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# FISH EGG SIZE VARIABILITY: BIOLOGICAL SIGNIFICANCE

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## ABSTRACT

Based on high–precision diameter measurements, volume and surface area of entire eggs and yolk spheres inside them were calculated in a number of fish species.

The results showed the eggs of various species to differ both in terms of their **dimensions** and **volume**, the differences being 5– and more than 70–fold, respectively.

Still larger differences were revealed in the yolk sphere size, the difference between the smallest and the largest eggs spanning 2 orders of magnitude.

The authors contend that the biological meaning of the differences involves adjustment of dimensions of an egg to its efficiency in providing appropriate oxygen supply to the developing embryo. The S/V (surface to volume) ratio, hence the gas exchange efficiency, depends on dimensions of both the egg and the oocyte surrounded by the perivitelline fluid confined by the membranes.

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The authors propose to replace the term "egg size", usually understood as egg dimensions, with "egg volume" or "egg weight".

**Key words:** fish, embryology, egg size

## INTRODUCTION

As shown by numerous publications dealing with conditions of life and reproduction of various fish species, fish eggs are highly diverse in terms of their size. The wealth of information on hand does not, however, translates into sufficient knowledge on mechanisms underlying the size variability observed.

It is characteristic that in most of the relevant papers, fish egg dimensions are treated as one, and in a way obvious, structural element with which to characterise a species' ontogeny, regardless of causal relationships between the species and its habitat [2, 4, 9–11, 20, 29, 39, 40, 42, 55].

Differences in egg dimensions have been related to the spawning season [4, 26, 37], fish individual size [3, 6, 8, 14, 18, 21, 25, 26, 32, 34, 37, 44, 47, 50], brood protection [49], or absolute fecundity [12, 48, 54].

A more in–depth analysis shows that each of the factors mentioned above plays a role and each opinion has an element of truth in it, but the opinions concerning effects of those factors on fish egg size in general may be questioned. What is or seems to be true in one species, is not necessarily so in another. In other words, the research on fish egg size lacks a common denominator in the form of a unifying theory which would explain the phenomenon in a more comprehensive and less eclectic and fragmentary manner than it does now.

It is in this context that we were prompted to review a large, fairly representative, body of data drawn from the ample literature and to complement those data with our high–precision measurements of eggs of several freshwater fish species [13, 28, 52]. This effort was aimed at relating, after the appropriate computations, the differences observed to those in the S/V (surface to volume) ratio. It is that ratio that directly affects the metabolic rate of the embryo surrounded by the membranes. Separate calculations of the ratio for eggs of different size should allow a more accurate determination of gas diffusion efficiency of various, differing in their surface area, egg parts during embryogenesis.

There are grounds to presume that it is the S/V ratio that, coupled with thermal conditions, explains the structural differences and allows to place the entire phenomenon within the developmental strategy of the class Pisces. To be able to colonize new, ecologically different habitats of the aquatic environment and to persist in them, individual species of the class have to be equipped (or have to equip themselves) with mechanisms enhancing survival and persistence under different ambient conditions, particularly with respect to temperature and oxygen supply. It is the interplay between those two factors that metabolic rates of poikilotherms are controlled by.

To some degree, the presumptions expressed above stem from our earlier research on the relationship between the rate of embryogenesis in some fish species and the S/V ratio and temperature. Our earlier observations [14, 15] as well as information supplied by numerous papers, particularly those by Zotin [54, 55] demonstrate that the dimensions of the entire egg are larger, sometimes substantially so, that those of the living structure inside the egg, i.e., the yolk sphere (surrounded by the vitelline membrane).

It seems that identification of the S/V ratios and coupling them with the number of thermal units determining the duration of embryonic development of a species will make it possible to arrive at a common denominator, a descriptor of the rate of change during embryogenesis. That, in turn, will facilitate deciphering the biological meaning of interspecific egg size variability. The extant huge set of data does not fully lend itself to solving this problem because it merely illustrates the size differences, without providing convincing answers to questions such as: why is it so? Why the size differences are so great? What is the biological significance of the variability? Those answers are important in the context of the evolution of the extremely species–rich class of the poikilotherm vertebrates in question and in view of their being able to colonize vast expanses of the highly diverse aquatic environment.

## MATERIALS AND METHODS

The study was conducted within 1995–2001 at the Department of Fish Anatomy and Embryology, Agricultural University of Szczecin and in the field laboratory situated on Lake Krzemień at Izdebno near Sieraków.

The study involved eggs of several freshwater fish species, greatly differing in size (1.25–5.01 mm diameter; Table 1).

The eggs, stripped from mature females, were fertilised and incubated in water the quality of which (temperature, dissolved oxygen content, etc.) was rendered similar, as much as possdible, to that of the native habitat of each species.

**Table 1. Mean (± standard deviation) dimensions, volumes, surface areas, and S/V ratios of hydrated eggs and yolk spheres in the fish species under study**

| Species | No. of eggs [n] | Diameter [mm] | | Volume, V [mm$^3$] | | Surface area, S [mm$^2$] | | S/V ratio | |
|---|---|---|---|---|---|---|---|---|---|
| | | egg | yolk sphere | egg | yolk sphere | egg | yolk sphere | egg | yolk sphere |
| Trout (*Salmo trutta* L.) | 778 | 5.01 ± 0.80 | 4.88 ± 0.59 | 71.12 ± 34.11 | 63.58 ± 22.72 | 81.00 ± 25.9 | 75.97 ± 18.11 | 1.23 ± 0.19 | 1.25 ± 0.15 |
| Rainbow trout (*Oncorhynchus mykiss* (Walb.)) | 75* | 4.9 ± 0.38 | 4.70 ± 0.37 | 62.77 ± 14.49 | 55.24 ± 15.75 | 75.94 ± 11.76 | 69.73 ± 10.80 | 1.23 ± 0.1 | 1.29 ± 0.10 |
| Pike (*Esox lucius* L.) | 212 | 2.68 ± 0.11 | 2.31 ± 0.11 | 10.33 ± 1.24 | 6.50 ± 0.87 | 22.90 ± 1.84 | 16.81 ± 1.51 | 2.23 ± 0.10 | 2.60 ± 0.12 |
| Lavaret (*Coregonus lavaretus* (L.)) | 186 | 2.61 ± 0.15 | 1.99 ± 0.16 | 9.42 ± 1.58 | 4.25 ± 1.05 | 21.49 ± 2.45 | 12.61 ± 2.07 | 2.31 ± 0.14 | 3.03 ± 0.25 |
| Whitefish (*Coregonus albula* (L.)) | 132 | 1.78 ± 0.10 | 1.34 ± 0.12 | 3.00 ± 0.50 | 1.29 ± 0.35 | 10.04 ± 1.10 | 5.68 ± 1.03 | 3.37 ± 0.18 | 4.52 ± 0.42 |
| Bream (*Abramis brama* (L.)) | 52 | 1.64 ± 0.04 | 0.99 ± 0.04 | 2.33 ± 0.18 | 0.51 ± 0.06 | 8.51 ± 0.45 | 3.09 ± 0.24 | 3.65 ± 0.10 | 6.07 ± 0.25 |

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|---|---|---|---|---|---|---|---|---|---|
| Three–spined stickleback (*Gasterosteus aculeatus* L.) | 70 | 1.52 ± 0.06 | 1.33 ± 0.33 | 1.83 ± 0.22 | 1.24 ± 0.15 | 7.23 ± 0.57 | 5.57 ± 0.44 | 3.96 ± 0.16 | 4.51 ± 0.17 |
| Bleak (*Alburnus alburnus* (L.)) | 40 | 1.48 ± 0.06 | 0.96 ± 0.04 | 1.71 ± 0.22 | 0.46 ± 0.06 | 6.90 ± 0.59 | 2.90 ± 0.25 | 4.06 ± 0.18 | 6.27 ± 0.28 |
| Rudd (*Scardinius erythrophthalmus* (L.)) | 30 | 1.33 ± 0.07 | 0.88 ± 0.11 | 1.26 ± 0.21 | 0.38 ± 0.14 | 5.62 ± 0.61 | 2.5 ± 0.63 | 4.50 ± 0.23 | 6.88 ± 0.85 |
| Spring Baltic herring (*Clupea harengus membras* (L.)) | 30 | 1.31 ± 0.02 | 0.78 ± 0.02 | 1.17 ± 0.07 | 0.25 ± 0.02 | 5.36 ± 0.20 | 1.90 ± 0.12 | 4.60 ± 0.09 | 7.73 ± 0.24 |
| Perch (*Perca fluviatilis* L.) | 55 | 1.28 ± 0.04 | 1.00 ± 0.05 | 1.10 ± 0.11 | 0.52 ± 0.08 | 5.15 ± 0.33 | 3.12 ± 0.31 | 4.69 ± 0.16 | 6.04 ± 0.31 |
| Goldfish (*Carassius auratus* (L.)) | 57* | 1.29 ± 0.05 | 0.95 ± 0.07 | 1.14 ± 0.14 | 0.46 ± 0.10 | 5.26 ± 0.42 | 2.86 ± 0.42 | 4.64 ± 0.18 | 6.34 ± 0.47 |
| Sun bass (*Leucaspius delineatus* (Heck.)) | 100 | 1.25 ± 0.04 | 0.86 ± 0.04 | 1.03 ± 0.10 | 0.34 ± 0.05 | 4.93 ± 0.33 | 2.35 ± 0.23 | 4.80 ± 0.16 | 6.96 ± 0.36 |

*** Eggs from a single female.**

Embryogenesis was monitored live, a particular attention being paid to the developing embryo's morphomechanics and the spatial distribution of individual embryonic structures, which was deemed useful for later analyses of development dynamics in eggs of different size. To monitor embryogenesis, two sets of equipment were used. Each set consisted of: ×2 objective Nikon microscope coupled with digital high resolution cameras; a monitor; a VCR; and a personal computer. One set of equipment was used to examine the developing egg from above, thus making it possible to measure egg diameter; the other set was arranged so as to examine the developing embryo in a side view, which made it possible to observe in detail changes in spatial arrangement of various embryonic structures [52].

The microscopic image (×100 magnification), projected on the monitor screen, was recorded on video cassettes. The video records were subsequently used to measure, with a high degree of accuracy (to 0.001 mm), the two (short and long) egg and yolk sphere axes (diameters). The measurements were effected with the aid of Multiscan computer software. The measurements were averaged for subsequent calculations of the volume ($V = 4/3 \cdot \pi r^3$) and surface ($S=4 \cdot \pi r^2$) of those spherical structures. The two diameters–based measurement procedure was proposed by Bartel [5]. The measurements were taken either on a sample of eggs stripped from a single female or on a sample consisting of eggs obtained from a number of females; the sample size ranged from 30 to 778 eggs.

The data obtained were subjected to statistical treatment employing the Excel 97 and Statistica PL software.

In addition to the data set obtained by measuring egg samples, an ample body of data on egg (and occasionally yolk sphere) size, provided by the relevant literature, was made use of as well.

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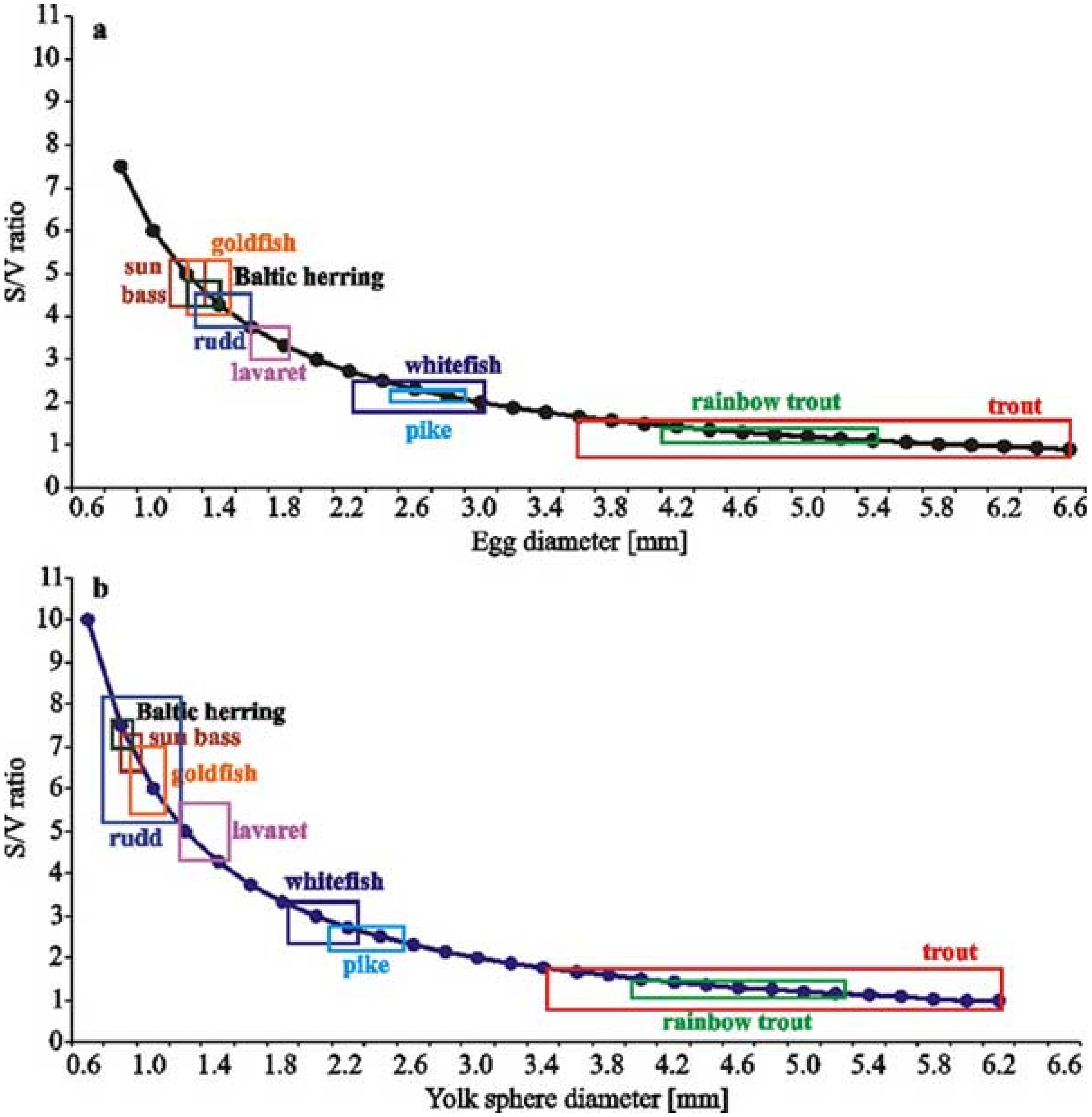
## RESULTS AND DISCUSSION

Before the results and literature data can be presented and interpreted, it is necessary to clarify some terms and concepts which have been given different connotations by various workers and have not always been defined precisely enough.

Foremost among those terms is the egg size, the size being usually reduced to dimensions. In our opinion, it would be more appropriate to regard the size in three, rather than in two, dimensions. This means that the egg **size** should be expressed as egg **volume**. The data in Table 1 and Fig. 1 demonstrate that, while the trout egg diameter (5.01 mm) is 4 times that of the sun bass egg (1.25 mm), the respective volumes (71.12 vs. 1.03 $mm^3$) differ by a factor of as much as 69!

**Fig. 1. The S/V ratio *versus* egg diameter (a) and yolk sphere diameter (b)**



Another term in need of clarification is the egg, usually applied to the **entire** egg, complete with the membranes, perivitelline fluid, and the yolk sphere, regardless of the fact that the yolk sphere, which is always much smaller than the entire egg, is the only living part of the egg.

Such a clarification is indispensable when considering the rate of embryogenesis, because the relative (%) contribution of living structures to the entire egg (a spherical space confined by the membrane minus the volume of the living structures) will translate directly into the metabolic rate, if only because it will be controlled by the area of contact with the surrounding medium relative to the volume of the living structure, *i.e.*, the S/V (surface to volume) ratio [15]. This means that, in the case of a hydrated fish egg, significant is only the surface of the **living structure**, the yolk sphere. After fertilization, significant becomes the yolk sac covered with ectoplasm and, later on, with the emerging germ layers and finally with the boundary structures (skin) of the developing individual.

When the terms and concepts concerning the basic structures are clarified in this manner,and once the necessary calculations have been made with relation to the yolk sphere (similarly to those made with relation to the entire eggs), the size differences become even more spectacular: 63.58 $mm^3$ in trout vs. 0.35 $mm^3$ in sun bass. That means that the trout egg yolk is as many as 182 times larger than the sun bass yolk sphere, although in terms of size the difference factor is as low as 5.67.

The data, collected from measurements (Fig. 1; Table 1) and drawn from the literature (Table 2) illustrate very pointedly the wide differences in size (entire egg volume), the differences being even larger in terms of the yolk sphere size. The entire egg volumes differ by as much as a factor of 100, while the yolk spheres differ by as much as several hundred times.

**Table 2. Egg size variability in selected fish species (after various authors)**

| Species | Diameter [mm] | | Author |
|---|---|---|---|
| | egg | yolk sphere | |
| Family: Arridae | | | |
| *Galeichthys feliceps* (Val.) | 19.0–21.0 | – | Bertin 1958 |
| | 15.7 | – | Tilney and Hecht 1993 |
| Family: Gymnarchidae | | | |
| *Gymnarchus niloticus* | 10.0 | – | Nikolskij 1971 |
| | 10.0 | – | Załachowski 1997 |
| Family:Osteoglossidae | | | |
| *Scleropages* sp. | 10.0 | – | Załachowski 1997 |
| Family: Salmonidae | | | |
| *Salmo salar* L. | 5.5–6.0 | – | Bertin 1958 |
| | 5.4–6.15 | – | Thorpe et al. 1984 |
| | 5.5–7.0 | – | Bartel 1991 |
| | 5.6–6.0 | – | Barus and Oliva 1995 |

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|---|---|---|---|
| *Hucho hucho* (L.) | 4.5–6.0 | – | Goryczko 1991 |
| | 3.6–6.0 | – | Barus and Oliva 1995 |
| | 3.87–5.96 | – | Bartel et al. 1999 |
| *Salvelinus alpinus* (L.) | 3.8–5.8 | – | Wallace and Aasjord 1984 |
| | 3.0–5.8 | – | Barus and Oliva 1995 |
| *Salvelinus lepechini* (Gmelin) | 5.20–6.05 | 3.60–4.40 | Pavlov et al. 1993 |
| *Thymallus arcticus baicalensis* Dybowski | 4–4.8 | 2.8–3.5 | Soin 1963 |
| *Thymallus thymallus* (L.) | 3.0–4.0 | – | Berg et al. 1949 |
| | 3.2–4.0 | – | Bertin 1958 |
| Family: Acipenseridae | | | |
| *Huso huso* (L.) | 3.6–4.0 | **–** | Detlaf and Ginsburg 1954 |
| *Acipenser gueldenstaedtii* Brandt | 3.0–3.5 | **–** | Berg et al. 1949 |
| *Acipenser baeri* Brandt | 2.5–2.7 | **–** | Sokolov 1965 |
| | 3.1–3.9 | **–** | Gisbert et al. 2000 |
| *Acipenser stellatus* Pall. | 2.7–3.2 | – | Detlaf and Ginsburg 1954 |
| Family: Cyprinidae | | | |
| *Chondrostoma nasus* (L) | 2.2 | 1.56 | Kryzanowski 1949 |
| *Rutilus rutilus* (L.) | 2.14 | 1.1 | Kryzanowski 1949 |
| | 1.93–2.48 | – | Cerny 1977 |
| *Rhodeus sericeus* (Pall.) | 2.1 | 1.95 | Kryzanowski 1949 |
| | 1.25–3.0 | – | Mlyniec 1991 |
| | 1.3–2.6 | – | Barus and Oliva 1995 |
| *Aspius aspius* (L.) | 1.9–2.1 | 1.4 | Lange et al. 1975 |
| *Leuciscus cephalus* (L.) | 1.99 | 1.27 | Kryzanowski 1949 |
| | 2.31 | – | Cerny 1977 |
| *Tinca tinca* (L.) | 1.9 | 1.0 | Kryzanowski 1949 |
| *Cyprinus carpio* L. | 1.5–1.8 | 1.2 | Kryzanowski 1949 |
| | 1.65 | – | Penaz and in 1983 |
| *Leuciscus idus* (L.) | 1.23–1.88 | 1.17–1.43 | Kryzanowski 1949 |
| | 1.7 | – | Barus and Oliva 1995 |
| Family: Cobitidae | | | |
| *Cobitis taenia* (L.) | 1.88 | 1.2 | Kryzanowski 1949 |
| | 1.80–2.80 | | Barus and Oliva 1995 |
| Misgurnus fossilis (L.) | 1.69–1.88 | 1.70–1.30 | Kryzanowski 1949 |

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| | | | |
|---|---|---|---|
| Family: Percidae | | | |
| *Perca fluviatilis* (L.) | 1.4–2.5 | 0.91 | Kryzanowski 1953 |
| | 2.0–2.5 | – | Bertin 1958 |
| | 2.0–2.5 | – | Anisimowa and Lavrovskij 1983 |
| *Stizostedion lucioperca* (L.) | 1.3–1.4 | – | Berg et al. 1949 |
| | 1.23–1.37 | – | Filuk 1962 |
| *Gymnocephalus cernua* (L.) | 1.07–1.23 | 0.79–0.97 | Kryzanowski 1953 |
| | 0.8–1.0 | – | Bertin 1958 |
| *Percarina demidoffi maeotica* (Kuznetziv) | 0.5–0.6 | – | Berg et al. 1949 |
| | 0.70 | 0.55 | Kryzanowski 1953 |
| Family: Anguillidae | | | |
| *Anguilla anguilla* (L.) | 1.1–1.2 | 0.84–0.85 | Prochorčik 1987 |
| Family: Gadidae | | | |
| *Lota lota* (L.) | 0.96–1.14 | – | Berg et al. 1949 |
| | 1.1–1.2 | – | Kryzanowski 1953 |
| | 0.8–1.0 | – | Bertin 1958 |
| Family: Osmeridae | | | |
| *Osmerus eperlanus* (L.) | 0.9–1.11 | – | Berg et al. 1949 |
| | 0.9–1.0 | – | Kazanowa 1954, Bertin 1958 |
| | 0.95 | – | Gottwald and Nagiec 1967 |

Where do those differences come from? What is their cause? What is their biological significance? Those are questions the exhaustive and convincing answers to which have not always been possible to give.

In our opinion, the answers should be sought in general laws governing the developmental strategy of the class Pisces, the strategy having been from the beginning controlled by the need to find structures and physiological mechanisms that would enable the fish to dwell and persist under constantly changing conditions of the aquatic environment. Without such strategy, the expansion of the class and the emergence of new forms would not have been possible. To summarise, without such strategy, the evolution and the record–breaking, among vertebrates, number of taxa could not have been achieved.

When looking for the “common denominator”, mentioned in the Introduction, which would explain the great diversity of fish egg size, it was assumed that for life processes to proceed and for the energy stored in the yolk sac to be released it is necessary for oxygen to access the egg. Consequently, it was deemed necessary to focus on borders through which oxygen penetrates into the egg and to refer to a principle formulated a hundred years ago by Rubner [43]. That principle relates the amound of substances, oxygen in this case, diffusing from the ambience into an organism to the area of a bordering surface (a membrane, a layer of the

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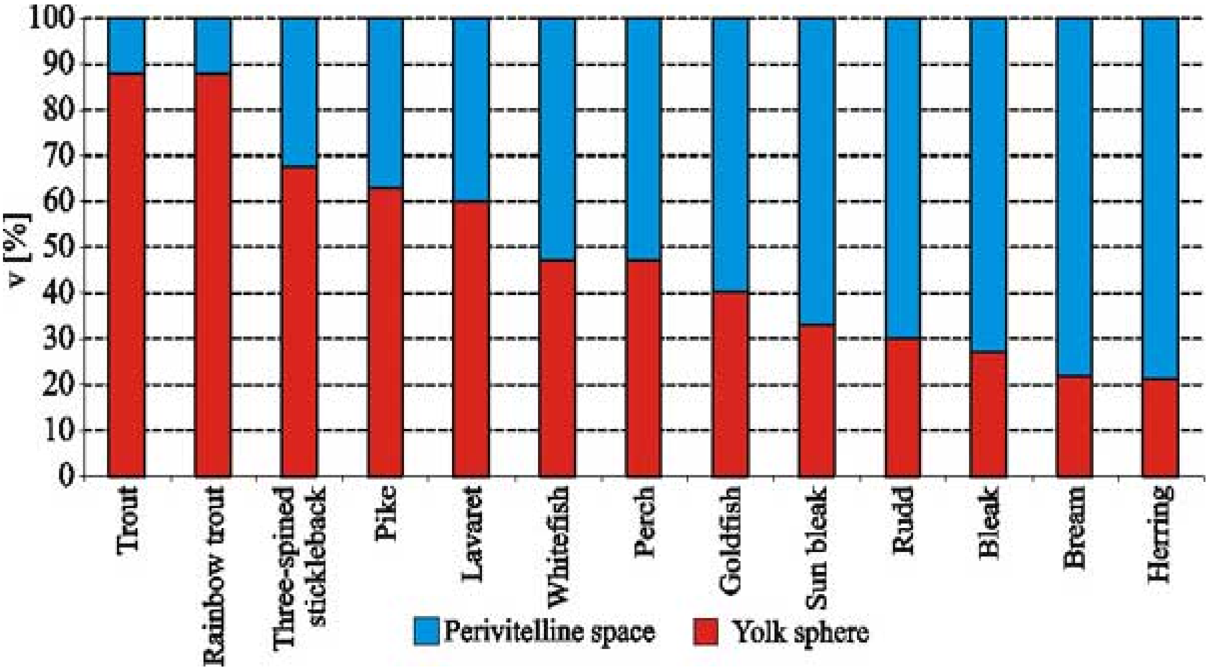
perivitelline fluide, perivitelline membrane, skin) corresponding to a unit volume of the organisms, which can be expressed with the already mentioned S/V ratio (Fig. 1).

A special explanation is necessary with respect to an interesting phenomenon presented by a **higher** relative contribution of the yolk sphere, a living part of the egg, to a large egg; for instance, the contribution is about 88% in the salmon egg [54] and decreases, with decreasing egg size, to as little as 30% (cyprinids) and less (Fig. 2).

**Fig. 2. Relative yolk sphere volume inside hydrated eggs of different species**



It seems that the relationship in question is an important element in the developmental strategy of a species. At a usually higher absolute fecundity, per unit weight, of thermophilous fish, for the reasons discussed above and concerning the S/V ratio, female gametes have been evolving towards smaller size, with a consequent reduction in the yolk sac. In the interest of a hatching individual requires that the embryo remain within the egg membranes for as short a time as possible, with a prospect of meeting the oxygen demand in a more active way after hatching [51]. The hatching larva (not only for that reason) had to be maximally advanced in its development, sufficiently motile, and relatively large, which would not have been possible with an egg having a limited relative volume of the perivitelline space (Fig. 3a). Conditions under which a pre–hatching embryo could fit the space within the membranes exist when the perivitelline space is as large as possible, because the embryo is much (even 4–5 times so) longer than the yolk sphere diameter (Fig. 3b).

This problem is avoided by embryos hatching from large eggs in which life processes are slow enough (low incubation temperature) to the extent that the newly hatched larvae seem to be born prematurely, being poorly motile, relatively small and lightweight with respect to the yolk sphere mass. They fit perfectly in the little slit of the perivitelline space, their size (length) being about twice that of the egg diameter (Fig. 4).

**Fig. 3. Bream Abramis brama (L.)**
**A - a newly-hatched larva fully prepared for independent life in the water column;**
**B - embryo before hatching**

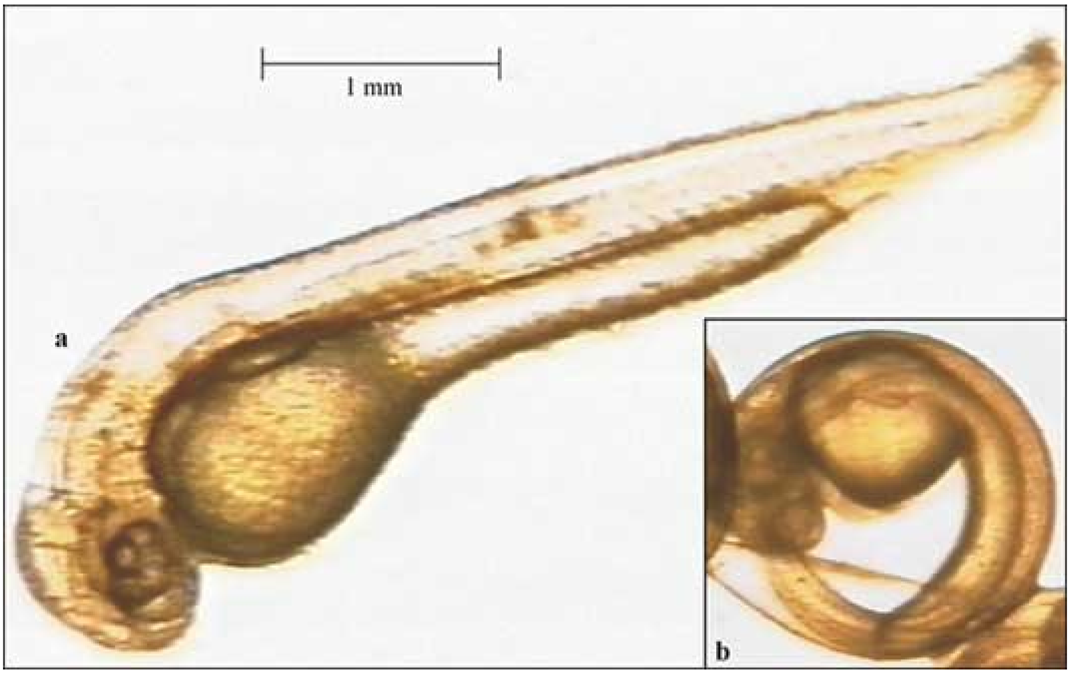


**Fig. 4. A sluggish trout (Salmo trutta L.) larva with a large yolk sac**

The size (volume) of an egg, or – more exactly – the volume of a particular "coating" of the yolk sphere in the form of the perivitelline fluid and membranes is used by some species as a device to maintain the egg's position in the water column. Thus, it indirectly serves as a buoyancy mechanism by adjusting the specific gravity of the **entire egg** to the density of the surrounding water medium and, consequently, ensures the zero buoyancy during the period of incubation.

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Finally, the biological meaning of egg size variability in most species producing medium–size and large eggs lies in that the size variations *per se* are not manifest only as interspecific differences, but are also visible as intraspecific variability observeable as differences between individuals, *e.g.*, differences in their age and body weight. The intraspecific variability is carried further to include size differentiation among eggs produced by a single female, as shown by previous research [15] and as confirmed by the present study (Fig. 5; Table 3).

**Fig. 5. Trout egg volume versus female weight (ANOVA, p<0.00)**

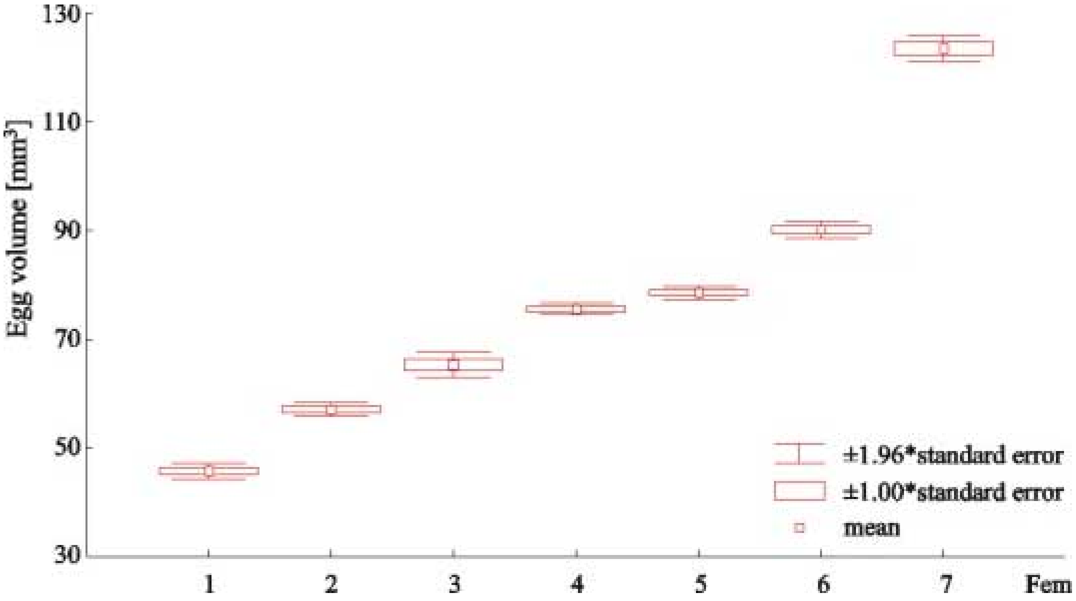

**Table 3. Size of trout (*Salmo trutta* L.) eggs obtained from different females (mean ± standard deviation)**

| Female No. | No. of eggs [n] | Weight after stripping [kg] | Total length [cm] | Mean egg diameter [mm] | Mean egg volume [$mm^3$] |
|---|---|---|---|---|---|
| 1 | 216 | 0.90 | 43 | 4.41 ± $0.36^a$ | 45.77 ± $10.89^a$ |
| 2 | 50 | 1.30 | 53 | 4.77 ± $0.13^b$ | 57.12 ± $4.75^b$ |
| 3 | 100 | 1.50 | 56 | 4.98 ± $0.30^c$ | 63.35 ± $11.44^c$ |
| 4 | 162 | 2.1 | 65 | 5.24 ± $0.16^d$ | 75.55 ± $6.76^d$ |
| 5 | 100 | 1.4 | 54 | 5.31 ± $0.14^d$ | 78.50 ± $6.06^d$ |
| 6 | 50 | 2.1 | 65 | 5.55 ± $0.12^e$ | 90.04 ± $5.91^e$ |
| 7 | 100 | 3.9 | 79 | 6.17 ± $0.20^f$ | 123.42 ± $12.13^f$ |

**Mean denoted with identical indices are not significantly different (Tukey's test; p>0.05).**

This latter constatation allows to conclude that the egg size variability is a specific mechanism ensuring perisistence of a population during short–term environmental changes disadvantageous for incubation. This conclusion is supported by, demonstrated earlier [14], cut–down of the duration (expressed in thermal units) of development of small eggs and extension of that period in larger eggs whose S/V ratio is less advantageous than that of the

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small eggs [15]. Even when some of the hatching embryos (larvae) perish, at least others will survive provided they hatch before or after the period of instantaneous hazard.

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