Effects of abiotic and biotic factors on hatching, emergence and survival in Baltic salmon 
*(Salmo salar* L.)*

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Umeå 1988

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AKADEMISK AVHANDLING

som med tillstånd av rektorsämbetet vid Umeå universitet för erhållande av filosofie doktorsexamen, framlägges till granskning torsdagen den 11 februari 1988, kl 10.00 i Hörsal C, LUO, (Johan Bures väg).

Examinator: prof. C. Otto, Umeå

Opponent: Dr. J-G.J. Godin, New Brunswick, Canada
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Abstract

This thesis deals with important factors that affect the temporal organization of emergence and early survival of Baltic salmon (*Salmo salar* L.). The study population was obtained from the Norrfors hatchery (63°50'N, 20°05'E), Umeälven (Ume river) in Northern Sweden. The main objectives of the thesis have been to study; a: the effect of female and egg characteristics on embryonic survival, b: the effect of egg size, temperature and photoperiod on the emergence pattern and c: the impact of early or late emergence on survival in relation to predation and limited territorial space.

The main results are summarized as follows: (1) Fecundity and egg size increased with increasing weight of females. No effect of female size were found on egg colour. Longer impoundment and later stripping increase egg colour. Egg mortality was not correlated with egg colour. Stripping date was found to have the strongest effect on mortality. (2) Egg size had no effect on the timing of emergence but fry of different egg size emerged synchronously. Fry from large eggs left the gravel as heavier fry and with a larger proportion of yolk left compared to fry from small eggs. (3) The number of days and number of degree days from hatching to 50% emergence decreased exponentially with increasing temperature. Synchronization of emergence increased with increasing temperature. Fry emerged with more yolk at 12 °C compared to 6 °C. (4) Eggs kept in a LD 16:8 light regime hatched mainly during the light period, while eggs kept in constant darkness hatched continuously over a 24 hour period. Alevins kept at different light regimes (light>4h) from hatching until emergence left the gravel during the dark period. Daylength had no effect on the annual onset of emergence. (5) In a laboratory stream channel, predator presence at emergence increased mortality especially in early emerging fry. If the predator was introduced after completed emergence high mortality was noted among late emerging fry. The presence of fish predators and a limited territorial space for fry seemed to make early and late emergence hazardous and to favour a "peak" emergence. In the presence of a predator the fry changed their behaviour by reducing their swimming activity.

Key words

Baltic salmon, *salmo salar*, eggs, egg colour, alevins, fry, photoperiod, temperature, hatching, emergence pattern, synchronization, survival.
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1. LIST OF PAPERS

This thesis summarizes and discusses the papers listed below, and they will be referred to by their Roman numerals.


II. Brännäs, E. Synchronous emergence of Baltic salmon fry (*Salmo salar* L.) originating from eggs of different size. Manuscript.


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2. INTRODUCTION

Salmon (*Salmo salar* L.) eggs are large and need the fast flowing water of rivers to develop. Food resources for large fish are more abundant in the sea compared to the situation in the rivers. The salmon cope with these two resources and has thus evolved an anadromous life pattern. They spend the first year(s) in rivers, migrate to the sea as smolts, stay in the sea one or several years and return to their natal rivers to spawn. The life in the lotic environment of the Baltic salmon is summarized in Fig. 1.

![Figure 1](image_url)

**Figure 1.** A schematic picture of the stream life of the salmon from spawning of the adults to the smolt run.

In Northern Baltic salmon rivers, the adults return to spawn from late June until September. When they reach their spawning grounds they remain in shallow pools until final maturation. In October – November, the salmon spawn in rapids with coarse gravel. The female spawns several times during 3–14 days. Each time she digs a hollow with her tail and releases about 100 eggs. Each egg batch is simultaneously fertilized by the male(s) and then covered with gravel (Jones 1959).
The eggs remain in the gravel, and they develop slowly during the winter (December through April) when the temperature is about 0.1 °C. Hatching takes place in mid or late May. Alevins hatch with a tissue to yolk proportion of about 1:3 (dry weight). They remain within the redd and the yolksac is successively absorbed. During this period the alevins have a positive geotactic and a negative phototactic behaviour. This behaviour keeps them within the redd (Noakes 1978). When the yolksac absorption is nearly completed the young salmon, now called fry, emerge from the gravel to start external feeding. To attain a normal swimming posture they fill the swimbladder with air at the water surface. After emergence the young salmon defend territories, and they "sit and wait" for drifting live food (Kalleberg 1958). After 1–4 years depending on geographical location and population characteristics they pass through physiological and behavioural changes that result in a smolt migration into the sea (Lundqvist 1983).

The emergence and the smolt run start and end the bottom dwelling life of the young salmon. These two habitat shifts have principal ecological properties in common. The fry leave the gravel and the smolts migrate to the sea in a predictable seasonally timed pattern. A change of habitat at the best time of the year involves adaptive tactics to ensure the highest levels of survival probabilities in a seasonally variable environment. Further, the two habitat shifts also involve an increased risk of predation. Accordingly, the adaptive responses of the fish to these events have similarities; emergence as well as seaward smolt migration mainly take place while the fish are protected by darkness and they both occur within a narrow time range. Numerous studies have focused on the abiotic and biotic factors involved in the smoltification and the smolt run. However, apart from studies directly related to hatchery practice relatively few studies have focused on the emergence of salmon.
3. SUMMARY OF PAPERS I TO V

I. Egg characteristics and hatchery survival in a Baltic salmon, *Salmo salar* L., population.

These studies used Baltic salmon populations at the Norrfors hatchery on River Ume (63°50'N, 20°25'E) in Northern Sweden. Migrating salmon were caught, artificially spawned and their progeny released as smolts to compensate for the loss of natural spawning grounds due to hydroelectric power plants. Female weight, length, size, colour and number of eggs as well as spawning date and number of days in impounding reservoir were related to egg characteristics. The eggs originated from 302 females of both wild and hatchery reared origin. Special interest was focused on the colour of the eggs. Fecundity and egg size increased with increasing weight of the females. However, the females of a wild origin had a higher fecundity and smaller eggs than the cultivated ones. Increasing number of days spent in impounding reservoirs and late stripping date increased egg colouration. No effect of female size was found on egg colour. The mortality was not correlated with egg colour but death rates exceeding 50% were only found among pale and medium coloured sibling groups. The covariation between parent fish and egg qualities revealed that a late stripping date had the largest effect on mortality.

II. Synchronous emergence of Baltic salmon fry (*Salmo salar* L.) originating from eggs of different size.

Small, medium and large eggs were kept separately in simulated redds at constant temperature (10.3 °C) and in daylength (L19:D5) conditions. All fry, independent of original egg size class emerged synchronously within a week. Fry from large eggs were significantly heavier than fry from small eggs. This may confer fry from large eggs an initial advantage when competing for territories, and also
reduce the risk of predation on these fry. Larger fry also emerged with a higher proportion of yolk/tissue which enabled them to tolerate a long period of food shortage compared to small fry.

III. Emergence of Baltic salmon (*Salmo salar* L.) in relation to temperature: A laboratory study.

Newly hatched yolksac alevins were kept in simulated redds in a constant light regime (L12:D12) but at different temperatures; 6.3, 10.3 and 12.2 °C, respectively. The number of days and number of degree days from hatching to 50% emergence decreased exponentially with increasing temperature. Synchronization of emergence increased markedly with increasing temperature. Optimal temperature for incubation of yolksac alevins was 10 °C which gave the heaviest fry at emergence and the lowest death rate. Fry kept at 6 °C had the lowest mean weight at emergence and the highest death rate. Fry emerged at an earlier developmental state with more yolk at 12 °C compared to 6 °C. Baltic salmon alevins had a faster developmental rate during the gravel phase compared to the Atlantic salmon from Canada.

IV. Influence of photoperiod and temperature on hatching and emergence of Baltic salmon (*Salmo salar* L.).

Eggs kept in a L16:D8 light regime hatched mainly during the light period, while eggs kept in constant darkness hatched continuously over a 24 hour period. Emergence from a simulated redd kept under different light regimes (light>4 hours) but at a constant temperature (11.5 °C) was well synchronized with the dark period. The fry started to emerge just before the dark period and the highest number left the gravel during the first dark hour. In continuous darkness fry exhibited a
tendency for a persistent emergence pattern. The pattern resembled the photoperiod cycle to which they were previously exposed. Neither the length of the yolksac phase nor the length of the emergence period was affected by the photoperiod. In cold water (7.1–8.0 and 11.5 °C) the emergence was mainly nocturnal. At high temperature (14.5 °C) the diel pattern of emergence changed and a major proportion of fry left the gravel during the light hours. In addition, at high temperatures the alevins spent a shorter time in the substrate, and they emerged during a shorter period of time compared to emergence in cold water.

V. Effects of predation and territory on survival of early and late emerging Baltic salmon fry (Salmo salar L.): A laboratory study.

Early, peak and late emerging fry were marked and exposed to fish predators (Salmo trutta) in a laboratory stream channel during and after completed emergence. Predation during emergence caused high mortality in early emerging fry and low mortality among late emerging fry. On the other hand, predation after emergence of all groups (early peak and late emerging fry) caused high mortality among the late emerging fry, while those emerging early showed a high survival rate. Here, high survivorship in early emerging fry suggests a territorial advantage. The presence of fish predators and a limited territorial space seem to make early and late emergence hazardous and to favour a "peak" emergence. Also, the locomotor activity of fry with and without the presence of a fish predator was measured. Swimming activity was low in the presence of a predator.
4. DISCUSSION

4.1 Abiotic factors effecting the timing for hatching and emergence

Temperature:

Time from hatching until emergence showed an inverse nonlinear relationship with increasing temperature (III). Temperature is the abiotic factor that has the prime control on annual timing of emergence. Since the developmental rate of fish as well as secondary production are closely related to temperature, the optimal time to emerge has influenced the optimal time for spawning through natural selection (Bams 1969). In northern Sweden the salmon spawn in October – November, while in Scotland the spawning takes place later in November – December (Jones 1959). This difference in spawning time is probably related to differences in water temperature and hence affecting developmental rates of salmon offspring to synchronize the fry to emergence while the drifting food is abundant during early summer. Bams (1969) also suggested that a developmental rate that is adopted to the specific environmental conditions may be selected for. Accordingly, my results indicate that the rate of development from hatching to emergence was doubled in Baltic salmon (30 d in 10 °C) compared to data presented on the Atlantic salmon (60 d in 10 °C) from the South of Canada (Dill 1970). Although both results are comparable by means of similar experimental design, the validity of the difference needs to be confirmed by additional data.

In my studies fry emerged with a varying amount of yolk remaining but the mean proportion of yolk left at emergence increased with increasing temperatures (IV). Since the yolk reserves are used at a faster rate at a high temperature, the result indicates that the fry leave the gravel in a state that corresponds to the developmental rate at each temperature. An earlier emergence at a high temperature may be adjusted so that the time available for the fry to learn external feeding is constant, independent of temperature.
Light:

Salmonid alevins' reaction to light is initially negative (Dill 1970) and then it changes to a positive one at emergence (Noakes 1978) or after emergence (Dill 1970). In Atlantic salmon alevins, Dill (1970) recorded the first negative reactions to light 5–10 days after hatching. The hatching of Baltic salmon eggs was synchronized to the external LD cycle (IV). After the hatching enzymes have been released a normal hatching needs swimming movements of the embryo to occur (Bams 1969). An increased hatching was found during the light hours, and this may be caused by an increased number of swimming movements mediated by light. The initial appearance of proteins involved in the photoreceptor reactions was studied by means of immunocytochemistry in the same population of Baltic salmon (Östholm et al. 1987). An early differentiation of pineal light receptors starting 2 days after eying of the eggs at 6 °C was demonstrated. However, the photoreceptors of the retina did not show any immunoreaction until after hatching (Östholm et al. 1987). These results indicate that the embryos have functional photoreceptors in the pineal organ well in advance of hatching. The involvement of pineal photoreception in the synchronization of diel rythms in fish is well documented (Eriksson 1971; vVeen 1981).

The photoperiod did not affect the onset of annual emergence (IV). However, the diurnal timing was well synchronized to the external LD cycle (IV). Nocturnal emergence is a general feature of salmonid fry as reviewed by Godin (1982). I noted, however, a switch in the emergence pattern from a nocturnal one at a temperature up to 12.2 °C to a diurnal one in 14.5 °C (IV). According to Hayes et al. (1983) the order of embryonic development was particularly advanced for eye development. My results indicate that the fry emerging at the highest temperature were photopositive at the time for emergence (IV).
The negative response to light that is developed already at hatching and persists until emergence (III) is one important mechanism that secures the alevins to stay in the gravel. Further, the negative phototactic behavior ensures that the fry leave the gravel to fill their gas bladder in protection of darkness. According to Bams (1969), alevins of sockeye salmon (*Oncorhynchus nerka*) develop the potential for a geotactic directed behaviour well before emergence actually takes place. At the time of emergence a negative response to light will guide the alevins to leave the gravel substrate at the onset of darkness. When the feeding starts the fry become active during the light hours since they use visual cues for feeding (Chapman 1966).

### 4.2. Biotic factors affecting early survival

The impact of egg size on early survival has received considerable interest among scientists. The strongest relationship between a number of variables of hatchery reared salmon was found for increasing female size leading to increasing fecundity and egg size (I). Svärdson (1949) proposed that if large and small eggs had the same chances of survival an increased fecundity with smaller eggs would be favoured by genetic selection. He also suggested that a higher survival of large egg progeny would work against such selection. However, all findings reveal that with increasing size of salmonid females, the eggs increase by number as well as by size (Thorpe et al. 1984). Large eggs result in larger fry at emergence (II). Large salmonid fry have a better survival rate both in the field (Bagenal 1969) and under hatchery conditions (Craik & Harvey 1984; Wallace & Aasjord 1985). Elliott (1984) modified Svärdson's original proposal for the reproductive strategy of brown trout (*Salmo trutta*) and suggested that both egg size and fecundity are maximized. Besides mortality caused by reduced viability of small versus large eggs, differences in timing of emergence due to egg size must be considered as a factor influencing
future survival. However, I found no difference in emergence pattern of small versus large eggs (II). In deviation, the large fry emerged in synchrony with small ones but with a larger tissue weight and a higher proportion of yolk remaining (II). These factors may be important to reduce predation in large fry (Taylor & McPhail 1985) and also to reduce the effect of late arrival in territorial competitions (Chapman 1962; Thorpe et al. 1974). In addition, large fry with large yolksacs can obviously withstand poor feeding conditions for longer periods of time (Bagenal 1969).

By migrating to the sea where food is abundant the salmon females increase their weight rapidly. An increased weight of females leads to more and larger eggs which should increase the fitness of their offspring.

Besides access to and competition for good feeding conditions, predation has exerted an important role in the synchronization of emergence (Godin 1982). Upon emergence, the salmon fry remain connected to positions on the river bottom after some initial dispersal. An aggressive territorial defence soon develops (Kalleberg 1958). Mason & Chapman (1965) found that early emerging sockeye salmon fry had territorial advantages over later emerging fry. I also found a high survival rate of the first emerging fry when they were allowed to settle territories in the absence of predators (V). However, when predators were already present at emergence the advantage of having an early access to plenty of territorial space was outweighed by an elevated relative predator pressure (V). Although fry reacted promptly in the presence of a predator by reducing their swimming activity they were still very susceptible to predation, at least under my experimental stream conditions.

Fry emerging prior to peak emergence are more likely to be consumed by predators because of their low numbers. Also, fry emerging late are obviously more susceptible to predation, because of lack of territorial space. The most favourable time to emerge from the gravel ought to be early within the bulk of all other fry.
Similar strategies that result in swamping of predators are used by other animals in situations where they are especially vulnerable (Daan & Tinbergen 1979). Conclusively, patterns of food availability in the stream, intraspecific competition for territorial space and predator pressure all seem to have contributed to evolving a narrow, synchronized emergence pattern within Baltic salmon population.
5. ACKNOWLEDGEMENTS

I thank Prof. Lars-Ove Eriksson, Dr. Hans Lundqvist and Prof. Christian Otto for support, encouragement and valuable comments on my papers. Mr. Harald Johansson at the Norrfors Hatchery offered all eggs I needed for my experiments. He and Mr. Bertil Öhman always helped me during my visits (as annually predictable as the spawning and hatching of salmon) to the hatchery.

I thank the following people for support during the past years; everybody at the department for a friendly and joyful atmosphere; Prof. Karl Müller, former Head of the department, for giving support to the working group on Salmon; Mr. Göran Andersson and Mr. Gunnar Borgström for technical assistance; Mrs. Görel Marklund for drawing the pictures; and Mrs. Joyce Clarke for improving the English in some of the papers. Finally, I thank my husband Kurt for statistical help and support and my two daughters Lisa and Kajsa for teaching me how to concentrate in a chaotic surrounding.

This thesis has partly been financed by the Natural Science Research Council (NFR) and by the Swedish Forestry and Agricultural Research Council (SJFR).
6. REFERENCES


