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REPRODUCTIVE TRAITS AND THEIR EFFECT ON EMBRYOS AND LARVAE OF VENDACE, *Coregonus albula* (L.). PART III. SIZE AND VIABILITY OF LARVAE

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A B S T R A C T. Length of vendace larvae at hatching (5103 measurements) varied slightly between groups originating from different lakes and between years of spawning. The length depended on egg dry weight and on time of hatching within the total time of hatching in batches. The latter factor (time) negatively affected yolk sac volume. Dry weight of larvae did not vary much; it amounted to ca 70% of egg dry weight. High survival of embryos (from fertilization to hatching) resulted in high correlation between larval and egg dry weights, and vice versa. Vitality of starving larvae appeared to be best determined by egg or larval dry weight.

Key words: EGGS, HATCHING PERIOD, LENGTH and WEIGHT SURVIVAL OF LARVAE

INTRODUCTION

The significance of egg size for viability of fish larvae was demonstrated by many authors (Kamler 1992). In vendace, starvation time of larvae (i.e. time to 50% death) - an index of viability - positively correlated with diameter, dry weight and energy content of eggs as well as with dry weight and energy content of larvae (Wilkońska, Żuromska 1988), but there were also examples of no effect or even some on a negative relationship (Kamler 1992). Modifying effect of temperature on larval size was also observed (Kamler 1992). Blaxter (1992) quoted data on the effect of incubation temperature on length or dry weight of larvae of 12 species; in 10 of them the relationship was negative. In vendace, low constant incubation temperature resulted in longer larvae than at high temperature but with respect to the size of yolk sac the relationship was just opposite (Łuczyński et al. 1984, 1986). In turn, size of larvae and their yolk sac can influence larval viability.

In view of the above mentioned influence of temperature on the size of yolk sac at hatching the controversial findings of no or even negative effect of egg size on larval viability could probably result from not considering the yolk size at hatching. The

latter could be small even from larger eggs if hatching is delayed and vice versa (Łuczynski et al. 1984, 1986).

Survival of incubated eggs of vendace depended on energy content in eggs and on sperm motility or percentage of good sperm. However, these variables explained utmost 29 per cent of the survival variability. The greatest fraction of the variations remained not explained. It was concluded that the egg and sperm quality did not always manifest itself in survival of embryos (Wilkońska et al. 1994).

In this paper attention is focussed on variability of larval size and of mortality in vendace larvae. As in case of incubation period the question is on significance of egg and sperm characteristics in predicting larval size and mortality. In particular, it was interesting to find out whether larval mortality (at starving) would so distinctly correlate with egg and larvae characteristics as demonstrated by Wilkońska and Żuromska (1988) who analyzed just one season (1985/86) samples of vendace.

MATERIAL AND METHODS

The same collection of vendace from four lakes (ISG, LUT, MAR, NAR) sampled in 1986, 1987, 1989 was used in this study as in Part II on egg incubation (Wilkońska et al. 1994), but due to high mortalities the material used in this paper was smaller. Also data on eggs and larvae collected during the spawning seasons 1984 from the same four lakes and in 1985 from three out of the four lakes were also included since they were not fully utilized (Wilkońska 1992, Wilkońska Żuromska 1988).

In 1985, 1986, 1988 and 1990 samples of larvae were taken at or just after the days of abundant hatching. Hence, such a series of samples enabled examination of size of larvae and their of yolk sacs during the hatching period.

Larvae were measured either by means of measuring microscope or simply on plotting (millimeter) paper. Yolk sac length (l) and height (h) were measured in larvae of 1984/85 and of 1985/86 seasons, yolk sac length only in larvae of 1989/90 season. It was assumed that yolk sac is roughly a prolate spheroid (Blaxter and Hempel 1963 after Luczynski et al 1984), hence, its volume equals:

$$V = 0.5236 \cdot l \cdot h^2$$

Table 1 shows the setup of data related to larval length. Note large numbers of measurements made during 3 seasons except 1989/90.

TABLE 1

Data on the measurements of larval length in vendace

SEASON	LAKE				
	ISG	LUT	MAR	NAR	TOTAL
1984/85 Each female mated with one different male					
n. of batches	13	10	9	14	46
samples/batch*	1 - 4	1 - 2	1 - 4	1 - 5	
total samples	39	15	19	40	113
n. of larvae	580	173	281	570	1604
mean length, mm	8.76c	8.61a	8.83bc	8.86b	8.78
SD=0.461			Range: 6.5 - 10.38		
1985/86 Each female of ISG and of MAR mated with 2 to 5 males except one which got just 1 male					
n. females/males	8/26	-	5/24	5/6	18/56
n. batches	26	-	24	6	56
samples/batch	1 - 4	-	2 - 5	2 - 5	
total samples	79	-	78	19	176
n. of larvae	1163	-	1106	264	2533
mean length, mm	8.45a	-	8.73a	8.72a	8.60
SD=0.426			Range: 7.3 - 9.98		
1987/88 Each but 2 females mated with different male; 2 females - with 2 males each					
n. females/males	8/9	10/11	8/8	6/6	32/34
n. batches	9	11	8	6	34
samples/batch	1 - 6	1 - 6	1 - 4	1 - 6	
total samples	34	35	23	21	113
n. of larvae	224	219	134	153	730
mean length, mm	9.16a	8.98a	9.06a	9.72a	9.16
SD=0.537			Range: 7.4-11.2		
1989/90 In ISG females mated with 1, 2 or 3 males, in LUT with 1, in NAR with 2 males in one case					
n. females/males	10/12	4/5	1/1	5/6	20/24
n. batches	17	5	1	6	29
samples/batch	1 - 4	1	1	1 - 2	
total samples	28	5	1	8	42
n. of larvae	130	21	24	41	216
mean length, mm	7.21a	6.28b	7.44a	7.20a	7.23
SD=0.525			Range: 5.85 - 8.62		

In 1986/87 season larvae were not measured but their dry weight was estimated in 16 batches (Table 2).

* Samples of up to 20 larvae from batches were taken at different dates when hatching was abundant, hence, they were not of the same size neither taken at fixed time intervals. The same letters at mean lengths denote insignificant differences.

In 1985 (larvae originated from spawning in 1984), in 1986, 1987 and in 1988 (spawning 1987) dry weight of just hatched larvae was estimated by drying groups of up to 30 fish to a constant weight at 55 °C in a desiccator over NaOH, in 1986 - energy content was estimated in a microbomb calorimeter (see Wilkońska et al. 1993)

In 1987 and 1988 a simple experiment with 18 and 48 batches, respectively, of known origin was performed to check possible differences in viability of starving larvae. Available number of larvae (from 3 to 40 per batch, average 20) were kept in 1 liter jars filled with lake water and dead larvae were counted and removed every day. The jars were placed in flowing water tanks. Temperature was recorded but not controlled.

Data of a similar experiment with vendace larvae from the same lakes performed in 1985 and in 1986 (but with greater numbers per batch, averages were: 35 and 45 in respective years) were used in this paper because they were not fully utilized in Wilkońska and Żuromska (1988).

STATISTICAL ANALYSIS

Multiple regressions of larval length on available egg and sperm characteristics and on the day of hatching were computed for every of seasonal data sets using the method of stepwise variable selection. Similar computations were performed for yolk sac size. This procedure allowed to find out these independent variables which best explain (predict) larval length or yolk sac size, respectively. The remaining variations - i.e. of real length of larvae minus that expected from regressions - were subject to the analysis of variance.

Larvae originated from batches of eggs of single females were incubated separately. In 1985/86 season eggs of several females were divided into 2 to 5 aliquots and each was fertilized with different males, hence, there were several batches of half sibs. In other seasons few of such combinations survived (Table 1). During hatching period samples of larvae were taken at the days of or just after abundant hatch, up to 6 times from a batch. Thus, there were basically 5 levels of classification of larvae: 1 - by origin (lake), 2 - by females, 3 - by batches in females (i.e. by males), 4 - by samples (days of measurements) in batches, 5 - by individual measurements in samples. Such a hierarchic design was applied to the 1985/86 collection only. In three other collections 4 levels were distinguished, i.e. levels 2 and 3 were combined into one, "batches in

lakes", because of too few multiple pairings. This could supply data for a nested (or hierarchic) analysis of variance if subordinate groups were chosen at random and, ideally, if numbers of subgroups within groups were equal (Sokal and Rohlf 1981). However, it was not possible to follow the rigid design; the highest level (lakes) was fixed, females and males were randomly selected but numbers of larvae in batches could not be kept equal simply because of varying embryo mortality. Also sampling of larvae within batches was dictated by the course of hatching (days of mass hatching). Therefore, analysis of variance performed on such sets of data violates the basic assumptions and testing of mean squares (variance) by means of F ratio is inconclusive and provides very rough estimates. Hence, variance components would be biased and were not calculated. Even so, such an analysis allows for rough assessment of significance of certain sources of variation.

RESULTS

SIZE OF LARVAE

The total length of larvae varied little between lakes in particular years (Table 1). Variation within season was small, from 5.1 to 7.3% of respective means (Table 1, SD to mean ratios). Variations between years were inconsistent; e.g. ISG had small larvae in 1986 and 1990 but not so in the other two years, MAR had largest in 1985 and 1988 but not so much in the other years, etc.

The larvae were smallest in 1990 but this cannot be attributed to the egg size from which they hatched (Wilkońska et al 1993). Because of the effect of incubation temperature on larval size (Łuczyński et al. 1984, Blaxter 1992) it is likely that sudden rise of temperature (from 1.5 to 8°C) at the end of incubation caused quick hatching of less developed embryos. High mortality of embryos was observed in this group of batches (Wilkońska et al. 1994).

Mean dry weight of larvae in four seasons were practically the same (Table 2, such measurements were not taken in 1990) and so were ratios of larva to egg dry weight (c. 72%). Variations within seasons were much greater than in case of length (C.V. was 10.9 to 18.1%). In two first seasons these weights (egg and larvae) were very strongly correlated (0.86 and 0.911 respectively) while in the third one such a correlation was insignificant (0.362) and in the last one it was weak (0.601).

TABLE 2

Dry weight of larvae

SEASON	N of batches	DRY WEIGHT		
		mg/larva	SD	% of egg d.wt.
1984/85	33	0.547	0.071	73.2
1985/86	52	0.525	0.057	70.9
1986/87	16	0.554	0.078	68.4
1987/88	32	0.554	0.077	75.8

But it should be born in mind that egg dry weight was estimated from subsamples at spawning time while larval dry weight from (obviously) different subsamples about 3 to 4 month later.

Larval dry weight appeared an exponential function of length :

$$1985/86 - E(d.wt. larva) = 0.009546 l t^{1.8457}$$

$$1987/88 - E(d.wt. larva) = 0.036701 l t^{1.2471}$$

and length determined 36.9 and 24.5% of weight variations in respective seasons (*E* - stands for *Estimated* value).

Measurements of energy content in larvae made in 1985/86 season resulted in the estimates as follows:

$$mean\ energy\ content = 12.96\ J/larva \quad (SD = 1.615, N = 50\ batches)$$

$$mean\ energy\ value = 24.6\ J/mg\ d.\ wt.$$

Larval energy content equals 68.0% of energy content of eggs before fertilization and 95.7% of energy value (per mg d.wt.) of eggs.

Multiple regressions of larval length on several variables (stepwise selection) were computed separately for every of four sets of data (Table 1). Egg dry weight or egg diameter (in 1987/88) and subsequent day of hatching explained from 11 to 43.9% of the larval length variability. Both egg variables have a positive (if significant) effect (Table 3). Other available egg characteristic as well as, rather obviously, sperm characteristics appeared insignificant in affecting larval size.

TABLE 3

Regressions of larval and yolk sac size on egg size and days of hatching. In brackets is per cent of variation determined by a given independent variable

DEPENDENT VARIABLE: total length of larvae					
INDEP. VARIABLE:	Constant	egg dry wt.	days	total R ² % ¹⁾	(d.f)
1984/85	7.5759	+1.15293 [6.33]	+0.03196 [17.36]	23.69	(1598)
1985/86	6.5957	+2.72331 [32.18]	ns	32.18	(2527)
1989/90	6.2399	+1.08915 [6.26]	+0.055631 [4.71]	10.97	(212)
INDEP. VARIABLE:		egg diameter	days		
1987/88	-0.16314	+4.91174 [38.58]	+0.019526 [5.31]	43.89	(1596)
DEPENDENT VARIABLE: yolk sac volume					
INDEP. VARIABLE:	Constant	egg dry wt.	days		
1984/85	-0.17716	+1.53686 [32.46]	-0.01063 [4.42]	36.86	(1597)
1985/86	-0.57041	+1.58461 [58.44]	-0.012182 [6.90]	65.34	(2523)
DEPENDENT VARIABLE: yolk sac length					
1989/90	1.138336	+0.57579 [10.17]	ns	10.17	(213)

¹⁾ Determination coefficient

TABLE 4

Decrease of length and height of yolk sac with subsequent hatching days in 1984/85 samples

LAKE*	N	DECREASE PER DAY (in 1/1000 mm)		DETERMINATION % (R ²)	
		length	height	length	height
ISG	173	8.36	10.97	13.1	36.3
LUT	578	3.46	8.32	21.3	34.4
NAR	624	0.01	9.14	22.6	24.7

* In lake MAR regression of yolk sac on days insignificant

Wilkońska and Żuromska (1988) calculated correlation between **mean** total length of larvae and **mean** egg diameter in 53 samples of 1985/86 season; it was equal 0.655. Here we calculated regression of **individual** length measurements on **mean** egg dry weight (per batch) which appeared better then on egg diameter.

Similar computations revealed that yolk sac volume increased with egg dry weight (Table 3) and the latter explained 32.5 and 58.4% of the volume variations. The yolk sac volume decreased along with the progress of hatching time (days, Table 3) but this factor appeared rather weak, determining utmost 6.9% of yolk variability (Table 3, 1985/86 season).

Luczyński et al. (1984) observed that yolk sac length changed slower than its height and the same relationship was found here (Table 4). Hence, insignificant effect of "days" on the yolk sac length in 1989/90 season (Table 5) seems misleading; if volumes were estimated then they could appear to diminish along with time of hatching.

Analysis of variance (Table 5) shows that the egg size had stronger effect than time of hatching on larval length in 3 seasons but 1984/85. After these effects were accounted for, the remaining variations of larval length (sums of square deviations from multiple regression) consisted mostly of that within samples i.e. between larvae of homogeneous groups. Although "origin" produced statistically significant contribution to variation of larval length in 1984/1985 (see Table 5, left side: $F=6.42$) no reasonable explanation can be offered for the effect of lakes. As mentioned above, differences between lakes were inconsistent.

Differences between batches and between samples were rather insignificant (after the effect of egg size and days of hatching had been taken care of). The male effect calculated for 1985/86 set of data appeared also insignificant (Table 5, left side, 1985/86 season).

The sources of variations can be summarized in three groups (Table 6). Thus, after the effect of egg size and day of hatching had been taken into account the variations of larval length could be considered random. That is, variations between lakes and years and due to female and male do not seem significant with respect to larval size and cannot be predicted.

Differences in yolk volume between lakes and batches (i.e. females) seem significant 1984/85 sample (Table 5, right side). The overall variation of yolk volume was much greater than that of larval length; coefficients of variation for yolk were 41.1%

TABLE 5

Analysis of variance of larval length and yolk sac volume

Variable	LENGTH of LARVAE				YOLK VOLUME			
	Sum of squares	df			SS	df		
1984/85								
Egg d. wt	26.1321		t=10.3		29.7487		t=20.8	
Days	71.9068		t=19.1		4.0283		t=11.0	
			MS	F			MS	F
Origin (lakes)	33.0543	3	11.0181	6.42	12.6775	3	4.2258	9.55
Between batches within lakes	72.1123	42	1.7170	3.90	18.5896	42	0.44261	5.78
Between samples in batches	29.5170	67	0.4406	3.63	5.1280	67	0.07651	5.31
Between larvae in samples	181.1634	1491	0.12151		21.4624	1488	0.01442	
TOTAL	413.7860	1603			91.6344	1600		
1985/86								
Egg d. wt.	55.3804		t=7.8		16.6411		t=15.2	
Days	n.s.				2.8707		t=6.3	
			MS	F			MS	F
Origin	0.8121	2	0.4061	1.33	0.0429	2	0.02145	0.42
Between females in lakes	4.5644	15	0.3043	2.14	0.7686	15	0.0512	4.50
Between batches (males) in females	5.3979	38	0.1421	1.14	0.4321	38	0.01137	2.29
Within batches between samples	14.9841	120	0.1249	2.19	1.1508	120	0.00497	1.07
Between larvae	134.3490	2357	0.05700		10.8893	2357	0.00462	
TOTAL	215.4884	2532			32.6956	2532		
1987/88					(yolk sac not measured)			
Egg diam.	80.9858		t=22.3					
Days	11.1346		t= 8.3					
			MS	F				
Origin	9.5213	3	3.1738	2.35				
Between batches in lakes	40.4924	30	1.3497	4.37				
Between samples in batches	24.4163	79	0.3091	4.0				
Between larvae	43.3401	617	0.07024					
TOTAL	209.8905	729						
1989/90					YOLK SAC LENGTH			
Egg d. wt.	3.7145		t=3.6		0.9056		t=5.5	
Days	2.8018		t=3.4		ns			
			MS	F			MS	F
Origin	4.1046	3	1.3682	3.14	0.8425	3	0.2808	5.11
Between batches in lakes	10.4468	24	0.4353	1.45	1.3175	24	0.0549	1.08
Between samples in batches	4.2166	14	0.3012	1.54	0.7105	14	0.05075	1.72
Between larvae	34.0700	174	0.1958		5.1301	174	0.02948	
TOTAL	59.3565	215			8.9062	215		

TABLE 6

Percent of total sums of squares (deviations) attributed to three groups of sources
of variations of larval length (%)

Season	EGG DRY WT. and DAY of HATCH	LAKES, FEMALES, SAMPLES	WITHIN SAMPLES
1984/85	23.7	32.5	43.8
1985/86	25.7	12.0	62.3
1987/88	43.9	35.1	20.6
1989/90	11.0	31.6	57.4

and 30.4% (1985 and 1986, respectively) and for larval length - 2.8 to 7.2% of respective averages. It is reasonable to assume that larval size at hatching can vary within certain limits determined primarily by egg size while yolk sac size can vary more being utilized by larvae for growth and metabolism.

VIABILITY OF STARVING LARVAE

Time till first death in batches, till 50% mortality i.e. so called "Hunger Potential" (Jager after Łuczyński 1986) and till 100% death did not vary much between seasons except 1986/87 (Table 7). Temperature during larval period differed between seasons what should have affected mortality rates.

Mean times to 50% mortality in 1986/87 and 1987/88 did not differ significantly showing much larger variability (Table 7). Origin of batches (lakes) had no significant effect.

Survival of starving larvae obviously depends on the amount of yolk sac resources at hatching and on the rate of their utilization for metabolism and growth of larvae (Kamler 1992). Yolk amount depends on the resources in eggs which, in turn, are closely related to egg dry weight or egg diameter. It also depends on incubation period; the longer it lasted the smaller were yolk sacs (Table 3, Łuczyński et al. 1984). But also larger (heavier) eggs had longer hatching periods (Wilkońska et al. 1994, and examples in Kamler 1992, p. 123) which reduces yolk sacs. Thus, egg size affects positively yolk resources directly and also negatively via its effect on hatching time.

TABLE 7

Survival times of starving larvae: average number of days when first mortalities occurred (vtb), when 50 % (vt50) and when 0 % (vt0) survived

Season	N	vtb	C.V.	vt50	C.V.	vt0	C.V
1984/85	50	22.1	12.2	30.3a	9.6	36.0	9.0
1985/86	56	26.1	12.1	32.6b	9.7	37.4	11.3
1986/87	17	19.6	34.0	30.3ab	17.1	43.8	19.7
1987/88	48	22.6	34.8	28.8a	23.8	33.7	20.6

Means (vt50) with the same letter denote insignificant differences.

TABLE 8

Selected predictors of survival time of starving larvae till 50 % mortality

Season	N of batches [#]	Independent variables	Determination		
			R ²	sign of correlation	p
1984/85	35	yolk sac volume	0.006	-	ns
1984/85	33	larval dry weight	0.171	+	0.017
1985/86	54	yolk sac volume	0.197	+	0.0008
1985/86	50	egg dry weight	0.345	+	0.0000
1985/86	52	larval dry weight	0.236	+	0.0000
1986/87	18	not any variable significant			
1987/88	25	larval dry weight	0.203	+	0.024
1987/88	48	egg dry weight	0.045	+	0.145
Two seasons combined*:					
1986-88	38	larval dry weight	0.107	+	0.0453
1986-88	66	egg dry weight	0.054	+	0.0612
1986-88	62	egg protein content	0.044	+	0.0904

[#] Some data on independent variables were missing

* See Table 7, column vt50

Underlined variables are the only significant ones in multiple regression. Regressions for the last two years included weights by numbers of larvae in batches which varied greatly (see MATERIAL AND METHODS above).

The rate of yolk absorption in larvae depends, at least, on temperature, oxygen level and light (Kamler 1992). We did not study these processes.

With regard to data from 1984/85 and 1985/86 seasons the available independent variables were: diameter, dry weight and energy content of eggs and length, dry weight and energy content of larvae as well as yolk sac volume. In 1986/87 and of 1987/88 also data on protein and lipid content of eggs (average per batch), on percent of spermatozoa without any deformities and on their motility were available (Wilkońska et al. 1993) but yolk sac was not measured.

Yolk sac volume (measured in 1984/85 and 1985/86 seasons, Table 8) appeared fairly well correlated with larval mortality in one season only. If stepwise variable selection was applied then the only significant regressions were on larval dry weight (Fig. 1a) or on egg dry weight (Fig. 1b) in respective seasons (Table 8). It should be emphasized that survival of embryos (until hatching) was fairly high during those seasons viz. 36.8 and 53.3% respectively. Probably that is why stronger relationship was revealed in 1985/86 season.

Small number of batches available for starvation experiment in 1986/87 season (Table 8, N=18) due to very low survival of embryos at hatching (average = 1.85%) resulted in a lack of any relationship between larval viability and any egg or larval traits.

In the next season more embryos survived (average was 8.4% from fertilization till hatching) and more batches were available (Table 8). Larval viability appeared best predicted again by larval dry weight although 23 measurements of the latter were missing. In the combined sample (two last seasons) also this trait was the best predictor, however, rather weak. Scattered points in Fig. 1c would have been more concentrated if their weights (i.e. numbers of larvae in batches) were somehow taken into account. Two other independent variables are shown (Table 8) the influence of which was insignificant but indicate a positive trend as expected.

Significance of embryos mortality also emerged from correlations between egg and larval dry weight (Table 2); it was weakest for 1986/87 (with egg mortality of 98.2%), next comes 1987/88 (with 91.6%), 1984/85 (with 63.2%) and finally 1985/86 (with mortality of 47.5 %).

Considering that sampling of any independent variables was not exactly random, that egg characteristics were obtained before fertilization (in autumn) and that numbers of larvae (and yolk sacs) for estimation of averages in batches (in following

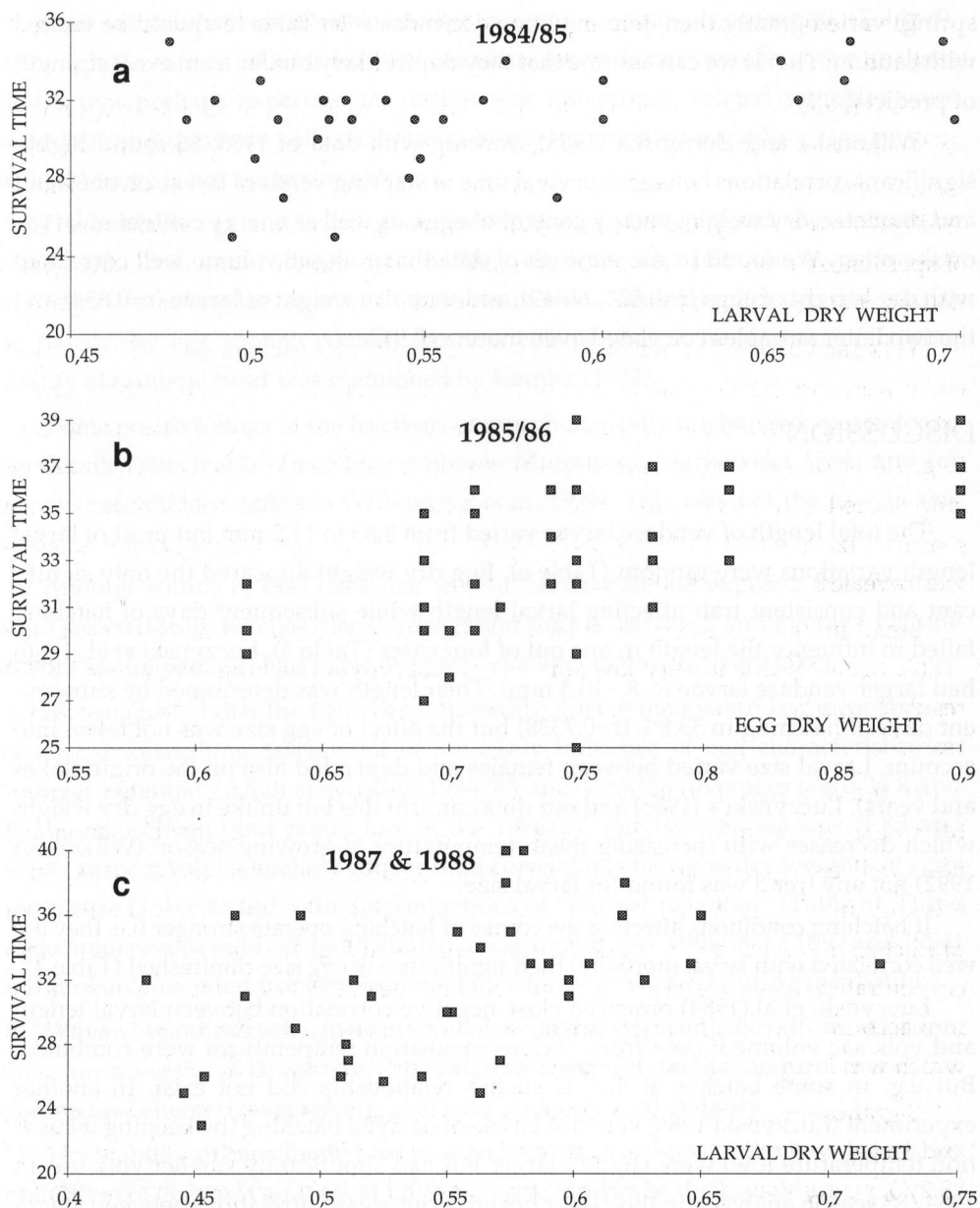


Fig. 1 Survival time to 50% death of fasting vendace larvae versus larval dry weight (a,c) and egg dry weight (b) in respective seasons.

spring) varied greatly then determination coefficients (in Table 8) should be treated with caution. That is we can assume that they depict likely but far from exact strength of predictability.

Wilkońska and Żuromska (1988) working with data of 1985/86 found highly significant correlations between survival time of starving vendace larvae on one hand and diameter, dry weight, energy content of eggs, as well as energy content of larvae on the other. We found in the same set of data that yolk sac volume well correlated with dry weight of eggs ($r=0.821$, $N=49$), and with dry weight of larvae ($r=0.854$) and the two latter variables correlated even more: $r=0.912$.

DISCUSSION

The total length of vendace larvae varied from 5.85 to 11.2 mm but most of larval length variations were random (Table 6). Egg dry weight appeared the only significant and consistent trait affecting larval length while subsequent days of hatching failed to influence the length in one out of four cases (Table 3). Łuczynski et al. (1986) had larger vendace larvae (c. 8 - 10.5 mm). Their length was determined by subsequent days of hatching in 53.8% ($r=0.7338$) but the effect of egg size was not taken into account. Larval size varied between females and depended also on the origin (lakes and years). Łuczynski's (1986) and our data confirm this but unlike in egg dry weight which decreases with increasing mean temperature of growing season (Wilkońska 1992) not any trend was found for larval size.

If hatching conditions affecting the course of hatching operate stronger (i.e. they are well correlated with larval mortality) then significance of egg size diminished (Table 3).

Łuczynski et al. (1984) observed close negative correlation between larval length and yolk sac volume if data from various incubation temperatures were combined. But e.g. in some batches at 4.9° C such a relationship did not exist. In another experiment (Łuczynski 1986) vendace larvae of delayed hatching (by keeping incubation temperature low) were slightly larger but had significantly smaller yolk sac. In 1984/85 season analyzed in this paper negative but weak correlations between length and yolk sac volume appeared in data from three lakes (ISG $r=-0.208$, LUT $r=-0.339$, NAR $r=-0.211$) and in data of MAR it was positive, $r=+0.172$. In 1985/86 it was also positive what concurs with the fact that influence of egg dry weight was strongest (Table 3, $R^2 = 65.34\%$) but that of days weak.

Yolk sac volume was a weak (if any) predictor of "hunger potential" (Table 8). Although the role of yolk for survival of fasting larvae is obvious the above analysis shows that perhaps experimental design was not proper, related variables were biased or/and the mere yolk sac volume (roughly estimated assuming regular geometrical form) is not the best measure.

The available egg and larval characteristic appeared interrelated (see Wilkońska et al. 1993, 1994, and Tables 3 and 5). They all determine yolk sac resources, but mortality of starving larvae were best determined by either larval or egg dry weight or, hardly, by egg protein content. Positive role of protein in eggs and offspring vitality of rainbow trout was mentioned by Kamler (1992).

Some positive effect of the fractions of morphologically unchanged spermatozoa on viability survival of *Tinca tinca* embryos (Żuromska, Markowska 1984) and for survival of vendace embryos (Wilkońska et al. 1994). This was not the case in this study.

Another source of bias consisted in that vendace larvae exposed to starvation were selected from batches disregarding their time of hatching and average volume of yolk sac (in batches) had to be accepted whatever days they were taken.

It is suggested that the embryonal mortality during incubation is a more important factor disturbing assessment of the likely influence of egg characteristics on "hunger potential". High survival in 1984/85 and 1985/86 (averages were 36.8 and 53.2%, respectively) but rather low in the 1986/87 and 1987/88 seasons (1.85 and 8.38%, respectively) somehow concur with correlations between dry weights of eggs and larvae (Table 2) and with determinations of "hunger potential" (Table 8). These various survivals could not be attributed to egg quality (see Wilkońska 1992 and 1994) and probably resulted from environmental factors (not studied during incubation).

We can hypothesize that low survival of incubated eggs indicates strong selection, thus, low diversity of larvae (since the fittest only survived) what, in turn, masks (i.e. diminishes) effects of average egg characteristics on larval viability.

The viability of starving fish larvae can be considered one of the best criteria for evaluation of egg, milt and larval traits as characteristics of their quality.

In one of the earliest investigations of this kind (Vladimirov 1965) correlations (r) between egg (and female) characteristics and offspring viability in *Rutilus rutilus heckeli* and *Abramis brama* were either insignificant or rather weak. E.g. for viability and egg diameter it was between $r=0.22$ and $r=0.44$, for viability and egg specific

weight $r=0.56$ in *R. r. heckeli* i. e. this characteristics explained utmost 32% of viability variations, a fairly high value but considerably less than nondetermination coefficient (68%). These and other relationships appeared often curvilinear.

Kato and Kamler (1983) found that linear and gravimetric properties of rainbow trout eggs had no or little predictive value for embryo survival. They quote several papers about that kind of relationships which, however, appeared not always significant. Vendace embryo survival was only slightly determined by egg characteristics (Wilkońska et al. 1994).

In a recent work on reproduction *Fundulus heteroclitus* (L.) (Marteinsdottir and Able 1992) egg size was positively related to survival of larvae only in populations (subspecies) with large eggs but there was no correlation in populations with small eggs. Delayed hatching had a negative effect on survival time of starving larvae. If we assume that the survival time depends on yolk sac resources then this observation concurs with that of Luczynski et al. (1984, 1986) viz. that delay of hatching resulted in diminishing of yolk sac and, therefore, in reduced viability.

Considering weak relationships between larval vitality and egg or larval characteristics it looks like not any of these traits can be considered predictive. Except extreme cases environmental factors and inherent variability mask any possible effect of those characteristics.

The other criteria for evaluating egg and milt characteristics would be growth and survival of foraging fish since at such fish efficiency of metabolism and of feeding behaviour are manifested. In starving larvae behaviour does not matter. Vladimirov (1965) observed that the greater was viability of starving larvae the slightly less it was among fed larvae originating from the same batch of eggs. He stated that causes of mortality in each case were different. In feeding larvae survival was best if they originated from eggs of medium content of lipids, protein and carbohydrates but data for supporting this observation were not very convincing.

Thus, it looks like physical and simple biochemical egg properties will have poor predictive value for offspring viability also at later stages.

Also fertilizability and survival of embryos of vendace was hardly determined by sperm motility and fractions of sound spermatozoa as well as by egg characteristics (Wilkońska et al. 1994). Hence, it is not surprising that larval viability hardly depends on egg quality and unexplained variations were by far greater.

That kind of research might therefore look futile if the main problem were egg and sperm quality criteria (as the title of Kato and Kamler's (1983) paper "Criteria for evaluation of egg quality ..."). However, the bulk of information, though discrediting the practical value of the various rather simple traits, have at least shown:

- low predictability of larval size and viability on the basis of physical and biochemical properties of egg and milt as in the case of embryo survival,
- necessity of considering joint and simultaneous effect of possibly related egg, milt and larval traits on larval (and embryo) viability,
- significance of external factors at any stage of embryonal and larval development, therefore, need for careful experimental design including control of external factors,
- importance of disturbing effect of embryonal mortality on assessment of any relationship between larval and egg or milt characteristics.

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STRESZCZENIE

CECHY REPRODUKCYJNOŚCI I ICH WPŁYW NA EMBRYONY I LARWY SIELAWY (*Coregonus albula* L.). CZĘŚĆ III. WIELKOŚĆ I ŻYWOTNOŚĆ LARW

Analizowano wielkość larw wylęgłych z jaj sielawy pozyskanych w czasie tarła w latach 1984, 1985, 1986, 1987 i 1989 z 4 lub 3 (w 1985 r.) jezior. Długości (pomiar 5103 osobników) larw poszczególnych jezior różniły się niewiele, nieco większe różnice zaobserwowano pomiędzy latami. Długości te były wyraźnie zależne od suchej masy jaj i od dni lęgu w próbie: im później się legły, tym były większe. Objętość woreczków żółtkowych zależała również od suchej masy jaj i od dni lęgu, lecz inaczej niż długość; im później się legły tym mniejszy był woreczek.

Badano także kaloryczność i suchą masę larw w nawiązaniu do kaloryczności i suchej masy jaj.

W ciągu 4 sezonów badano przeżywalność głodzonych larw. Stwierdzono istotną lecz słabą zależność pomiędzy liczbą dni do momentu przeżycia 50% larw a suchą masą jaj lub larw. Wskazano na małą użyteczność fizycznych i biochemicznych właściwości jaj i mlecza do przewidywania wielkości i żywotności larw.

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