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Growth of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) related to egg size and temperature

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Abstract

Time from fertilization to eyed ova, hatching, and complete yolk absorption was studied in relation to egg size (44.7, 68.6, and 100.7 mg) and temperature (5, 10, and 15 °C). The temperature 15 °C was first used from the eyed ova stage because newly fertilized eggs could not survive this temperature. After first feeding (at complete yolk absorption) the growth of the fish was followed 260 days at 5 °C, 175 days at 10 °C, and 130 days at 15 °C. The time it took to eyed ova, hatching, and complete yolk absorption was independent of egg size. The weight and energy content at hatching increased with increasing temperature, whereas the weight and energy content at complete yolk absorption was highest at 10 °C. There were no significant differences in growth between fish hatched from eggs of different sizes.

Keywords: growth, rainbow trout, egg size, temperature.

Introduction

Dahl (1919) showed that large eggs produce larger fry than do small eggs. This finding is generally accepted. Further Dahl said: 'Fish born in possession of a small amount of food-matter grow, under otherwise similar conditions, practically during the whole of their life, much slower, on the average, than fish born with a large amount of matter.' This statement is of course more difficult to prove because Dahl uses expressions as 'whole of their life' and 'much slower'. Some authors find that fish hatched from bigger eggs show a higher rate of growth, e.g. Wallace & Aasjord (1984) for Arctic charr, *Salvelinus alpinus* (Linné, 1758). They followed the fish for 138 days post hatch. Other authors find that fish from bigger eggs are bigger but they do not have a higher growth rate than fish from smaller eggs, e.g. Escaffre & Bergot (1984) which followed the growth of rainbow trout for 58 days post hatch. Other authors find that the relationship between egg size and size of fry is lost early. For rainbow trout Springate & Bromage (1985) found that four weeks after first feeding there was no relationship between egg size and fry weight.

In these studies it can be difficult to see if a fish is bigger only due to a bigger start weight or if the bigger fish also has a higher rate of growth. It is therefore necessary to include a parameter which is independent of temperature and fish size (within a certain specified group) but which might be dependent of egg size.

Rasmussen & From (1991) estimated the values of the different parameters in a growth model for rainbow trout. In this model enters a parameter (named h_1) which is an expression of the feed intake independent of temperature and fish size. If this parameter is calculated for fish originating from different egg sizes it can be tested if the fish eat different amounts of feed. According to Rasmussen & From (1991) the amount of feed eaten can be described as:

$$dR/dt = fh(T)w_t^m ,$$

where

dR/dt = ration per day, feeding rate
$h(T)$ = coefficient of anabolism, temperature dependent
T = temperature (°C)
m = exponent of anabolism
f = feeding level (can vary from 0 to 1)
t = time (day).

The feeding level is defined as the fraction eaten of the maximum quantity which can be eaten ($0 \leq f \leq 1$) at a given temperature. The feeding level for a starving fish is 0, and for a fish eating the maximum ration $f = 1$. There is general agreement about the assumption that the feeding rate increases with increasing temperature up to a maximum point beyond which the feeding rate decreases. If, only temperatures below the temperature for maximum feeding rate are considered, $h(T)$ can be described as:

$$h(T) = h_1 \cdot \exp(h_2 \cdot T),$$

where h_1 and h_2 are constants.

In this way we have:

$$dR/dt = fh_1 \cdot \exp(h_2 \cdot T)w_t^m \qquad (1)$$

If we conduct feeding experiments with $f = 1$, i.e. maximum feeding without waste of feed, and insert the values for h_2 and m estimated by Rasmussen & From (1991) and for w_t insert, w_t = the mean of the start and final weight in the experiment, h_1 can be calculated.

The present study was carried out to compare progeny from different egg sizes at different developmental stages, and to see if there are differences in relative feed intake and growth of the fish related to egg size.

Material and methods

Bregnballe (1967) showed that the size of fish eggs is related mostly to the age and not the size of the broodstock fish, in such a way that age of fish and size of eggs is positively correlated. Therefore, eggs were taken from three age groups of rainbow trout, 2 (1.5 kg), 3 (2-5 kg), and 4 (6-7 kg) years old. In advance we could not be sure of finding eggs with an adequate uniformity in weight (±5%), so the procedure was as follows: First, ten females from the smallest size group had their eggs mixed.

From this batch of eggs 600 specimen were blotted in a moist cloth, and weighed individually in grammes with four decimals. After this, the weight of the eggs was examined, and if it turned out that the variation in the weights was more than ±5% all the eggs were discarded, and ten new females were stripped. When a batch with enough uniformity was found, the 600 weighed eggs from this batch were discarded, and the rest of the eggs of the batch were fertilized by a mixture of milt from 22 three years old males of about 1.5 kg. The milt was added to the eggs and mixed by hand. The eggs were now placed in one hatching through at 5.0 °C (±0.2 °C) and two hatching throughs at 10.0 °C (±0.2 °C). The procedure was repeated for the two other size groups of brood stock fish using the same 22 three years old males. In this way we had three hatching throughs (each with one different size groups of eggs) at 5 °C and six hatching throughs at 10 °C. These six throughs consisted of two with the smallest eggs, two with the medium sized eggs, and two with the largest eggs.

At the eyed ova stage three of the hatching throughs (one with the smallest eggs, one with the medium sized eggs, and one with the largest eggs) were moved from 10 °C to 15.0 °C (±0.2 °C). In this way we ended up with nine hatching throughs so we had each of the three size groups of eggs placed at the three different temperatures. The reason why eggs first were placed at 15 °C at the eyed ova stage is that newly fertilized eggs cannot survive at this temperature.

A sample of eggs (about 200 from each size group) was collected for analysis. The eggs were blotted in a moist cloth and analysed for dry matter and energy content by means of chemical oxygen demand, COD. For description of the analyses see From & Rasmussen (1984).

At hatching, a sample of 100 embryos from each of the nine batches was taken. The embryos were weighed individually in grammes with four decimals, and analysed for dry matter and energy content. At the time for complete yolk absorption, again 100 specimens from each of the nine batches were weighed individually in grammes with four decimals, and analysed for dry matter and energy content.

As mentioned, we wanted to find h_1 from (1) in order to compare the relative feed intake by the fish originating from the three different egg sizes. In growth experiments it is usually implicitly assumed that two fish of equal weight, compared under the same environmental conditions during a certain time period, have equal growth rate irrespective of how they have obtained their weight at the start of the growth. Maybe this assumption is not true, and to eliminate any possibly effect of prior feeding on h_1 the fish were fed *ad libitum* by electrical feeders each 15 minutes both day and night. In this way the feeding level f can be put to 1. This procedure took place from the first feeding (at complete yolk absorption).

The feed used was commercial dry feed Brande 3800/50. Analyses carried out, showed that dry matter of the different batches ranged from 91.53 to 93.65% with a mean of 92.94%. The energetical value ranged from 1.47 to 1.56 g COD/g dry matter with a mean of 1.51 g COD/g dry matter.

If growth experiments with maximum feeding rate ($f = 1$) are conducted, h_1 can be calculated from (1). Therefore, such experiments were carried out for the different batches of fish to see if there should be any significant difference in the values of the h_1's. At 5°C one maximum feeding experiment was carried out for 33 days from 227 days after first feeding for each of the three size categories. Before and after the experiments the fish were starved for 140 hours to ensure that the fish were weighed with empty stomachs, see From & Rasmussen (1984). At 10 °C three maximum feeding experiments with each of the three size categories were carried out for 12 days for each experiment from 66 days, from 122 days and from 163 days after first feeding for each size category. Before and after the experiments the fish were starved for 92 hours to weigh the fish with empty stomachs (From & Rasmussen, 1984). At 15 °C three maximum feeding experiments were carried out for 12 days for each experiment from 48 days, from 81 days and from 118 days after first feeding for each of the three size categories. The fish were starved for 68 hours before weighing, see From & Rasmussen (1984). In all we conducted 21 growth experiments, namely three (one for each size group) at 5 °C, nine (three for each size group) at 10 °C, and nine (three for each size group) at 15 °C.

In the period between the growth experiments the fish were again fed *ad libitum* each 15 minutes by the electric feeders.

From the experiments h_1 was calculated from (1). The total amount of pellets divided with the number of fish and days gives dR/dt. T = temperature was known. The start mean weight was called $w(0)$ and the mean weight after n days for $w(n)$. $(w(0) + w(n))/2$ gives w_t in formula (1) and the values for h_2 and m from Rasmussen & From (1991) were inserted.

After the start and final weighing subsamples of fish were collected for analysis for dry matter and energy content. The number of fish for analysis was at follows: At 5 °C and the first experiment at 10 °C and 15 °C: 100, at the second and third experiment at 10 °C and 15 °C: 25.

Results and discussion

Weight at the different stages. Efficiency of energy conversion between the stages

The weight of the eggs at stripping before adding of water is shown with 95% confidence limits in Table 1.

Table 1. Weight at stripping (before water absorption).
Wet weight given with 95% C.L.

Size group	Wet weight, g	Weight, g COD	Dry matter, %
Small	0.0447±0.0002	0.0295	41.14
Medium	0.0686±0.0002	0.0440	41.55
Large	0.1007±0.0007	0.0639	41.11

The eggs in the experiment were not weighed after water absorption but other 100 eggs were weighed individually before and after water absorption. it was found that the water gain by water absorption was 17.2% (±4.1%).

The weight (with 95% confidence limits) at hatching and complete yolk absorption can be seen in Table 2. If the embryos at hatching from the same size of eggs

Table 2. Weight at hatching and complete yolk absorption. Efficiency of energy conversion from stripping to hatching and complete yolk absorption. Wet weight given with 95% C.L.

Temp., °C	Size group	Stage	Wet weight, g	Weight, g COD	Dry matter, %	Efficiency, %
5	Small	Hatching	0.0471±0.0010	0.0242	34.82	82.03
		Absorption	0.0841±0.0016	0.0186	15.87	63.05
	Medium	Hatching	0.0728±0.0010	0.0374	37.71	85.00
		Absorption	0.1150±0.0017	0.0281	17.77	63.86
	Large	Hatching	0.1083±0.0014	0.0565	36.24	88.42
		Absorption	0.1532±0.0023	0.0415	19.13	64.95
10	Small	Hatching	0.0472±0.0012	0.0277	34.89	93.90
		Absorption	0.0884±0.0016	0.0218	17.57	73.90
	Medium	Hatching	0.0731±0.0014	0.0420	36.52	95.45
		Absorption	0.1182±0.0017	0.0328	19.03	74.55
	Large	Hatching	0.1101±0.0026	0.0595	35.23	93.11
		Absorption	0.1665±0.0030	0.0479	19.29	74.96
15	Small	Hatching	0.0488±0.0011	0.0289	36.50	97.89
		Absorption	0.0801±0.0038	0.0197	17.72	66.90
	Medium	Hatching	0.0750±0.0008	0.0431	36.01	97.95
		Absorption	0.1128±0.0021	0.0308	18.88	70.00
	Large	Hatching	0.1145±0.0024	0.0604	35.03	94.52
		Absorption	0.1622±0.0085	0.0430	18.53	67.29

are compared at the three different temperatures it is seen that the weight in COD increases with increasing temperature ($p < 0.05$). This was also found by Kamler & Kato (1983) who incubated spawn from rainbow trout in parallel at 9, 10, 12, and 14 °C till complete resorption of yolk sac. For larvae at complete yolk absorption these authors also found that the weight increased with increasing temperature, whereas we find that larvae have maximum weight at 10 °C. This can maybe be explained by the fact that we compared 5, 10, and 15 °C, whereas the highest temperature in Kamler & Kato (1983) was 14 °C. Maybe 15 °C contrary to 14 °C exceeds the optimal temperature for yolk absorption.

Further, the efficiency =

$$\left(100 - \frac{\text{energy at stage 1} - \text{energy at stage 2}}{\text{energy at stage 1}}\right) \%$$

is shown in Table 2. The efficiencies are dependent of temperature ($0.01 < p < 0.05$) and independent of egg size ($p > 0.05$).

Beacham, Withler & Morley (1985) investigated chum *Oncorhynchus keta*, (Walbaum, 1792) and coho salmon *O. kisutch*, (Walbaum, 1792) and Kazakov (1981) investigated Atlantic salmon, *Salmo salar* Linné, 1758 and found that the weight difference between egg samples became more pronounced during the yolk sac absorption period. Phillips & Dumas (1959) who investigated brown trout, *S. trutta* Linné, 1758 found the opposite, namely that the weight difference between two egg samples became less apparent during the sac-fry stage. If the weights and energy contents in Tables 1 and 2 are compared it is seen that the weight differences between the newly fertilized eggs are not altered ($p >> 0.05$) measured both as energy and wet weight at hatching. The weight differences are not altered during the yolk sac stage measured as energy, but the difference measured as wet weight becomes less pronounced during the yolk sac stage.

Duration of the different stages

The duration of the period from fertilization to eyed ova, the period from eyed ova to hatching, and the period from hatching to complete yolk absorption is shown in Table 3. The durations given represent 50% values as not all eggs from a given batch will hatch on the same day. From the table it can be seen that the duration of the different stages is independent of egg size ($p >> 0.05$). Beacham, Withler, & Morley

Table 3. The duration in days of the different stages. The days are 50% values.

	Size group	Duration in days 5°C	10°C	15°C
Fertilization to eyed ova	Small	38	20	
	Medium	34	19	
	Large	33	21	
Eyed ova to hatching	Small	15	9	6
	Medium	33	13	8
	Large	30	12	3
Hatching to complete yolk absorption	Small	55	23	16
	Medium	52	22	13
	Large	49	21	18

(1985) found the same for chum and coho salmon. The duration of the period from fertilization to hatching can only be found at the two temperatures 5 and 10 °C because no eggs were placed at 15 °C before the eyed ova stage. If the number of day degrees at 5 and 10 °C is found for the period from fertilization to hatching it is found that the number of day degrees is independent of both egg size and temperature ($p >> 0.05$). In mean for the three egg sizes we find that it takes 322 day degrees from fertilization to hatching at 5 °C and 313 day degrees at 10 °C. This is in good accordance with Schäperclaus (1961) who has 333 day degrees at 5 °C and 314 at 10 °C from fertilization to hatching.

Growth experiments

The values of h_1 found from the 21 growth experiments are shown in Table 4. h_1 is independent of egg size and temperature ($p >> 0.05$), and therefore the specific growth rate is not influenced by egg size. But the fish hatched from the larger eggs should retain their initial size advantage. In our experiments the large eggs are weighing more than twice as much as the smallest eggs. Further, at the three differ-

Table 4. h_1 on basis of COD measurements from the different growth experiments.

	5°C	10°C	15°C	Mean
Small	0.0930	0.1289 0.1290 0.1309	0.0767 0.1314 0.1339	0.1177
Medium	0.1128	0.1492 0.1348 0.1293	0.0814 0.1479 0.2022	0.1368
Large	0.1180	0.1838 0.1237 0.1061	0.0679 0.1198 0.1191	0.1198
Mean	0.1080	0.1351	0.1200	0.1248

ent temperatures the newly hatched fry from the largest eggs also weigh more than twice as much as the fry from the smallest eggs. To see how big the weight difference would be under identical environmental conditions after a longer period of time we have calculated the weights by means of the growth equation described by Rasmussen & From (1991). We have chosen the temperature 10 °C and $f = 0.5$ which means that the fish eat 50% of what they possibly could eat. We have chosen this value for f as we think this is about the maximum feed intake under natural condi-

Table 5. Weight after one year of feeding and feeding level = 0.5.

		Start weight		Final weight	
Temp. °C	Size group	Wet weight g	g COD	Wet weight g	g COD
10	Small	0.0884	0.0218	163.2	77.0
	Medium	0.1182	0.0328	169.3	80.2
	Large	0.1665	0.0479	175.2	83.4

tions. The weights after one year of feeding are shown in Table 5. It is seen that the fish from the largest eggs only are weighing 7-8% more than the fish from the smallest eggs. So, it seems fair to suggest that the effect of egg size early in the life of the young fish will be overshadowed by genetical and environmental factors.

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