

Olli Urpanen

Spatial and Temporal Variation in
Larval Density of Coregonids and
Their Consequences for Population
Size Estimation in Finnish Lakes



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Dedicated to fishers in Lake Gennesaret

ABSTRACT

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Diss.

Early life stages are important in both population ecology and management of fishes. Vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) have a prominent role in Finnish lake ecosystems and ecosystem services due to their economical and ecological status; thus a proper sampling method is needed for abundance estimation of coregonids in different life stages. In this thesis, horizontal, vertical and temporal patterns of coregonid larval distributions in many natural populations were studied and their effects on larval population size estimations were analysed. Hatching time and length of coregonid larvae predicted by otolith analyses revealed that the vast majority of larvae hatched within two weeks after ice-off. Although growth rate of larvae seemed to be affected by larval density, clear size-selective mortality was not observed during the first weeks of larval life. Estimated larval density within sampling site showed temporal stability over time-scales from weeks to years. Sampling site densities at distances less than 2 km were predictable from each other whereas site-specific densities at distances over 2 km were not. Larval vertical distribution varied greatly between years and populations and a simple vertical distribution model was included in the procedure for estimating larval population size. This additional component substantially affected the annual density estimates of larval coregonids. In an applied part of this thesis, time series data for coregonid larvae were analysed together with fish mass removal data. No effect of cyprinid and percid removal on coregonid larvae densities was observed. Nevertheless, collection of time series data with a reliable method can be highlighted as a prerequisite for long term population studies and more extensive understanding of species-species interactions in aquatic environments.

Keywords: Coregonid; larval; population size; vendace; vertical; whitefish.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV. In addition, some unpublished data are presented. O. Urpanen wrote the first version of the papers which were then finished with the co-authors. He was responsible for collecting, identifying and counting larvae from six lakes in 1999-2007 as well otolith preparation in 2001. He was also involved in otolith analysis and data analysis, except of mortality estimates by bootstrap (II) and BACI-analysis (IV).

- I Urpanen O., Huuskonen H., Marjomäki T. J. & Karjalainen J. 2005. Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae. *Boreal Environment Research* 10: 225-238.
- II Urpanen O., Marjomäki T. J., Viljanen M., Huuskonen H., Sarvala J., Helminen H. & Karjalainen J. 2007. Spatio-temporal distribution of vendace (*Coregonus albula* (L.)) larvae in Finnish lakes. *Fundamental and Applied Limnology, Advances in Limnology* 60: 221-230.
- III Urpanen O., Marjomäki T. J., Viljanen M., Huuskonen H. & Karjalainen J. 2009. Population size estimation of larval coregonids in large lakes: Stratified sampling design with a simple prediction model for vertical distribution. *Fisheries Research* 96: 109-117.
- IV Urpanen O., Keskinen T., Marjomäki T. J., Sakomaa V., Salo H., Syrjänen J., Viljanen M. & Karjalainen J. 2011. Effects of mass fish removal on coregonid larval abundance in a large mesotrophic lake. *Fundamental and Applied Limnology, Advances in Limnology* (in press).

1 INTRODUCTION

1.1 Recruitment variability in fish populations

Understanding processes affecting population dynamics of fish is essential for fisheries managements (Myers 2001). One of the main questions and thus, one of the most targeted research subjects of both freshwater- and marine fish biology, has been recruitment variability, i.e. variation in year-class strength (e.g. Rose et al. 2001). Large inter-annual recruitment variability is typical for vendace and whitefish populations (Hamrin & Persson 1986, Viljanen 1986, Salojärvi 1987, 1992, Helminen 1994, Auvinen et al. 2000, Karjalainen et al. 2000) and is to a large extent determined by unpredictable, density-independent factors (Eckmann et al. 1988, Marjomäki 2003). Density-dependent population regulation also has a role in density fluctuations (Salojärvi 1992, Marjomäki 2003), and has been suggested to be the reason for cyclicity in year-class strength fluctuations of vendace (Aass 1972, Hamrin & Persson 1986, Helminen et al. 1993, Huusko & Hyvärinen 2005).

Vendace and whitefish have a significant role in Finnish lake ecosystems since many medium-size and large lakes with meso-oligotrophic trophic status are inhabited by abundant populations of these coregonid species. Vendace catches constitute a major source of income for commercial inland fishers in Finland and the other Nordic countries (Nyberg et al. 2001, Marjomäki et al. 2004, Sipponen et al. 2006). Many external and internal factors directly or indirectly affecting coregonid population fluctuations have been listed (see reviews by Salojärvi 1992 and Marjomäki 2003). These studies conclude that the between-year variations in year-class strength are a consequence of very high mortality from spawning to recruitment. Moreover, year-class fluctuations occur synchronously in many vendace populations (Valkeajärvi et al. 2002, Marjomäki et al. 2004), which implies similar environmental factors (e.g. weather conditions) simultaneously affecting larval survival directly over a larger geographical scale.

1.2 Early life stages as a part of the recruitment process

Recruitment variability in fish originates from very high and unpredictable mortality during egg and larval stages (Pepin & Myers 1991). The larval phase of fish is defined as the period from hatching to the moment when juvenile characteristics emerge (Hubbs 1943, Rass 1946, Copp & Kovác 1996). For freshwater fish, mortality over this period averages 96.4 % (Houde 2002). Even minor changes in mortality or growth rates during any phase of early life stages can generate multifold recruitment variations (Houde 1987, 2002). Many recruitment hypotheses related to food density and predation at the larval stage have been presented: critical period (Hjort 1914), match/mismatch (Cushing 1975), bigger-is-better (Miller et al. 1988) and stage duration (Houde 1987) hypotheses. Later, Leggett & Leblois (1994) concluded in their review that a major link between food abundance at the time of first feeding and recruitment success (Hjort's "critical period") was not supported. On the contrary, they found general congruence with recruitment and seasonal timing of plankton production and larval abundance (Cushing's "match/mismatch") although relationships were weak. Further, they suggested that size-dependency (Miller's et al. "bigger-is-better") and predation (Houde's "stage duration") may be important but cannot be supported unequivocally as major factors affecting recruitment. All these hypotheses indicate that the main essential variables in larval population and recruitment studies are hatching time and size as well as growth rate of larvae (Jones 2002). Nevertheless, predictions of hatching time and lengths in the field among spatio-temporal distribution patterns of coregonid larvae are still poorly understood.

Mortality rate of eggs and yolk-sac larvae is independent of size, but decreases as the size of externally feeding larvae increases (Pepin & Myers 1991). Larger and faster growing individuals are generally considered to be less vulnerable to predation than smaller larvae (Miller et al. 1988) because of a lower number of potential predators and better escape ability. Conversely, under some circumstances, larger and fast growing larvae are more vulnerable to predation compared to smaller larvae due to the higher predator encounter rate (swimming speed and pigmentation) of larger individuals (e.g. Pepin 1991, Litvak & Leggett 1992). The importance of starvation decreases with increased larval size (Miller et al. 1988) but still promotes a serious risk because of the high metabolic rates and low energy reserves of larvae (Fuiman 2002).

The survivors of a year-class are suggested to be exceptional individuals (Rice et al. 1993) with greater likelihood of survival due to their size, but in stable environments behaviour of larvae may be more important than size for survival and recruitment (Fuiman & Cowan 2003). According to models by Letcher et al. (1996), both internal and external factors had equal effects on cohort survival. Larval growth capacity explained most variance in survival derived from internal factors. Of the external factors, most variability in survival was explained by the predator size. Starved fish will be eaten more

often due to the interaction of predation and starvation (Letcher et al. 1996). Cowan et al. (2000) concluded that food-limited growth of larvae contributed significantly to recruitment variability. It has also been stated that retention and accumulation of essential fatty acids (EFA) in the early life stages have high importance for fish recruitment success, and the availability of these EFAs for fish larvae is strongly dependent on the primary source of carbon in the food-chain (Bell & Sargent 1996, St John et al. 2001). Free amino acids (FAA) are of high importance for yolk-feeding larvae as a source of metabolic fuel (Kamler 2008). More recently, Perga et al. (2009) found a significant contribution of terrestrial carbon sources to copepods and, further, to growth of early larval stages of whitefish. Thus, variation in the spring plankton bloom peak may have a significant effect on the recruitment process. Thus Cushing's match/mismatch theory may also operate in Finnish coregonid populations. From this point of view, detailed information about the hatching time in the field in relation to ice-off is essential. Zooplankton production under ice cover is low and if a large proportion of larvae hatch under ice cover this might result in poor survival.

Populations of piscivorous fish, especially perch (*Perca fluviatilis* L.), may regulate the size of vendace stock due to predation and prevent recovery of stock from the prolonged low stock phases (Helminen & Sarvala 1994, Heikinheimo 2001, Valkeajärvi & Marjomäki 2004). Perch predation on vendace larvae (Huusko & Sutela 1992, Huusko et al. 1996, Haakana et al. 2007) and juveniles (Jaatinen et al. 1999, Tolonen 2000) has been observed, but between-lakes or between-years variation of predation intensity exists (Huusko et al. 1996, Vuorimies & Tolonen 1999). Predation pressure depends on the size distribution of both prey and predator (Mittelbach & Persson 1998, Cooper & Stankowich 2010) and the significance of perch as a predator has been thought to increase as vendace larvae reach the size of 12-14 mm (Huusko & Sutela 1992, 1997). Vendace larvae have also been found from the diets of minnow (*Phoxinus phoxinus* L.), whitefish (*C. lavaretus* L.), ruffe (*Gymnocephalus cernuus* (L.)) (Huusko & Sutela 1992, 1997), brown trout (*Salmo trutta* (L.)) (Vehanen et al. 1998) and smelt (*Osmerus eperlanus* (L.)) (Haakana & Huuskonen 2009), but no evidence that their predation is an important regulator of vendace abundance has been reported.

1.3 Early life stages in the context of fisheries management

Long term sustainability of fish stocks is a key objective in fisheries management. Stock-recruitment analyses are central for management decisions. Estimates of survival rates and abundance during early life stages play an important role in fishery management (Rutherford 2002) providing cost-effective means for forecasting recruitment (Karjalainen et al. 2000) and potential yield. Monitoring of larval abundance is needed to produce basic information for the decision makers to prevent biological and economical

overfishing. This precautionary fisheries management policy is also recommended for vendace fisheries since high larval abundance is a prerequisite for abundant recruitment in vendace (Helminen et al. 1997, Karjalainen et al. 2000). Knowledge of larval and nursery areas is required for the reliable estimates of larval fish abundance over years (Urho 2002) and thus development of effective sampling systems for coregonids are also needed.

1.4 Population size of larvae: sampling methods

Estimates of larval fish density and size distribution are key issues in understanding year-class strength. The difficulty of obtaining density estimations with sufficient accuracy is widely recognised, especially for larval fish stages and in large water bodies (Nellen & Schnack 1975, Treasurer 1978, Bagenal & Nellen 1980).

Several methods ranging from drags and sleds (Quadri 1960, Madenjian & Jude 1985) to various pushed or pulled nets (Smith & Richardson 1977, Leslie et al. 1983, Morse 1989, Karjalainen et al. 1998) have been used in studies of larval fish. From the beginning of the 1980s, coregonid larvae have been collected with seine nets (e.g. Hakkari 1983, Bogdanov 1992, Viljanen & Karjalainen 1992, Valkeajärvi & Bagge 1995), many types of push/pull nets (Salojärvi et al. 1981, Sarvala et al. 1988, Wanzenböck et al. 1997), larval trawls (Næsje et al. 1986a, Eckmann 1989) and drift nets (Næsje et al. 1986b). Also, strengths and limitations of different sampling gear have been studied intensively (Barkley 1972, Jessop 1985, Choat et al. 1993, Isermann et al. 2002, Claramunt et al. 2005) providing guidelines for the most appropriate sampling method for different size larvae of given fish species. A bow-mounted push net has shown to be an adequate sampling gear both in littoral and pelagic areas for the comparable catches between these habitats (Claramunt et al. 2005). The suitability of different methods for the sampling of larval coregonids in Finnish lakes has also been studied extensively as the efficiency of seine nets and bongo nets for sampling vendace and whitefish larvae has been compared (Viljanen 1987, Karjalainen & Viljanen 1992, Viljanen & Karjalainen 1992, Viljanen et al. 1995, Karjalainen et al. 1998). The mean size of larvae was higher in seine nets than in bongo nets (Viljanen 1987). Further, a bongo net fitted in front of a boat gathers more larvae compared to a bongo net pulled behind a boat. On a lake-wide scale, bongo netting produces more representative samples than seining (Huusko et al. 1988, Karjalainen & Viljanen 1992) and thus a modified bongo net sampling based on these previous studies has been widely used (Karjalainen et al. 2000, Karjalainen et al. 2002, Sutela et al. 2002, Marjomäki et al. 2004).

Besides the effects of sampling gear on the accuracy of abundance estimates, survey design must provide adequate spatial and temporal resolution to account for dispersion and patchiness of many aquatic organisms in different habitats (Cyr et al. 1992, Pepin & Shears 1997, Claramunt et al.

2005). Larval habitats of many species in lakes and reservoirs are typically found in nearshore areas (Auer 1982). Larvae may favour certain area of a lake due to better environmental conditions for their survival and growth, and thus larvae may be aggregated in dense shoals in some habitats whereas other habitats are inhabited by only low numbers of larvae (Urho 1996, 2002). However, sampling is often focused in open pelagic areas whereas more fragmented and shallow littoral areas are avoided (Sammons & Bettoli 1998) due to sampling difficulties (Leslie et al. 1983).

Exactness (high precision and/or accuracy) of larval fish abundance estimates is generally linked to the sampling procedure used (Downing et al. 1987, Frank 1988) and recognized bias can be reduced already through appropriate sampling design (Urho 1997). Observations are almost always spatially auto-correlated at some scale (Caeiro et al. 2003) and the scale can be quantified using semi-variogram analysis (Clark 1979). Minimum distance of sample pairs independent of each other is important for the sampling plan (Flatman et al. 1987). Stratified random sampling produces more precise estimates in spatially auto-correlated circumstances compared to simple random sampling (Caeiro et al. 2003). Precision of abundance estimation can be increased by increasing sample volume and/or by taking greater number of replicates (Cyr et al. 1992, Urho 1997, Karjalainen et al. 1998).

2 OBJECTIVES

The main aim of this thesis was to analyze horizontal, vertical and temporal patterns of coregonid larval distributions and to utilize this information from the field studies in improving the density estimation method for larval coregonids. Density estimates of larval fish with high accuracy and precision are needed to solve the complex recruitment dynamics of vendace, and thus the following more detailed objectives were focused on:

- (a) hatching time and length of coregonid larvae in field populations (I),
- (b) daily growth rate and size-selective mortality during the first weeks of larval life (I),
- (c) spatial and vertical distribution of coregonid larval density over time-scale from weeks to years (II, III),

and, based on the above mentioned, a further aims were:

- (d) to integrate the information about the observed spatial and vertical variation of larval distribution in order to improve the estimation method of larval abundance (III),
- (e) to offer a practical and economic method for future long-term monitoring of larval coregonids (I, II, III),

and finally,

- (f) to apply the improved larval density estimation method for analysing the effects of a fish mass removal on vendace and whitefish density (IV).

3 MATERIAL AND METHODS

3.1 Study lakes

Data for publication I were collected during 1989-2002 from lakes Pyhäjärvi (South-West Finland), Southern Konnevesi, Puruvesi (Harvanselkä) and Paasivesi (Table 1, Fig. 1). In II, larval sampling was performed in lakes Pyhäjärvi (South-West Finland), Päijänne (Tehinselkä), Puulavesi, Northern Päijänne, Southern Konnevesi, Northern Keitele, Paasivesi, Onkamo, Puruvesi (Harvanselkä) and Oulujärvi in years 1990-2005 (Table 1, Fig. 1). Publication III was based on data gathered from lakes Puruvesi (Harvanselkä, Hummonselkä), Paasivesi and Southern Konnevesi in 1999-2008 (Table 1, Fig. 1). Lakes Southern Konnevesi, Puulavesi, Onkamo and Pyhäjärvi (South-West Finland) were used as control areas when the impacts of fish removal on density of vendace were studied in Lake Northern Päijänne (IV). More comprehensive details of the study lakes are presented in the original publications.

TABLE 1 Years of coregonid larvae data used in original publications (I, II, III, IV) and this thesis (T), and density/population size estimation method A and/or B used (see more in chapter 3.2.2) in different lakes.

Lakes	Vendace larval data from years				Density/population size estimation method
	Otolith	Developmental stage	Vertical aggregation	Density/population size (ind. ha ⁻¹)/(million ind.)	
Oulujärvi			99-07 ^(T)	04-05 ^(II) , 99-06 ^(T)	B ^(II)
Northern Keitele			99-01, 03-07 ^(T)	04-05 ^(II) , 99-01, 03-08 ^(T)	B ^(II)
Southern Konnevesi	01 ^(I)	00-02 ^(I) , 01-03, 05, 07 ^(III)	99-07 ^(III, T)	01 ^(I) , 03-05 ^(II) , 99-07 ^{(III)*} , 99-07 ^(IV) , 99-10 ^(T)	A ^(III, IV, T) , B ^(I, II, III)
Onkamo			99-07 ^(T)	01-05 ^(II) , 99-07 ^(IV) , 96-06 ^(T)	A ^(IV, T) , B ^(II)
Paasivesi	01 ^(I)	89-01 ^(I) , 06-08 ^(III)	99-08 ^(III, T)	01 ^(I) , 90-91 ^(II) , 99-07 ^{(III)*} , 93-09 ^(T)	A ^(III, T) , B ^(I, II, III)
Puruvesi, Hummonselkä		06-07 ^(III)	99-07 ^(III, T)	99-07 ^{(III)*} , 93-09 ^(T)	A ^(III, T) , B ^(III)
Puruvesi, Harvanselkä	01 ^(I)	92-01 ^(I) , 06-07 ^(III)	99-07 ^(III, T)	01 ^(I) , 98 ^(II) , 99-07 ^{(III)*} , 93-09 ^(T)	A ^(III, T) , B ^(I, II, III)
Puulavesi			99-07 ^(T)	04-05 ^(II) , 99-07 ^(IV) , 99-10 ^(T)	A ^(IV, T) , B ^(II)
Northern Päijänne			99-07 ^(T)	04-05 ^(II) , 99-07 ^(IV) , 99-10 ^(T)	A ^(IV, T) , B ^(II)
Päijänne, Tehinselkä			00-07 ^(T)	04-05 ^(II) , 00-10 ^(T)	A ^(T) , B ^(II)
Pyhäjärvi, South-West	01 ^(I)	96-01 ^(I)		01 ^(I) , 99-05 ^(II) , 99-07 ^(IV) , 93-10 ^(T)	A ^(IV, T) , B ^(I, II)

*) Larvae abundance expressed as population size (million individuals)

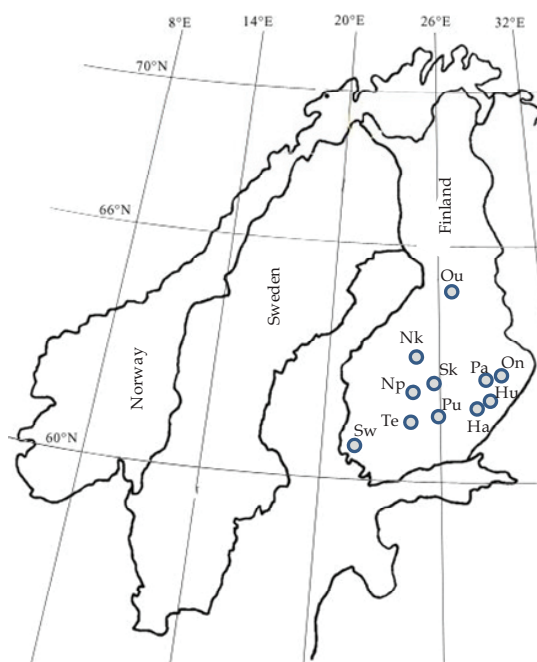


FIGURE 1 Study lakes. Ou=Oulujärvi, Nk=Northern Keitele, Sk=Southern Konnevesi, On=Onkamo, Pa=Paasivesi, Hu=Puruvesi (Hummonselkä), Ha=Puruvesi (Harvanselkä), Pu=Puulavesi, Np=Northern Päijänne, Te=Päijänne (Tehinselkä) and Sw=Pyhäjärvi (South-West).

3.2 Population size of larval vendace

3.2.1 Larval sampling (I, II, III, IV)

Estimation of larval population size was based on consistent bongo net sampling (Karjalainen et al. 1998) in all lakes studied. A stratified random sampling design with typically 20 littoral and 10 pelagic sampling sites (1 km x 1 km) in each lake was used annually. Sampling of each littoral site covered five strata (Fig. 2): stratum *I* (from shoreline to 0.5 m of bottom depth), stratum *II* (0.5-1 m), stratum *III* (1-2 m), stratum *IV* (2-4 m, but in Lake Southern Konnevesi 2-7 m and in Lake Puulavesi 2-10 m) and stratum *V* (pelagic). Larvae were sampled with a manually pushed tube net (mouth area 0.028 m²) from stratum *I* and with bongo net (mouth area 0.24 m²) from strata *II-V* (Fig. 3). The tow speed of the bongo net varied from 1.1 m s⁻¹ to 1.7 m s⁻¹ (2.2 knots to 3.2 knots). A mean (\pm S.D.) sample volume was 1.5 \pm 1.3 m³ in the each tube net tow and 101.1 \pm 23.0 m³ with each bongo net tow. The volume of each sample was measured by a flow meter. Generally, two bongo nets were used in each sampling tow. In stratum *II*, two samples were taken from a depth layer of 0-30 cm and pooled. In strata *III*, *IV* and *V*, one net sampled the depth layer of 0-30

cm and another net sampled the 30-60 cm layer (Fig. 2). Besides this general sampling system, pelagic areas of lakes Paasivesi (2006-2008), Puruvesi, Harvanselkä (2006-2007), Puruvesi, Hummonselkä (2006-2007) and Southern Konnevesi (2001-2003, 2005 and 2007) were sampled more intensively. Sampling covered vertical depth layers of 0-30 cm, 30-60 cm, 60-90 cm, 90-120 cm, 120-150 cm and 150-180 cm in lakes Paasivesi, Puruvesi (Harvanselkä and Hummonselkä), and 0-60 cm, 60-120 cm, 120-180 cm and 180-240 cm in Lake Southern Konnevesi. Further, pelagic area of L. Paasivesi was sampled with HYDRO-BIOS® MultiNet® Midi in 2008 covering water depth layer from 0 to 50 m.

The annual sampling was performed within the weeks after ice-off, i.e. during April to the beginning of June, depending of the lake and year. Samples were preserved in a 1:1 mixture of 70 % ethanol and 1 % formalin. Species identification was based on pigmentation and counts of myomeres as described by Karjalainen et al. (1992). Length of larvae was measured (TL, nearest 0.01 mm) and they were weighed for fresh and dry mass (mg, nearest 1 mg). The developmental stage of larvae was categorized into four classes: 0 = no yolk left, 1 = 1-33 % of yolk left, 2 = 34-66 % of yolk left and 3 = 67-100 % of yolk left. Wind speed and cloudiness were estimated visually during sampling in each lake and were categorized on scales 0-12 m s⁻¹ and 0-8, respectively.

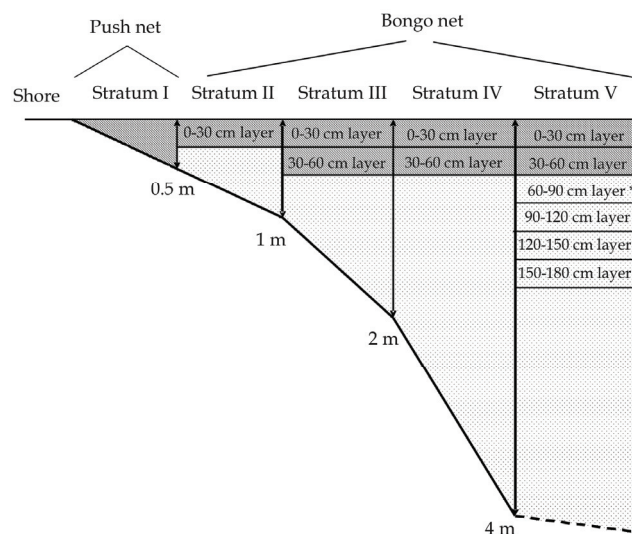


FIGURE 2 Overview of different sampling strata (I, II, III, IV and V) and water depth layers (0-30 cm, 30-60 cm etc.) sampled. Density of depth layers based on either sampling (▨) or prediction (□); for more details see chapter 3.2.2).
*=Sampled in certain years and lakes (for more details see text above).

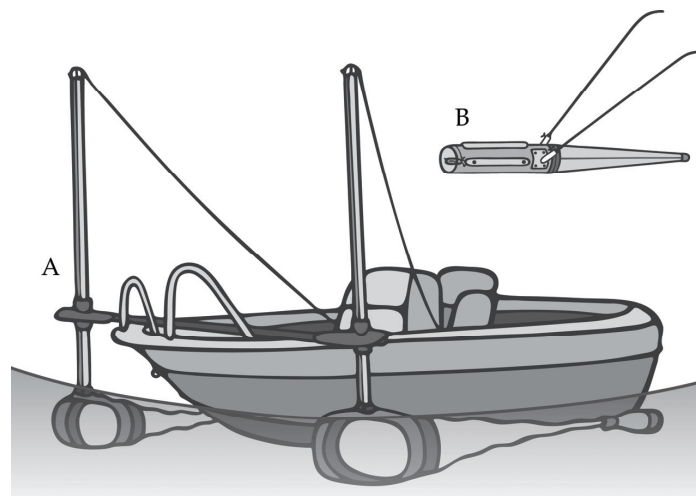


FIGURE 3 Illustration of bongo net (A) and push net (B) used in coregonid larval sampling in this thesis (drawing by Kirsti Pusa).

3.2.2 Larval density estimation (I, II, III, IV)

The total number of larvae in a given lake was expressed as individuals ha^{-1} and was calculated from the stratified sampling according to Krebs (1989) and Karjalainen et al. (1998, 2000). Estimates were based on two methods referred as A and B. Method A (new) was applied in IV and method B (old) in I and II. In III, both methods A and B were used (Table 1).

Method A is an improved version of method B (III) and the main simplifications in the method B are: 1) in every lake and year, the number of the larvae in the pelagic stratum in water layers deeper than 1 m was accounted for by multiplying the mean density of larvae at the depths of 0-1 m by a constant coefficient (2 and 1.5 for vendace and whitefish, respectively) in the estimate of total density of pelagic strata. 2) In the littoral strata III and IV, the simple arithmetic mean of the density estimates from 0-30 cm and 30-60 cm was applied as the estimate for the mean density from surface all the way to the bottom. Thus, no vertical aggregation index was used when the densities were extended to produce the estimates of the whole-lake population. 3) Only four horizontal strata were used in the stratified sampling design (in the method A stratum IV was added, see Fig. 2). 4) The areas and volumes of the littoral strata were re-estimated for method A using more observations on strata widths and shoreline lengths. Besides these differences between methods A and B, data for the larval vertical distribution were included in method A. Vertical distribution of larvae was expressed as the ratio of the larval densities at two different water depth layers (0-30 cm and 30-60 cm). This index of larval aggregation (VA) was calculated by equation

$$VA = d_2 / d_1$$

where d_1 is density of larvae (individuals 100 m^{-3}) caught in the upper depth layer and d_2 is density of larvae (individuals 100 m^{-3}) caught in the lower depth layer. The ln-transformed index value 0 means equal larval densities in both the depth layers sampled. Negative index values indicated that the larval abundance in the lower depth layer was lower than that in the upper layer. The analysis of lake- and year-specific variation in VA was based on nearly 7000 larvae samples in III and an even more comprehensive data set (ca 15000 samples) in this thesis.

The population size for a whole lake in III and IV was estimated by method A (Table 1) with the following procedure. First, stratum- and depth layer-specific observations of larval abundance were used to estimate the whole lake average density (individuals 100 m^{-3}) for each stratum and depth layer. Secondly, the average density in each stratum was estimated based on observed densities at the depth layers of 0-30 cm and 30-60 cm and VA-predicted densities at depth layers of 60-200 cm. The density of larvae at depth layers of deeper than 200 cm was assumed to be negligible and was omitted from larval population estimates. Thirdly, the stratum-specific average densities were weighed by the estimated volumes of the different strata and added together to produce the larval population size estimate (million individuals) for the whole lake. In strata *I*, *II* and *III*, the volumes included depth layers from surface to bottom and in strata *IV* and *V* from surface to a depth of 2 m.

Observed larval densities in depth layers of 0-50 m and the VA-based density estimates produced by method A were compared by calculating modelling efficiency according to Mayer & Butler (1993) (III).

3.3 Age and growth determinations (I)

The age of coregonid larvae was determined from otoliths (sagittae). Sagittae were dissected from larvae under a dissecting microscope at magnifications of $\times 48$ -320. Then sagittae were mounted on a microscope slide with a drop of glycerol and covered by a coverslip. Measurements of otoliths (radius, maximum diameter of hatch check and counts of daily growth increments) were made with a compound microscope at $\times 125$ -1250 magnification. Firstly, daily increment count of otoliths was made by two persons without information of the other person's results. Secondly, the mean number of these two counts was tuned with experimentally determined daily increment - fish age -regression (Huuskonen & Karjalainen 1995). The relationship between larval total length and otolith radius was described by Monastyrsky's (1930) equation (I). Larval length at age i was also back-calculated by the method of Monastyrsky. The instantaneous daily growth rate in length between time of hatching and capture was calculated for each larva based on otolith data (I). The mean growth rates were also calculated based on average mean length

estimates for field samples. Growth rates produced from otolith and field samples were compared to confirm that larvae taken for otolith analysis were a random sub-sample of the larval population for a given lake and year.

3.4 Spatial distribution of larvae (II)

The pattern of larval spatial distributions over time-scales from weeks to years was investigated for 10 lakes. Larvae were assumed to disperse with a pattern of isotropy, i.e. the same spatial structure existed in all directions of lake area. The larval density differences between two sampling sites were expressed as their squared differences (γ):

$$\gamma = [Z(x_i + h) - Z(x_i)]^2$$

where $Z(x_i)$ is abundance at site x_i , where x was defined by latitude and longitude in two-dimensional space. $Z(x_i + h)$ is another abundance value separated from x_i by a distance h measured in kilometres. The distances between sampling sites were categorized in 2 km classes (0-2 km, 2-4 km etc.) and γ between sampling size densities at distances 0-2 km and 2 km onwards were analysed.

Estimates of instantaneous total mortality between two sampling occasions (first within a few days after ice-off and second two weeks later) were calculated for the 2004 data set of Lake Southern Konnevesi. The effect of fixing sampling sites on precision of mortality estimates were illustrated by a bootstrap re-sampling procedure with 5000 repeats. New samples of 20 observations were picked from the original data set. When simulating the fixed sampling design, sampling sites of the first survey were randomized and combined with the real observations of second survey samples of that site. When simulating the random sampling design, the sampling was carried out independently from both sets.

3.5 Mass fish removal and monitoring (IV)

Mass fish removal has been widely used as a biomanipulation method, but mostly in small and shallow lakes (Olin et al. 2006, Jeppesen et al. 2007). Mass fish removal in large boreal lakes with thermal stratification, long ice cover and high inflow of nutrients in spring have been conducted less often and its biomanipulative effects are thought to be different from in shallow lakes (Horppila et al. 1998, Olin et al. 2006). An intensive mass fish removal was performed during 2001-2004 in a mesotrophic Finnish lake basin (Northern Päijänne) with a total phosphorus concentration of 15 mg m⁻³ and water colour of 40 mg Pt l⁻¹. The lake area is 15700 ha and the area of mass fish removals

covered 4600 ha. The purpose of the mass fish removal project (Development of lakes Northern Päijänne and Jyväsjärvi – rehabilitation of fishery) was firstly to change the fish community structure towards more abundant stocks of commercially valuable species such as coregonids, and secondly to increase the overall recreational value of the lake area. Thus, percids and cyprinids were the main targets and were mainly caught by trap nets. The project was conducted during open-water seasons by the professional fishers. The effects of mass removals on the fish community were monitored by multimesh gillnet fishing with a stratified random sampling design.

Coregonid larvae have been sampled in lakes Northern Päijänne, Puulavesi, Onkamo and SW Pyhäjärvi since 1999 as part of the CORNET (Finnish Coregonid Stock Research and Fisheries Network) research programme. Thus, there was a good opportunity to combine data from these two projects to more extensive research. The larval population size estimation method developed by Karjalainen et al. (1998, 2000) and improved in II and III (method A, see above in methods) provided a way to investigate the abundance of coregonid larvae under a large biomanipulated lake area and in the three control lakes.

The effect of mass fish removal on coregonid larval densities in northern Päijänne was analyzed using asymmetric analysis of variance, i.e. a Beyond BACI (Before-After-Control-Impact) design (Underwood 1992). Newly hatched coregonid larval densities were estimated for three years before and six years after the beginning of fish removal. Larval densities calculated for the same time period in lakes Southern Konnevesi, Onkamo, Puulavesi and Pyhäjärvi (South-West Finland) were used as controls.

4 RESULTS AND DISCUSSION

4.1 Hatching, growth and size-selective mortality of larvae (I, II)

The average back-calculated hatching lengths of vendace and whitefish larvae caught from natural populations ranged from 6.8 mm to 8.0 mm and from 8.8 mm to 11.0 mm, respectively and significant differences between populations were found. Generally, vendace larvae caught in the second survey had a significantly greater back-calculated hatching length than that of larvae caught in the first survey. The vast majority of larvae hatched within two weeks after ice-off. Larvae caught from the littoral and pelagic areas had the same average hatching time. Hatching occurred on average after ice-off in all lakes studied (I) and the results are in agreement with previous work by Sarvala et al. (1988) and Karjalainen et al. (2000). Since exactness of density estimation is a key target in many growth and mortality studies, knowledge of the larval hatching time is necessary for correct timing of sampling. Thus, the results in publication I could potentially provide useful information for the schedule for sampling larval coregonids. However, differences in spring temperature development, rate of larval mortality and variation in sampling schedule may induce considerable inter-annual and inter-lake variation in larval densities and their estimates. Therefore, in practice it may be difficult to increase the precision of density estimates by "better" sampling scheduling. A minimum requirement for higher precision is higher frequency of sampling; instead of one sampling, having two samplings with a one week interval between them. Although the majority of larvae had hatched by the first survey, larval sampling will always underestimate the total number of hatched larvae due to high mortality in the larval stage (Karjalainen & Viljanen 1994).

Estimation of larval mortality rate requires two consecutive surveys and the use of fixed sampling sites increases the precision of within-season mortality estimates (II). However, mortality based on the decrease of abundance between consecutive surveys may be overestimated due to their increasing ability to avoid the samplers when schooling (Karjalainen & Viljanen

1992). Due to equal hatching times and growth rates of larvae originating from the littoral and pelagic areas, larval samples gathered from these two zones can be used as comparable replicates in larval data analysis (suitability of sampling method for larval coregonids is discussed in more detail in section 4.3). The average back-calculated growth rates during the few first weeks after hatching ranged from 0.03 mm d⁻¹ to 0.06 mm d⁻¹ for vendace and from 0.03 mm d⁻¹ to 0.05 mm d⁻¹ for whitefish and agreed with earlier field observations (Sarvala et al. 1988, Karjalainen & Viljanen 1992).

Estimates of hatching length and time as well as an average daily growth rate of larvae were based on the back-calculation from otolith data (I). Otolith growth is continual without resorption (Campana & Thorrold 2001) throughout the lifetime even under periods of starvation (Campana & Neilson 1985). Since the development of otolith microstructure examination in the early 1970s (Pannella 1971), determination of daily growth rate of larval fish from daily growth increments has provided a new approach for early life history studies (Campana & Neilson 1985, Campana & Jones 1992). The precision and accuracy of growth back-calculation based on otoliths has been widely discussed (e.g. Campana 1990). Slowly growing fish tend to have larger otoliths than fast growing fish of the same size, which may cause underestimation of previous length-at-age in slowly growing fish. In larval fish, difficulties in correct interpretation of otolith increments are a more significant source of bias (Klink & Eckmann 1992). Formation of subdaily increments limits identification of daily increments in Finnish coregonids (Huuskonen & Karjalainen 1993, 1995), whereas in Central Europe daily increments were easily distinguished (Eckmann & Pusch 1989). Thus, Huuskonen (1999) suggested that the daily increment formation is indirectly affected by latitude since formation of increments differed between northern and southern populations. The number of subdaily increments increased with multiple feedings per day in experimental conditions (Neilson & Geen 1982, Campana 1983), possibly due to increased metabolic rate (Huuskonen & Karjalainen 1998). Later, Eckmann (2000) concluded that feeding frequency seems to be the most important factor in increment formation for coregonids. Growth rate estimates based on the back-calculation from otolith data corresponded well with growth rates predicted from field observations of mean length (I). In addition, daily increment counts were tuned (see methods above) and hence age and growth estimates seem to be sufficiently accurate and precise despite some weaknesses of the analyses in northern latitudes. It is also worth noting that otolith analysis is practically the only way to estimate hatching lengths, age and early growth rate of wild larvae. Scales, other hard parts, fin rays or spines are not formed prior to hatching and complete formation of these does not occur until late metamorphosis (Jones 2002). Hence, these cannot be used in larval ageing. Indeed, publication I was the first study where hatching lengths of coregonids were estimated from larvae caught purely from nature, producing new basic information on the ecology of coregonid larvae. In previous studies (Huuskonen & Karjalainen 1993, Huuskonen & Karjalainen 1995, Huuskonen et

al. 1998) artificially incubated larvae were used and hatching occurred under laboratory conditions.

4.2 Spatial and vertical distribution of larvae (II, III)

Very high variation in density of vendace larvae between lakes and years was observed (I-IV, Fig. 4) emphasizing the need for a good quality density estimation method for population ecology studies and fisheries management. Nevertheless, estimated distributions of larval density within sampling sites showed temporal stability over time-scales from weeks to years (II). Correlations between density estimates from two within-season surveys and two surveys in consecutive years at the same sampling site were significant. Wind-driven currents have been proposed to affect spatial distributions of larvae (Huuskonen et al. 2002), but this may be rather exceptional due to the temporal stability of distribution pattern over years (II). Indeed, temporal stability of larval distribution may arise from the fact that the main spawning areas and thus, larval hatching areas, remain the same over time, as proposed by Huuskonen et al. (2002). At distances of less than 2 km, the average difference between density estimates was lower than that of distances from 2 km upwards. Thus, sampling site densities at distances less than 2 km were to some extent predictable from each other whereas site-specific densities at distances over 2 km were not. Effects of larval spatial distribution on different sampling designs are discussed in section 4.3.

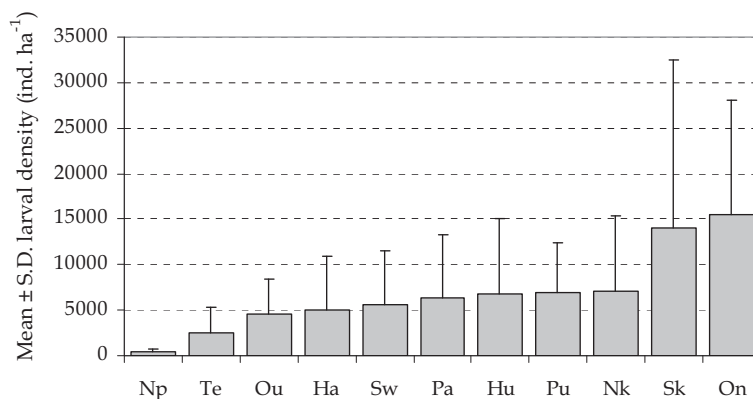


FIGURE 4 Mean (\pm S.D.) annual average density estimates of vendace larvae in study lakes calculated by method A (improved in III). Study lakes and years: Np=Northern Päijänne (1999-2010), Te=Päijänne (Tehinselkä) (2000-2010), Ou=Oulujärvi (1999-2006), Ha=Puruvesi (Harvanselkä) (1993-2009), Sw=Pyhäjärvi (South-West) (1993-2010), Pa=Paasivesi (1993-2009), Hu=Puruvesi (Hummonsälkä) (1993-2009), Pu=Puulavesi (1999-2010), Nk=Northern Keitele (1999-2008), Sk=Southern Konnevesi (1999-2010) and On=Onkamo (1996-2008).

Besides the variation in horizontal distribution of larvae within a lake (II), population density estimates are also affected by vertical the distribution of larvae (III). The vertical distribution of vendace and whitefish larvae showed high inter-annual and between-lake variation (Fig. 5). In general, larvae were aggregated near the water surface in both littoral and pelagic areas. A major part of larvae were in the uppermost 0-30 cm and 0-60 cm of depth layers in the littoral and pelagic areas, respectively. The gradient near the surface was steep and results of whole water column sampling (depth layer of 0-50 m) indicated high larval orientation towards the water surface (97 % of total vendace larvae occurred in the top 0-2 m layer). A tendency of newly hatched coregonids to aggregate near the water surface has been documented in several studies both in nature (Faber 1970, Eckmann 1989, Karjalainen et al. 1998) and experimental conditions (Ylönen et al. 2004, 2005) and is a consequence of the positive phototactic behaviour of larvae (Shkorbatov 1966, Viljanen et al. 1995) and their preference for warmer water layers during early spring (Eckmann 1989). A positive correlation between larval vertical aggregation (VA) and wind force found in this thesis indicates a mixing effect of harsh environmental conditions on larvae due to their poor swimming ability. Moreover, larval vertical aggregation was more surface-oriented in humic lakes compared to lakes with lower water colour (Fig. 5) and under cloudy weather conditions. These results are in agreement with previous findings by Ylönen et al. (2004, 2005) as they suggested that the larval vertical position was associated with solar radiation and perhaps also avoidance of UV-radiation. Häkkinen et al. (2002) suggested that coregonid larvae are UV-B tolerant and able to avoid increased UV-radiation.

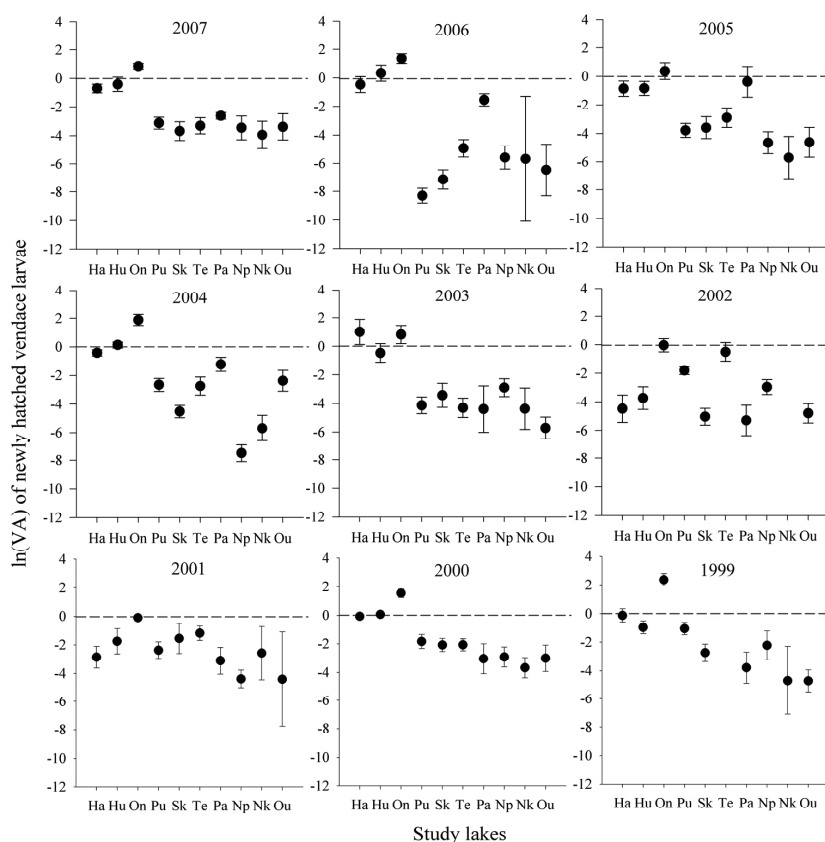


FIGURE 5 The mean $\ln(VA)$ values (\pm S.E.) of newly hatched vendace larvae in the study lakes during 1999-2007 (see descriptions of VA in chapter 3.2.2). Ha=Puruvesi (Harvanselkä), Hu=Puruvesi (Hummonseltä), On=Önkamo, Pu=Puulavesi, Sk=Southern Konnevesi, Te=Päijänne (Tehinseltä), Pa=Paasivesi, Np=Northern Päijänne, Nk=Northern Keitele and Ou=Oulujärvi. Lakes are ordered along the x-axis based on their water colour from clear lakes to humic lakes.

4.3 Factors contributing to the accuracy and precision of population size estimates of coregonid larvae (I, I, III)

Since the early life stage is known to be significant in the recruitment complex of fish (Bradford & Cabana 1997, Cowan and Shaw 2002) including vendace (Auvinen et al. 2000, Karjalainen et al. 2000, Houde 2002, Marjomäki et al. 2004) due to high mortality, a main goal is to develop a best available method for larval population estimation. The aim of abundance estimation is to produce accurate (i.e. unbiased) and precise (i.e. low variance) estimates of larval density.

Selectivity of samplers and its effect on the required sample number and volume has been discussed in many studies (Barkley 1964, Cyr et al. 1992). Thereafter, the sampling method for larval coregonids has been developed and the density estimation has been based on the bongo net method in Finnish lakes (Karjalainen & Viljanen 1992, Viljanen & Karjalainen 1992, Karjalainen et al. 1998). The area of the mouth opening, towing speed and mesh size are the most important factors (among many others) affecting the suitability of bongo net sampling in respect of its efficiency (Barkley 1972, Murphy & Clutter 1972, Hernandez et al. 2011). Mesh size is one of the basic factors not only because it affects catchability of newly hatched larvae, but also in terms of minimizing net avoidance or net extrusion, the most documented sources of bias in larval collection with plankton nets (Barkley 1972, Johnson & Morse 1994). The mesh size used in coregonid larvae bongo net sampling in Finland has been based on studies by Posgay & Marak (1967) and Nellen & Schnack (1975) modified by Viljanen (1987) (Fig. 6). According to Viljanen (1987) and Karjalainen & Viljanen (1992), a bongo net with mesh size 500 μm can be used successfully for coregonid larvae up to 15 mm total length. Larval hatching length in nature (I) confirms these previous perceptions that this sampling gear is suitable for newly hatched coregonids (Fig. 6). The influence of towing speed on catchability of fish larvae is generally recognized, indicating higher net avoidance of larger larvae at low speed (Colton et al. 1980, Thayer et al. 1983). The magnitude of this bias is both size- and species-specific and thus dependent on patchy distributions and diurnal migrations of larvae (Noble 1970). Colton et al. (1980) found that herring (*Clupea harengus membras* (L.)) larvae up to 21 mm total length were adequately gathered with a bongo net even at a low speed of 0.77 m s^{-1} (1.5 knots). Thus, for newly hatched coregonid larvae sampling with an average towing speed of 1.4 m s^{-1} (2.7 knots) can be assumed adequate. Moreover, speed of samplers explained a smaller proportion of catch variability than sampling day and depth (Hilden & Urho 1988) and thus sampling design can be assumed to be highly important (Urho 2002). Night catches often exceed day catches in many fish larvae because of visual avoidance of samplers by larvae (Thayer et al. 1983, Rehberg et al. 2009). Vendace larvae are highly phototactic, aggregating near the water surface in daytime, and day catches are found to be higher than night catches when larvae are distributed more evenly in vertical water column (Viljanen et al. 1995).

The use of a bongo net in larval sampling also has some limitations. Firstly, sampling among dense macrophyte beds may be difficult due to net-clogging which may cause biased density estimates. Lakes harbouring stocks of coregonids in Finland are typically meso-oligotrophic with only a low proportion of vegetated shores (Tolonen et al. 2001) and thus, their effect on larval population estimates can be regarded as rather negligible. Secondly, strong wind conditions may cause low precision for the vertical depth layer sampling (Fig. 6). The sampling design used in I-IV was based on a large number of samples for a given lake, relatively long sampling hauls (over 4 min.) and as large volumes of filtered water (approx. 100 m^3) as in larval studies in the marine environment (Pepin & Shears 1997, Lyczkowski-Shultz & Hanisko

2007). By taking into account these known limitations, it was assumed that bongo net sampling would produce reliable estimates of larval coregonid density.

The precision of estimates can be increased by increasing sampling effort and by accounting for larvae distribution patterns (Urho 1997). Annual random picking of sampling sites should be favoured if the goal of larval monitoring is to produce the least biased long-term average estimates (II). A minimum distance of 2 km between adjacent sampling sites produces independent observations (II). In contrast, better detectability of between-year variation in larval density and higher precision within-season mortality estimates can be achieved by utilizing fixed sampling sites over long time period (Quist et al. 2004, II).

Abundance of larval coregonids has been monitored intensively in Finnish lakes for nearly 20 years, producing a large dataset for early life-stage studies (Helminen et al. 1997, Auvinen et al. 2000, Karjalainen et al. 2000, Marjomäki et al. 2004). All previously published larval abundance studies have been based on stratified bongo net sampling (e.g. Karjalainen et al. 2000) with good within-lake horizontal coverage (Karjalainen et al. 2000, 2002, Marjomäki et al. 2004). The vertical distribution of coregonid larvae has been shown to vary both in time and space due to environmental factors (e.g. Viljanen et al. 1995, Karjalainen et al. 1998, Ylönen et al. 2005, III). Thus, in III was analysed in more detail whether larval population size estimates were affected by the vertical distribution patterns of larvae (Fig. 6). The average density estimates of larvae were 30 % and 37 % lower for vendace and whitefish, respectively, if produced by the updated method A including the lake- and year-specific coefficient of vertical aggregation (VA). Field samples, have until now, usually been gathered from a depth layer of 0-200 cm. Observed and VA-predicted density estimates for depth layers below 60 cm were in reasonable correspondence. Thus, the method A produced adequate estimates for average total density without the sampling from the deeper layers (> 60 cm) and thus sampling time and resources can be saved both in the field and the laboratory.

Many factors affecting the reliable estimates of larval population abundance have been documented including sampling system, larval characteristics and environmental factors (Fig. 6). Besides these factors, data for lake morphometrics were taken into account in estimation of population size. Of course, this induces some error in population size estimates caused by uncertainty in the morphometrics data. Firstly, variation of volumes of different strata was included in method A which increases random variation of population size estimates. On the contrary, fixed volumes of strata may cause biased results. Secondly, estimates of volumes of strata are dependent on shoreline length and its measurements from maps with sufficient accuracy are in turn dependent on scale, causing biased results to some extent. Thirdly, the slope of the bottom profile in a given lake is based on observations in field and must also take account of potential source of errors also. In Lake Southern Konnevesi, the effect of the changes in these volume coefficients between

methods A and B was only 13 % of the annual population estimates of vendace larvae.

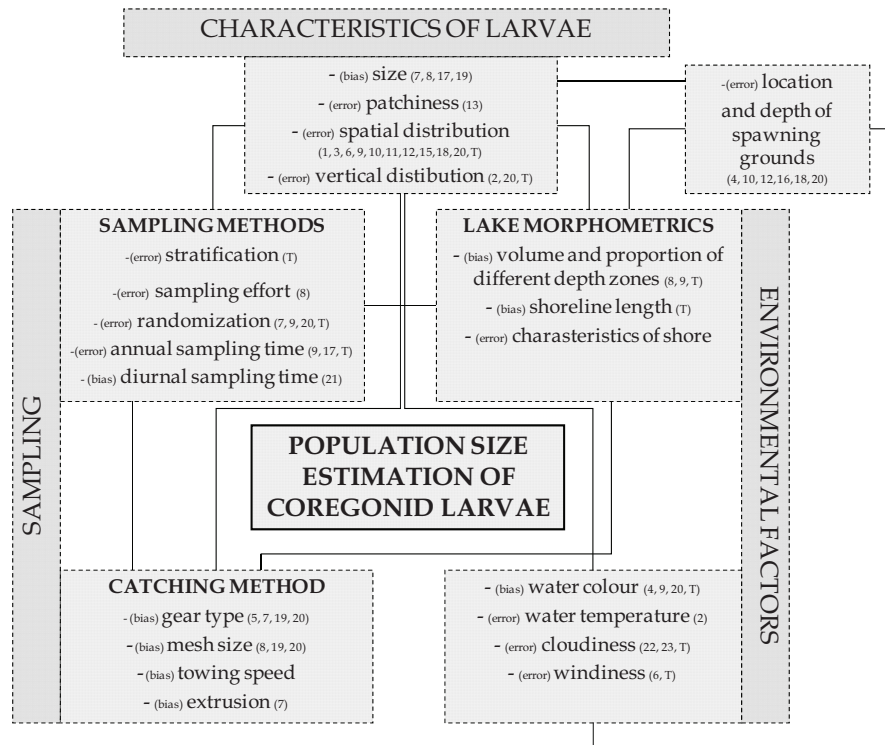


FIGURE 6 Schematic illustration of factors and sources of uncertainty affecting population size estimation of coregonids larvae produced by method A. References: 1=Bagge & Hakkari 1987, 2=Eckmann 1989, 3=Eckmann & Pusch 1989, 4=Heikkilä et al. 2006, 5=Huusko et al. 1989, 6=Huuskonen et al. 2002, 7=Karjalainen & Viljanen 1992, 8=Karjalainen et al. 1998, 9=Karjalainen et al. 2000, 10=Karjalainen et al. 2002, 11=Lahnsteiner & Wanzenböck 2004, 12=Lahti 1992, 13=Lehtonen 2008, 14=Lindström 1962, 15=Næsje et al. 1986a, 16=Nissinen 1972, 17=Sarvala et al. 1988, 18=Sarvala et al. 1994, 19=Viljanen 1987, 20=Viljanen & Karjalainen 1992, 21=Viljanen et al. 1995, 22=Ylönen et al. 2004, 23=Ylönen et al. 2005. T=investigated in this thesis.

4.4 Effects of spatial and temporal patterns on the recruitment of larval coregonids (I, II)

Although hatching size of fish larvae is commonly considered to be determined by egg size (Viljanen & Koho 1991, Fuiman 2002), it is not always evident (Uusi-Heikkilä et al. 2010) and has not been found to correlate with recruitment variability (Pepin & Myers 1991). Thus, differences between populations in their hatching size may not contribute significantly to recruitment variability of vendace. Growth rates differed significantly between populations, being higher

in lakes Southern Konnevesi and Paasivesi than in lakes Puruvesi (Harvanselkä) and Pyhäjärvi (South-West Finland). In pooled data, a significant negative correlation between larval growth rate and density was found. This has also been observed in net enclosures (Karjalainen 1992). Besides population-specific growth rate differences, growth rate of larvae within the population caught in the first survey were higher than in the second survey. However, larval growth rate in littoral and pelagic areas was equal, as can be expected based on their feeding success in both zones (Sutela et al. 2002). Growth rate of coregonid larvae is tightly connected to water temperature (Rey & Eckmann 1989, Luczynski 1991, Koho 2002) which in turn affects the availability of plankton food (Hansen et al. 2010, Rahkola-Sorsa et al. 2011) and thus positively affects larval survival (Auvinen 1988, Huusko & Sutela 1998). During the first two weeks after hatching the yolk-sac larvae of vendace start to prey effectively on zooplankton (Karjalainen 1991, Karjalainen & Viljanen 1992, 1994) and yolk reserves become exhausted within three to four weeks after hatching (Karjalainen & Viljanen 1992). Despite the high energy requirements of larvae (Karjalainen et al. 1995, 1997), larval predation did not necessarily depress the zooplankton density (Karjalainen 1992, Rahkola-Sorsa et al. 2011) and thus food shortage may not be enough to cause recruitment failures. Polyunsaturated fatty acids (PUFAs) are essential for fish development (Sargent et al. 1999, Tocher 2010). Thus, the effect of UV-B radiation on coregonid larvae survival (i.e. their normal development and growth) may be controlled indirectly by depletion of PUFAs in their zooplankton diets since total lipid content of some microalgae are reduced by increased UV-B radiation (Arts & Rai 1997).

Observed larval length distributions in the second survey were generally wider compared to length distributions of larvae caught in the first survey. After standardization, length distributions were not significantly skewed, indicating that larger larvae were not relatively more abundant after the first weeks of larval life. Thus, no clear evidence for size-dependent mortality of these coregonid larvae populations was observed. Mortality during first weeks was rather random in relation to larval size and size differences increased as spring progressed. Size-selective mortality of vendace larvae is found indirectly in the field (Helminen & Sarvala 1995) and in laboratory conditions (Koho & Viljanen 1998). In contrast, detection of size-driven mechanisms in the field may be difficult due to density estimation difficulties caused by larval patchiness, school density or size (Fig 6). Regardless of the extensive discussion about size-selective processes during early life stage, clear density-dependent effects in larval fish populations have been suggested to be rare (Cushing 1983, Fortier & Harris 1989, Persson et al. 2000) or to exist with high time-specific variation caused by strong dependence on environmental conditions (e.g. water temperature) and intrinsic developmental schedules (Gagliano et al. 2007).

4.5 Estimation of coregonid larvae abundance as part of a mass fish removal project in a large lake (IV)

A low density of newly hatched vendace larvae was observed in Northern Päijänne throughout the study period implying low spawning stock size compared to the control lakes (Fig. 4). Regardless of slight increases in total densities of larval coregonids, no significant differences in densities were found either between the northern and southern parts of the study area or between before and after time periods. The highest larval density of vendace in Northern Päijänne was observed in 2007 when high densities were found in two control lakes also implying synchronization between population variations (cf. Marjomäki et al. 2004). Results of BACI-analyses confirmed that the mass removal of cyprinids and perch from Northern Päijänne did not have any significant effect on the densities of larval coregonids. Reproductive outputs of coregonids were not affected by a manipulative treatment and some reasons can be hypothesised. Firstly, recruitment of the coregonids in Northern Päijänne is not regulated by the predation and competition of perch or cyprinids and secondly, mass fish removal was not efficient enough to decrease the population size of perch and cyprinids to a level which would influence the coregonid recruitment. On the other hand, the data contained high variation due to larval patchiness and thus, the test power of BACI-analyses remained low. However, effects of biomanipulation on lake ecosystem are not straightforward. For example, expansion of larval cyprinids after biomanipulation has been detected in several lakes in Finland (Olin et al. 2006). Intensive fishing of a perch population may also cause compensatory effects leading to strong year-classes (Romare & Bergman 1999, Karjalainen et al. 1999, Keskinen 2008) and/or accelerated growth rates of individual fish. Additionally, in large lakes, perch and roach are able to co-exist in large quantities without stunted growth rates due to their effective ability to use different habitats and food resources (Horppila et al. 2000). In this study, fish removal was insufficient to affect the densities of larval coregonids, which is in agreement with the results of Haakana et al. (2004). Thus, we conclude that clear effects of mass fish removal may be difficult to achieve on a large scale. Nevertheless, long time-series data, as collected in this thesis, are needed for more comprehensive analyses of species-species interactions in large lake ecosystems.

5 CONCLUSIONS

Variability in recruitment has prominent biological consequences and substantial implications for management of fish stocks. Understanding factors behind this complex requires long-term monitoring at various life stages. Without proper methods, results from monitoring are potentially misleading and may cause inadequate mortality estimates, and thus uncertain recruitment predictions at the population level. High and unpredictable recruitment variation is a typical feature of many vendace populations (Marjomäki et al. 2000) and causes of this variation have been widely discussed from the turn of the last century onwards (Järvi 1919). As in many fish populations in marine and freshwaters (Houde 2002), high mortality in the early life stages of vendace is well established (Karjalainen et al. 2000).

The general aim of this thesis was firstly to increase knowledge of horizontal, vertical and temporal patterns of coregonid larval distributions. Secondly, these results were examined in the context of larval sampling design and population size estimation. Back-calculated hatching lengths and times as well as larval growth rate during the mixed feeding period and later, externally feeding stages, provided us with a specified sampling design. Results of larval spatial and vertical aggregations over temporal scales from weeks to years yielded valuable additional information for the sampling design. Further, larval population size calculated with data for larval vertical aggregation patterns produced lower and less biased density estimates compared to the method used previously. A reliable long-term average density estimate may be achieved by using a random sampling design and restricting sampling to the 0-60 cm depth layer. Thus, both time and financial resources can be saved. In summary, the use of a bongo net enables a large volume of water to be sampled in a relatively short time also in shallow and fragmented littoral areas. A previous method (Karjalainen et al. 1998, Karjalainen et al. 2000) with recent development shown in this thesis, has improved the estimation procedures for coregonid larvae population size. Accuracy and precision of larval population size estimates of coregonids are affected by many sources of uncertainty. True dynamic variation in larval population densities between years and lakes is, however, multifold

compared to biases and errors in larval estimates (Karjalainen et al. 2000, IV) rendering the method suitable for field monitoring.

In an applied part of this thesis, time series data for coregonid larvae were analyzed together with mass fish removal data. Regardless of the insignificant effects of mass fish removal on larval coregonids, collection of continuous data with a reliable method is a prerequisite for these kinds of population studies. Thus, long-term monitoring helps us comprehend species-species interactions in complex aquatic environments.

Long-term studies of many populations in all life stages should be a standard practice for the better understanding of the coregonid recruitment variability. Indeed, significance of reproduction and development during early ontogeny is becoming an increasingly important target in recruitment predictions for vendace, since mortality from spawning to hatching seems to be high and unpredictable as concluded already by Marjomäki (2003) and later by Urpanen et al. (2011). However, from a broader point view, the whole Finnish inland fishery system and management of valuable fish stocks are in a critical stage. At present, a gap exists between fisheries science and actual fisheries practice. Unfortunately, this “human response” has received only little attention and practical answers to improving fisheries management are rare (Fulton et al. 2011). We should move on towards more a comprehensive ecosystem-based fisheries management policy (Hilborn 2011) including definition of functional management regions, increased stakeholder engagement as well as new scientific answers (Jennings & Rice 2011). Thus, the significance of long-term monitoring of fish stocks should be realized and accepted in all level of fisheries organization from shareholders to policymakers and should be included in an inland fisheries management policy in the near future.

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*” Ei anna erämaa armoa maisterillekaan, kun sille päälle sattuu.
Pieni ja voimaton on täällä ihminen ja avuton ihmisen tieto ” *)*

A. E. Järvinen (1953): Tunturi huutaa

*) A. E. Järvinen (1953): Screaming fjeld “In a harsh day, wilderness gives no mercy, not even to M.Sc. Tiny and weak is human and his knowledge faltering”. (Translated by O. Urpanen)

YHTEENVETO (RÉSUMÉ IN FINNISH)

Muikun ja siian poikastiheyksien spatiaalinen ja ajallinen vaihtelu ja sen vaikutukset poikasmääräarviointiin

Ensimmäisten elinviikkojen aikana kalojen poikasista kuolee huomattava osa. Siksi poikasvaiheenaikaiset tapahtumat voivat aiheuttaa kalastettavaksi tulevan vuosiluokan koon (=rekryyttimäärä) huomattavia vaihteluita eri vuosina. Myös muikun rekrytoituvien yksilöiden kokonaismäärä vaihtelee merkittävästi eri vuosina ja eri populaatioiden välillä. Toimivan kalastuksensäätelyn kannalta on tärkeää pystyä ennustamaan mahdollisimman varhaisessa vaiheessa kalastettavan vuosiluokan koko, joka muikulla määräytyy ensimmäisen kasvukauden aikana. Suomen järvissä muikunpoikaset kuoriutuvat keväällä, Etelä- ja Keski-Suomessa tavallisesti huhti-toukokuun vaihteessa ja Pohjois-Suomessa toukokuun aikana. Vastakuoriutuneiden poikasten määrän mahdollisimman tarkka arvioiminen on tärkeää, jotta kalastettavan vuosiluokan runsautta voidaan ennustaa. Näin voidaan ennakoida mahdollisia kalastuksensäätelytoimenpiteitä, joita alhaisen tai runsaan kannan vaihe edellyttäisi. Tämä on erityisen tärkeää sellaisilla järviolueilla, joilla harjoitetaan muikun ammattimaista kalastusta.

Tässä väitöskirjassa tutkittiin muikun- ja siianpoikasten kuoriutumisaikankohtaa ja -kokoa useissa suomalaisissa järvissä sekä pyrittiin arvioimaan niiden vaikutuksia kuolevuuteen poikasten ensimmäisten elinviikkojen aikana. Näiden lisäksi tarkasteltiin muikunpoikasten alueellista jakaumaa ja jakauman samankaltaisuutta eri viikkoina ja vuosina. Alueellisen jakauman lisäksi tutkittiin myös poikasten syvyysjakaumaa. Poikasjakaumissa tapahtuvien ajallisten ja paikallisten muutosten vaikutuksia tarkasteltiin suhteessa käytettyyn poikasten näytteenottomenetelmään ja sen toimivuuteen sekä vuosittaisiin kokonaispoikasmääräarviointeihin. Poikasmäärän arviointimenetelmää sovellettiin tässä väitöskirjassa myös vähempiarvoisten kalalajien tehokalastushankkeessa, jossa selvitettiin erityisesti särjen ja ahvenen poistokalastuksella saavutettavia muikukantaan kohdistuvia vaikutuksia laajalla vesialueella.

Muikun- ja siianpoikasten kuoriutumisaikankohtaa ja -kokoa tutkittiin neljällä järvellä otoliittien (=kuuloluut) avulla. Otoliittianalyysit osoittivat, että suurin osa poikasista kuoriutuu jäiden lähtöä seuraavien kahden viikon aikana, vaikka ensimmäisten ja viimeisten poikasten kuoriutumisaikankohdissa voi olla jopa neljän viikon väli. Poikasnäytteitä kerättiin useilta järviltä jäiden lähdön jälkeisellä viikolla ja toisen kerran kahden-kolmen viikon kuluttua jäiden lähdöstä. Havainnot osoittavat, että yhteen näytteenottoon perustuva poikasmäärän arvioiminen tuottaa riittävän hyvän arvion kevään kokonaispoikasmäärästä. Suuren poikasvaiheenaikaisen kuolevuuden vuoksi on kuitenkin huomattava, että näytteenoton perusteella laskettu poikasmäärä on aina aliarvio luonnossa kuoriutuvien poikasten todellisesta kokonaismäärästä. Poikasten kuolevuutta voidaan arvioida tekemällä vähintään kaksi näytteenottoa. Poikasten kasvunopeus näytti olevan hieman hitaampi suuremmissa poikastiheyksissä. Ensimmäisten elinviikkojen aikana ei kuitenkaan havaittu selvää poikasten

koosta riippuvaa kuolevuutta, vaan kuolevuus näytti olevan enemmän satunnaista, ja siten erikokoisilla poikasilla oli samanlaiset mahdollisuudet selvitä.

Väitöskirjassa tutkittiin myös poikasten sekä alueellista että syvyysuuntaista jakaumaa. Poikasten jakaumissa havaitut erot olivat suuria vuosien ja järvien välillä. Tietyllä järvellä runsaimmat poikasmäärät esiintyivät aina samoilla alueilla huolimatta näytteenottoviikosta tai -vuodesta. Poikastiheyden näytepisteiden välinen vaihtelu oli vähäisempää, jos näytepisteiden etäisyys toisistaan oli alle 2 km, kuin kauempana toisistaan sijaitsevien pisteiden välillä. Kun näytteenottopaikkojen etäisyys on yli 2 km, näytteenottopaikkojen poikastiheyksiä voidaan siis pitää toisistaan riippumattomina, ja tätä tietoa voidaan hyödyntää näytteenoton suunnittelussa. Pitkällä aikajaksolla vuosittain satunnaistetut näytteenottopisteet tuottavat keskimäärin vähemmän harhaisen poikasmääräarvion kiinteisiin näytteenottopisteisiin verrattuna. Toisaalta vuosien välinen poikasmäärävaihtelu havaitaan tarkemmin, mikäli vuodesta toiseen käytetään samoja näytteenottopisteitä. Yleisesti poikaset olivat kuoriutumisen jälkeen kerääntyneet lähelle veden pintaa, vaikka niiden syvyysuuntainen jakauma vesikerroksessa vaihteli huomattavasti sekä vuosien että järvien välillä. Tummavetisemmissä järvissä poikasten suhteellinen osuus lähellä pintaa oli suurempi kuin kirkasvetisissä järvissä. Tyynellä säällä poikaset olivat myös kertyneet lähemmäs pintaa kuin tuulisella säällä. Syvyysjakaumaa kuvattiin tutkimuksessa ns. sammumiskertoimen avulla, ja vuosittainen järven kokonaispoikasmääräarvio oli keskimäärin n. 30 % pienempi, mikäli tämä sammumiskertoimen vaihtelu 0–60 cm:n vesikerroksessa otettiin laskennassa huomioon. Tulokset osoittavat myös, että 0–60 cm:n syvyysvyöhykkeestä laskettua sammumiskerrointa käyttämällä kyetään arvioimaan 60 cm:n vesikerrosta syvemmällä olevien poikasten määrä luotettavasti ilman, että sieltä tarvitsee ottaa lainkaan näytteitä. Näin näytteenotossa voidaan säästää aikaa ja kustannuksia sen vaikuttamatta merkittävästi lopputulokseen.

Väitöskirjan soveltavassa osassa poikasnäytteenotto- ja tiheysarviolaskentamenetelmiä käytettiin osana laajempaa kokonaisuutta. Pohjois-Päijänteellä toteutetun, lähinnä särkikalojen ja ahvenen, poistokalastuksen vaikutuksia alueen muikku- ja siikakantaan tutkittiin sekä ennen että jälkeen tehokalastuksen. Tehokkaasta kalastuksesta ja suuresta poistetun kalan määrästä huolimatta kalastuksella ei havaittu vaikutusta alueen muikun- ja siianpoikasten määriin. Tähän saattaa vaikuttaa se, ettei kalastus ollut riittävän tehokasta suhteessa suureen pinta-alaan tai että poistetut kalalajit eivät säädelleet alun perinkään kyseisen järven muikku- ja siikakantoja, vaan kutukannat ja niistä seuraavat poikastiheydet olivat jostain muusta syystä hyvin alhaiset useisiin muihin järviin verrattuna. Toisaalta on huomioitava, että tilastollisen testin voimakkuus jää aina melko alhaiseksi, jos aineiston sisältämä hajonta on suurta poikasten laikuittaisuuden vuoksi, eikä siihen voida vaikuttaa merkittävästi edes näytemäärää lisäämällä. Mahdolliset pienet muutokset voivat siis jäädä havaitsematta aineistoon aineiston suuren hajonnan vuoksi.

Vesiekosysteemien toiminnan ymmärtäminen vaatii pitkien aikasarjojen tutkimusta, ja siksi niiden kerääminen on välttämätöntä tulevaisuudessa. Suo-

nessa aiemmin käytettyä ja tässä väitöskirjassa edelleen kehitettyä siikakalojen poikasten arviointimenetelmää voidaan käyttää apuna tällaisen tiedon keräämisessä, kun näytteenottoon ja poikasten populaatiokoon arvioimiseen liittyvät epävarmuustekijät otetaan huomioon.

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ORIGINAL PAPERS

I

**GROWTH AND SIZE-SELECTIVE MORTALITY OF VENDACE
(*Coregonus albula* (L.)) AND WHITEFISH
(*C. lavaretus* L.) LARVAE**

by

Olli Urpanen, Hannu Huuskonen, Timo J. Marjomäki & Juha Karjalainen
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Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae

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Urpanen, O., Huuskonen, H., Marjomäki, T. J. & Karjalainen, J. 2005: Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae. *Boreal Env. Res.* 10: 225–238.

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⁻¹ in SW Pyhäjärvi, 0.1–3.4 kg ha⁻¹ in Paasivesi and 0.2–16.0 kg ha⁻¹ 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⁻¹. 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⁻¹. 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

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

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

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 α with the Bonferroni method ($\alpha1 = 0.05/n$) 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) ($-2\sum_i^n \log p_i$ 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.

Table 1. Density of newly hatched vendace and whitefish larvae (ind. ha⁻¹ (95% confidence limits)) in study lakes during first survey in 2001.

Lake	Density, ind. ha ⁻¹ (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)

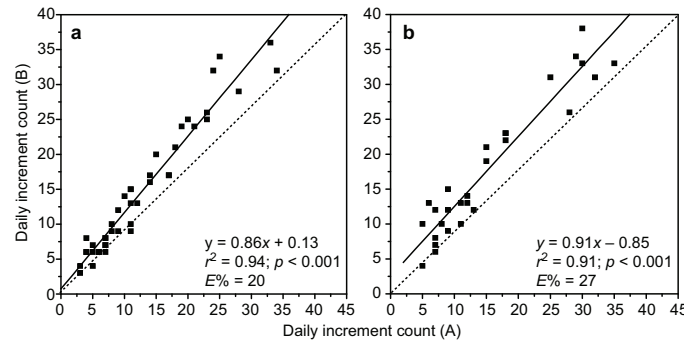


Fig. 1. Relationship between daily growth increment counts counted by two persons (A and B) in (a) vendace ($E\% = 20$, $a = 0$, $b = 1$, $n = 43$) and (b) whitefish ($E\% = 27$, $a = 0$, $b = 1$, $n = 28$) larvae. The 1:1 line is shown by a dotted line.

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

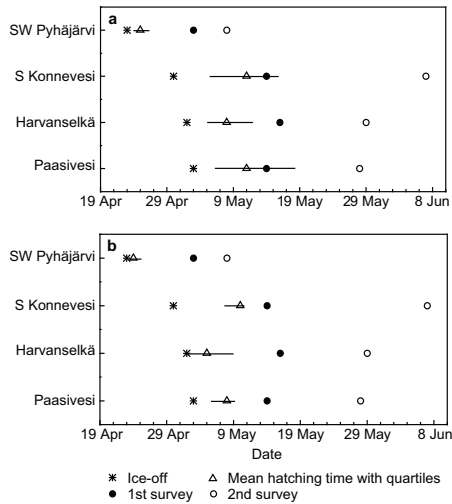


Fig. 2. Mean hatching time with quartiles of vendace (a) and whitefish (b) larvae in the study lakes in 2001. Times of surveys and ice-off are also shown.

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 (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	

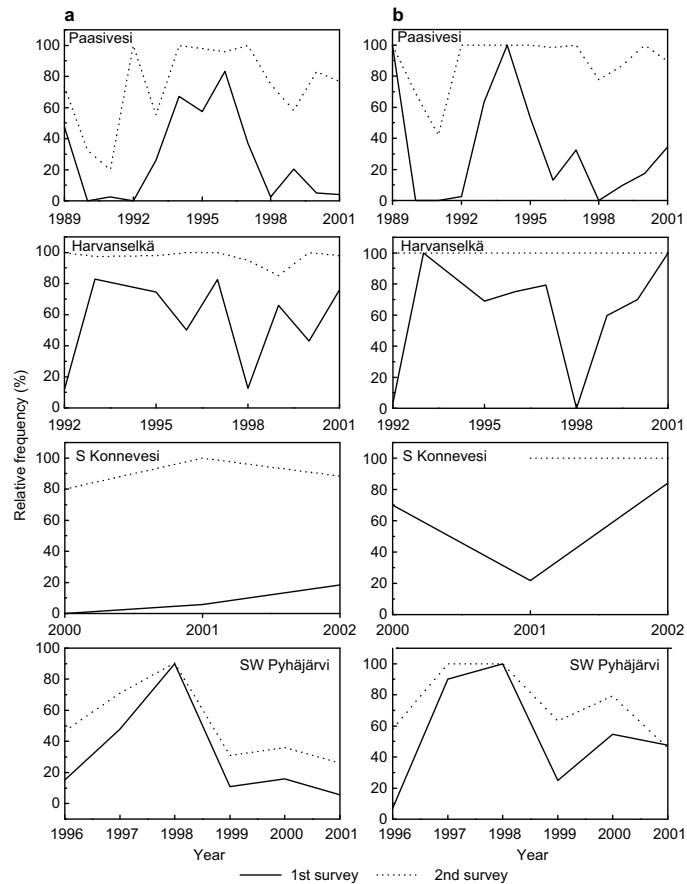


Fig. 3. Relative abundances of (a) vendace and (b) whitefish larvae with empty yolk sacs in the study lakes during 1989–2002 at the first and second surveys. Data of years 1989–2000 and 2002 from CORNET (Finnish Coregonid Stock Research and Fisheries Network) research project (unpublished). Note that 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

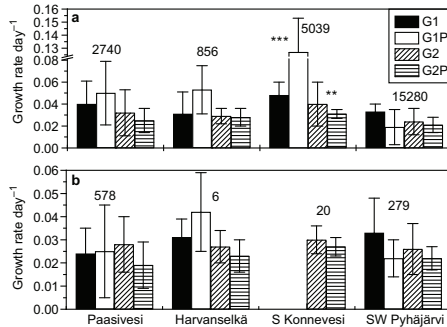


Fig. 4. Mean growth rates and standard deviations of (a) vendace and (b) whitefish larvae in the study lakes in 2001. The growth rates calculated from different data indicated as follows: G1 = growth rate between hatching and first survey back-calculated from otolith data, G1P = growth rate between hatching 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⁻¹) 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⁻¹) and growth rate of larvae (d⁻¹, both surveys combined) calculated individually by sampling areas. Statistical significance of Spearman's correlation coefficient (1-tailed) with a correction of α 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		

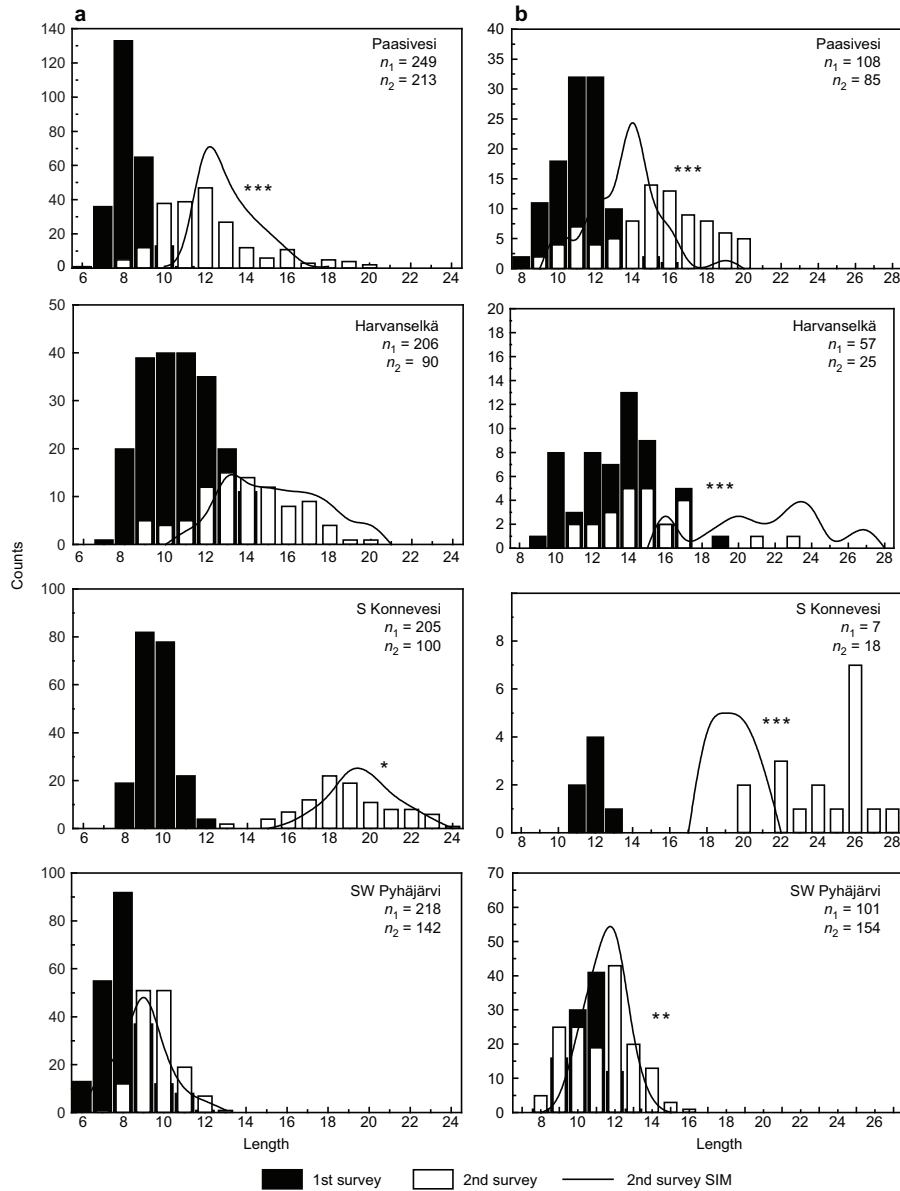


Fig. 5. Length distributions for (a) vendace and (b) whitefish larvae in the study lakes in 2001. The observed distributions in the first survey are indicated as 1st survey, observed distributions in the second survey as 2nd survey and the simulated distributions of the second survey as 2nd survey SIM. 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⁻¹) and S Konnevesi (5039 ind. ha⁻¹) when compared with mean densities of these lakes during 1992–2000 (3250 ind. ha⁻¹ and 29 619 ind. ha⁻¹, respectively). The density of whitefish larvae was low, e.g. in S Konnevesi only 20 ind. ha⁻¹ whereas the mean densities during 1984–1993 were 2200 ind. ha⁻¹ (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⁻¹) 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

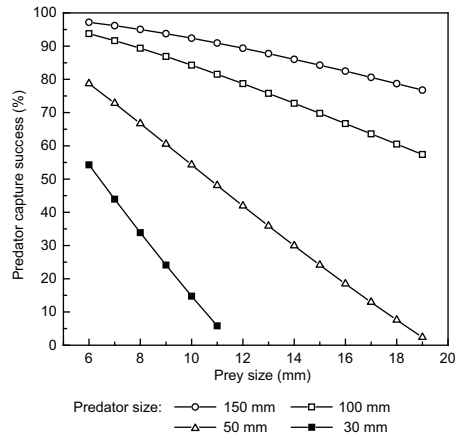


Fig. 6. Effects of a predator size on the mortality of the fish larvae modelled with the method of Miller *et al.* (1988). Prey size-scale corresponds to the sizes of coregonids larvae in first weeks of their life history.

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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