

## **Utilization of the yolk in rainbow trout alevins (*Salmo gairdneri* Richardson) : effect of egg size**

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**Summary.** Changes in body weight and yolk weight were studied in rainbow trout alevins fasted at 7 °C and originating from either big eggs or small eggs of the same female.

A model has been proposed to describe the changes in body and yolk weight which occurred between hatching and the end of yolk resorption. Maximal body weight was reached later and was higher in alevins from big eggs than from small eggs. The yolk was resorbed more quickly by alevins from small eggs.

Egg size did not seem to influence yolk water content, initial specific growth rate (8.5 %) or yolk conversion efficiency (70 %).

Body water content increased through the fasting period up to a limit value of 91.4 %, which was the same for both classes of alevins. This level was reached more quickly by alevins from small eggs.

These results suggest that original egg size had both a quantitative and qualitative effect on the early development of alevins.

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### **Introduction.**

Salmonid alevins cannot ingest exogenous food when they hatch. Apart from nutritive substances dissolved in the water and absorbed through the gills and skin, yolk stores are the only source of food before the esophagus opens and the first meal is taken.

The amount of yolk available at hatching depends on original egg size and also on incubation conditions, particularly temperature (Gray, 1928b ; Heming, 1982) and oxygen supply (Hamor and Garside, 1977).

According to Privol'nev *et al.* (1970a), original egg size affects only the amount of yolk present at hatching but not the size of the alevins or their further growth. On the contrary, other authors report that alevins from big eggs have the following advantages over those from small eggs : lower embryonic loss (Gall, 1974 ; Pitman, 1979) bigger size at hatching (Gray, 1928a ; Fowler, 1972) and at the first meal (Kazakov, 1981), larger size retained after several weeks of feeding (Fowler, 1972 ; Bilton, 1971), better survival when put into a natural environment or fasted (Bagenal, 1969). Since these aforementioned studies compared eggs from different females, the differences could be due not only to original egg size but to other maternal effects (age, spawn, genotype).

The aim of the present work was to determine the mode of early development and of the utilization of the yolk in rainbow trout alevins from different-sized eggs of the same female.

## Material and methods.

Two successive experiments were carried out on a fish farm at Lees-Athas (Pyrénées-Atlantiques, France) in water at a constant temperature of 7 °C. In each experiment, a female rainbow trout (4 years old) presenting ova of heterogeneous size was crossed with two males. Fertilization was carried out by the wet method of Petit *et al.* (1973) using the « 532 » diluent of Billard (1977).

The eggs of each family were sorted at the eyed-stage. Only those having a diameter of less than 3.7 mm (« small » eggs) or more than 4.2 mm (« big » eggs) were used ; the two groups were kept separately. 895 eggs were kept from female 1 (eviscerated body weight = 1,965 g) and 2 656 eggs from female 2 (eviscerated body weight = 4,250 g). In experiment 2, every crossing was replicate (table 1).

From the end of hatching to the free-swimming stage (69 to 71 days after fertilization, depending on the female), a sample of 10 animals was taken from each group every 7 days, then every 3 days from the free-swimming stage to the 50 %-mortality stage (at which 50 % of the hatched alevins were dead). The fish were fixed and conserved in 10 % formol until analysis. After a minimal interval of one month, the fixed alevins were dissected to separate the yolk from the body. Body and yolk weights were determined in each sample (mean of 10 regrouped animals) in the wet state and in the dry state (after 24 h at 104 °C) to  $\pm 0.1$  mg.

The formula used to describe change in dry body weight (x) (\*) as a function of time (t) was :

$$x = 4 x_m Z (1-Z)$$

$$\text{with } Z = \frac{1}{1 + e^{\lambda(tm-t)}}$$

The three parameters  $x_m$  (maximal x value in mg),  $t_m$  (time needed for x to reach  $x_m$ , expressed in days after fertilization) and  $\lambda$  (coefficient of growth) were estimated by the general method for calculating non-linear regressions (partial derivatives) with a PSI.80 microcomputer. This formula was chosen from the trend of curve reported by Gray (1928a).

Change in dry yolk weight (y) as a function of time was calculated using the formula :

$$y = 4 x_m (\alpha - Z)^2$$

This function introduced only one extra parameter,  $\alpha$  (Z value at which the function as well as its derivative was 0), which could be estimated using the  $x_m$ ,

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(\*) The function x (t) used was a solution of the differential equation (Lefort, 1967) :  $x' = \varepsilon x - \int_0^t x(t) dt$ , where  $\varepsilon$  was the initial specific growth rate ( $x'/x$ ). The coefficient  $\varepsilon$  differed little from  $\lambda$  because :  $\varepsilon = \lambda \frac{e^{\lambda t_m} - 1}{e^{\lambda t_m} + 1}$  and  $e^{\lambda t_m}$  was higher than 500 in the present case. The second term of this equation could be interpreted as a decrease in growth due to metabolites accumulated by the organism from fertilization to time t. The coefficient c was inversely proportional to  $x_m$  ( $c = \lambda^2/2x_m$ ).

$t_m$  and  $\lambda$  values found for  $x$  and the experimental values of  $y$  from samples containing at least 50 % of sac fry. The plot of this function gave a curve tangent to the  $x$ -axis (time) when yolk weight was zero. This function was used only in the interval  $0 < t < \theta$  ( $\theta$  = time needed for complete yolk resorption). It was chosen from the trend of  $y(t)$  curves reported by Lasker (1962) for sardine, Johns *et al.* (1981) for flounder and Heming (1982) for salmon and is one of the solutions of the differential equation (Gray, 1928a)

$$-y' = x' + kx$$

where the coefficient  $k$  (mg of dry yolk weight consumed per mg of dry body weight per day) was the proportion of consumption unrelated to growth and corresponded to :

$$k = \lambda (2\alpha - 1)$$

The time needed for complete yolk resorption was computed by the formula :

$$\theta = t_m + \frac{1}{\lambda} \log \frac{1-\alpha}{\alpha}$$

We used the conversion rate of yolk into body weight given by Blaxter (1969) :

$$\frac{x_m}{Y_0 - Y_{(t_m)}} \text{ which is little different from } \frac{1}{4\alpha - 1}$$

Statistical analysis was carried out using the  $t$ -test and analysis of variance (Snedecor and Cochran, 1971) to compare alevins from small and big eggs. Data on hatching and 50 %-mortality stage were compared by a two-way (male and egg size) analysis of variance. Hydration of the body and yolk were not linearly correlated with time. Body and yolk water contents were compared by a two-way variance analysis, with time and egg size as fixed effects.

## Results.

1) *Hatching and survival (table 1).* — The duration of incubation (number of days between fertilization and onset of hatching) varied significantly ( $P < 0.01$ ) between experiments and between males but not between egg classes. The duration of hatching (number of days between the onset and end of hatching) was between 3 and 4.5 days for all the groups. Hatching finished 49 and 48 days after fertilization in experiments 1 and 2, respectively.

The percentage of hatched eggs differed ( $P < 0.001$ ) between experiment 1 (95 %) and experiment 2 (85 %). This percentage was higher ( $P < 0.05$ ) in big-egg groups (mean : 94 %) than in small-egg groups (mean : 88 %). The 50 %-mortality stage was reached 11 to 12 days earlier by alevins from small eggs (table 3). A male effect ( $P < 0.05$ ) was also observed at this stage.

TABLE 1  
Group characteristics.

Experiment	Parental origin	Egg diameter (mm)	Number of eyed-eggs	Hatching		
				Duration of incubation (days)	Duration of hatching (days)	% of hatched eyed-eggs
I	♀ 1 ♂ 1	< 3.7	202	44	4.5	87
		> 4.2	374	45.5	3	97
	♀ 1 ♂ 2	< 3.7	106	45	4	91
		> 4.2	213	46	3	99
II	♀ 2 ♂ 3	< 3.7	205	45	3	80
		< 3.7	205	45	3	83
		> 4.2	434	44.5	3	87
	♀ 1 ♂ 4	> 4.2	434	44.5	3.5	83
		< 3.7	299	44	4	83
		< 3.7	299	44	4	83
		> 4.2	390	43.5	3.5	89
		> 4.2	390	44	3.5	91
		> 4.2	390	44	3.5	91

2) *Change in body weight.* — To determine changes in body weight, the data of the two males were pooled for each intrafemale egg class (non-significant male effect).

Whatever the original egg size, dry body weight of alevins increased after hatching, reaching a maximum, then decreased before complete yolk resorption (fig. 1).

The growth coefficient ( $\lambda$ ) between hatching and the time at which all the alevins had resorbed the yolk was estimated by using the model adjusted to the data (with a mean relative error of less than 10 %, table 2). This growth

TABLE 2  
Parameters of variations in dry body weight.

Parameters					
Origin	Number of data	Curve adjustment MRE (*)	Growth coefficient (%/day) $\lambda \pm$ SD	Maximal dry weight $x_m \pm$ SD	Number of days needed to reach $x_m : t_m \pm$ SD
♀ 1 small eggs	16	4.73	$8.9 \pm 0.8$	$9.09 \pm 0.18$	$74.02 \pm 0.03$
	19	3.39	$8.2 \pm 0.3$	$14.60 \pm 0.16$	$77.01 \pm 0.01$
♀ 2 small eggs	33	8.46	$8.7 \pm 0.9$	$7.71 \pm 0.18$	$72.48 \pm 0.03$
	35	4.73	$8.4 \pm 0.4$	$15.14 \pm 0.16$	$75.50 \pm 0.02$

$$(*) \text{ MRE} = \text{mean relative error (\%)} = \frac{\sum \left[ \frac{x - X}{X} \cdot 100 \right]}{n}; X = \text{theoretical dry body weight.}$$

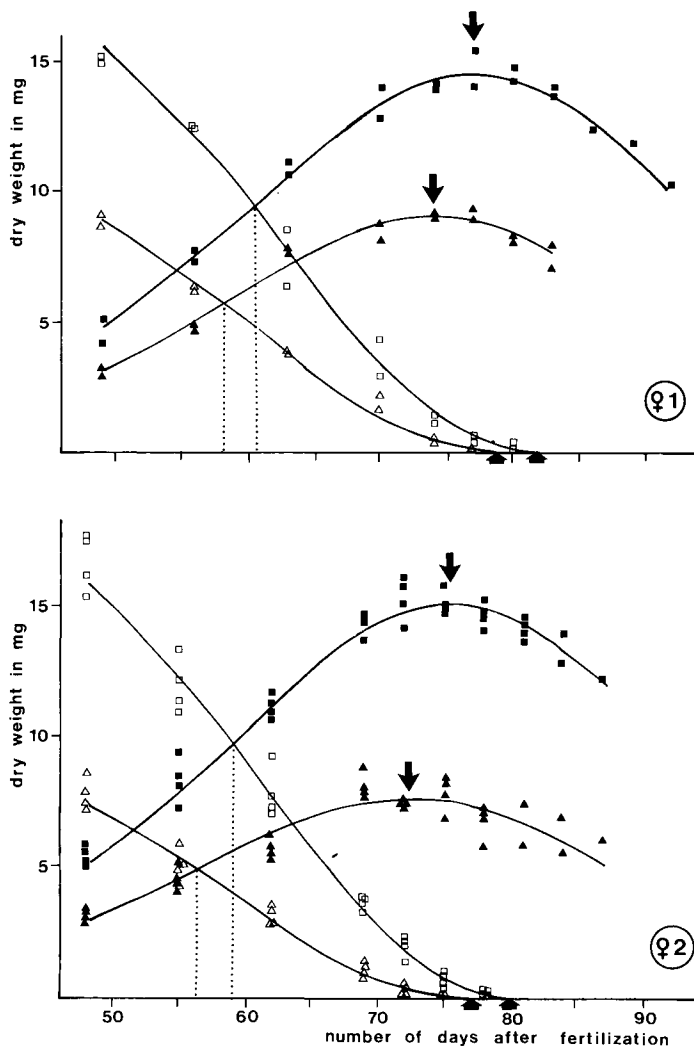


FIG. 1. — Variations in dry weight of body and yolk of small and big-egg alevins.

- Mean body weight of yolked alevins : ■ big-egg alevins ; ▲ small-egg alevins ; ↓ calculated maximal weight.
- Mean yolk weight of alevins (only groups utilized for calculating the theoretical curve) : □ big-egg alevins ; △ small-egg alevins ; ◆ full resorption of the calculated yolk.

coefficient was higher in small-egg alevins than in big-egg ones but no significant difference was seen between the two classes ; its mean was 8.5 % (table 2). This model enabled us to show that maximal weight ( $x_m$ ) depended on egg size and was reached quicker by small-egg than big-egg alevins (estimated deviation of 3 days).

Between the stages of maximal weight and 50 % mortality small-egg alevins of female 2 lost 31 % of dry body weight and big-egg alevins 35 %. In female 1, big-egg alevins lost 43 % of this weight (tables 2, 3).

3) *Body water content* (fig. 2). — The body water content of both classes of alevins fixed in 10 % formol increased significantly from hatching to the 50 %-mortality stage.

At the same number of days after hatching, the small-egg alevins were more hydrated ( $P < 0.001$ ) than big-egg animals. However at hatching, no significant difference was seen between the two classes. At the 50 %-mortality stage, all the alevins had a mean body water content of 91.4 %.

4) *Yolk resorption*. — At hatching, the absolute and relative amounts of dry yolk weight stores were higher in big-egg alevins than in small-egg ones (table 3). At this stage, the small-egg alevins had a yolk mean value of 8.2 mg (72 % of alevin weight) and big-egg alevins 16.2 mg (76 % of alevin weight). By the free-swimming stage (69 to 71 days after fertilization), some fish had resorbed the yolk. The stage of complete yolk resorption in 50 % of the animals was reached earlier in small-egg alevins than in big-egg ones (fig. 3). There was a difference of 2.5 to 3 days.

Parameter  $\alpha$  (table 4) was similar between alevin classes and between females. This parameter had a mean value of 0.605, resulting in a  $k$  value of about 0.018 mg of dry yolk weight consumed per mg of dry body weight per day for every group.

The theoretical curves of yolk resorption obtained from mean estimates of  $\alpha$  (0.605) and  $\lambda$  (8.5 %) were coherent with the observed values (fig. 1). These curves showed that small-egg alevins reaching the stage where dry body weight

TABLE 3  
*Alevin characteristics at hatching and 50 % mortality stage.*

Experiment	Parental origin	Egg diameter (mm)	Hatching			50 % mortality stage	
			body weight	yolk weight	% yolk/weight alevin	Number of days after fertilization	Body weight
I	♀ 1 ♂ 1	< 3.7	2.8	9.13	77	*	*
		> 4.2	4.24	15.12	78	105	8.41
	♀ 1 ♂ 2	< 3.7	3.18	8.77	73	*	*
		> 4.2	5.07	14.95	75	107	8.23
II	♀ 2 ♂ 3	< 3.7	3.17	8.07	72	92	6.05
		> 4.2	5.20	17.01	77	103	9.85
	♀ 2 ♂ 4	< 3.7	3.27	7.57	70	93	4.65
		> 4.2	5.72	16.42	74	105	9.69

\* Data missing.

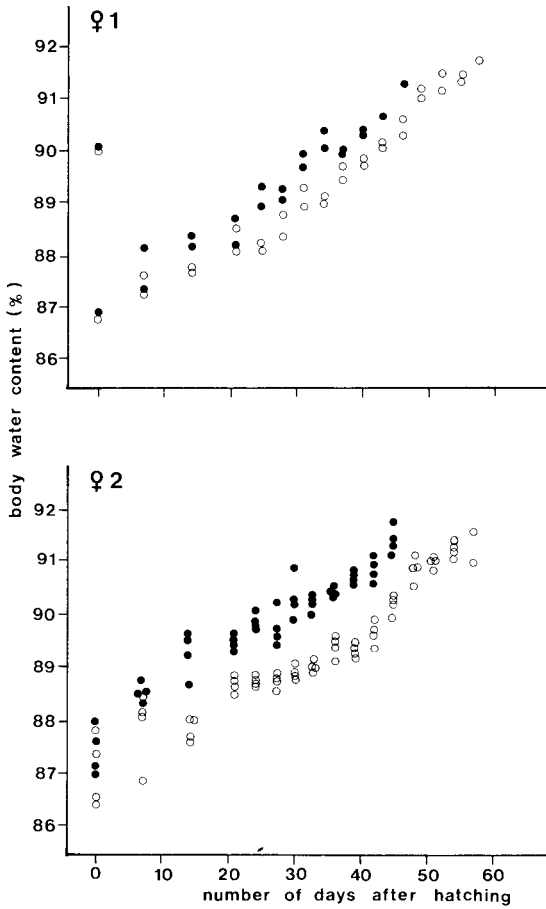


FIG. 2. — Variations in alevin body hydration between hatching and the 50 %-mortality stage.  
 ● small-egg alevins ; ○ big-egg alevins.

TABLE 4  
*Parameters of yolk resorption.*

Parameters					
Origin	Number of data	$\alpha \pm SD$	Yolk ( $y_0$ ) at fertilization (mg)	Overall conversion rate	Resorption time $\theta$ (days)
♀ 1 small-eggs	12	$0.609 \pm 0.007$	13.4	69.6	79
big eggs	14	$0.608 \pm 0.006$	21.5	69.8	82
♀ 2 small-eggs	24	$0.601 \pm 0.007$	11.1	71.2	77
big eggs	29	$0.606 \pm 0.004$	22.1	70.2	80

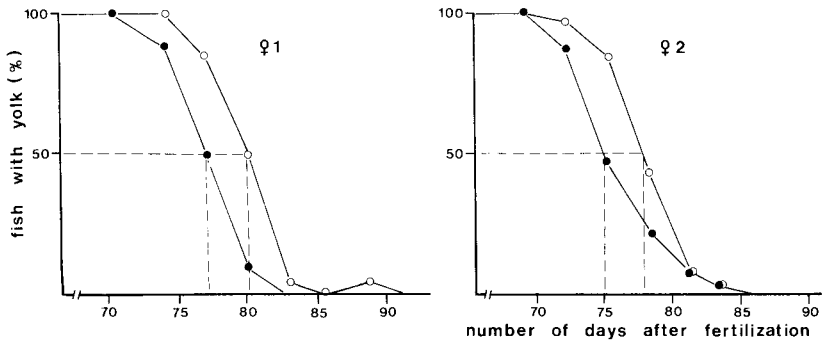


FIG. 3. — Variations in the percentage of yolked fish.

♀ 1 = 20 fish per sample ; ♀ 2 = 40 fish per sample ; ● small-egg alevins ; ○ big-egg alevins.

was equal to dry yolk weight maintained an advance of 2.5 to 2.8 days over big-egg alevins ; they also had resorbed the yolk completely 3 days before the big-egg alevins (table 4).

The extrapolation of these curves to the initial time gave an estimate of the amount of yolk at fertilization and of the overall conversion rate of the yolk (table 4). This rate was not different between alevin classes and its mean was 70 %.

5) *Yolk water content* (fig. 4). — Yolk water content increased significantly ( $P < 0.001$ ) between hatching and the free-swimming stage at which all the alevins still had yolk stores. This content increased from 49 to 53 % for female 1 and from 49 to 59 % female 2 but did not differ between egg classes.

## Discussion.

Size deviations between the egg classes studied in the present work were wide but not exceptional in salmonids. In Atlantic salmon, the volume of the biggest eggs, computed from the diameter, may reach 1.5 times the volume of the smallest eggs of the same female (Privol'nev *et al.*, 1970b). Intraspecific variation is even wider, egg volume varying between 1 and 3 (Bagenal, 1971).

The present work was carried out on fish fixed in 10 % formol. It is well known that this fixative brings about changes in body length and weight compared to that of live fish (Hay, 1982 ; Heming and Preston, 1981) ; nevertheless, it allows animals fixed under the same conditions to be compared (Heming, 1982).

The fact that yolk water content is identical at the same age in big and small eggs of the same female suggests that the chemical composition of the yolk is perhaps also identical and that the differences observed between egg classes could be attributed directly to the amount of yolk stores rather than to their nature.



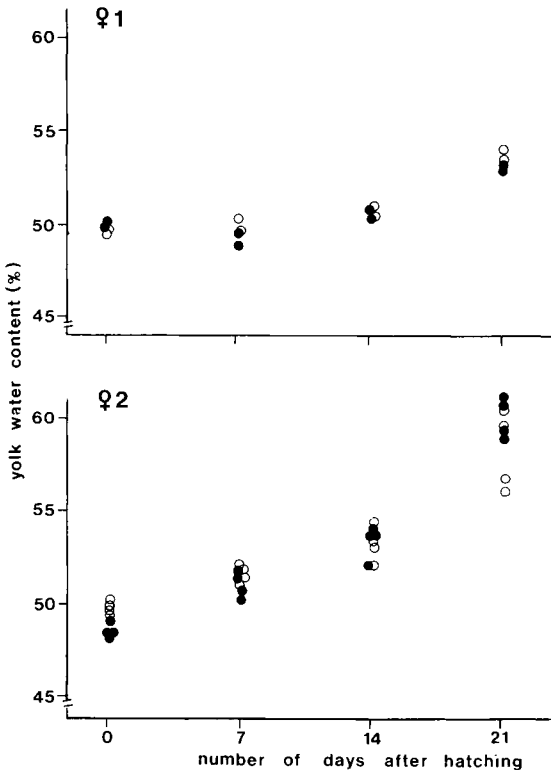


FIG. 4. — Variations in alevin yolk hydration between hatching and the free-swimming stage.  
 ○ small-egg alevins ; ○ big-egg alevins.

While Gray (1926) studying *fario* trout and Peterson and Metcalfe (1977) studying Atlantic salmon consider that body water content of alevins and of yolk remains constant during yolk sac resorption, our results indicate that these contents increase slightly but significantly with time. A variation in yolk hydration does not seem to have been reported up to now. On the other hand, an increase in body hydration identical to that we observed (+ 4 %) between hatching and the 50 %-mortality stage was reported by Ehrlich (1974a, b) in alevins of sardine and herring.

In the model proposed by Gray (1928a), the time when maximal weight is reached coincides with the same time as the end of yolk resorption. According to our results, there is an interval of several days between these two times. This difference has been the object of controversy (see Heming, 1982), but it appears to be a general occurrence because it has been reported in herring (initial dry yolk weight : 0.3 mg) by Blaxter (1969) and in chinook salmon (initial dry yolk weight : > 150 mg) by Heming (1982).

The present study shows clearly that the body weight of big-egg alevins was higher and the amount of yolk (expressed in absolute terms and in percentage of

body weight) greater than in small-egg alevins. These data contradict the conclusions of Privol'nev *et al.* (1970a) and Kazakov (1981) in Atlantic salmon, but confirm those of Blaxter and Hempel (1966) in herring.

Apart from evident differences in size scale, there are more subtle differences in chronological development between the alevin classes. Body weight began to decrease earlier and yolk was exhausted more rapidly in small-egg alevins, while the hatching date was not affected by original egg size. Blaxter and Hempel (1963) reported more rapid resorption in small-egg alevins when they compared the eggs of different populations, but they did not show intrafemale differences.

The model proposed in the present work gives a satisfactory approximation of variations in body and yolk weight, at least for the period between hatching to the end of yolk resorption. After that, body weight values may tend to be underestimated. This model shows that the dissimilarities observed between alevin classes can be attributed to different rates of body growth (dissimilar values of parameters  $x_m$  and  $t_m$ ) and not to a difference in the rate of yolk utilization (same value of parameter  $k$  : 1.8 %).

In our experimental conditions (7 °C), the theoretical value for the overall conversion rate of yolk, from fertilization to the time maximal body weight was observed (Blaxter, 1969), was about 70 % for both alevin classes ; this value is close to those of Heming (1982) in chinook salmon (69 % at 6 °C) and 65 % at 8 °C), but it must be confirmed by measuring the true initial amount of yolk.

Death by starvation did not appear to be related either to a minimal critical weight or to a constant relative decrease in body weight in relation to maximal weight. Weight loss in big-egg alevins at the 50 %-mortality stage was slightly higher than that of small-egg alevins. Body water content (91.4 %) at the 50 %-mortality stage was identical in all the groups studied which otherwise showed different survival times according to egg size and genetic origin. The small-egg alevins reached this critical value sooner.

In conclusion, alevins appear to be affected quantitatively (body weight) as well as qualitatively (water content) by the amount of yolk available initially.

*Reçu en novembre 1983.*

*Accepté en mars 1984.*

*Acknowledgements.* — We wish to thank Mr. and Mrs. Cazenave for care and sampling of the alevins, M. S. Kaushik for adapting the non-linear adjustment program, Messrs, J. M. Blanc and B. Fauconneau for critical reading of the paper and Mrs. A. Daifuku for its English translation.

**Résumé.** *Utilisation du vitellus chez l'alevin de truite arc-en-ciel (Salmo gairdneri Richardson) : effet de la taille de l'œuf.*

Les variations du poids du corps et du poids du vitellus ont été étudiées chez des alevins de truite arc-en-ciel issus soit de gros œufs, soit de petits œufs provenant de la même femelle et maintenus à jeûn à 7 °C.

Un modèle est proposé pour décrire ces variations entre l'éclosion et la fin de la résorption du vitellus. Le poids corporel maximum est atteint plus tardivement et est plus

élevé chez les alevins issus de gros œufs que chez ceux issus de petits œufs. Chez ces derniers le vitellus est épuisé plus rapidement.

La teneur en eau du vitellus, le taux de croissance spécifique initial (8,5 %) et le taux global de conversion du vitellus (70 %) ne semblent pas influencés par la taille de l'œuf.

La teneur en eau du corps augmente au cours du jeûne jusqu'à une valeur limite de 91,4 % commune aux deux classes d'alevins. Cette valeur est atteinte plus rapidement chez les alevins issus de petits œufs.

Ces résultats suggèrent que la taille de l'œuf d'origine a une influence quantitative mais aussi qualitative sur le développement de l'alevin.

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