

REPRODUCTIVE TRAITS AND THEIR EFFECTS ON EMBRYOS AND LARVAE OF VENDACE, *COREGONUS ALBULA* L. PART I. FISH AND GONAD ATTRIBUTES

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ABSTRACT. Egg and milt quality of vendace collected from four lakes over four spawning seasons was analyzed. Particular attention was paid to the degree of determination of some reproductive attributes by somatic characteristic and by environment. Vendace in these lakes differed greatly with respect to growth rate and to abundance, but variation of the majority of gonad attributes did not exceed 20 % of their overall means. Age of females explained utmost 13.4 per cent of variability of egg diameter, of egg dry weight, of egg caloric content and of lipids in eggs. Origin of fish and years of collecting were responsible for a greater fraction of variance of egg and of testicle attributes. Majority of the variability remained unexplained indicating large variance within samples which masks the other effects.

Key words: VENDACE, EGG QUALITY, MILT QUALITY

INTRODUCTION

The first study dealing with vendace reproduction in Poland concerned gonad development (Backiel 1952) and was followed by an extensive investigation into the fecundity of this fish (Zawisza, Backiel 1970), and then by a series of studies on reproduction success of the fish in Mazurian lakes (Wilkońska, Żuromska 1982, Żuromska 1982a,b). Analyses of egg quality in relation to some traits of females including their origin appeared later (Kamler, et al. 1982). Long term estimates of egg quality and of females traits began in 1981, data on milt quality were collected since 1985 and laboratory experiments on embryo and larval mortality were carried out (Wilkońska, Żuromska 1988, Wilkońska 1992). Many results of these studies were summarized by Kamler (1992).

This long series of research in vendace reproduction revealed the detrimental effect of eutrophication including biotic (predation on eggs) and abiotic (e.g. oxygen deficit) factors responsible for egg mortality. Effects of atmospheric conditions during the season preceding spawning upon ovaries appeared rather clear e.g. lakes from northern Finland had smaller eggs and poorer in dry matter than those from Poland (Kamler et al. 1982), egg dry weight correlated negatively with mean seasonal tem-

perature (Wilkońska, Żuromska 1988, Wilkońska 1992). With respect to fecundity this relationship was positive (Zawisza, Backiel 1970, Wilkońska 1992) i.e. there was greater number of eggs in warmer lakes or in warmer years irrespective of fish size. However, significance of the trophic status of lakes for egg and milt has remained contradictory (Wilkońska, Żuromska 1988, Wilkońska 1992).

Several egg attributes were found to depend on the age of fish although the strengths of these relationships were not assessed (Kamler et al. 1982, Kamler 1992). Data on milt of vendace are limited to just one attribute (% of unchanged live spermatozoa) and to one year collection (Wilkońska, Żuromska 1988).

The situation drafted above justifies further studies. As exemplified above, any egg and milt quality characteristic can be affected by environment and is related to certain fish characteristics e.g. age. Variations of environmental conditions and of somatic characteristics of fish can increase variability of egg and of milt quality. The question we try to answer here is what a set of factors (considered as independent variables) and to what extent contribute to the variability of certain reproductive attributes. Such an approach has not been found in the available literature. Thus, this paper, being the first in a series, presents evaluation of 1986-1989 data on reproductive traits of vendace with the emphasis on predictability i.e. on the degree of determination of the traits by fish characteristics and by the environment.

MATERIAL AND METHODS

Fish (10 to 15 of each sex in every sample) were collected from four lakes: Isąg (thereafter abbreviated ISG), Lutry (LUT), Maróz (MAR) and Narie (NAR) at the culmination of the spawning periods, i.e. late November - early December of 1986 through 1989. Fish were caught in gill nets, hence, selectively but attempts were made to collect all available size classes. The methods applied here were basically those of Kamler, Żuromska (1979) with minor modifications. The following parameters were assessed in the:

1. fish: body length, gutted weight, age from scales; and from the dried (at 60°C) homogenate of fish muscles the following parameters were estimated:
 - a) percent of lipids in dry matter (in 1987 only) using the method of Dowgiałło (1980),
 - b) percent of protein (1988 only) using the method of Lowry et al. (1951),
 - c) caloric value in the microbomb calorimeter (Klekowski, Bęczkowski 1973) in 1987 and 1988, [Original measurements were in calories, the conversion is $4.187 \cdot \text{cal} = \text{joules}$],

2. eggs from each female:

- a) percent of eggs without symptoms of resorption (from ca 300 eggs per sample),
- b) diameter of 30 unswollen eggs,
- c) wet weight (in 1989 only)
- d) dry weight of egg (from ca 30 eggs dried at 60°C to a constant weight in a desiccator over NaOH),
- e) energy content,
- f) lipids (1986, 1987),
- h) protein (1986-1988), the last three as in muscle analyses,

3. sperm from each male:

a) percent of morphologically unchanged spermatozoa without any deformities of heads or flagellae, calculated from dry preparations - saline (1:1) diluted sperm stained with 5% eosin plus 10% negrosine (4:1) - examined under an immersion in 10 fields (Żuromska, Markowska 1984),

b) motility of spermatozoa (in 1986 and 1987 only) i.e. duration (of progressive motion of most of them, activated in water: three small portions of sperm from each male was observed under 200 magnification until almost all spermatozoa but the last 2-5 ceased moving forward, oscillatory motions were disregarded and average of three measurements was (Żuromska 1981),

c) density of spermatozoa (per mm²) from saline treated samples examined in Thoma-Zeiss chamber, three per male (Żuromska 1981) in 1986 and 1987 only.

4. testicles from males in 1986 and 1988: protein value of dry matter.

For the numbers of the examined fish see Table 1.

RESULTS

CHARACTERISTIC OF THE LAKES AND OF VENDACE

Four growing seasons (May - October) preceding autumn collections of fish varied at least with respect to the mean temperature: 14.36 °C in 1986, 13.44 °C in 1987, 15.07 °C in 1988, and 14.31°C in 1989.

The four lakes: Isąg (ISG), Lutry (LUT), Maróz (MAR) and Narie (NAR) are of different size, depth, shoreline development and trophic status. Vendace population was most abundant in MAR, in NAR of fair size in ISG and LUT it has been almost vanishing (Table 2).

TABLE 1

Summary of characteristics of fish and gonads collected in 1986 through 1989 from lakes
ISG, LUT, MAR, NAR

| | Num- ber of fish | Mean | C.V. % | Range | Samples lakes | from years |
|---|------------------------|---------------------|--------|--------------|------------------|------------|
| FEMALES | | | | | | |
| Age | 192 | (2,3) ¹⁾ | | 2 - 6 | 4 | all |
| Body length(cm) | 193 | 18.3 | 14.2 | 14.5 - 28.2 | 4 | all |
| Gutted Weight(g) | 193 | 65.1 | 57.1 | 23 - 249 | 4 | all |
| Muscles: | | | | | | |
| protein % dry wt | 20 | 54.7 | 18.1 | 40.8 - 68.5 | 2 | 1988 |
| lipids % dry wt | 54 | 15.75 | 19.0 | 11.3 - 22.3 | 4 | 1987 |
| energy cal/dry wt | 79 | 6.70 | 5.3 | 5.6 - 7.29 | 4 | 1987-1988 |
| (J/dry wt.) | | 28.1 | | 23.4-30.5 | | |
| Gonads: | | | | | | |
| Eggs without resorption % | 187 | 93.9 | 13.2 | 15 - 100 | 4 | all |
| Egg diameter(mm) | 192 | 1.63 | 4.3 | 1.47 - 1.8 | 4 | all |
| C.V. diameter within fish ²⁾ | 192 | 4.67 | 26.7 | 2.64 - 10.6 | 4 | all |
| Egg dry wt.(mg) | 193 | 0.749 | 13.2 | 0.545-1.026 | 4 | all |
| Egg wet wt.(mg) | 54 | 2.275 | 14.1 | 1.72 - 3.19 | 4 | 1989 |
| Egg specific wt. | 54 | 1.004 | 6.9 | 0.897- 1.196 | 4 | 1989 |
| Egg hydration % | 54 | 65.2 | 3.7 | 59.8 - 74.2 | 4 | 1989 |
| Egg protein: | | | | | | |
| mg/egg | 139 | 0.300 | 20.7 | 0.174-0.493 | 4 | 1986-88 |
| % dry wt. | 139 | 40.8 | 15.2 | 25.6 - 61.0 | 4 | 1986-88 |
| Egg lipids: | | | | | | |
| mg/egg | 90 | 0.197 | 23.7 | 0.125-0.342 | 4 | 1986-87 |
| % dry wt. | 90 | 23.9 | 18.9 | 18.6 - 41.5 | 4 | 1986-87 |
| Egg energy: | | | | | | |
| cal/egg | 192 | 4.90 | 13.7 | 3.0 - 6.81 | 4 | all |
| (J/dry wt.) | | 20.5 | | 17.5-28.5 | | |
| cal/mg dry wt. | 192 | 6.56 | 8.8 | 5.26 - 7.67 | 4 | all |
| (J/dry wt.) | | 27.5 | | 22.0-32.1 | | |
| MALES | | | | | | |
| Age | 242 | (2,3) ¹⁾ | | 2 - 6 | 4 | all |
| Body length (cm) | 243 | 17.9 | 10.2 | 14.5 - 23 | 4 | all |
| Gutted weight(g) | 232 | 62.3 | 35.9 | 26 - 142 | 4 | all |
| Muscles: | | | | | | |
| protein(% dry wt) | 30 | 48.4 | 8.2 | 42.2 - 58.6 | 3 | 1988 |
| lipids (% dry wt) | 40 | 17.46 | 15.5 | 11.5 - 24.9 | 4 | 1987 |
| energy(cal/dry wt) | 79 | 6.718 | 4.12 | 6.04 - 7.24 | 4 | 1987,88 |
| (J/dry wt.) | | 28.1 | | 25.3-30.3 | | |
| Gonads: | | | | | | |
| Good sperm ³⁾ (%) | 242 | 22.8 | 70.7 | 0 - 83.7 | 4 | all |
| Motility (s) | 110 | 51.5 | 34.0 | 0 - 86 | 4 | 1986-87 |
| Density '000/mm ³ | 83 | 82.7 | 37.7 | 25.8 - 189 | 4 | 1986-87 |
| Protein % dry wt. | 79 | 36.2 | 26.2 | 19.1 - 63 | 3 ⁴⁾ | 1986,1989 |

1) Age groups 2 and 3 constituted 83 % in females and 84 % in males.

2) About 30 eggs from each fish measured.

3) Morphologically sound spermatozoa, i.e. without any deformities of head and of flagellum.

4) From lake LUT - 3 fish only, ignored.

TABLE 2

Selected characteristics of lakes and of vendace stocks

| | ISG | LUT | MAR | NAR |
|------------------------------|--------|---------|---------|---------|
| Area, ha | 396 | 691 | 333 | 1240 |
| Mean depth, m | 14.0 | 7.2 | 11.9 | 9.8 |
| Max. depth, m | 54.5 | 20.7 | 41.0 | 43.8 |
| Shorline, m ha ⁻¹ | 44 | 28 | 44 | 54 |
| Type | b-meso | eutroph | eutroph | a-meso |
| Catches kg ha ⁻¹ | 10.8 | 3.2 | 21. | 13.6 |
| mean 1975-89 | | | | |
| trend | down | down | up-down | up-down |

Condition of the fish differed somewhat between the lakes (year 1987 stood out with respect to males in ISG, Table 3) but **growth in weight** in ISG and mother lake differ by a factor of 2 or 2.5 if one compares weights at age 3 (Table 4, last column). Similar differences of growth between ISG, MAR and NAR were found in 1981 to 1985 (Wilkońska, Żuromska 1988).

TABLE 3

Constants in equations describing weight-to-length relationships: gutted weight = a · (length)^b

| | a | b | Coefficient of determination | Estimated weight at 17 cm |
|-----------------|---------|--------|---------------------------------|------------------------------|
| FEMALES | | | | |
| ISG | 0.01140 | 2.9824 | 78.2 | 53.3 g |
| LUT | 0.00903 | 2.9824 | 74.0 | 42.2 g |
| MAR, NAR | 0.06042 | 2.3555 | 83.2 | 47.8 g |
| MALES | | | | |
| ISG 1987 | 0.00722 | 3.2411 | 66.8 | 57.2 g |
| ISG other years | 0.00553 | 3.2411 | 76.4 | 53.8 g |
| LUT, MAR, NAR | 0.00533 | 3.2411 | 88.8 | 51.8 g |

TABLE 4

Constants (c,d) in equations $w(t)=c*EXP(d*t)$ describing gutted weight of vendace ,w(t), at age t

| LAKES | c | d | Coefficient of determination | Estimated w(t) at t=3 |
|---------------|------|---------|---------------------------------|--------------------------|
| FEMALES | | | | |
| ISG | 52.8 | 0.28924 | 62.1 | 125.7 g |
| LUT, MAR, NAR | 23.1 | 0.23684 | 78.5 | 47.0 g |
| MALES | | | | |
| ISG | 73.0 | 0.08930 | 32.1 | 95.4 g |
| LUT, MAR, NAR | 27.4 | 0.2012 | 50.1 | 50.1 g |

The proximate composition of muscles was slightly different in sexes (Table 1) but statistically significant difference concerns lipids only, viz. females 15.75%, males 17.46%. The effect of fish age appeared rather weak except that on protein content in female muscles where it was exceptionally strong and followed a second degree equation (parabola, see Table 5). Slight effect of (guttled) weight was detected in one set of data only, i.e. in the caloric value of female muscles.

TABLE 5
Regressions of muscle compounds (y.) on fish attributes and fractions of variations of y. (R^2 , %) explained by the attributes and/or by environment.

| | FEMALES | MALES |
|---|---------|--|
| LIPIDS, 1987 only | N=54 | N=47 |
| no effect of age, weight, lakes | | $y_1 = 14.2 + 1.285 \cdot \text{age}$, $R^2 = 9.07$ |
| | | lakes ineffective |
| PROTEIN, 1988 only | N=20 | N=30 |
| $y_2 = -7.73 + 34.52 \cdot (\text{age}) - 4.02 \cdot (\text{age}^2)$, $R^2 = 84.4$ | | $y_3 = 54.3 - 2.04 \cdot (\text{age})$, $R^2 = 17.0$ |
| lakes ineffective | | lakes ineffective |
| CALORIC value, 1987 & 1988 | N=80 | N=79 |
| $y_4 = 7.06 - 0.192 \cdot (\text{age}) + 0.00245 \cdot (\text{wt})$, $R^2(\text{age}) = 12.6$, $R^2(\text{wt}) = 4.0$ | | $y_5 = 6.92 - 0.0627 \cdot (\text{age})$, $R^2 = 6.4$ |
| effect of: year=21.7%, lakes=49.5% | | year-no, lakes=50.6% |

Effect of years and lakes was assessed by ANOVA after the effect of age and weight of fish was taken into account and they could be disclosed with respect to the caloric value of muscles. This effect appeared fairly pronounced but inconsistent both in females and in males (Fig. 1, compare lakes ISG and NAR in both years). The fast growing ISG vendace did not differ from the other ones in any consistent manner. These results are rather obscure, most likely due to inadequate samples.

FRACTION OF GOOD EGGS

Kamler et al. (1982) found that mean per cent of vendace eggs without resorption in 10 samples (range from 97.7 down to 62.4 %, from 8 lakes, and 2 lakes over 2 years) correlated with fertilizability and with survival of embryos till the morula stage (rank correlation $r(s) = 0.818$, our computations from their data). However, if the ranking was on fractions of fish having good eggs and providing high survival of embryos, the correlation was insignificant ($r(s) = 0.5644$, $df = 8$, NS).

The fractions of apparently good eggs (without detectable resorption, Table 1) in the ovaries were over 80 percent in most (171 out of 187) females with the only exception of the sample of 1988 from lake LUT where numerous tapeworms (Cestoda) and small, unripe eggs were observed. Otherwise fish size and age, years and lakes

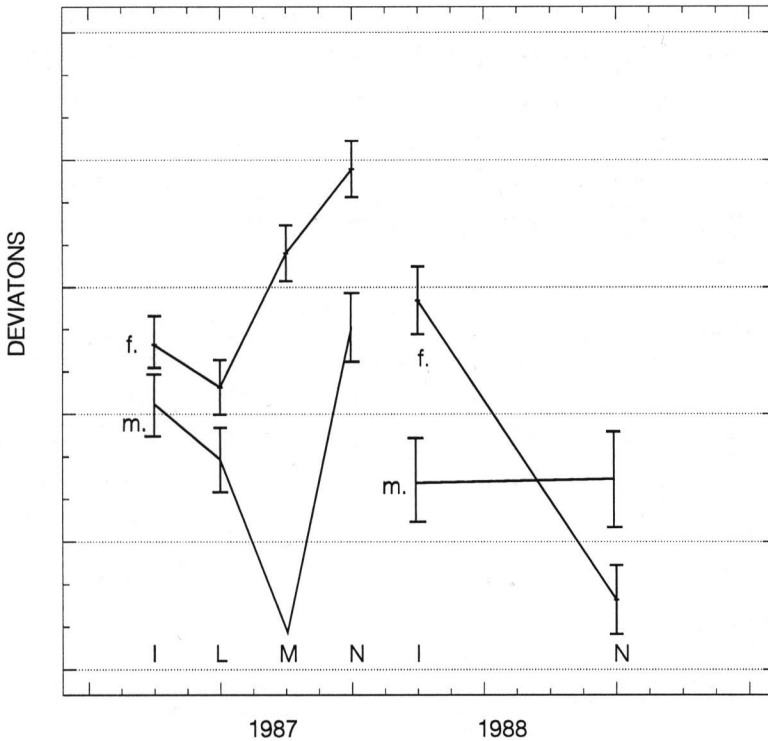


Fig. 1. Energy value of muscles in females (f) and in males (m) expressed as mean deviations of observed from predicted values (see Table 5). Means for lakes are joint by lines in respective sexes and years, confidence limits - vertical lines. Letters I, L, M and N stand for the four lakes

had no effect. In the batches from 19 females all developing embryos died till the stage of eye globules, but these females had from 69.4 to 100% good eggs (Wilkońska et al. in prep.).

All the above evidence shows that fraction of good eggs can be affected by environmental factors and this results in varying number of mature eggs but not in offspring survival.

SIZE, WEIGHT OF AND WATER CONTENT IN EGGS

Egg diameter varied little (Table 1) and depended on age and age squared, although the degree of determination was weak (Table 6). Fish length, weight and condition had no effect. The relationship was :

$$E(\text{diameter, mm}) = 1.424 + 0.1226 \cdot (\text{age}) - 0.0157 \cdot (\text{age})^2 \quad (1)$$

where $E()$ stands for the *estimated value*.

TABLE 6

Fractions (%) of total variability of egg attributes (dependent variables) explained by gutted weight and age of fish, by origin (lakes) and years, or by other variables

| DEPENDENT VARIABLES | Diameter r | Dry weight | Wet weight | Protein | | Lipids | | Energy | | Hydra- tion % | Specific weight |
|--|--------------------|--------------------|---------------|-----------------|------------------------|----------------|--------|------------|-------------------------|------------------|--------------------|
| | mm | mg | mg | mg | % d.w. | mg | % d.w. | cal/egg | per mg | % | |
| Sample size | 192 | 192 | 54 | 139 | 139 | 90 | 90 | 191 | 191 | 54 | 54 |
| INDEPENDENT VARIABLES | | | | | | | | | | | |
| Gutted weight | - | - | - | 9.0 | 10.9 | - | - | - | - | - | - |
| Age | 11.3 ^{y)} | 5.2 | - | - | - | 13.4 | 9.1 | 12.6* | - | - | - |
| Lakes | 9.7 | 7.0 | 13.2 | 5.3 | insing. | 12.4 | 15.8 | 7.4 | insign. | 19.0 | 13.3 |
| Years | insign. | 15.9 | | 24.7 | 13.2 | 27.1 | 29.0 | 9.3 | 63.6 | - | - |
| | | | (1989) | (3 years only) | | (2 years only) | | | | (1989 only) | |
| Interact. (L*Y) | 10.2 | 10.5 | - | 10.8 | 18.7 | 10.8 | 18.6 | 8.6 | 9.3 | - | - |
| UNEXPLAINED | 68.8 | 61.4 | 86.8 | 50.2 | 57.9 | 36.3 | 27.5 | 62.1 | 27.4 | 81.0 | 86.7 |
| OTHER VARIABLES | | | | | | | | | | | |
| Muscle protein | | | | | 49.5** (1988, N=20) | | | | | | |
| Muscle energy | | | | | | | | | 13.0 (1987-88, N=79) | | |
| Egg dry weight | | | | | | | 58.5 | | | | |
| Egg wet weight | | | | | | | | | | 6.6 | |
| Egg protein | | 32.6 | | | | | | | | | |
| Egg lipids | | 25.6 | | | | | | | | | |
| | 1986-87, N=89 | | | | | | | | | | |
| Occurrence of significantly large and small mean values in years | | | | | | | | | | | |
| large values | 1987 in 3 lakes | ? | | 1986 in 3 lakes | | 1986 | | 1987, 1988 | | | |
| small values | 1988 in 3 lakes | 1988 in 3 lakes | | 1988 | | 1987 | | 1986, 1989 | | | |

* Egg diameter depends on age and age square (see text)

** Negative effect

The equation describes a parabola (Fig. 2) with maximum diameter at age 3.9, close to that in many vendace samples analyzed by Kamler et al. (1982) with respect to egg dry weight.

Two factor (i.e. years and lakes) ANOVA of egg diameter minus the diameter predicted for age (see equ. 1) showed high value for interaction (lakes · years, Table 6). This implies the effect of these factors as being vague. Lakes considered in particular years differed little or not at all. Scattered points (Fig. 2) illustrate effects of the differentiation due to origin and years and a lot of within the sample variability.

Egg dry weight varied three times as much as the diameter (Table 1) and the two parameters correlated, $r=0.753$. Moreover:

$$E(\text{egg dry wt}) = 0.6763 + 0.02595 \cdot (\text{age}) \quad (2)$$

Contrary to Kamler et al. (1982) factor „age²” appeared insignificant, and regres-

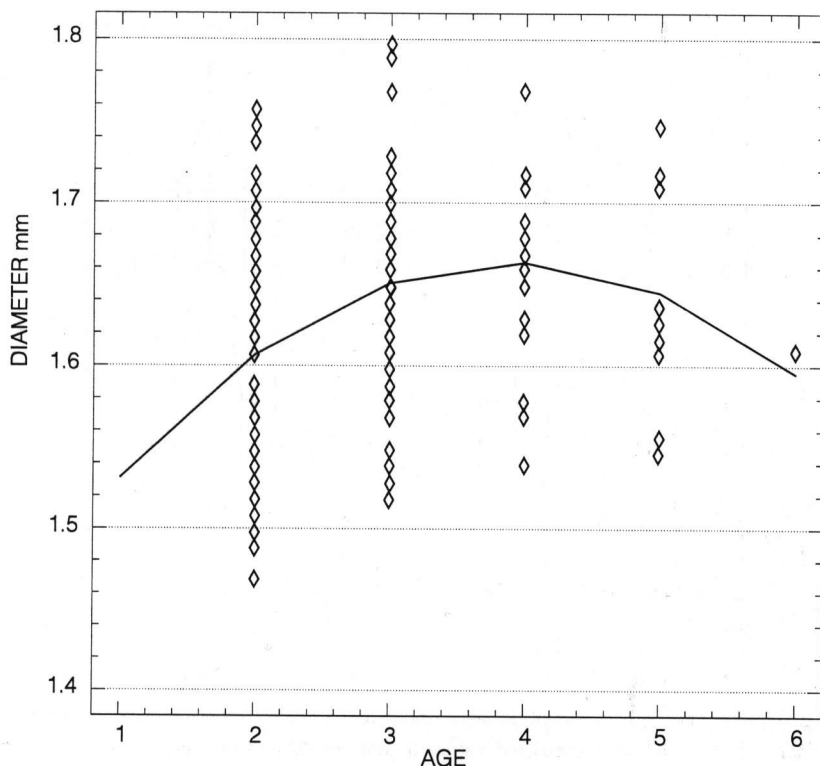


Fig. 2. Egg diameter versus age of fish; points - individual fish, line - equation (1)

sion (2) explained 5.2 percent of the variations only (Table 6) what may be due to a small numbers of old fish.

Averages of the dry weight were roughly parallel to the averages of egg diameter (Fig. 3, after the effect of age was subtracted) but, again, high interaction between lakes and years (Table 6) made separation of their effects inexplicit. One can infer from Fig. 3 that lake LUT had the smallest and the lightest eggs in 3 years, the largest eggs were those from MAR in 1986 and 1989, the years of very similar temperatures (see p. 7). Data on egg dry weight of vendace collected over 8 years showed the same inconsistency with respect to the lakes (Wilkońska 1992).

In 1988 - the warmest season - the eggs had significantly smaller dry weight than in 1989. In the period 1981-1989 a negative correlation between the mean seasonal temperature and the egg dry weight was found, the former explaining as much as 25% of egg variability (Wilkońska 1992).

Coefficient of variation of egg diameter within females (Table 1) did not correlate with the respective means but was found to vary between years (years explained 6 % of total variability); in each lake maximum coefficient of variation

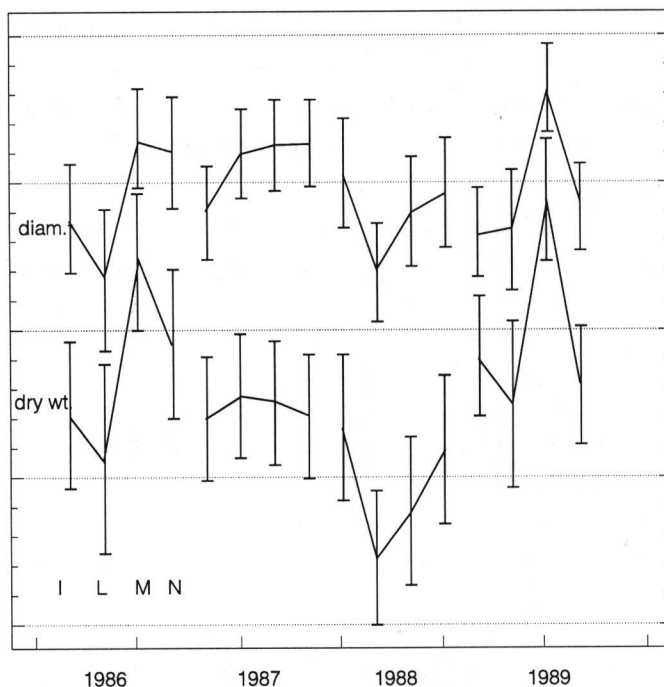


Fig. 3. Egg diameter and egg dry weight in lakes (indicated by letters) over four years expressed as mean deviations of observed from predicted values (equations (2) and (3), respectively) with confidence limits. Ordinates for the respective values shifted, scale the same

appeared in 1988 (the warmest year), minimum in the next year and the two years differed significantly. Differences between the lakes were not significant.

Wet weight and hydration (fraction of water by weight) showed rather small variations but they were measured in fish from 4 lakes in one year only (Table 1). They were not affected by any fish characteristics. Significant effect of lakes was found for hydration only, in MAR smaller than in NAR. Obviously, wet weight correlated with dry weight ($r_{dw}=0.743$) and egg diameter ($r_{di}=0.741$, $N=54$).

Fraction of dry weight in wet weight decreased with the increase of the latter, but hydration - increased:

$$E (\% \text{ dry wt}) = 39.157 - 1.927 \cdot (\text{wet wt, mg}) \quad (3)$$

$$\text{and } E (\% \text{ hydration}) = 60.84 + 1.926 \cdot (\text{wet wt, mg}) \quad (4)$$

tough the determination coefficient was low, $R^2=6.6\%$. In the set of data of 1981 season ($N=33$, the same lakes but LUT, unpublished) a very similar relationship was found, viz.:

$$E (\% \text{ dry weight}) = 40.83 - 2.592 \cdot (\text{wetwt, mg}) \quad (3a)$$

and the determination was 16.7 %. Thus, the larger the eggs (average in female) the greater the fraction of water and the smaller of dry matter.

Mean fractions of water and dry matter in the wet weight of eggs (averages 34.8 and 65.2 %, respectively) in the 1986-89 samples were very similar to those of 1981 collection, viz. 34.7 and 65.3 %, respectively, although the eggs were heavier, wet wt. = 2.354, dry wt. = 0.8134 mg (Wilkońska, unpublished).

Specific weight (Table 1) did not differ from 1 mg mm^{-3} and varied very little.

PROXIMATE COMPONENTS OF DRY WEIGHT

There was less protein (per dry weight) in eggs than in muscles, but with respect to lipids the reverse relation was noted (Table 1). These comparisons, however, are based on one year data only.

Protein content increased with the weight of the fish, but lipids in the eggs increased with the age. The same applies to the **average fractions of protein and of lipids** in dry weight of the eggs:

$$E(\text{protein cont.}) = 0.2592 + 0.65178 \cdot (\text{fish wt}/1000) \quad (4)$$

$$E(\text{protein \% dry wt}) = 36.30 + 0.07196 \cdot (\text{fish wt}) \quad (5)$$

$$E(\text{lipid cont.}) = 0.1275 + 0.02465 \cdot (\text{age}) \quad (6)$$

$$E(\text{lipid \% dry wt}) = 21.35 + 1.62 \cdot (\text{age}) \quad (7)$$

Each regression determined utmost 13.4 % of total variability of respective characteristics (Table 6). These results differ from those of Kamler et al. (1982); they fitted second degree equations to the data on protein and lipid content in vendace eggs plotted versus age but did not give estimates of determinations. As in the case of dry weight (equation 2) this difference may have resulted from the small number of old fish in our samples.

Effect of lakes was either weak or inconsistent and that of years fairly consistent. With respect to protein, the minimum occurred consistently in 1988 (the warmest) in each lake but maxima were either in 1986 (ISG, LUT, MAR) or in 1987 (NAR).

Lipids in 1986 (estimated over two years only) appeared higher or not different from the level in 1987 (coolest) in each lake; averages were 0.222 mg/egg and 29.1 % or 0.175 mg/egg and 23.4 % in the respective years.

The fractions of protein (Table 1, average 40.8 %) and of lipids (23.9 %) did not vary with egg size or with egg dry weight but the two components were negatively correlated : $r = -0.219$ (very weak determination).

ANOVA of dry weight for lakes including covariates of protein, lipids and years produced the results as follows:

| From multiple regression: | | | | | |
|----------------------------|--------------|------------|-----------|----|----------------|
| | Coefficients | sign.level | S.squares | df | % contribution |
| Constant | 0.2541 | .0000 | | | |
| protein | 0.7041 | .0000 | 0.2347 | 1 | 32.6 |
| lipids | 1.1749 | .0000 | 0.1848 | 1 | 25.6 |
| year | 0.0290 | .0615 | 0.0121 | 1 | 1.7 |
| From analysis of variance: | | | | | |
| between lakes | | .0043 | 0.0422 | 3 | 5.9 |
| residual | | | 0.2468 | 83 | 34.2 |
| TOTAL | | | 0.7206 | 89 | 100.0 |

This analysis of dry weight variations based on two years data with protein and lipids measurements, differs from that based on 4 years data but excluding effects of protein and lipid content (see above, Fig. 3 and Table 6). The latter revealed dominating effect of external factors on egg dry weight (33.4 %) and significant though small effect of age, while the former (two years): a small contribution of lakes (5.9%), insignificant of years, and no detectable effect of fish age. This is because the contents of protein and of lipids depended on years and lakes, and was affected by fish weight and age (Table 6).

ENERGY IN EGGS

One can expect that protein and lipids contribute to the **energy content** (cal per egg) at mean rates 5.5 and 9.5 cal per mg (23.0 J and 39.8 J, respectively) of the respective substance. The three measurements were made in 1986 and 1987 only, but for all 4 lakes (90 fish). Multiple regression computations of energy content (cal per egg) on protein and lipids (mg per egg), including effect of the year, resulted in the estimates as follows :

| | Coefficients | S.E | Comments |
|-------------------|--------------|--------|--------------------------|
| Constant | 0.2894 | 0.414 | not sign. diff. from 0 |
| protein | 5.5777 | 0.7759 | not sign. diff. from 5.5 |
| lipids | 8.5549 | 1.2284 | not sign. diff. from 9.5 |
| year ('86 or '88) | 0.8259 | 0.1141 | sign. diff. from 0 |

This result justifies forcing the intercept to be 0. Recalculation of data under this assumption produced coefficients for protein and lipids equal 5.81 and 9.17 cal.mg⁻¹ also close to the theoretical mean values.

Analysis of variance showed that in the two years when the analyses were made, 33.4 per cent of the total variations (sum of squares) of energy content per egg could be attributed to protein level, 4.9 per cent to lipids, 22.2 per cent to years, and 7.9 per cent to lakes (interaction insignificant). (Compare the results of regressing dry weight on protein and lipids above). High fraction i.e. 31.2 per cent of the total variation remained unexplained.

In the whole set of data (192 fish) the energy content appeared strongly associated with the dry matter content in eggs:

$$E(\text{cal cont}) = 1.01104 + 5.196 \cdot (\text{dry wt}), R^2 = 58.3\% \quad (8)$$

Wilkońska, Żuromska (1988) found that:

$$E(\text{cal cont}) = -0.065 + 6.144 \cdot (\text{dry wt}), R^2 = 71.9\%, (N = 25) \quad (8a)$$

If the effect of dry weight or its components is ignored then:

$$E(\text{cal. cont}) = 2.6716 + 1.3374 \cdot (\text{age}) - 0.1759 \cdot (\text{age})^2 \quad (9)$$

($R^2=12.6\%$, maximum expected at age 3.7, while for diameter it was 3.9). Consequently, if dry weight, age and age squared were used as independent variables, the latter two (i.e. age) appeared insignificant in affecting the energy content because age influenced dry matter of eggs, hence, indirectly also the energy content.

In 14 out of 15 samples of vendace (ranging from 23 to 30 fish in each) Kamler et al. (1982) found parabolic relationship between caloric equivalent (=content) and age, and respective coefficients ranged as follows:

| regression: constant | coeff. on age | coeff. on age ² |
|----------------------|----------------|----------------------------|
| from 2.11 to 11.82 | 0.397 to 1.407 | -0.2661 to -0.0168 |

Our estimates fall within these ranges. However, the strength of the quoted regressions was not shown nor the regressions on dry weight of eggs were calculated.

As in the case of egg diameter and of dry weight, effect of lakes and years was assessed for caloric content after the effect of age (equ. 9) had been subtracted. The results are shown in Table 6. In 1986 and 1989 the means of caloric contents for lakes were similar as for dry weight and of the sequence: LUT, ISG, NAR, MAR, and LUT was significantly lower than MAR. In 1987 and 1988, the years of extreme temperatures, there was no significant difference between the lakes.

Energy value (cal per mg dry weight, Tables 1, 6) did not depend in a significant way on any attributes of fish, nor on egg size, but variation between the years

explained as much as 63.6 % of the total. It is interesting that in the years of quite different temperature regime (1987 and 1988, Fig. 4) the energy values of eggs were significantly higher than in the apparently similar years of intermediate thermal regime (1986 and 1989). Effect of lakes was inconsistent.

It should be noted that energy value of eggs and muscles was positively, though not strongly (Table 6), related:

$$E(\text{egg cal. val.}) = 4.99 + 0.294 \cdot (\text{muscle cal. val.}) \quad (10)$$

ATTRIBUTES OF SPERM AND TESTICLES

Among four attributes of testicles, **per cent of good spermatozoa** only were estimated in fish from 4 lakes over 4 years (Table 1). The varied widely and a small fraction (i.e. 8.93 %, Table 7) of the variation was explained by fish (gutted) weight.

$$E(\% \text{ good sperm}) = 9.95 + 0.2163 \cdot (\text{fish wt}) \quad (11)$$

In 1986 per cent of good sperm was the lowest, in 1989 - the highest (Fig. 5). With respect to the lakes no consistent sequence occurred.

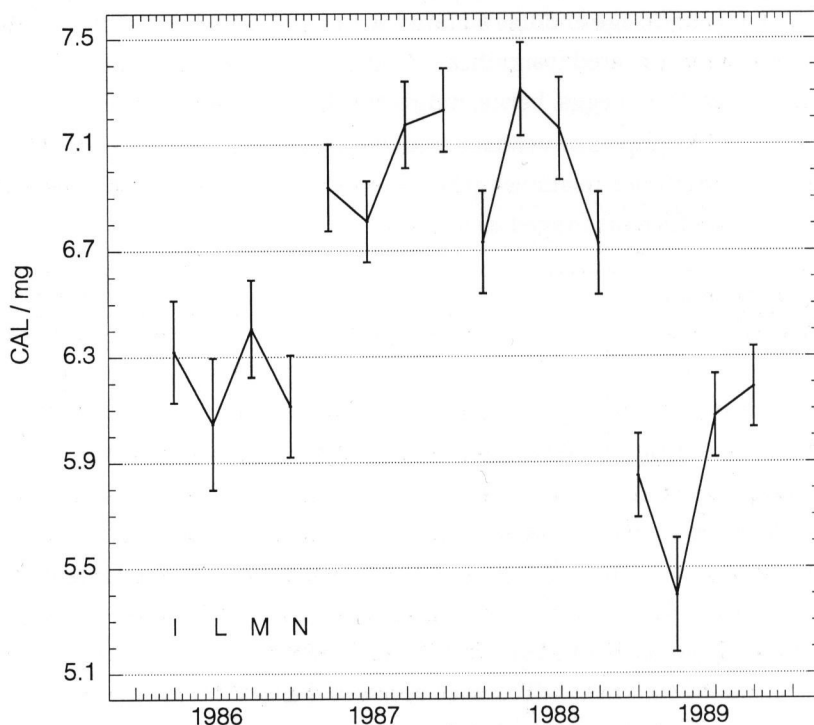


Fig. 4. Energy value (calories per mg dry weight) in eggs. Points and lines as in Fig. 3.

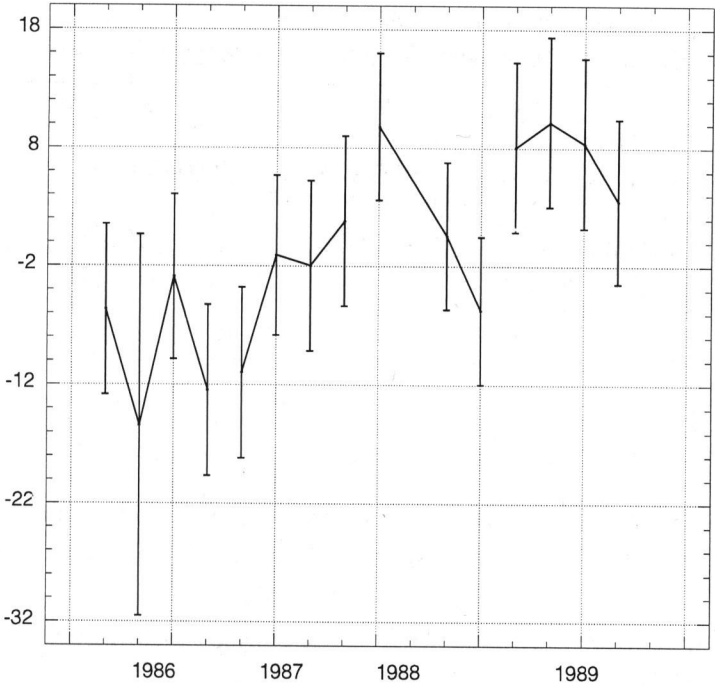


Fig. 5. Mean deviations of percent of good sperm from predicted levels - see equation (10). Sequence of lakes and years as well as meaning of lines and points as in Fig. 3

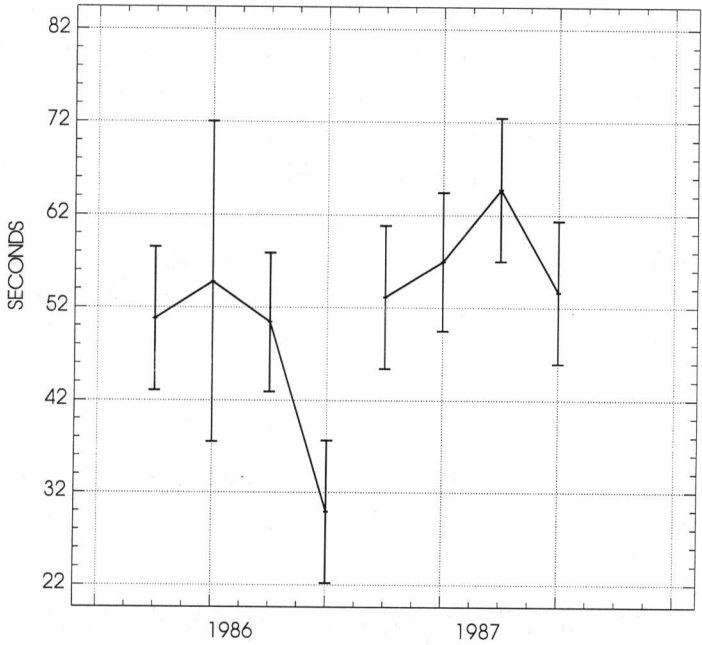


Fig. 6. Mean sperm motility (seconds). Sequence of lakes as in Fig. 3

TABLE 7

Fractions (%) of total variability of testicle characteristics attributable to fish and to environment

| DEPENDENT VARIABLES | '86-89 | '86, '87 | '86, '88 | ('88) | '86, '87 |
|-----------------------|--------------|---------------|-------------------|--------|------------------------------|
| | Good Sperm % | Motility sec. | Protein % dry wt. | | Density '000/mm ³ |
| Sample size | 232 | 110 | 79 | (30) | 83 |
| INDEPENDENT VARIABLES | | | | | |
| Fish age | - | - | - | (5.4) | - |
| Fish weight | 8.9 | - | - | (58.6) | - |
| Years | 12.1 | 9.4 | 40.7 | - | 5.0 |
| Lakes | insign. | 7.3 | inign. | (14.4) | 5.7 |
| Interaction (Y · L) | 7.6 | 6.0 | 5.8 | - | 6.3 |
| Good sperm | - | 13.2 | - | - | - |
| Muscle protein | - | - | - | (24.7) | - |

Motility of spermatozoa (two years only) appeared well correlated with the former trait ($r=0.3638$), on the average slightly better in 1987 than in 1986, but the differences between the lakes were inconsistent (Fig. 6).

Protein (per cent) in testicles (Table 1) was strongly associated with both gutted weight and age of the fish in 1988 only:

$$E(\text{prot. testes}) = 19.78 + 0.242 \cdot (\text{fish wt}) - 1.959 \cdot (\text{age}) \quad (12)$$

As in the case of protein in eggs, in 1986 the protein level in testicles was higher than in 1988 (and this coincidence should be emphasized), but the differences between the lakes were inconsistent (Fig. 7). This parameter correlated positively with protein in muscles ($r=0.4971$, $N=20$, year 1988 only).

Sperm density varied independently of any traits.

Effect of external factors on male gonads appeared much lower than on ovaries (compare Tables 6 and 7). Only protein levels showed significant (and consistent in every lake) decrease from higher level in 1987 to lower in 1988, explaining 40 % of total variation (Fig. 7).

GONADS AND MUSCLES

Negative correlation between protein value (% dry wt) of eggs and that of muscles suggests some trade-off between somatic and reproductive metabolism in the females:

$$E(\text{egg prot. val.}) = 49.72 - 0.2226 \cdot (\text{muscle prot. val.}) \quad (13)$$

(determination =0.495, $N=20$). But note that protein value in muscles of females

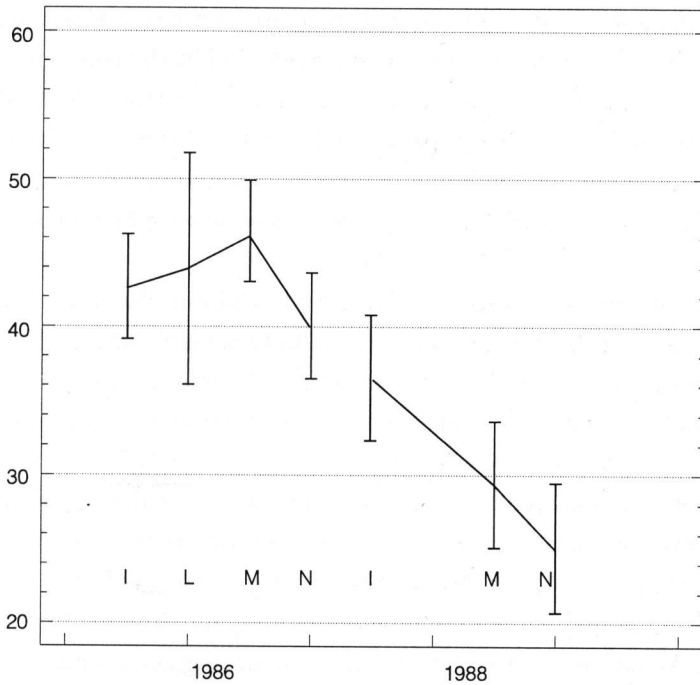


Fig. 7. Mean protein value in testes, per cent dry weight

appeared to be a parabolic function of age (Table 5), although with a medium strength.

This was not the case with respect to lipids in females but energy content in eggs and muscles ran parallel (equ. 10). In males the protein in gonads increased as that in muscles. Hence, there was not any trade-off.

$$E(\text{testes prot. val.}) = -5.917 + 0.74 \cdot (\text{muscle prot. val.}) \quad (14)$$

(determination=0.242, N=20)

It seems that the available data on the relationships between muscle and gonad composition are inconclusive.

DISCUSSION AND CONCLUSIONS

Although vendace in the four lakes differed greatly with respect to growth and even more to abundance (by a factor of 7) the reproductive attributes did not differ so much. The overall variability was not great (Table 1, column C.V.%). The ratios of maximum to minimum average of the reproductive attributes in 16 samples (4 lakes

in 4 years) ranged from 1.08 (egg diameter) to 1.59 (per cent of lipids in eggs). Data of Kamler et al. (1982) on vendace from 5 Polish and 4 Finnish lakes show these ratios equal to: 1.11 for egg dry weight, 1.09 for per cent of protein and 1.90 for per cent of lipids in dry matter of eggs. It is almost trivial that these attributes are restrained and cannot deviate from a certain level, securing perpetuation of populations, unless catastrophic situations occur. An example of such a catastrophe was an infestation of vendace with *Cestoda* in lake LUT in 1988.

Kamler et al. (1982) produced evidence that in 14 samples from 9 lakes (considered separately) egg dry weight, protein and lipid contents and caloric equivalents depended on age of fish (parabolic relationship). We found that a better predictor for protein content was (gutted) weight but also that any trait of gonads could hardly be predicted from the measured attributes of the fish (Table 6 & 7). The most significant effect of age of fish explained 13.4 percent of lipid content in the eggs. Unlike vendace samples quoted by Kamler (1992), egg dry weight did not show such a relationship with age. This may be due to insufficient number of older fish in our samples. But Kamler et al. (1982) did not estimate the degree of determination.

Also, unlike Kamler et al. (1982), protein content in eggs depended on fish weight (Table 6) but not on age. However, protein value of muscles (1 year data only) showed exceptionally strong (84.4 %) parabolic relationship with age (Table 5) and the two protein levels (in eggs and in muscles) were negatively correlated. Protein value of testicles in 1988 appeared strongly related to fish weight; protein in muscles appeared negatively affected by age. All other testicle traits (and the whole set of protein data) varied rather independently of the fish size or age.

The picture looks obscure and this is in part due to sample sizes and, no doubt, also due to the masking effect of variability within sample (=population), between homogeneous fish. It seems, however, that such a shape (parabolic or any convex curve) involves biological phenomena. Growth rate in many fish (annual increase of body weight) plotted against age follows a convex curve. Suppose that the egg size (EG) tends to increase with age (t) at a steady rate, say $+A$, and that at the same time there are age dependent factors that inhibit this rate (effect of ageing), say equal to $-B \cdot t$, then we get:

$$\text{rate of egg size change} = \frac{d(EG)}{dt} = A - B \cdot t$$

and upon integration:

$$EG = A \cdot t - \left(\frac{B}{2} \cdot t^2\right) + \text{constant}$$

Relationships between muscle and gonad chemical composition in females and

males suggest that females build up gonads on the expense of soma but this was not the case in males. Dąbrowski (1985) found evidence that in female vendace „the body stores are mobilized for purpose of reproductive tissue energy increment” a month or so before spawning and it concerns mainly lipids. Our findings do not contradict his (lipids were not analyzed) and also suggest that allocation of energy intake may be different in vendace males. This requires further studies.

Significant interaction of lakes and years exhibited different reaction of the majority of reproductive traits to similar atmospheric situation in different lakes. Thus, separation of the effect of atmospheric conditions from that of the lake environment is difficult. However, coefficient of variation of egg diameter within females, and energy value of eggs, did not differ between the lakes in any year, but the effect of years was consistent; minimum occurred in 1989, which preceded high levels in 1988, the warmest year. This agrees with the negative correlation between temperature and egg dry weight found by Wilkońska (1992). Considering high correlation of caloric content with dry weight in eggs ($r=0.764$) one can expect that the warmer the season the greater the energy per unit dry weight in eggs, as shown above.

Wilkońska and Żuromska (1988) concluded that egg quality (dry weight and caloric content) in vendace from eutrophic lake MAR was very good, but from the a-mesotrophic lake NAR it was poor in 1985. In 1987 and 1988 (of extreme seasonal temperatures) the lakes did not differ with respect to caloric content in eggs but in 1986 and 1989 (of very similar and intermediate temperatures) MAR had significantly higher content than LUT. Note that vendace in LUT was almost vanishing while in MAR - abundant (Table 1). Hence, there is no doubt about environmental effects but it remains unsolved which factors apart from seasonal temperature were responsible for egg quality: trophic level of lake, population abundance or other factors. Whatever combination of variables possibly affecting gonad characteristics was considered jointly there always remained a large fraction (from about 30 to almost 70 per cent) of unexplained variance (Tables 6, 7).

A major fraction of the latter is due to intra-population variability which masked the rather small effects of environment and masked the relationship between somatic and gonadal characteristics except for the number of eggs per fish (not considered here, Zawisza, Backiel 1970). What follows is that the reproductive traits analyzed in this paper are species specific and, as stated above, very much less than one could expect from variations of external and even of internal factors.

In order to illustrate the complex interrelations we summarized determination coefficients for the dry weight of eggs and its components (Fig. 8). This is somewhat similar to the schematic presentation of the pathways of direct and indirect effects of

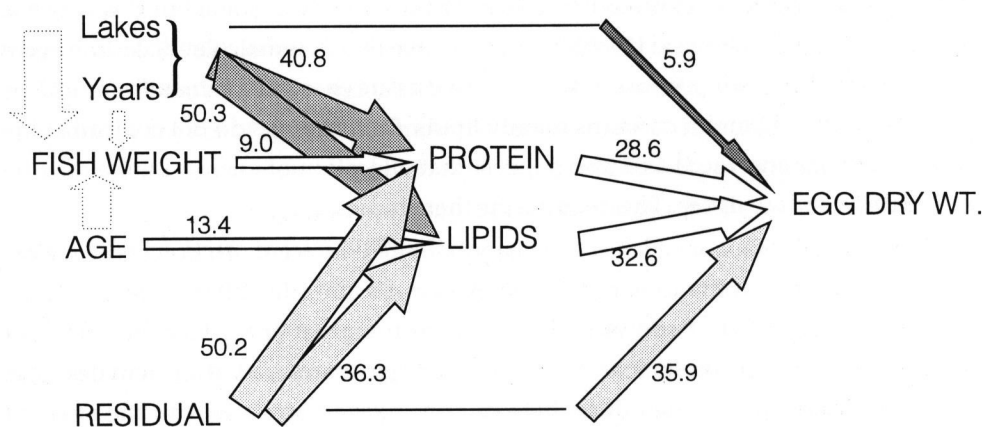


Fig. 8. Degree of determination (figures at arrows= percent of total sum of squares of deviations) of egg dry weight directly by protein and lipid contents and by "lakes" and via the two former components by fish and environmental attributes. Width of arrows show roughly differences between respective effects. "Residual" means coefficients of nondetermination. See text

various factors on fish offsprings in Kamler (1992, her Fig. 3.13). We tried here to quantify certain effects upon one important egg attribute. The quantities showing relative strength of effects are the percentages of total variability explained by the respective variables (factors). The quantities are based on either 2 or 3 year (protein) sampling in 4 lakes only and, therefore, are of limited value. Note that contributions of protein and lipids to the variations of dry weight appeared roughly equal. This apparently contradicts the respective fractions of these components in dry weight (see Table 1), but the latter are components while in the former case they have been considered factors of variability.

Influence of fish size and age was weak and indirect, via constituents of the dry weight of eggs. The same applies to the environmental effects („variations" of lakes and years assessed jointly) but they were stronger. We did not quantify the relationships between lakes/years and fish weight (growth) and between age and growth. This could be done on the basis of data in Tables 2-4.

A warning is appropriate here; the quantities illustrate determination of one selected trait by some factors and obviously differ from regression coefficients which allow for estimating the average level of the dependent variable affected by selected „independent" variables. Among the latter there are such as lakes and years, which are not necessarily linearly related. And we disposed of just four lakes - i.e. four vendace populations - a too small number for assessment of inter-environmental variability.

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STRESZCZENIE

CECHY REPRODUKCYJNOŚCI I ICH WPŁYW NA EMBRYONY I LARWY U SIELAWY,
COREGONUS ALBULA (L.). CZĘŚĆ I. CHARAKTERYSTYKA RYB I GONAD

Badania prowadzono przez 4 lata (1986-1989) na sielawie z 4 jezior mazurskich. Wszystkie osobniki mierzono, ważono i pobierano łuski do odczytu wieku. Z gonad żeńskich pobierano próby jaj do oceny średnicy, śmiertelności, kaloryczności oraz zawartości białka i lipidów. Jakość mlecza oceniano na podstawie ruchliwości i procentu niezdeformowanych plemników oraz zawartości białka w gonadach.

Mimo dużej zmienności w rozmiarach i wzroście ryb, zmienność cech związanych z rozrodem była niewielka.

Potwierdzono paraboliczny charakter zależności między wielkością jaj a wiekiem samicy, chociaż była ona zdeterminowana jedynie w 11.3%. Z wiekiem związane były również różnice w zawartości lipidów i kaloryczności jaj. Oceniane właściwości jąder i plemników okazały się praktycznie niezależne od wielkości i wieku samców. Znalaziono natomiast prostą korelację między zawartością białka a suchą masą mięśni i gonad.

Na przykładzie suchej masy jaj przedstawiono (rys. 8) stopień zdeterminowania tej cechy bezpośrednio: przez zawartość białka i lipidów oraz przez różnice pomiędzy badanymi populacjami z 4 jezior, a pośrednio: przez masę jednostkową i wiek ryb oraz wspomniane różnice między jeziorami i pomiędzy latami.

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