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DURATION OF EMBRYONIC DEVELOPMENT AND S/V (SURFACE/VOLUME) COEFFICIENT IN FISH EGGS

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ABSTRACT. S/V (surface/volume) coefficient was used to explain the nature of the relationship between length of embryonic development and egg size in fish. It was found that coefficient values were directly related to the rate of energetic processes in the tissues which determined the rate of embryogenesis and duration of embryonic development. From among a number of the examined fish species the smallest viz. the least favourable S/V coefficient (mean value 1.16) was observed in *Salmo trutta* L., a little better (mean value 2.19) - in *Esox lucius* L., and the most favourable and the biggest (mean 4.8) - in *Leucaspius delineatus* L. These differences result in different temperatures selected by particular fish species for their reproduction: low in case of big eggs and respectively higher in case of small eggs.

Key words: FISH, EMBRYONIC DEVELOPMENT, DEVELOPMENT RATE, EGG SIZE, S/V COEFFICIENT

INTRODUCTION

From among many factors which affect the rate of embryonic development in fish, i.e. also duration of embryogenesis, such as temperature (Reibisch 1902, Gray 1928, Embody 1934, Nikiforov and Trusov 1950, Hayes et al. 1953, Kowalska 1959, Lecyk 1965, Łuczyński and Kirklewska 1984, Herzig and Winkler 1968, Kujawa et al. 1997), water pH (Krishna 1953, Bilko 1977), or O_2 content (Murisier 1918, Garside 1959, Winnicki 1967, Chodżer 1974), the least attention has so far been paid to relations between duration of embryonic development and egg size (Kaj and Lewicka 1962, Bonisławska et al. 2000). Studies presented in this paper had to elucidate if these relations did exist, if yes - how were they expressed, what was their biological meaning, and - finally - to what an extent (if any) did they conform to an almost 100 years old idea of Rubner (1902, 1908) that the rate of physiological processes taking place in closed systems of definite living individuals depended on a coefficient which illustrated the ratio between organism surface (surface directly contacting the environment) and its volume, this ratio being expressed as S/V coefficient.

Fish eggs seem to be an ideal material for such studies: they are usually covered with transparent envelopes enabling direct observation of the insides and continuous registration of structural changes in course of embryogenesis.

Moreover, eggs obtained from females of the same species are fairly diversified as regards their size (Sklowier 1930, Kaj and Lewicka 1962, Steffens 1963, Liebiedev and Čžen Čžen-Diun 1963, Lugovaja 1963, Galkina 1969, Savostianova and Nikandrov 1976, Wallace and Aasjord 1984, Springate and Bromage 1985, Kazakov and Liašenko 1987, Pavlov et al. 1993, Bartel and Parlińska 1995, Dlaboga et al. 1998, Papała et al. 1998). Hence, when environmental factors remain identical, it is easy in laboratory conditions to precisely measure duration of embryonic development (from egg activation to larvae hatching) and express it in thermal units: degree-days (D°), or better - degree-hours (H°).

Differences in egg size are even greater between particular species (Kryžanowski 1949, Berg 1949, Rass 1953, Bertin 1958, Zotin 1961, Ginsburg 1968, Bagenal 1971, Pauly and Pullin 1988, Araujo-Lima 1994, Baruš and Oliva 1995), and this enables comparative studies.

It would be very interesting to reveal possible regularities in this respect and to check their expression in different species in relation to optimal reproduction temperatures selected by these species. Precise explanation and description of these phenomena would help our understanding the biological sense of considerable differences observed in egg size, and of the effects of the latter on the rate and course of embryogenesis.

It seems that some of the expected results would be of applied value for hatchery practices, as practical procedures tend not to pay enough attention to different egg size, while our earlier studies (Bonisławska et al. 1999) showed that this affects the results of egg incubation.

MATERIAL AND METHODS

Studies were carried out in 1997-2000, in autumn on sea trout (*Salmo trutta* L), early spring on pike (*Esox lucius* L.), and summer on white aspe (*Leucaspius delineatus* L.).

Fish eggs were artificially stripped, fertilised (using „dry method"), hydrated (water absorption and egg swelling) and distributed over plastic or glass incubation minichambers. These were supplied with running water which had been first filtered and aerated.

Incubation was carried out either in the laboratory of the Department of Fish Anatomy and Embryology in Szczecin (filtered water in a recirculation system - sea trout and pike), or in a field laboratory located in the village Izdebno, in which incubators (white aspe) were supplied with water pumped from the spawning grounds of this fish in a nearby lake.

Swollen eggs were measured along vertical and horizontal plane (lateral view in the methods used earlier) (Winnicki and Korzelecka 1997, Korzelecka and Winnicki 1998, Korzelecka et al. 1998), and a few average values obtained this way were used to calculate the mean egg diameter. This was needed to calculate egg surface ($S=4\pi r^2$) and volume ($V=4/3\pi r^3$). Results of these calculations were then taken advantage of to determine S/V coefficient. A sample consisted of 100 eggs.

Measurements were taken in egg sample from one female and in the mixed samples of eggs from a few females of the same species; duration of incubation (length of embryonic development) was calculated for all these samples and variants (eggs from one female, mixed samples, and eggs of different species) and expressed in thermal units - D^0 or H^{0*}.

RESULTS AND DISCUSSION

Observations and calculations made in course of the studies revealed some phenomena and processes which add to our knowledge on the relationship between rate of changes taking place during embryogenesis and egg size (as well as size of egg cells).

Considerable differences were observed as to the egg size not only between particular species, but also within the same species and even particular individuals (Fig. 1 and 2). Comparison of these data with the duration of embryonic development measured in thermal units point to considerable degree of inter-relation between egg size and length of embryogenesis (Fig. 3).

This phenomenon is in fact quite simple and logical, although its mechanism has not been fully explained as yet.

Having this in mind it was decided to take a closer view at the mechanisms determining these differences and their effects on embryogenesis. To achieve this we decided to calculate (check) how the discussed differences related to the S/V

* D^0 - product of days and mean daily temperature
H^0 - product of hours and mean hourly temperature

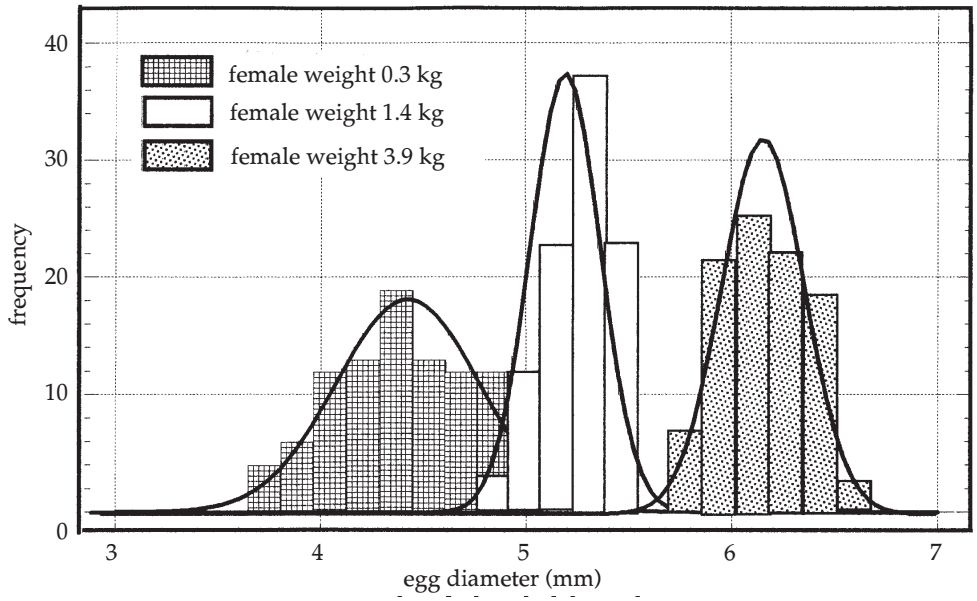

Fig. 1. Distribution of egg sizes in three females of sea trout (*Salmo trutta* L.)

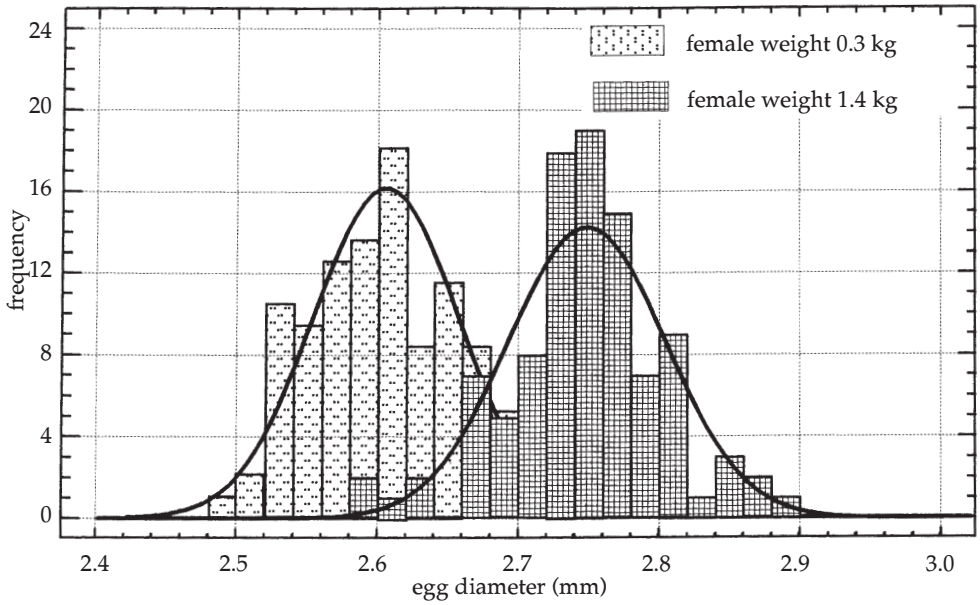

Fig. 2. Distribution of egg sizes in two females of pike (*Esox lucius* L.)

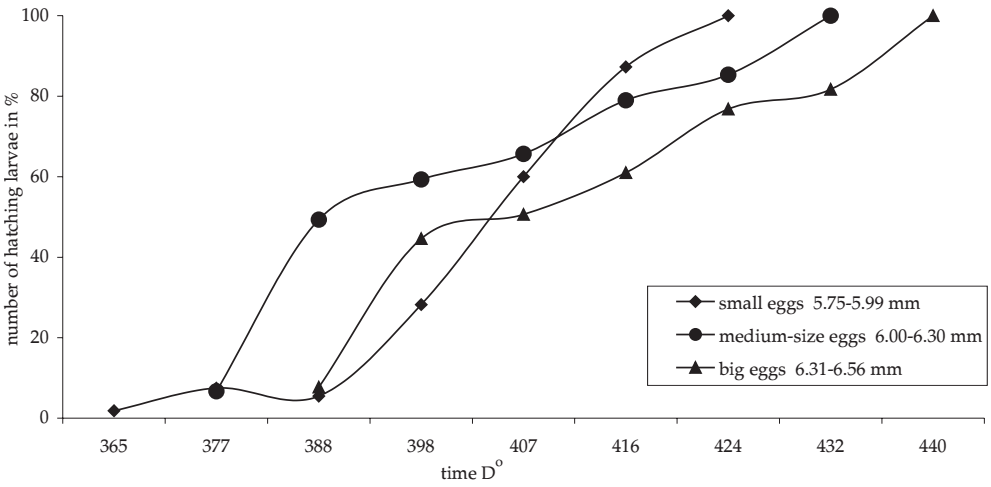

Fig. 3. Relationship between embryonic development and size of eggs of the same sea trout (*Salmo trutta* L.) female weighing 3.9 kg

coefficient which reflects the proportion between a unit of living structure (egg, yolk sphere) and volume of the observed object expressed in cubic units of the same metric value.

Proper calculations revealed (Fig. 4) that value of the S/V coefficient decreased as egg diameter increased and *vice versa* - they increased when egg size decreased.

Comparative analysis of these calculations revealed with no doubt that in discussing the development and rate of processes and internal transformations within a developing fish organism (egg) it was necessary to take into account the coefficient proposed by Rubner (1902, 1908). This coefficient explains effectiveness of the exchange of substances needed to maintain life processes between a living organism (embryo) and its surroundings. In this respect our study focused on gas exchange rate, which is directly related to the surface area through which the gas can diffuse

It is clear that when one takes into account „global" requirements for e.g. O_2 by a basic unit (cell, tissue) and assumes that they are similar in a small as well as big aggregate, it is easy to conclude that cells (tissues) in big aggregates (living objects) will be considerably handicapped compared to small aggregates. This is because in small aggregates S/V coefficient is much higher viz. also more favourable.

If this is so, then large and small living units (embryos in our case) staying (living) in the same temperature will be supplied with e.g. O_2 in a different rate per volume

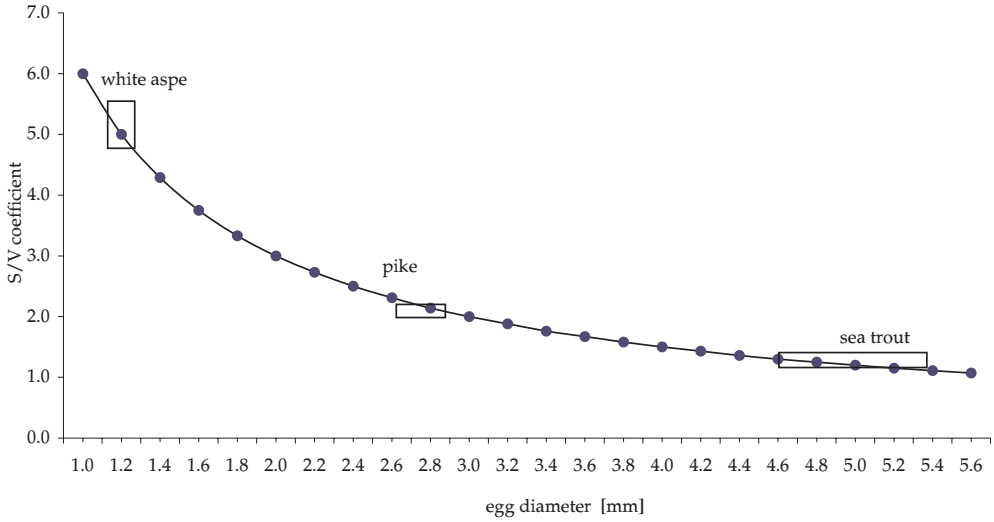

Fig. 4. Values of S/V coefficient depending on the size of eggs obtained from selected specimens of the analysed fish species

unit. This will result in a slow down of the energetic processes, thus - also of the rate of development.

Bearing this in mind it is easy to conclude that only the possibility of ensuring embryogenesis in lower temperature would be a way of compensating or „giving the same chances" to the embryos developing in big eggs; this is because temperature is the environmental factor which directly and precisely affects the rate of metabolism in a living organism, slowing it down in low values and speeding up in high (some authors even call the temperature an „imperative" factor).

This leads us directly into another conclusion on inter-relationships between egg size and the season selected by a species for its reproduction (egg incubation) so as to deal with a possibly optimal water temperature.

This conclusion is confirmed by the fact that in natural conditions big eggs are usually spawned at low water temperatures (salmonids), while small ones - in warm water.

A fish *Galeichthys feliceps* Val., however, does not conform to this pattern (Tilney and Hecht 1993, Załachowski 1997). It lays exceptionally big eggs and incubates them in its mouth, but this fact should be regarded rather as an „incident" that confirms the rule; the product of S/V coefficient and the number of thermal units in which

embryonic development of this fish takes place reveals that the result is quite comparable, within the range obtained for eggs of different sizes.

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STRESZCZENIE

CZAS TRWANIA ROZWOJU ZARODKOWEGO A WSPÓŁCZYNNIK S/V (POWIERZCHNIA:OBJĘTOŚĆ) JAJA U RYB

Badano zależność tempa embriogenezy i czasu trwania rozwoju zarodkowego u ryb – troć (*Salmo trutta* L.), szczupak (*Esox lucius* L.), słonecznica (*Leucaspius delineatus* L.) od wymiarów jaj tych ryb.

Taka zależność jest oczywista co stwierdzono już wcześniej, a potwierdzone zostało w niniejszych badaniach. Założono, że właściwą i w znacznym stopniu wyczerpującą odpowiedź na pytanie o mechanizmy zaobserwowanych współzależności może dać wprowadzenie do analiz współczynnika S/V (powierzchnia:objętość) tłumaczącego sprawność procesów wymiany gazowej między środowiskiem zewnętrznym i wewnętrznym żywego ustroju (w tym przypadku jaj ryb).

Współczynnik S/V jest w przypadku jaj wielce zróżnicowany i najmniejszy (oczywiście najmniej korzystny) u jaj dużych rozmiarów (troć) i kilkakroć większy (a zatem i korzystniejszy) u jaj małych (słonecznica).

Wartości współczynnika mają bezpośrednie przełożenie na szybkość procesów przemiany materii w tkankach warunkujących tempo embriogenezy i czas trwania rozwoju zarodkowego.

Oczywistą konsekwencją tego będzie wybór przez gatunek na porę tarła niskich temperatur otoczenia (jaja duże) i odpowiednio wyższych w przypadku jaj mniejszych rozmiarów.

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