

Mechanism of fluctuations in year class survival of
vendace (*Coregonus albula* (L.)) larvae - an individual
size based approach

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Academic dissertation

Helsinki 2002

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ISBN 952-91-5163-2 (paper pack)

ISBN 952-10-0737-0 (PDF)

<http://ethesis.helsinki.fi>

Yliopistopaino / Helsinki University Printing House
Helsinki 2002

Koho, J. 2000: Mechanism of fluctuations in year class survival of vendace (*Coregonus albula* (L.)) larvae – an individual size based approach

Abstract

Large variation in the vendace year class strength has been well documented. Although such fluctuations have been the subject of numerous research, no general explanation regarding their causes has been revealed. It is generally assumed that the variability in the recruitment of fish is initially originated from the early life history of fish via variability in the mortality of the eggs and larvae. In the present investigation, the development of vendace year classes from eggs to juvenile stages was studied in field conditions and in the laboratory. In addition, a computerized simulation modeling was applied.

Vendace spawners were caught with gill nets in the end of October and the beginning of November at their spawning grounds in different parts of Lake Saimaa (Pyhäselkä, Orivesi, Puruvesi, Haukivesi and Etelä-Saimaa) in Eastern Finland between 1985-1991. Ripe spawners of vendace were stripped and fertilized and water hardened eggs were transferred into the laboratory incubators. Thereafter, the eggs were divided into specific test groups. The practical laboratory experiments were carried out in the Karelian institute (University of Joensuu, Finland) and in the Finnish Game and Fisheries Research Institute, Saimaa Fisheries Research and Aquaculture (Enonkoski, Finland). In the field experiments, the eggs were incubated *in situ* in Lake Pyhäselkä. The effects of water temperature and oxygen concentration on the development of year classes were studied in laboratory and field conditions. In order to determine the instantaneous dry mass composition (energy, fat, protein) the elements H, C, N of the eggs and embryos were analysed at the different phases of the egg development. The metabolism of eggs was measured as the heat dissipation and, furthermore, estimated from the dry mass loss of the eggs and hatched embryos at different ages. The effects of zooplankton density and/or water temperature on the larval growth, survival, food selection and swimming activity were studied in the laboratory. The influence of the type of prey and temperature on the gastric evacuation rate of larvae was also examined. The computer simulations were applied to reveal the interactions between the larval survival and dry mass of eggs, water temperature, and predation pressure.

These studies showed that (1) the metabolic rate of the eggs depended on the egg size, (2) the duration of the incubation period affected the size of embryos, (3) survival of the larvae depended indirectly on the water temperature. It was found that both the decrease in incubation temperature and the increase in water temperature after hatching beneficially increased the survival of larvae when feeding was not the limiting factor. Furthermore (4), the survival of a year class was dependent on the interactions of egg size, water temperature, oxygen conditions, exogenous feeding conditions and, most of all, predation pressure.

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ACKNOWLEDGEMENTS

REFERENCES

ORIGINAL PAPERS (I-VI)

1. LIST OF ORIGINAL PAPERS

This thesis is based on the following articles, which are referred to by their respective Roman numerals in the text:

- I. Viljanen, M. and Koho, J. (1991): The effects of egg size and incubation conditions on life history of vendace (*Coregonus albula* (L.)). Verh. Internat. Verein. Limnol. 24:2418-2423.
- II. Koho, J., Penttinen, O.-P. and Viljanen, M.: Effects of environmental conditions on the energy metabolism of vendace (*Coregonus albula* (L.)) and whitefish (*Coregonus lavaretus* (L.)) embryos. Boreal Env. Res. Submitted.
- III. Koho, J.: Dynamics and composition of endogenous dry mass of vendace (*Coregonus albula* (L.)) eggs and embryos. Boreal Env. Res. Submitted.
- IV. Karjalainen, J., Koho, J. and Viljanen, M. (1991): The gastric evacuation rate of vendace (*Coregonus albula* L.) larvae predating on zooplankters in the laboratory. Aquaculture 96:343-351.
- V. Koho, J., Karjalainen, J. and Viljanen, M. (1991): Effects of temperature, food density and time of hatching on growth, survival and feeding of vendace (*Coregonus albula* (L.)) larvae. Aqua Fennica 21:63-73.
- VI. Koho, J. and Viljanen, M. (1998): Growth, survival, and swimming activity of vendace (*Coregonus albula* (L.)) larvae under different food conditions in the laboratory. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 50:61-71.

Contributions

Papers	I	II	III	IV	V	VI
Original idea	JK, MV	JK, O-PP	JK	JuK, JK	JK	JK
Design of experiments	JK	JK, O-PP	JK	JuK, JK	JK	JK
Data analysis	JK	JK, O-PP	JK	JuK	JK, JuK	JK
Manuscript preparation	MV	JK, O-PP	JK	JuK	JK	JK, MV

Docent Markku Viljanen served as responsible project coordinator.

2. INTRODUCTION

The interest in the rise and fall of fisheries, the annual variation in regional fish abundance, dates back for centuries. This interest is by no means restricted to academia as the economies of many coastal communities are closely tied to the fortunes and the misfortunes of the fisheries. Johan Hjort hypothesized (1914) that the fundamental reason for the yearly fluctuations of fisheries is the variability in mortality during the "critical period" in the early life history of fish (Sinclair 1997). The concept "critical period" of fish larvae is known as the time interval when the mortality is remarkably high (e.g. Pitcher & Hart 1982, p.159). The early life history of fish includes fertilization, the embryonic stages, larval periods and the initial stages of the juvenile life. In this dynamic period of the life cycle individuals undergo rapid changes in morphology, ecology, behaviour and habitat use. During these stages the mortality of young fish in the new year class may rise over 99%. Variation in the annual mortality in the early life of fishes, (*i.e.* eggs, larvae and juveniles) has been suggested to be the main factor causing the fluctuation of adult fish populations and fishery in both marine and freshwater environments (Chambers & Trippel 1997).

There has been a considerable amount of well-documented evidence showing the large variation in vendace year class strength (e.g. Järvi 1942, Nissinen 1972, Hamrin 1979, Hamrin & Persson 1986, Viljanen 1986, 1988, Salojärvi 1987, Auvinen 1988, Helminen *et al.* 1993, Helminen 1994, Helminen & Sarvala 1994, Sarvala & Helminen 1995, Huusko 1998). It has been proposed that competition for food between age groups, temperature, and predation are the main factors behind these fluctuations. Although these fluctuations have been subject of significant interest, their mechanisms are not yet understood and better insight is needed. In general, however, high abundance of vendace larval produces a high number of recruits (Karjalainen *et al.* 2000).

Water temperature has a fundamental effect on the fish eggs and larvae (McCormick *et al.* 1971, Colby & Brooke 1973, Christie & Regier 1973, Edsall & Colby 1978, Jezierska *et al.* 1979, Kamler & Kato 1983, Luczynski & Kirklewska 1984, Luczynski 1985, 1991, Böhling *et al.* 1991, Blaxter 1992, Steinarson & Björnsson 1999). The rise in water temperature increases the rates of metabolism and growth but, simultaneously, shortens the incubation time. Temperature influences the body size and the efficiency of yolk conversion into embryonic tissue (Braum 1978, Luczynski *et al.* 1984, Blaxter 1992). In general, the longer the incubation time is, the longer are the hatched coregonid embryos. Cold winters (embryonic period) associate with strong year classes of plaice (*Pleuronectes platessa* (L.)) (Pihl 1990). Positive correlation have been observed between year class strength of perch (*Perca fluviatilis* (L.)) and water temperature during growth season (Karås 1987, Böhling *et al.* 1991). Karås (1987) and Pihl (1990) concluded that the early predation was the major regulating factor for the year class strength of perch and plaice.

Predation may be a major factor in the total mortality of fish larvae (e.g. Houde 1987, Bailey & Houde 1989). The magnitude and nature of predation mortality may substantially affect the year class survival and size distribution (Rice *et al.* 1987, 1997). The relative body size is a crucial factor in predator-prey interactions (Werner 1974, Miller *et al.* 1988).

The problem (which has been an object of scientific interest for the last century) is complicated by the egg size; egg size controls the larval growth, survival, and even

recruitment in coregonids (Wilkonska & Zuromska 1988, Brown & Taylor 1992, Sarvala & Helminen 1995). What the combined effects of different factors are is not known, neither are the optimum conditions for the early life history of vendace.

The aim of this investigation has been to study the factors affecting the survival of vendace eggs and larvae. The main study objectives were:

1. to develop incubation and rearing methods for experimental studies on vendace eggs and larvae,
2. to study the chemical composition and its changes in eggs and embryos,
3. to study the effects of water temperature and oxygen concentration on the embryo size, the metabolic rate and the time of hatching,
4. to study the effect of food density and quality and the rearing temperature on the larvae growth and survival,
5. to construct an experiment-based population model to demonstrate and study the development and survival of vendace eggs and larvae,
6. to present the combined effect of the egg dry mass, water temperature and predation on vendace larval survival and, finally,
7. to plot the results of this summary using the "model eggs" and larvae of vendace.

Experimental work was carried out both in laboratory and field conditions. An experiment-based population model was then constructed to describe and study the population dynamics of the early life of vendace.

3. MATERIAL AND METHODS

3.1 Experiments with eggs, embryos and larvae

3.1.1 Study area and the experiment material

Vendace spawners were caught with gill nets at the end of October and the beginning of November between 1985-1991 from spawning grounds in different parts of the Saimaa lake system (Pyhäselkä, Orivesi, Puruvesi, Haukivesi and Etelä-Saimaa) in Eastern Finland. Ripe spawners of vendace were stripped and fertilized by the dry method at the approximate temperature of 6 °C lake water. The water hardened eggs were then transferred into laboratory incubators and, thereafter, divided into different experimental groups for laboratory and field conditions (I-VI).

3.1.2 Laboratory and field experiments

Laboratory work was carried out in the Karelian institute, University of Joensuu and in the Finnish Game and Fisheries Research Institute, Saimaa Fisheries Research and Aquaculture, Enonkoski. In the field experiments, the eggs were incubated *in situ* in Lake Pyhäselkä. The effects of the egg size and the incubation conditions (temperature, oxygen) on the survival, metabolism and hatching time of eggs were studied in laboratory and field conditions (I, II, III). The dry mass (mg) and the composition (elements H, C, N) of eggs and embryos were determined at different phases of development (III). The dry mass of eggs and embryos (I, III) were determined using an electronic micro-analysis balance. Individual eggs were put in aluminium containers. The empty containers were preheated to 500 °C in a furnace to reach constant weight. A

blank test (an empty container) and a repetition of weighing were used to check the correctness of the weighing process. Before weighing the eggs and embryos were dried at 60 °C at least over night. After drying they were kept in a desiccator. The maximum error in individual cases was estimated to be smaller than 0.005 mg. The weight effect of fungus infection on eggs was out of control. The instantaneous metabolism of vendace eggs was measured as the heat dissipation (II) and the cumulative metabolism was also estimated from the dry mass loss of the eggs and hatched embryos at different ages (II, III). The effects of zooplankton density and water temperature on the growth, survival, food selection and swimming activity of larvae were studied (V,VI). The influence of prey animals and temperature on the gastric evacuation rate of the larvae was examined in the laboratory (IV).

3.2 Modelling of eggs, embryos and larvae

3.2.1 Simulation experiments

The aim of the simulations was to summarize the interactions of eggs dry mass, water temperature and predation on larval survival of vendace. The simulation procedure follows the development of the new year classes of vendace. The procedure was carried out by a set of simulations and experiment-based calculations (Fig.1). The Systat and Minitab Statistical Software was adapted for the calculations.

The variation sources were studied; the first source of random variation was the variation in the egg mean dry mass at the population level (*i.e.* interannual variation in year classes or variation in different lakes (I) and the dry mass variation between single eggs at the individual level (*i.e.* variation in the year class). The simulated year classes are independent from each other. A simulated egg population represents the initial state of the year class (*i.e.* the fertilized eggs) (cf. III, Fig. 1). The mean dry mass of the year classes was generated from the normal distribution with the mean μ_1 and the variance σ_1^2 *i.e.* from $N(\mu_1, \sigma_1^2)$. This operation gave the mean μ_2 egg dry mass for the new year class. Eggs within this population were then generated from $N(\mu_2, \sigma_2^2)$.

The second variation source was the water temperature. The hatching time was linearly dependent on water temperature (I). Firstly, the incubation temperature for the developing year classes was taken from a temperature curve measured in the Finnish Game and Fisheries Research Institute, Saimaa Fisheries Research and Aquaculture, Enonkoski, in 1986-1987 (Fig. 2). After that, the temperature curves over the experimental period (0-90 years) for the year classes were constructed by generating a deviation ε for the measured curve (0-curve) from $N(0, \sigma_3^2)$. The daily water temperatures were then calculated by adding the deviation ε to the daily temperatures of the measured curve, where $\mu_3=1.88$ °C. In order to demonstrate the effect of temperature the value of σ_3^2 was set different for each (three) 30 year period. The length of the incubation period for each egg was taken from $N(\mu_4, \sigma_4^2)$, where $\mu_4 = 237.6 - 28.83(1.88 + \varepsilon)$, rounded to the nearest integer (cf. I, Fig. 1B). The length of hatching period results from the value of σ_4^2 , based on unpublished data. Examples of calculations are given for the 90 years (Table 1).

The third variation source studied in the year classes' survival was predation (P) on vendace larvae by a hypothetical predator. The size- and density-independent predation intensity (%) per day was mimicked. Every day a simple random sample was taken from the hatched larvae population. Daily predation (p) pressure (larval daily mortality) was

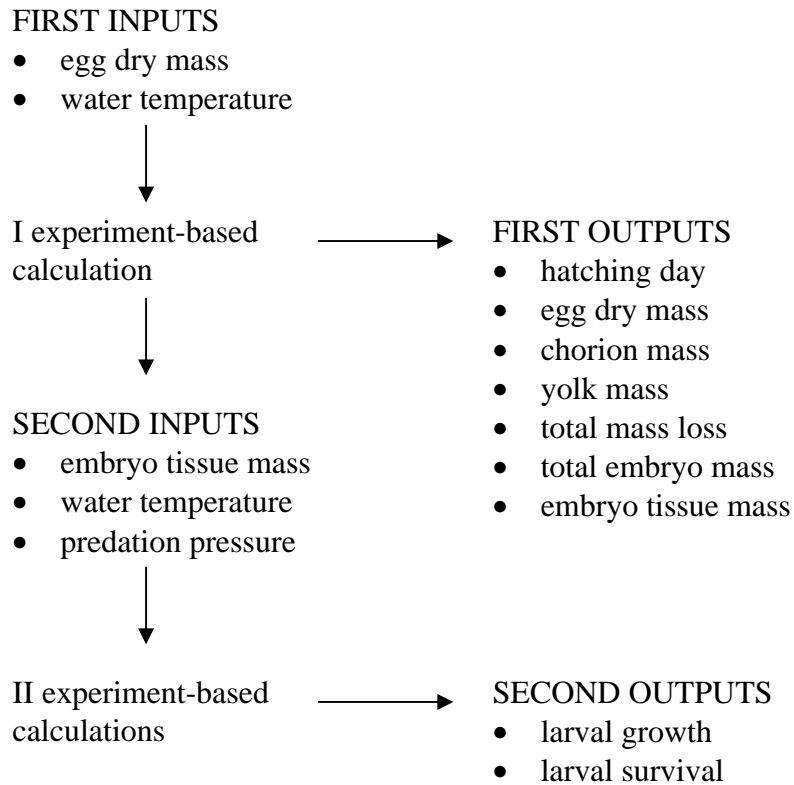


Figure 1. Diagram of the model design. In the first input the egg population and water temperature are generated from fertilization to the time of hatching. The first (I) experiment-based calculation produces the first outputs. Hatching day and the tissue mass of the embryo is needed for the second input, as well as, water temperature and, the predation pressure on vendace larvae. The calculation in the second phase produces the daily growth (size in dry mass) and survival of larvae. The whole process is fixed in real time (0-250 days), where the start point is the moment of fertilization (day 0). The terminal point is fixed on the larval size, which is the 5 mg in dry mass (20 mm for total length) or in alternative case on the day 250. Variation in the yearly survival of larvae is then viewed in the light of the separate and combined effect of e.g. egg dry mass, water temperature, and predation pressure on the yearly larval survival.

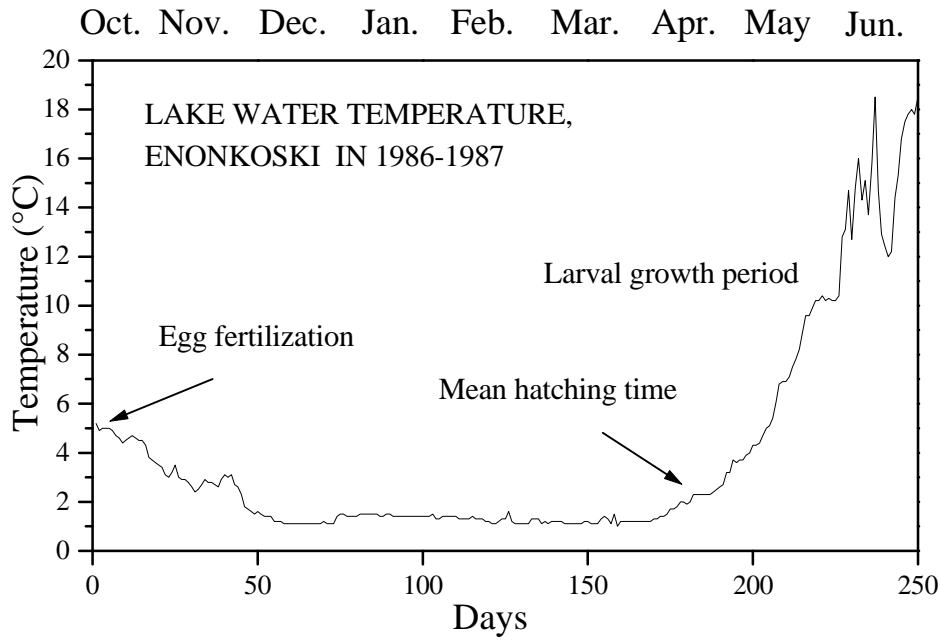


Figure 2. The temperature curve measured in the incoming water at the Finnish Game and Fisheries Research Institute, Saimaa Fisheries Research and Aquaculture, in 1986-1987 (Enonkoski, Finland).

Table 1. The simulation conditions: the means ($\mu_1, \mu_2, \mu_3, \mu_4$) and the variances ($\sigma_1^2, \sigma_2^2, \sigma_3^2, \sigma_4^2$) and their units used in simulation experiments for vendace eggs over three different 30-year periods. The values (g) of μ_2 , and μ_4 were generated. μ_1 is the expected value of mean egg dry mass of year class (III, Fig. 1), μ_2 is the mean egg dry mass of the same year class, μ_3 is mean water temperature (here 1.88 °C), μ_4 is the mean time of hatching, σ_1^2 is the variance of the expected value μ_1 . σ_2^2 is the variance of egg dry mass, σ_3^2 is the variance of water temperature and σ_4^2 is the variance of the length of incubation period. P is the predation pressure.

Years	μ_1 (mg)	μ_2 (mg)	μ_3 (°C)	μ_4 (d)	σ_1^2 (mg)	σ_2^2 (%)	σ_3^2 (°C)	σ_4^2 (d)	P (%d ⁻¹)
1-30	0.65	g	1.88	g	$2.5 \cdot 10^{-3}$	100	$5.625 \cdot 10^{-3}$	2.25	5
31-60	0.65	g	1.88	g	$2.5 \cdot 10^{-3}$	100	$50.63 \cdot 10^{-3}$	2.25	5
61-90	0.65	g	1.88	g	$2.5 \cdot 10^{-3}$	100	$455.6 \cdot 10^{-3}$	2.25	5

constant ($5\%d^{-1}$) during the simulated 90 years (cf. Houde 1987, Karjalainen *et al.* 2000). The effect of predation intensity on the larval mortality was separately studied using three different predation intensities. The effect of predation was followed until the end of the experiment (larvae size 5 mg in dry mass and about 20 mm in total length, see Fig. 7).

3.2.2 Experiment-based calculations

The framework of the experiment-based calculations during the endogenous feeding of the single egg is the equilibrium,

$$(1) m_e(0) = m_c(t) + m_p(t) + m_r(t) + m_y(t)$$

where $m_e(0)$ is the egg dry mass (mg) at the fertilization moment. Correspondingly, m_c is the dry mass of the egg chorion, m_p is the dry mass of the embryo tissue, m_r is the metabolism in form of the loss dry mass and m_y is the dry mass of the yolk at the moment of t . The excretion and germinal disc have been omitted from the calculations (cf. Kamler 1992).

3.2.3 Estimation for chorion- and embryo dry mass

At the hatching day (*HD*), the dry mass of the egg chorion (2) and the embryo tissue mass (3) were estimated:

$$(2) m_c(HD) = 0.1 m_e(0) \pm error$$

$$(3) m_p(HD) = m_e(HD) - m_c(HD) - m_y(HD)$$

The estimation of the chorion mass is considered in papers II and III. For model calculations the chorion dry mass was roughly rounded to 10% from the initial egg dry mass. The yolk dry mass was estimated (recalculated from yolk volume) in paper III (and see also 3.2.5). The embryo tissue mass m_p remains (from the total dry mass) after the subtraction of the egg chorion mass (m_c) and yolk dry mass (m_y).

3.2.4 Estimation for egg daily metabolism

Mature spawners of vendace (*Coregonus albula* (L.)) were caught with gill nets at the end of October in 1991 in Lake Pyhäselkä. Eggs were stripped and fertilized by sperm at approximately 6 °C temperature in lake water of pH 6.7. The vendace egg were incubated in a laboratory at the University of Joensuu and *in situ* in Lake Pyhäselkä with a temperature range of 0.1-6.0 °C. Details for experimental methods are given in references (I, III).

The effect of early egg dry mass on further egg metabolic activity (metabolic dry mass loss) was estimated. In this purpose the original data were analysed in respect of dry mass first as one group and then after division as different groups. The divisor between the groups (greater and smaller eggs dry mass) was the regression line calculated by the least squares method. Then the different groups were analyzed again in similar way with the least squares method. Prior to analyses eggs were arranged in homogenous groups in relation to the incubation temperature and age of embryos, enabling the slopes of the linear regression of the dry mass on time to be calculated between the groups. The metabolic dry mass loss (mgd^{-1}) relative to the early dry mass (mg) was estimated from the values on these slopes (Fig. 3).

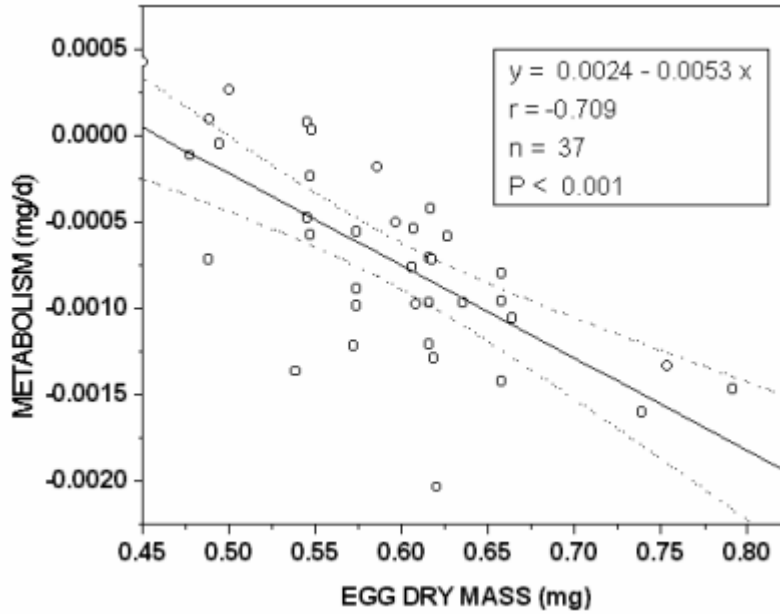


Figure 3. Regression of the metabolic dry mass loss (mgd^{-1}) on the early dry mass (mg) of vendace egg. The range of the incubation temperature was 0.1-6.0 °C. The points are the slopes (b) of the linear regression $m_e = a + bt$, where m_e is the dry mass of egg, t = time (in days) and a is the constant. 95% confidence limits of regression are given with broken lines.

The interactions between incubation temperature and the initial egg dry mass on the metabolic mass loss are roughly described in Fig. 4. The estimates for daily metabolism $m_r(t)$ over the incubation period is given in Table 2. Then, let $m_e(0)$ be the dry mass of an egg at the fertilization moment and let HD be the length of its incubation period in days. Furthermore, let $T(t)$ be the temperature of water on the day t . Daily metabolism $m_r(t)$ on the day t , is calculated (Table 2) by the equation (4):

$$(4) \quad m_r(t) = 0.00151 - (0.00286 m_e(0) + 0.00013 T(t)) m_e(0) / m_e(t-1)$$

Total metabolism $m_r(HD)$ is calculated as the sum of daily metabolism.

3.2.5 Estimation for embryo yolk dry mass

Ripe spawners of vendace were gill netted in two different parts of Lake Saimaa in 1989 and 1991 (I, III). Fertilized eggs were incubated in lake conditions and in the laboratory. In order to estimate the amount (mg) of yolk dry mass at the hatching moment the relationship between yolk volume (mm^3) and yolk dry mass was estimated (III). The dry mass of yolk was estimated using equation 5. The description of estimates for the remaining yolk dry mass ($m_y(HD)$) at the moment of hatching are given in Fig. 5 and in Table 2.

$$(5) \quad m_y(HD) = 0.02687 + 0.52655 m_e(HD) - m_c(HD) - 0.00089 HD$$

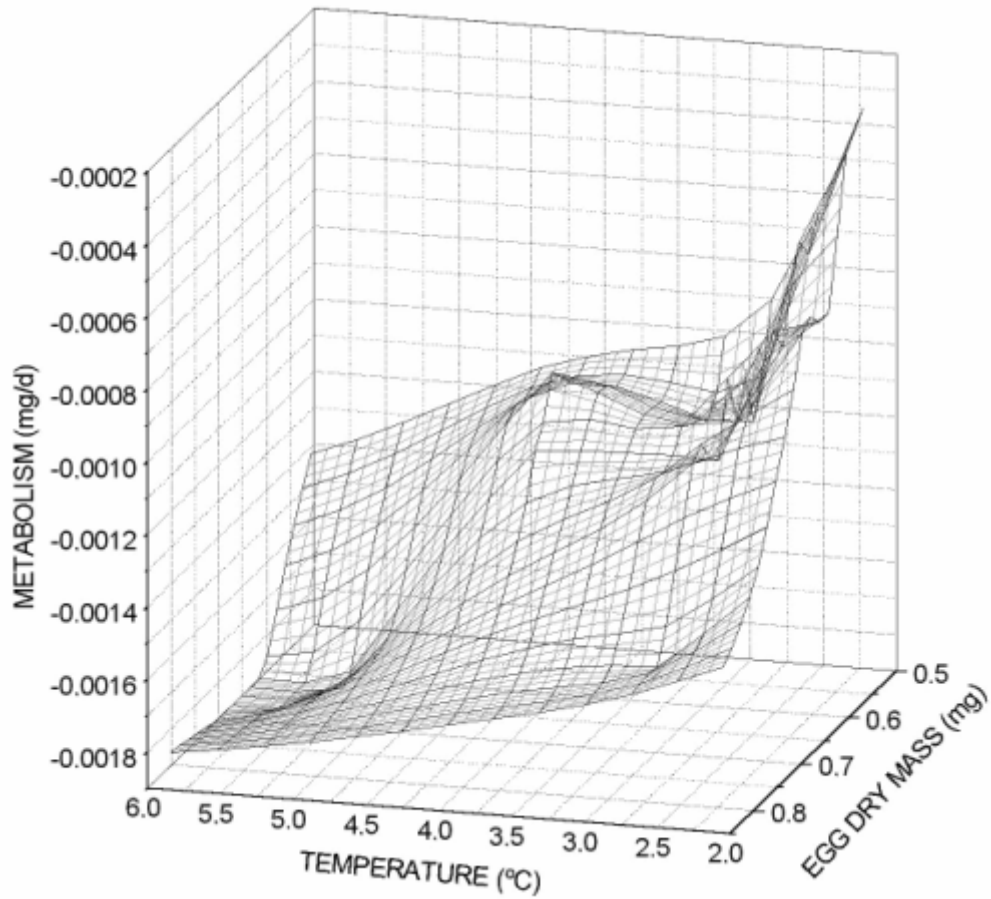


Figure 4. Daily metabolism (mgd^{-1}) of vendace egg in respect of water temperature ($^{\circ}\text{C}$) and early egg dry mass (mg). The equation of the surface graph is $m_r = a - (b m_e + c T(t))$, where m_r is the metabolism, m_e egg dry mass, a , b and c are the constants and T is the mean daily temperature on the day (t). The time dependent form for daily metabolism $m_r(t)$ on the day t was estimated (Table 2) from the model $m_e(t) = a - (b m_e(0) + c T(t)) m_e(0) / m_e(t-1)$, where $m_e(0)$ is the estimated dry mass of the egg at the moment of fertilization while $m_e(t-1)$ is the dry mass of the egg on the day ($t-1$).

Table 2. The models used for estimation of daily metabolism ($m_r(t)$) of vendace egg on the day t and the dry mass of yolk (m_y) resources on the hatching day (HD) of the embryo. The values and their standard errors (S.E.) of the model equipments are given. The form of the equations are given in text Figs. 4 and 5. The calculations were carried out by using the SYSTAT program.

Equation	$a \pm \text{S.E.}$	$b \pm \text{S.E.}$	$c \pm \text{S.E.}$	R^2	n
(4) $m_r(t)$	0.0015 ± 0.00023	0.00286 ± 0.00038	0.00013 ± 0.00003	0.81	37
(5) $m_y(HD)$	0.02687 ± 0.0177	0.52655 ± 0.02479	-0.00089 ± 0.00008	0.76	221

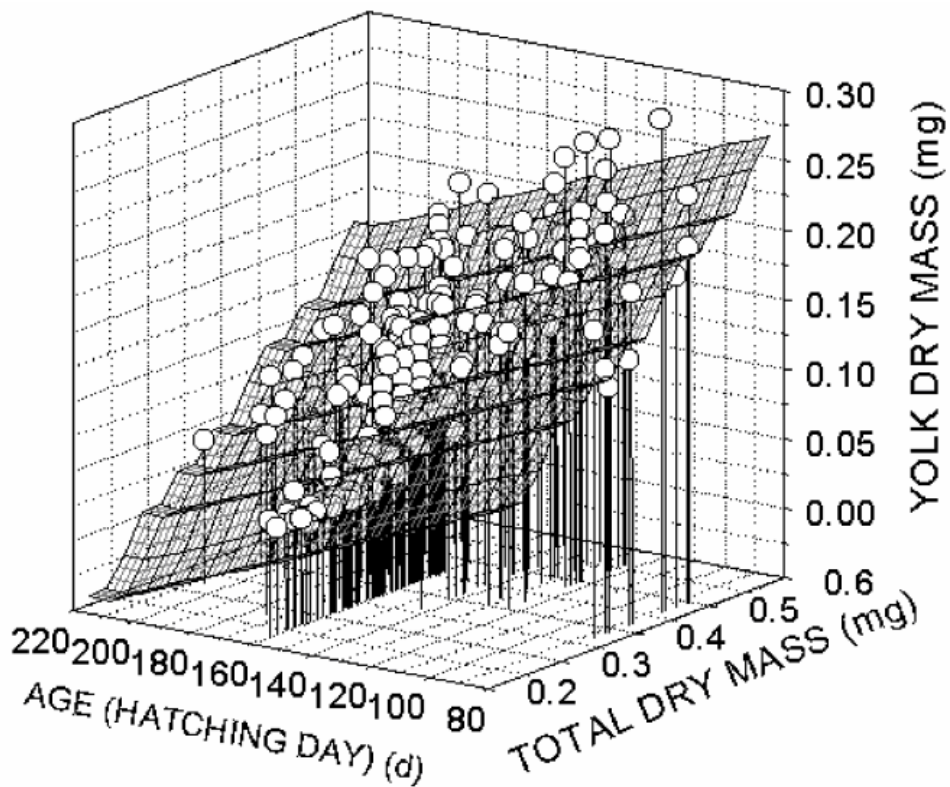
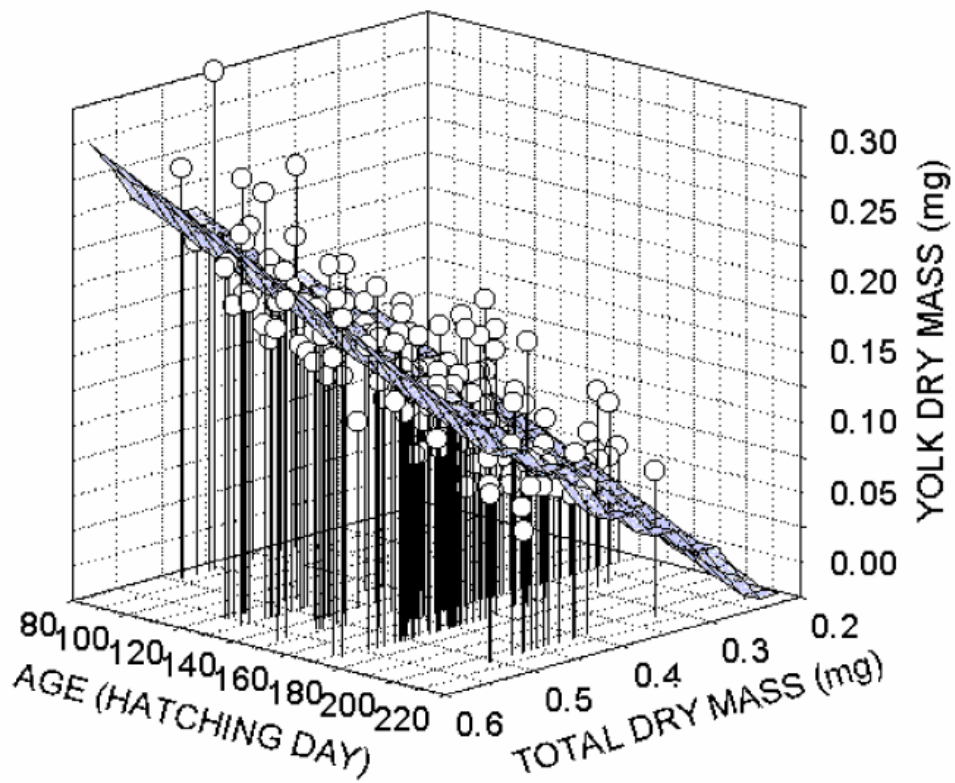


Figure 5. The estimation of the remaining yolk dry mass $m_y(HD)$ of embryos at the moment of hatching. The 3-dimensional graph was plotted from two sides. The form of the equation is $m_y(HD) = a + b m_p(HD) - c HD$, where a , b and c are the constants (Table 2).

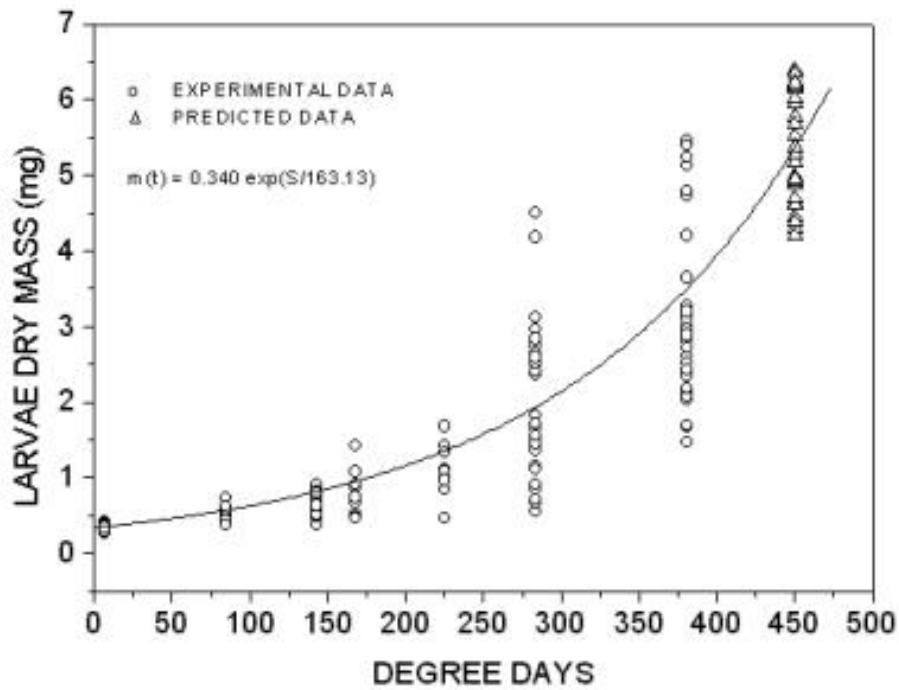


Figure 6. Regression of larvae dry mass on degree days is given above. Experimental and predicted data are given. The predicted data points were calculated by using the individual dry masses of hatched embryos (m_p) and the same course of degree days than in real experiment.

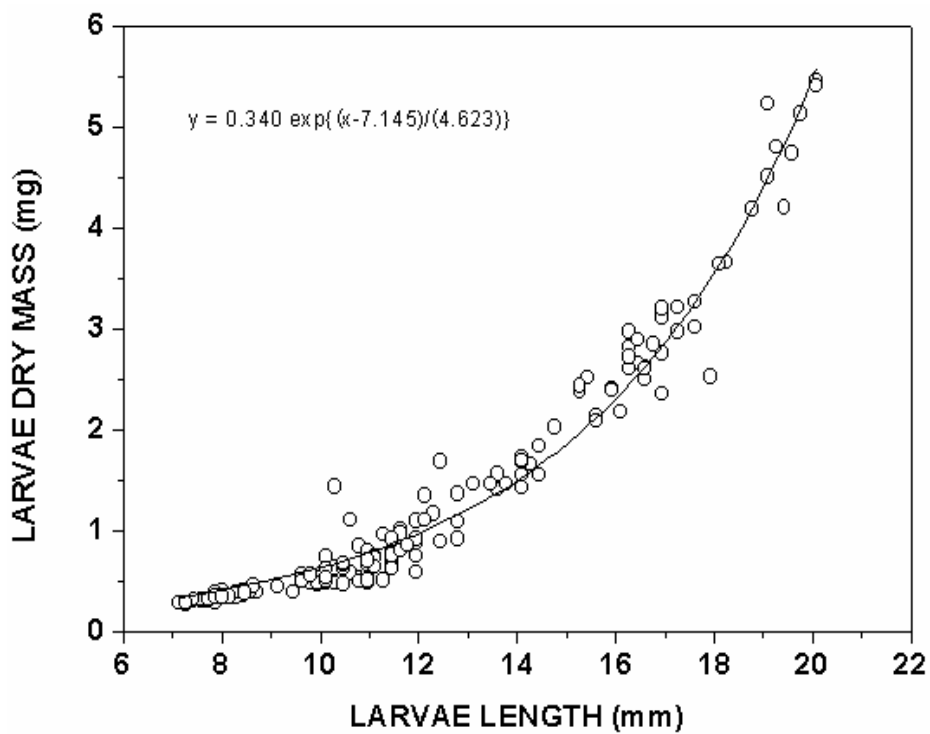


Figure 7. Regression of experimental larvae dry mass (mg) on the larvae length (mm). The data is the same as in Fig. 6.

3.2.6 Estimation for larvae growth

Newly hatched vendace larvae were reared in laboratory at three different temperatures 6.5 °C, 12.9 °C and 17.3 °C with living zooplankton (900 zooplankters/larva/day) in laboratory conditions over three weeks experimental period (unpublished data). In these laboratory conditions, the amount of food was alleged to be an unlimited factor for the larval growth and survival, based on works V and VI. The size (total length, mm, total dry mass, mg) of larvae were measured in the beginning, middle and at the end of experiment. The increase in dry mass of larva (m_l) on the day (t) was calculated in form:

$$(6) m_l(t) = m_p(HD) \exp(S/163.13), \text{ for } t=HD+1, \dots,$$

where $m_p(HD)$ is the dry mass of the single embryo tissue at the day of hatching and S is the degree-days calculated as the sum of daily temperature (°C) of water from the moment of hatching (Fig. 6). The relationship between larvae length (mm) and dry mass (mg) are also given in Fig. 7.

4. RESULTS

4.1 Dynamics of egg, embryo and larval dry mass

4.1.1 Egg and embryo dry mass and composition

The characterization of the egg size variables was carried out by measuring the diameter (D , mm), fresh mass (FM, mg), and dry mass (DM, mg) of the single eggs. The mean egg dry mass ($DM \pm SD$) was found to vary from 0.57 ± 0.05 mg to 0.65 ± 0.09 mg during one year (1987) in five lakes (I). Accordingly, in the constructed model population, the value of the egg dry mass varied from a minimum of 0.45 mg to a maximum of 0.90 mg within the population (III). Furthermore, the egg dry mass (DM, mg) decreased during incubation (I, II, III). The dry mass of newly hatched embryos varied between 0.25 and 0.55 mg, depending on their hatching time and, thus, the incubation temperature (I, II, III). The metabolic mass loss together with the chorion mass was found to be the main dry mass loss of eggs (II, III). The minimum mass of the living larva was between 0.20 and 0.15 mg; below which the larva was starving (V, VI). Energy, protein and fat mass decrease during incubation, hatching and starving (Fig. 8).

The main time-dependent changes in the vendace egg dry mass have been summarized in simulations Fig. 9. The total dry mass and mass deviation between individuals decrease. Opposite to this, metabolic mass loss increases during incubation. At the moment of hatching the total dry mass was divided into two parts; the embryo tissue and the remaining yolk dry mass.

4.1.2 Size dependent metabolic rate and embryo mass

The present simulations reveal a strong linear dependence on means between 1) larvae dry mass at the moment of hatching and initial egg dry mass (Fig. 10A), 2) larvae dry mass and total dry mass loss (metabolism) (Fig. 10B) and 3) the total dry mass loss (metabolism) and the initial egg dry mass (Fig. 10C). These results also show a strong scatter and, therefore, no dependence exists between the total dry mass loss and the hatching day of the year classes (Fig. 10C).

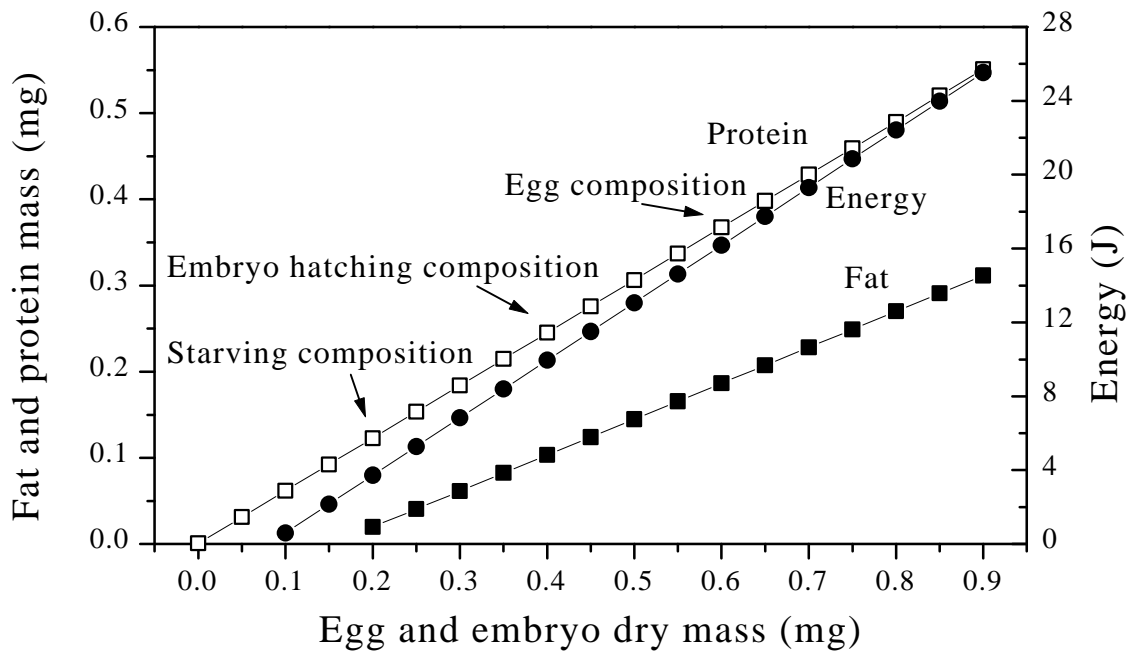


Figure 8. The lines of total energy (J), fat and protein mass (mg) on the dry mass (mg) of egg and embryos. Arrows indicate roughly the mean egg dry mass and mean embryo dry mass during hatching and starving. Fat mass [F] was calculated from the carbon mass [C] in fat by $F=1.304 C$; protein mass [P] from the nitrogen [N] by $P=6.25 N$; carbon in protein by $C=3.25 N$, and energy balance [E] by the equation $E=12.388 C-4.636 N$ (Brouwer 1965). The carbon and protein mass (mg) per egg and embryo dry mass [DM] (mg) were calculated by $DM=0.076+1.568 C$ and $DM=-0.001+10.22 N$, (III).

The estimated proportion of cumulative metabolism from the initial ($m_e(0)$) egg dry mass varied from 0.15 to 0.35 and the proportion of the embryo tissue mass varied from 0.42 to 0.62 of the initial egg dry mass.

4.1.3 Effects of water temperature and oxygen concentration on embryo size and larval survival

There is a strong linear dependence (negative) between the hatching day and the yolk mass (Fig. 11A), as well as a positive dependence between the hatching day and the embryo tissue mass (Fig. 11A). Accordingly, during the hatching period of 60 days the increase in the embryo tissue mass and the decrease in the embryo yolk dry mass were about 0.050 mg and 0.070 mg, respectively.

Larval survival depends on the incubation and, on the other hand, on the larval growth temperature (Fig. 11B). The survival of larvae also depends on the embryo dry tissue mass at hatching (Fig. 11C). Low water temperature maximizes the length of the embryo (Fig. 12A) and the hatching length of embryo has great effect on larval survival (Fig. 12B). According to these results, the beneficial high survival of year classes occurs

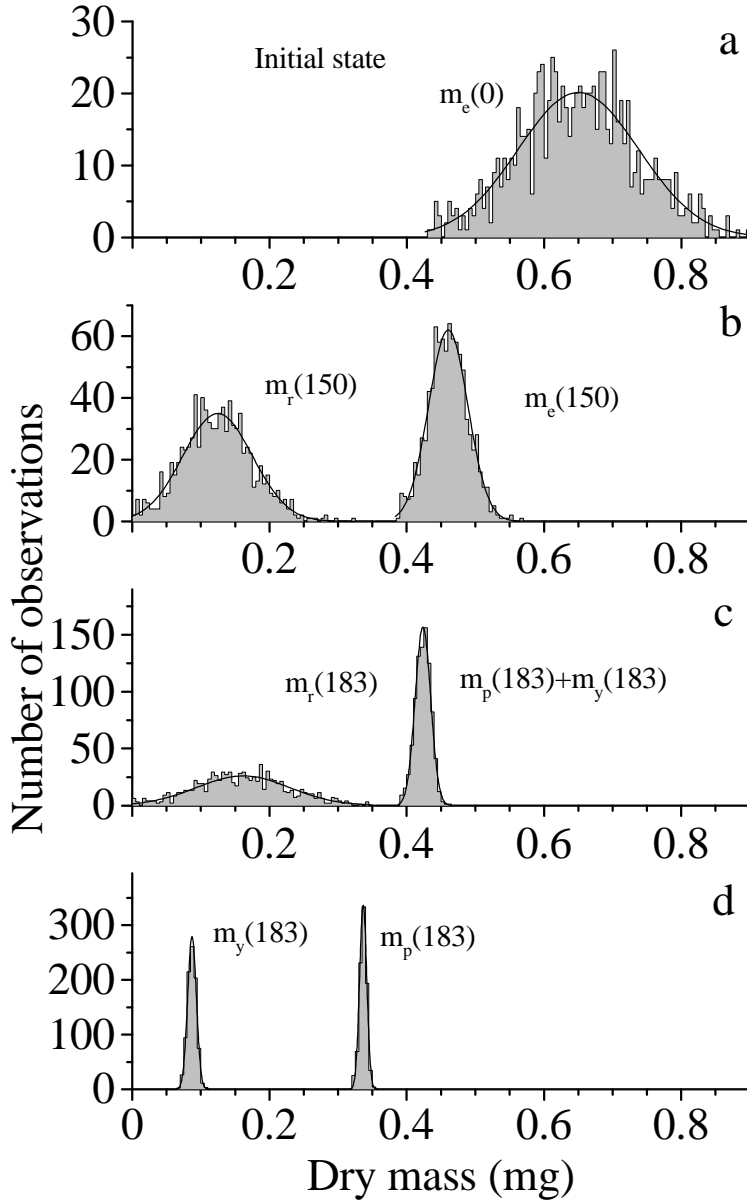


Figure 9. General outline of model outputs of the vendace egg dry mass (mg) at different phases of incubation. The initial state (a) is the dry mass distribution of the egg population at the moment of fertilization ($m_e(0)$). The total dry mass $m_e(t)$ and the dry mass of cumulated metabolism $m_r(t)$ before (b) and on the estimated mean hatching day (c) are given at the ages 150 d and 183 d, respectively. The total dry mass was divided (d) to the yolk dry mass remaining $m_y(t)$ and the dry mass of the embryo tissue $m_p(t)$ at the day of hatching. Here, the eggs ($N=900$) at the moment of fertilization $m_e(0)$ are simulated from $N(\mu_2, \sigma_2^2)$, where $\mu_2=0.65$ mg and $\sigma_2^2=0.008$ mg (III, Fig. 1). Incubation temperature over the experimental period used in this case was measured in Enonkoski between 1986-1987. The hatching day for each egg was generated from $N(\mu_4, \sigma_4^2)$, using $\mu_4=183$ d and $\sigma_4^2=2.25$ d.

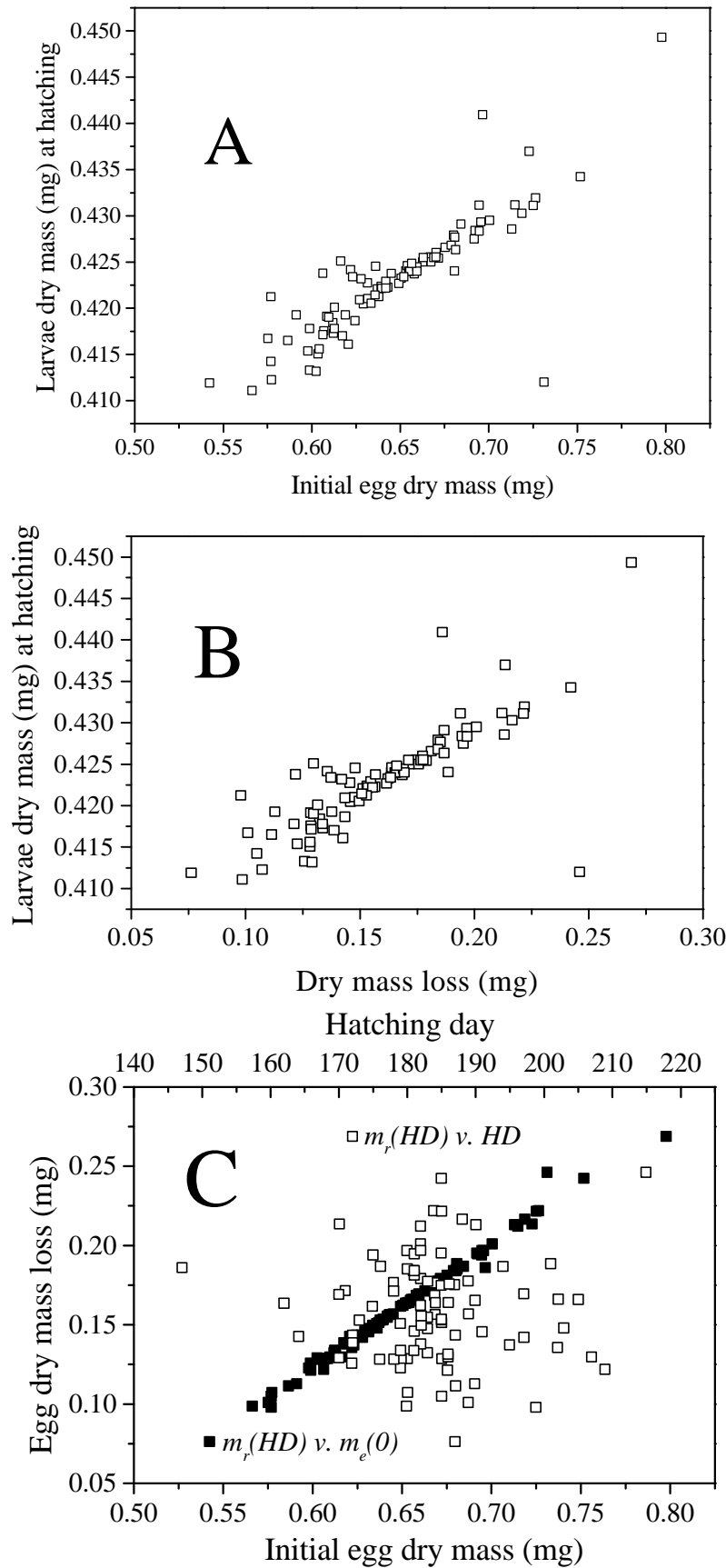


Figure 10. Scatter plots of: larval total dry mass (at hatching) on the initial egg dry mass (A) and on the dry mass loss (metabolism, m_r) (B). Scatter of egg dry mass loss versus initial egg dry mass (solid points) and hatching day (open points) are given in C. Each point represents the mean value of the year class (population size = 600). The simulation conditions are given in Table 1.

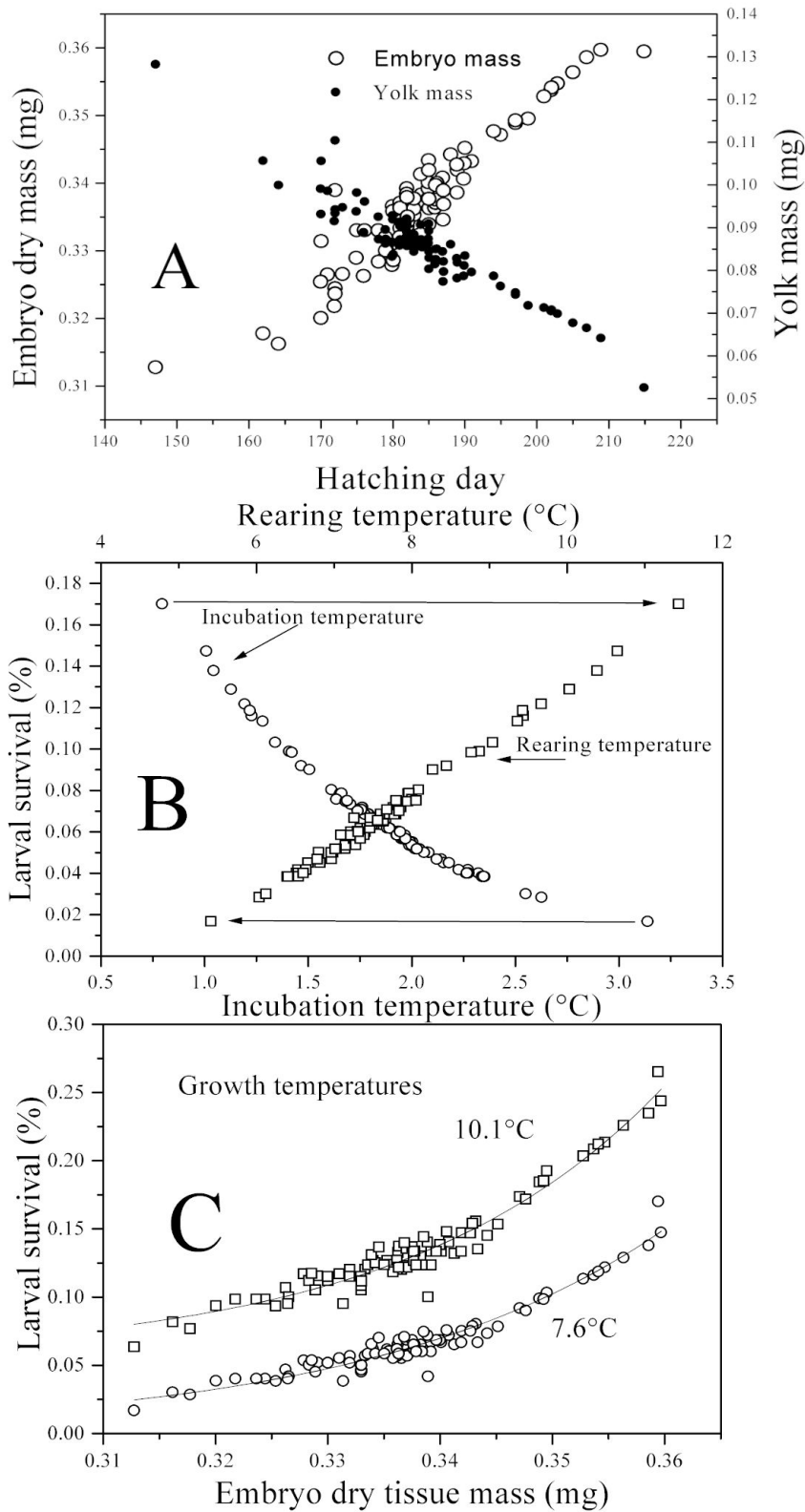


Figure 11. The effects of the temperature (hatching day) on embryos properties and larval survival (%) calculated from all hatched larvae. Embryo and yolk dry mass (mg) versus hatching day (A). Effect of mean temperature on the survival of larvae during incubation and rearing (B). The extreme temperature (shift from incubation to rearing) conditions are indicated by the long lateral arrows. The effects of larval dry tissue mass (at hatching) on the larval survival at two different rearing temperatures are given in C. Each point represents the mean value of the year class (population size = 600). The simulation conditions are given in Table 1.

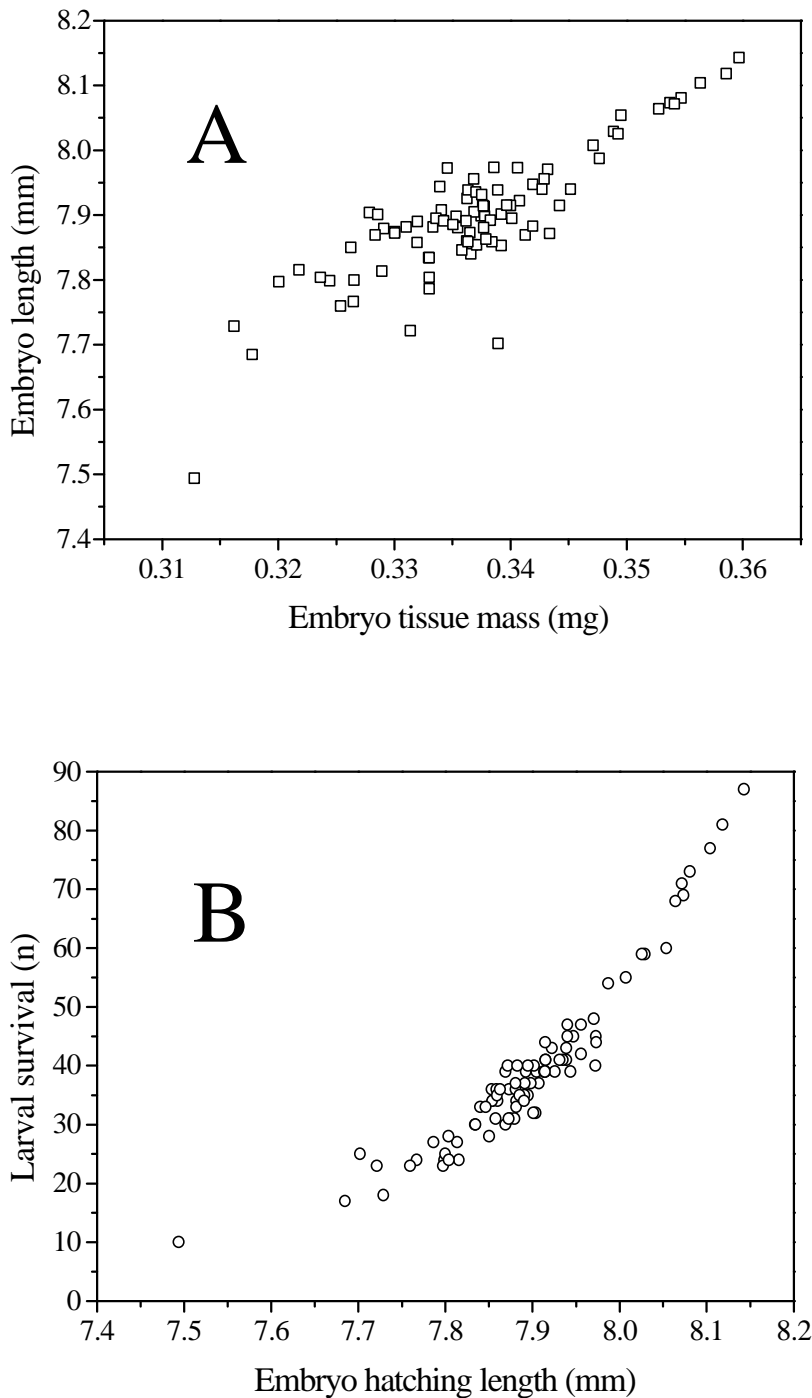


Figure 12. Scatter plots of embryo length (mm) on the embryo dry tissue mass (mg) A and larval survival (%) on the embryo hatching length (mm) B. Each point represents the mean value of the year class (population size = 600). The simulation conditions are given in Table 1. Length estimation based on unpublished data.

at a low incubation temperature, the growth temperature being as high as possible. In the opposite case, when the incubation temperature is high and growth temperature is low, larval survival is poor. The elongation of the incubation period increases the embryo dry (tissue) mass at hatching and, therefore, has a beneficial influence on the

survival of larvae. The phenomenon is more prominent if the growth temperatures are elevated.

The oxygen conditions influence the size and also directly survival of larvae. Embryos incubated in low oxygen concentration and high (3 °C) temperature were shorter with larger yolk volume than embryos incubated in high oxygen concentration and lower temperature (II). Survival was also lower in low oxygen concentration and high incubation temperature (3 °C) (II).

4.1.4 Endo- and exogenous feeding and larval growth

The accelerated loss of the metabolic dry mass loss (endogenous feeding) reached the maximum at the hatching point or soon after (II, III). The rate of such mass loss is highly dependent on water temperature (III). In all experiments, the larvae started to feed on exogenous food immediately or soon after hatching (V). The exogenous feeding of vendace larvae was selective (V). In a high zooplankton density, the larvae preyed on copepod nauplii as the primary exogenous food source but in restricted food conditions the prey in larvae guts was similar to the plankton composition in the tanks (V). The gastric evacuation rate was faster for copepod nauplii than larger copepods (IV). This evacuation rate also accelerated with the temperature rise (IV). Furthermore, the growth rate of larvae increased with increasing temperature and zooplankton density (V, VI). The starving of larvae was studied and discussed in paper VI. The simulated growth curves for larvae at three different temperatures are given in Fig. 13.

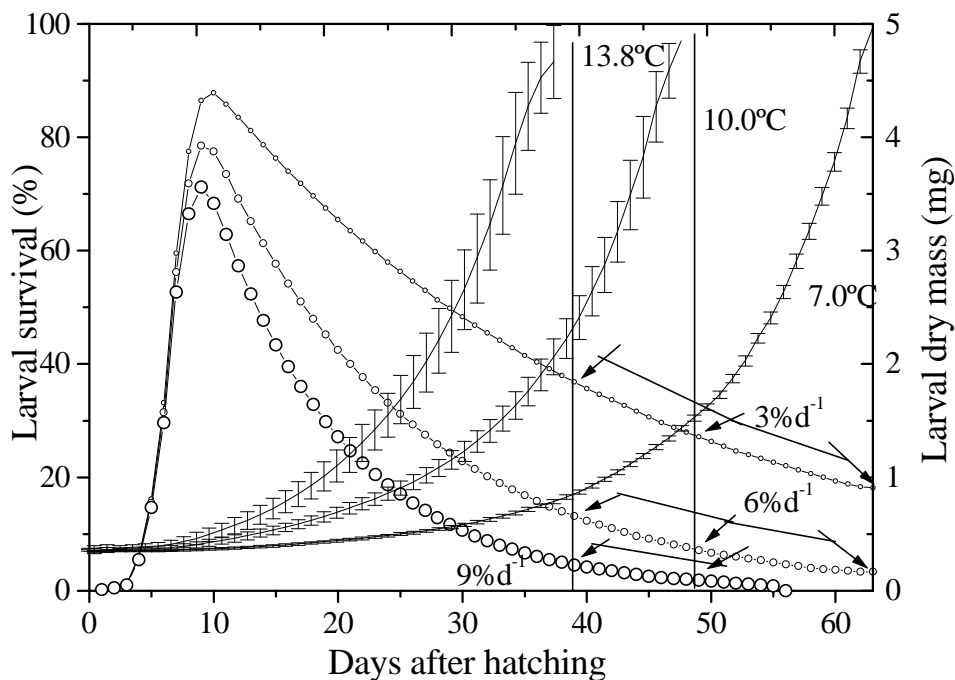


Figure 13. Larval survival (%) and growth (dry mass, mg) in three different temperatures and three different predation pressures (% d⁻¹). The vertical bars in growth curves indicate the daily SD values in dry mass of living larvae. The arrows indicate the proportion (%) of larvae still alive at the end of experiment (5 mg in dry mass, initial population size = 600).

4.2 Variability in survival during early life history

4.2.1 Effect of different predation intensity

The effects of three different predation intensities on the larval survival are illustrated in Fig. 13. On the one hand, differences in the water temperature (growth rate) caused differences in survival of larvae, although the predation pressure was constant. On the other hand, the differences in predation pressure level reflect very sensitively to larval survival. At the predation intensity 9d^{-1} no larvae survived to the end of the experiment at $7.0\text{ }^{\circ}\text{C}$ but about five percent survived if the rearing temperature was $13.8\text{ }^{\circ}\text{C}$. At the predation level 3d^{-1} about 18% of larvae survived to the end of the experiment at $7.0\text{ }^{\circ}\text{C}$. In all cases the larval density decreased markedly already during the hatching period.

4.2.2 Combined effects of egg dry mass and water temperature

The simulation results of the larval survival for 90 year period are summarized in Fig. 14. The simulations were carried out by solving the development of each year class and the year cycles were repeated for 90 independent times. The result shows that the variation of the year class survival depends simultaneously on the fluctuation of the temperature and on the larval mortality caused by predation. The increase of temperature fluctuation prominently increases the variation in the year class survival of vendace. For examination in more detail the variation in egg dry mass, total larval dry mass and metabolism (dry mass loss) is also given (Fig. 15).

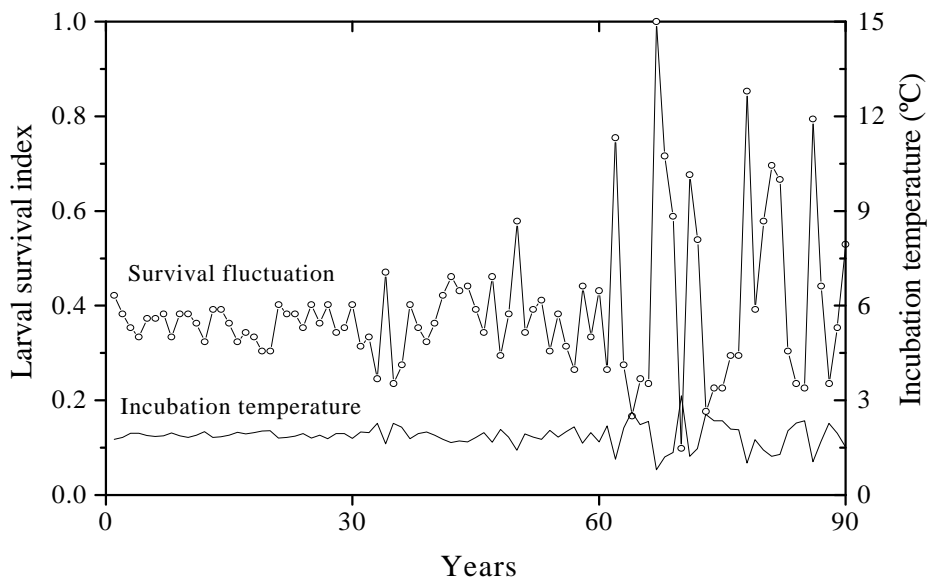


Figure 14. The simulated variation in larval survival index (0-1) at different incubation temperatures ($^{\circ}\text{C}$) over 90 independent year classes. Survival index 1 corresponds to the maximum survival rate (17%, calculated from all hatched larvae) and the minimum, 0.1, corresponds to the minimum survival rate of larvae (1.7%). Each point represents the survival of the year class (population size = 600). The simulation conditions are given in Table 1.

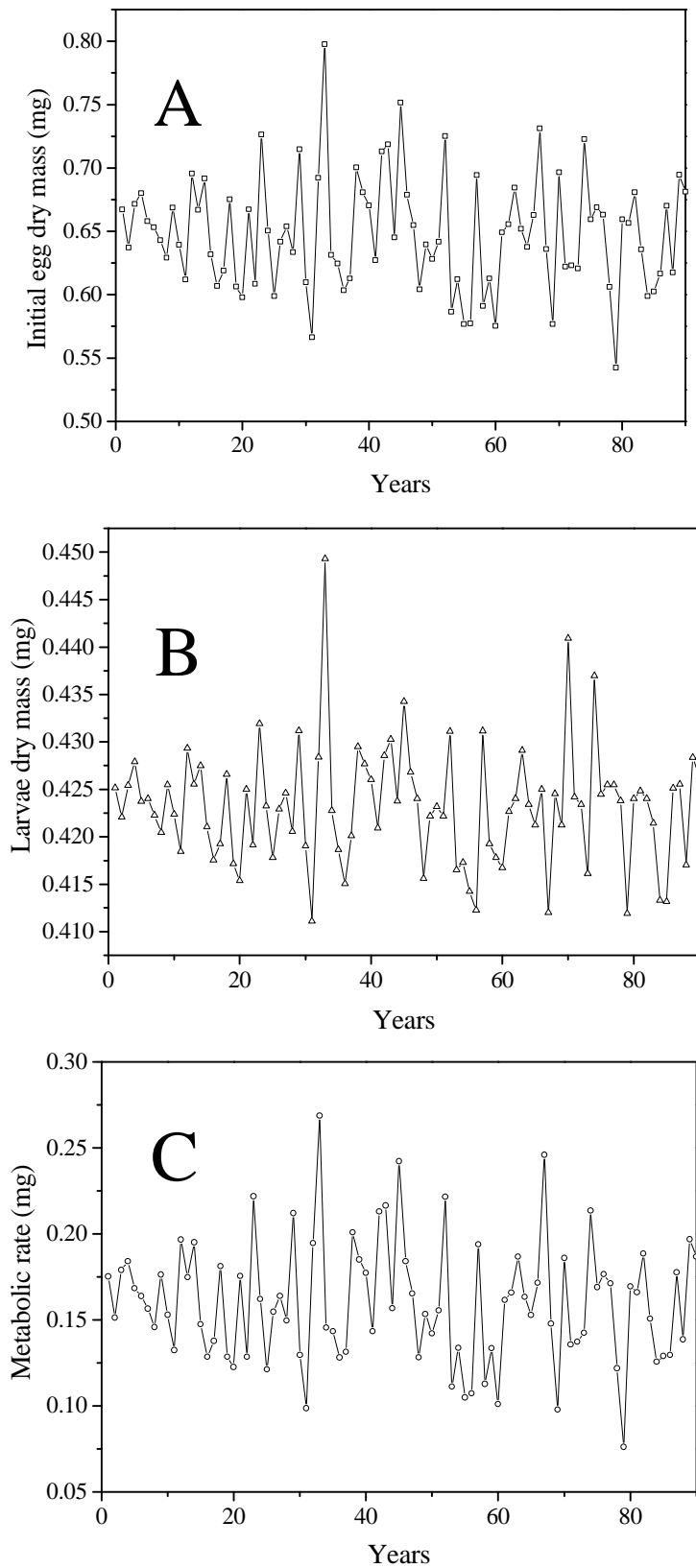


Figure 15. The simulated variation in egg dry mass (A), total dry mass of larvae at hatching (B) and total metabolism of eggs (C) over the 90 independent year classes. Each point represents the mean value of the year class (population size = 600). The simulation conditions are given in Table 1.

5. DISCUSSION

5.1 General study idea

In this study, to interpret the dynamics of the early life history of vendace, the early development has been reduced into the form of a simplified model (cf. Fig. 1) The connecting thought was to follow the total dry mass both of the individual and population level over the early life history of vendace. According to this study, combined effects of the variation in egg size, water temperature, hatching time, larval phase duration and predation pressure may cause enormous (many fold) fluctuations in the yearly survival of vendace larvae, although the initial population size (number of members) between the years is constant. The results do not represent any special lake. Obviously, egg size, water temperature and predation pressure work with different intensity in different lakes and in different years. Therefore the results can be applied e.g. when the purpose is to look for a common mechanism between lakes. There are no sources in the literature about combined effects of the egg size, temperature and predation pressure on the survival of vendace larvae. Because of this (different methods have been used in recent studies in the literature) it is impossible to make any direct comparison between the present study and earlier work.

The "dry mass" is the mass in which the water content is very low (caused by differences in air humidity during weighing process) or the mass is completely without water. In this study the effect of fungus infection on egg weight was out of control. Thus, there are some errors (obviously overestimated weight) in egg weighing results. However, when comparing different groups the effect of that error is very small. One can determine dry mass in any egg or larval developmental stage. The individual dry mass can be used as a way to the other important variables, e.g. size (egg diameter, larval length) carbon mass and energy (III, Platt *et al.* 1969, Sisula & Virtanen 1977, Gnaiger 1983, Lahti 1991). The idea of equivalence between energy and dry mass was applied to construct equation 1 (in 3.2.2). Details in egg composition and yolk dry mass were studied in paper III.

5.2 Variation in egg size

The mean egg dry mass varied from the minimum of approximately 0.55 mg to the maximum of 0.80 mg in simulated data for 90 years. In Finnish lakes, the mean vendace egg dry mass can vary from 0.57 mg to 0.65 mg (I), from 0.52 mg to 0.78 mg (Sarvala & Helminen 1995) and from 0.582 mg to 0.716 mg (Koho 1998). Some wider ranges of mean dry mass values for vendace eggs are reported from Polish lakes: 0.741-0.808 mg (Kamler & Zuromska 1979) and 0.4-0.9 mg (Wilkonska & Zuromska 1988). Egg size is considered in paper III with more detail. The individual eggs for each year class were generated by using 0.1 as the value of the coefficient of variation *i.e.* $\bar{x}/SD = 0.1$. The value of variation coefficient in Finnish lakes of different egg samples varied from 0.08 to 0.16 (I) and 0.1 to 0.21 (Sarvala & Helminen 1995). Increasing (in simulations) the value of the variation coefficient was impossible without omitting the smallest eggs, which had weak metabolic rate. Therefore, the dry masses of the simulated eggs correspond roughly to the dry masses of eggs in real vendace populations. Variation in the egg size is considerable (and even greater than in simulations) both between lakes and years as well as between individuals of the same population. It is also important to notice that the frequency in variation (simulated variation in different years) in egg dry mass do not represent any special trend observed in lakes. The focus of simulations was

to generate random variation in egg dry mass for initial state of early life of vendace. Random variation in egg size and in the described population structure produces some maximum and minimum values per decade. The size-dependent processes follow the variation in egg size. Therefore, the total (yolk+embryo) hatching mass of larvae, and the cumulated metabolic rate also vary according to egg size over years. Total dry mass is related to total carbon mass and energy of eggs and larvae; the greater the dry mass, the better is larval ability to resist starving (Blaxter & Hempel 1963, Blaxter 1969, Dabrowski 1989). On the one hand, metabolic mass (yolk mass) is lost to new individual tissues (embryo tissues) and maintenance. Thus, egg metabolic rate (mass loss) may be a good indicator for fish larval quality and survival (cf. Kamler 1992). On the other hand, in restricted food conditions the metabolic requirement leads to starving of fish larvae.

The dry mass of just hatched vendace larvae depends on the initial egg size and the hatching time. Karjalainen (1998) reported slightly over 0.4 mg dry mass for just hatched vendace larvae. The minimum dry mass (and energy) of fish larvae represents the so-called "point of no return"-state, which depends also on the temperature and food conditions (III, VI, cf. Blaxter & Hempel 1963, Dabrowski 1981, Dabrowski & Luczynski 1984, Dabrowski *et al.* 1984). When the larvae approach the minimum life mass (III, V, VI), the ratio of inorganic/organic matter changes. This change may cause a serious problem for the starving animal and this needs more research.

5.3 Hatching and the "critical period"

The hatching ecophysiology of vendace is known very well (Luczynski 1984^a, Luczynski 1984^b, Luczynski & Kirklewska 1984, Luczynski & Dettlaff 1985, Luczynski *et al.* 1986, Luczynski *et al.* 1987, Luczynski & Kolman 1987). The effect of water temperature on the time of hatching for whitefish and vendace has been predicted in models (I, Colby & Brooke 1973, Luczynski & Kirklewska 1984).

In this study, the used model and temperature curve give a mean hatching time of 183 days at the water temperature of 1.88 °C for vendace. Correspondingly, the calculation according to the model by Luczynski & Kirklewska (1984) gives only 152 incubation days for vendace in the same mean temperature. So, there is a clear difference between these model results. The genetic variation between Polish and Finnish populations may be the reason for this phenomenon (embryonic development rate). Although these models work at different absolute levels they however give very similar relative outputs; equal shifts in the mean incubation temperature correspond to equal shifts in hatching time.

The egg and larval size have a positive relation also within species (I, see also Fig. 15, Blaxter & Hempel 1963, de Ciechowski 1966, Kjørsvik *et al.* 1990, Brown & Taylor 1992, Gisbert *et al.* 2000). Low water temperature and good oxygen conditions maximize the length of the incubation period and also the dry mass and length of the embryo body (Figs. 11A, 12A). Prolonged incubation time increases the length of the embryo but decreases the yolk volume (I, III, Luczynski *et al.* 1984). Length increase enables the embryo to catch prey and escape the predators via better swimming ability (cf. Fig. 12B). The benefit from delayed hatching (good growth conditions in lakes) can be applied in aquaculture practice (Luczynski 1984^c, Luczynski & Kolman 1985).

Low temperature (0.5-1.0 °C) is high enough for embryonic development to continue but low enough to keep the metabolic cost of the embryo low and to prevent premature hatching. After hatching, the embryo body mass may show a downward trend before the complete resorption of the yolk (III). Larvae resist this metabolic depletion of body tissues by starting exogenous feeding much before the yolk material runs out (V). Together with the water temperature, the hatching size of the embryo is a very important factor for larval growth and survival during the exogenous feeding period (Fig. 11C). During the years 1965-86 the mean water temperature ($\bar{x} \pm SD$) measured at 10 m depth in 20 Finnish vendace lakes in March was 1.38 ± 0.431 °C (Valkeajärvi 1988). Although, the temperature data published by Valkeajärvi are roughly similar to the simulated thermal conditions in the present study (during the last 30 years $\bar{x} \pm SD = 1.88 \pm 0.675$ °C), the temperature simulations do not represent any special lake. Vendace spawning depth varies greatly between lakes: vendace eggs were sampled at less than 10 m depth in Lake Suomunjärvi and Lake Onkamojärvi (Viljanen 1988) but at 8-22 m depth in Lake Puruvesi (Nissinen 1972). Thus, the temperature curves also vary greatly between lakes and spawning areas.

On the one hand the purpose of simulations was to generate similarity and on the other hand variation, in water temperature. By help of nearly constant water temperature the effect of variation in egg size was studied. By help of simulated variations in water temperature the effect of temperature on egg and larval development and survival was then considered.

For simulations the starting point was a single temperature curve (Fig. 2). Some similarities between all possible incubation curves for autumn spawning vendace can be concluded: first the autumn period with decreasing temperature, then the steady winter period and finally the spring period with rising water temperature. But in a lake the eggs (also of the same year class) develop to some extent in different temperatures. In the model the eggs and larvae of the same year class were incubated and reared following the same temperature curve, which decreased the variation for the hatching size of larvae caused by thermal factors. The realism of the model could be improved with more exact temperature curves from the egg and larvae development areas.

The instantaneous population density (N_t) and the slope of the general mortality curve $N_t = N_0 e^{(-zt)}$ in constant daily mortality (z) is dependent also on the initial (N_0) population density (Heat 1992). If the curve of survival does not indicate a steep descent, there is no critical period (Pitcher & Hart 1982, p. 159) at all, although the daily mortality may be strong.

According to the literature, the daily mortality by predation on larval fish varies widely, e.g. 5-20% d^{-1} (Houde 1987), or even 40% d^{-1} (Leiby 1984) among different fish species. Thus, the variation in mortality rate can be initiated from variation in predation pressure (a change in the amount of predators). The daily mortality of vendace larvae varies widely (0.3-7% d^{-1} , recalculated) between years and lakes, observed by Karjalainen *et al.* 2000. The simulations over 90 years indicated a strong combined effect between water temperature (regulating factor of hatching time and larval growth rate) and the predation pressure. Due to lack of information about the intensity and variation in different years mortality caused by predation pressure value was kept constant (5% d^{-1}). The effect of the predation pressure sensitivity on mortality was studied separately using three different hypothetical predation pressure (Fig. 13). When the larval size is at its minimum (*i.e.* point of no return state), the predator / prey size-relation is at its maximum. This relation is considered to be important in determining the level of the size-dependent (or stage specific) larval mortality of fish (Miller *et al.* 1988). A strong predation by minnow on vendace larvae was observed in field conditions (Huusko & Sutela 1997). According to my own new experiments perch (*Perca fluviatilis* (L.)) can harvest the whitefish larvae quickly (unpublished data).

A consistent survival curve with the concept of the "critical period" can be observed in paper V, Fig. 6 and VI, Fig. 2. In both cases, the time of mortality was linked with the inadequate amount of food. The direct starving of vendace larvae is, however, a very unlikely alternative in some lake conditions (VI, cf. Huusko 1998). A dramatic decrease in larval density may be caused by predation on larvae, as has been shown in this study. The swimming activity (escape ability) of larvae may be weakened already before the final starving (VI, cf. Mesa *et al.* 1994).

Predation pressure may be size-independent or size-dependent (Chambers & Trippel 1997). The size-dependent predation may be positively or negatively correlated with prey (larvae) size (Cowan *et al.* 1997). Thus, the size-dependent paradigm (*i.e.* mortality rate generally decreased as mean size of members of the year class increases) may not always be true (Cowan *et al.* 1997). Modelling of recruitment based on average individuals only is not always appropriate because of the possibility of selective mortality soon after hatching. The small differences between individuals could have large effects on their probability of survival (Houde 1987, Miller *et al.* 1988, Cowan *et al.* 1997). In the present model the effect of individual tissue mass and length on the larval survival was revealed to be an important factor.

In a hypothetical condition (cf. Huusko 1998) with starving larvae the first limiting factor for survival of the larval year class is lack of fat. When the total dry mass approaches 0.2 mg the fat mass is about zero and the composition of the embryo is weighted by protein. In a laboratory experiment (V, VI), vendace larvae reached "the point of no return" (50%-mortality) when their dry mass had dropped between 0.20-0.15 mg.

5.4 Mechanism of variation in year class survival

The egg size, hatching size and larvae sizes, water temperature, oxygen and feeding conditions (during yolk-, mixed- and exogenous feeding) and predation are all important factors affecting the survival rate of young coregonids.

In Lake Puruvesi (1961-1970) a two-year cycle in vendace population strength was observed (Nissinen 1972). Every other year a strong year class was born from the dominating 1+ age group. In Lake Pyhäjärvi the asymmetrical (density-dependent) food competition between age groups causes the persistent two-year cycle in the strength of vendace year classes (Helminen 1994). According to that hypothesis, age group 0+ will have a competitive advantage during summer and this strong year class will suppress the reproductive output of older vendace. The details of the mechanisms of these fluctuations are unknown.

If density-dependent regulation (mainly a deterministic process, cf. Strange *et al.* 1992) occurs the importance of deterministic factors must mask the effects of stochastic (e.g. weather conditions) factors. Sarvala and Helminen (1995) observed in Lake Pyhäjärvi (SW Finland) that the dry mass of vendace eggs was a good predictor for the ensuing year class size. According to the present study the dry mass of egg alone is insufficient property for larval survival. Larval survival is greatly dependent on predation pressure and the total larval mortality by predation is greatly dependent on the growth rate of larvae. The growth rate of larvae is, in turn, greatly dependent on hatching mass of embryo tissue and water temperature. In the present study the egg dry mass was calculated versus the larval properties at the hatching moment. Egg dry mass reflected clearly to the total dry mass of larvae. If the big eggs were incubated in lakes where the thermal conditions enable the incubation period to become long enough, the advantage of being big would also come in the form of a greater total metabolic rate and tissue mass of the embryo. Thus, the egg dry mass-dependent regulation requires enough quality for environment conditions, too. Huusko (1998) concluded that the vendace larval survival and recruitment was functions of the resource limitation of food resources in the preceding season of vendace and other planktivorous fish species in Lake Lentua. The decline in the larval survival was suggested to be primarily caused by food-deprivation (Huusko 1998). Obviously, the food conditions in different lakes are different and the generalisation of the temperature limited growth conditions (used in present study) can be applied only if the food conditions are comparable to each other.

The effect of an environmental variable can be useful or harmful on the survival depending on time (development stage of fish) and absolute value of the variable. The incubation temperature may be harmfully high, but the same temperature is too low for growth during exogenous feeding. The "medium" temperature (about 3-5 °C), which is unnecessary high for egg development, but too low for exogenous growth, is indirectly critical (increase in duration of vulnerable larval period) for larval survival. Thus, the temperature has a very different "optimum" range for different life stages of fish. In the best case the transition period between two different life stages should be as short as possible.

According to Christie & Regier (1973) Lawler (1959) found that cold winters were associated with larger whitefish year classes in Lake Erie. Christie & Regier (1973) reported that year class strength of whitefish correlated negatively with spawning season (November) temperatures but positively with temperatures in April, during hatching time. If the temperature in the lake water column remains too high in the autumn, it reflects on the oxygen and thermal conditions during the following winter. During winter, the water (bottom) temperature increases gradually (II). The tendency of the oxygen concentration change is "opposite" to that of the water temperature (II). When the temperature rises the oxygen content decreases and the oxygen minimum appears just when the ice breaks. At that moment (hatching time), the need for oxygen is at its maximum value (II). The deeper the lake is, or the higher its eutrophication level is, the greater are these changes during the winter. The effects of oxygen and temperature were studied in more detail in paper II. Failure in incubation conditions produce smaller hatching size (length, tissue mass), expose larvae to a prolonged larval phase and thus, a higher mortality rate by fish predation. In addition, this can be supported in (eutrophicated) lakes where the fish assemblage includes abundant predators. So, if the egg development starts under unfavourable conditions, the future of eggs also looks gloomy. Yearly variation in incubation results together with predation pressure cause yearly variations in larval survival and generate fluctuations of adult vendace population (cf. Karjalainen *et al.* 2000)

6. CONCLUSIONS

The individual fish egg is a functional unit and the rate of life processes of the egg are controlled by both internal and external factors. The outer surface of the egg chorion separates the egg from the environment. Via the egg surface the remaining metabolic products (mainly C, H, O, N) and energy (heat) flow to the environment. In poikilothermic fish egg the rates of these processes are strongly controlled by water temperature.

As was demonstrated in this study, mean size of eggs and individual eggs between years can be generated from the descriptive statistics of the population. The dry mass spectrum of an egg population can be described with a single top frequency distribution. On the one hand, a shift on the left side (between minimum and the top) of this distribution changes the described property and its frequency in the *same* direction. On the other hand, a shift on the right side of the distribution always changes the described property and frequency in *opposite* directions. Consequently, an increase in absolute energy per egg (on the right side) partly requires the cost of a number of individuals.

It is generally hypothesized that the fluctuation in year class size of fish is based on differences in early mortality of fish. In case of vendace the stock fluctuations may vary from more regular (e.g. a strong year class every second year) to very irregular or to more or less complete absence of year classes. The model presented here produces two kinds of variation, which are independent from each other: firstly, the variation and its consequences fixed in egg size and secondly, the variation originated in environment (*i.e.* incubation temperature). On the one hand, the bigger the egg dry mass the bigger the total hatching mass. On the other hand, the longer the incubation period the bigger the embryo tissue mass. Thus, differences in egg size and hatching time cause differences in start points of larval period.

Even a constant initial population size and a constant predation pressure during larval period of different durations is sufficient to cause enormously high differences in survival of larval year class. High incubation temperature, low oxygen concentration, low water temperature and low food density after hatching increase the predation mortality of larvae by minimizing the growth rate of larvae. Opposite low incubation temperature, high oxygen concentration, high water temperature and high food density after hatching decrease the larval predation mortality by maximizing the larval growth rate at the right time and thus minimizing the duration of the "critical period".

This study reveals that the results from field observations, experimental studies *in situ*, in the laboratory and model descriptions are possible to join together in a "virtual reality". The model presented here consists of both deterministic and stochastic factors. Depending on the stage of the fish life, both of these processes work in changing intensity. Simultaneously, when metabolism works for embryo growth (mainly in a deterministic way) at the cost of mass loss in the yolk, a sudden encounter with a predator may shift the whole larva to another compartment of food webs.

This work indicates that it is possible to develop the model study in the direction of more detail also concerning early life history of vendace. We can follow the development from egg to juvenile stage of vendace also by the model. This early version of the model needs to be developed. One of the most important work fields lays in the accuracy of the required estimates and in the testing of their validation. For the time being it is impossible to compare the model results with results from real lakes. The reason for this is the lack of the real daily temperature curves between the moment of fertilization and the end of larval stage of vendace. This is complicated by the great dispersion of vendace larvae between the littoral and pelagic zone (Karjalainen *et al.* 2001, Sutela *et al.* 2001). The other problem is the lack of estimates of predation pressure (between years) in lakes. According to the present model the total larval survival is very sensitive to differences in predation pressure; in addition, there is no practical method to distinguish between the larval mortality caused by predation and that caused by lack of food. I hope, however, that detailed modelling of the early life history of fish may open a new window for studying fish stocks in light of different environmental scenarios, like global warming.

ACKNOWLEDGEMENTS

The experimental part of this study was carried out at the Karelian Institute, Department of Ecology and Department of Biology, University of Joensuu. I wish to thank the staff of both departments. I thank my first supervisor Dr. Markku Viljanen and Prof. Heikki Hyvärinen. I am also grateful for the good working facilities provided by these departments. I also thank Prof. Juha Karjainen for fruitful co-operation. Dr. Jorma Piironen is thanked for his help. I am grateful to Prof. Hannu Lehtonen who later conducted my work and for his patience during the last years. Hannu Lehtonen and the staff of the Department of Limnology and Environmental Protection at the University of Helsinki have given me additional scientific views. This work has been supported by the Academy of Finland, the Foundation for Research of Natural Resources in Finland, the National Graduate Programme in Fish Biology and Fisheries and by my aunt Elina Iukkanen. The support of Leena and my daughter Liina was also irreplaceable.

The "time- and place-independent" model calculations in co-operation with Esko Valtonen was unforgettable. Thanks to him there were no problems without solution. I hope that I some day can continue the fruitful work together with Esko. Tvärminne Zoological Station was an excellent point of support during the last years. The support and the patience of the staff have been endless. Here I remember Laila Keynäs and Raija Myllymäki with special gratitude. The formulating of the last sentences was possible by help of Magnus Lindström, Tarja Katajisto, Marja Koski, Eva Sandberg-Kilpi, Riggert Munsterhjelm, Antti Nevalainen and Jouko Pokki. I am also greatly indebted to Professor Åke Niemi for many interesting discussions at the coffeetable and for his continuous support. Leena Nurminen, and Magnus Lindström have kindly checked the English texts. The research plans for the future and the already started new investigations have been made possible thanks to Walter and Andrée de Nottbeck foundation. Finally I wish to thank all my relatives and friends, among them especially my mother Eva, my brothers Yrjö and Reino and my neighbours Kari Koho, Peter Boldt, Risto Toivanen, Toivo Paju and Maria Fagerlund.

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