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Initial feeding time of Atlantic salmon, *Salmo salar*, alevins compared to river flow and water temperature in Norwegian streams

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Synopsis

The time of initial feeding of Atlantic salmon, *Salmo salar*, alevins in ten geographically widespread Norwegian streams was estimated theoretically by combining data on spawning time and models describing the time from fertilization to hatching and from hatching to initial feeding at different temperatures. The point of initial feeding was correlated with water flow and water temperature regimes. Initial feeding was avoided in all rivers during spring peak flow, and before water temperature reached 8° C. Two different strategies were indicated: (1) initial feeding may take place before the culmination of the spring flow or (2) after the peak spring flow. The choice of strategy depends on temperature and flow regimes in each river.

Introduction

Salmonid survival rates vary between locations and yearclasses. Mortality is particularly high during the weeks immediately following emergence from the gravel and initial feeding and is generally regarded as density dependent (Allen 1951, LeCren 1973, Mortensen 1977a, b, Elliott 1984).

In most northern rivers, Atlantic salmon, *Salmo salar* L., alevins start feeding in a period when the water flow is too high for detailed field studies. Therefore, existing knowledge about the biology and timing of the initial feeding of alevins of salmon in northern streams is limited.

The development time from fertilization to hatching is mainly temperature dependent. A model describing the development time for Atlantic salmon at different water temperatures was proposed by Crisp (1981). This model was shown to be satisfactory also for temperatures close to 0° C by Heggberget & Wallace (1984) and Wallace & Heggberget (1988). Corresponding data describing the development time from hatching to 50-percent initial feeding were recently given by Jensen et al. (1989). Hence, when spawning time and water temperature in a river are known, the time of initial feeding can now be estimated. In the present study, data on time of spawning and temperature regime from ten geographically widespread Norwegian streams are applied to estimate initial feeding time of alevins of Atlantic salmon. Based on lower threshold growth temperatures (Allen 1940, 1941, Jensen & Johnsen 1986) and experiences from Norwegian salmon farming regarding initial feeding (Refstie 1979) it is hypothesized that initial feeding takes place when water temperature reaches 7–8° C in spring.

Methods

Data on spawning time in the 10 rivers were collected from brood stock hatcheries, and represent mean time of spawning over a period of five to ten years. Release of gametes was conducted artificially, and fish were sampled for degree of ripeness 1–2 months before spawning peaked. Peak spawning was defined as the period when about 50 percent of the females were ripe, which normally varied by 5–10 days from one year to another. The dates on which the first and last females matured were also recorded, providing data on the length of the spawning periods.

The development time of Atlantic salmon eggs from fertilization to hatching was computed according to Crisp (1981), equation 1b:

$$\log D = b \log (T - \alpha) + \log a = -2.6562 \log (T - (-11.0)) + 5.1908, \quad (1)$$

where D = incubation time (days), T = temperature (°C), and a, α and b are constants (Crisp 1981). Results from hatching experiments performed at temperatures between 2.4 and 12°C were available to Crisp (1981). Additional experiments at temperatures between 0.1 and 1.3°C have later been performed by Heggberget & Wallace (1984) and Wallace & Heggberget (1988), who concluded that Crisp's equation 1b satisfactorily described the time from fertilization to hatching also at temperatures close to zero.

Development time at different temperatures in the range 3.9–10.4°C from hatching to 50-percent initial feeding was estimated by Jensen et al. (1989):

$$D = a\,T^{b} = 472\,T^{-1.27}, \quad (2)$$

where D = number of days after hatching, T = temperature (°C), and a and b are constants. Most of their experiments were performed with the river Vefsna strain, one of the populations included in this study.

The date of 50-percent initial feeding was calculated by using mean water temperature for 10-day intervals, estimating the fraction of total development for each short period. The length and peak of the initial feeding period correspond to the length and peak of the spawning period. Hence, peak of initial feeding was defined as the period when 50 percent of the alevins started feeding.

Water flow and water temperatures were measured by the Norwegian Water Resources and Electricity Board, Hydrological Department. The median flow over a ten year period is used in most rivers (normally 1976–1985). In the river Stryneelva the median flow for the period 1930–1960 is used, and in two rivers (Suldalslågen and Lærdalselva) which are both regulated for hydroelectric purposes, water flow and water temperature data from a period before regulation (1962–1977 and 1961–1973, respectively) are used. Mean water temperatures for 4 to 17 years were available.

The rivers are situated along the Norwegian coast between 59 and 70°N (Fig. 1).

Results

The peak spawning took place between 18 October and 10 January in the ten rivers, and usually lasted for five to ten days in each river (Table 1). The duration of the entire spawning period lasted from 17 days in river Numedalslågen to 56 days in river Stryneelva.

The peak of hatching was estimated to take place between 20 April and 10 June in the ten rivers studied, at a water temperature of 4.5–6.8°C.

The peak of initial feeding was estimated to take place between 24 May and 11 July in the ten rivers studied (Table 2). In all rivers the period from the start to the end of initial feeding was considerably shorter than the spawning period. The duration of the initial feeding period varied from 5 days in Numedalslågen to 29 days in Stryneelva.

The water temperature at peak initial feeding varied from 8°C in the river Stryneelva to 13°C in the rivers Drammenselva and Imsa. In the other rivers the temperature at peak initial feeding was 9–12°C.

Alevins avoid initial feeding at peak flow in all rivers, and peak initial feeding takes place at between 17 and 74 percent of peak flow (Fig. 2). In the river Stryneelva, alevins start feeding before peak flow, while in the other nine rivers they start feeding afterwards.

Fig. 1. Map of Norway showing the rivers studied.

Table 1. Spawning time of the ten Norwegian Atlantic salmon populations. Peak spawning represents the time when 50 percent of the females matured.

River	Start spawning	Peak spawning	End spawning
Altaelva	5 Oct	18–23 Oct	5 Nov
Vefsna	20 Oct	25–31 Oct	15 Nov
Driva	20 Oct	25 Oct–5 Nov	28 Nov
Rauma	25 Oct	1–5 Nov	20 Nov
Stryneelva	5 Nov	18–23 Nov	1 Jan
Lærdalselva	15 Oct	23–28 Oct	20 Nov
Suldalslågen	1 Jan	5–10 Jan	27 Jan
Imsa	2 Nov	28 Nov–3 Dec	24 Dec
Drammenselva	10 Nov	1–5 Dec	20 Dec
Numedalslågen	3 Nov	10–15 Nov	20 Nov

Discussion

Temperature and development time to initial feeding in Atlantic salmon have also been investigated by Kane (1988). At 4° C the results are similar to Jensen et al. (1989), but at higher temperatures this interval lasts for up to 13 days more. While Jensen et al. (1989) used live animals as food, Kane (1988) considered fish to be ready for exogenous feeding when the yolk constituted 5% of the total alevin wet weight, referring to Thorpe et al. (1984). However, it seems unlikely that alevins at high temperatures (e.g. 10° C) wait until yolk for only two more days is left before they start exogenous feeding.

For fish species living in temperate and cold areas with a restricted growing season, strong selection pressure is exerted on accurate reproductive control for optimal fitness. Offspring from individuals breeding at any time of the year other than the ideal, would appear to have limited chances of survival.

Several studies of salmonids indicate that there are few, or only minor, differences in temperature response between families or populations during embryonic development. Except in some quite genetically distinctive populations of chum salmon, *Oncorhynchus keta,* no stock adaptations were detected in development rates of embryos of this species in British Columbia (Beacham & Murray 1986, 1987), or in disparate populations of Atlantic salmon in Norway (Wallace & Heggberget 1988). This suggests that given a particular thermal regime in a river, the time of hatching of salmon embryos in that river depends on the time at which the salmon spawn. Since the duration of incubation is known to depend on temperature regime, a linking of spawning time to a stream temperature triggers spawning at a time which will result in hatching at a specific and presumably optimal time for survival (Heggberget 1988).

Due to long time selection we expect that in each population the majority of alevins start feeding and emerge from the gravel when the environmental conditions are favourable for highest possible survival. In competition with other juveniles for the most suitable territories, the fish size is important. Le Cren (1973) concluded that there was a hierarchy associated with size and the more favourable territories. In some laboratory experiments with coho salmon, *Oncorhynchus kisutch,* Chapman (1962) found that size was the principal factor governing hierarchy arrangement. Differences as small as 1 mm were found to be important. Gardiner & Geddes (1980) recorded higher energy content in larger individuals of Atlantic salmon than in smaller ones of the same year-class. Hence, among smaller fish occupying less favourable territories, higher mortality may be expected. For this reason an early start of the growing season is important.

The lowest temperature recorded for growth of Atlantic salmon in the Matamek River in Quebec (Gibson 1978) and the Little Sevogle River, New

Table 2. Estimated date for initial feeding in ten Norwegian Atlantic salmon populations. The estimations are based on knowledge of spawning time and water temperature in each river. The duration of the incubation period is calculated from equation (1), and the time from hatching to initial feeding from equation (2).

River	Start of period	Peak of period	End of period
Altaelva	8 July	10–12 July	15 July
Vefsna	5 July	7–9 July	12 July
Driva	20 June	23–26 June	30 June
Rauma	21 June	23–25 June	28 June
Stryneelva	20 May	3–6 June	18 June
Lærdalselva	21 June	22–25 June	3 July
Suldalslågen	27 June	29 June–1 July	4 July
Imsa	15 May	23–25 May	30 May
Drammenselva	17 June	21–23 June	26 June
Numedalslågen	17 June	19–21 June	22 June

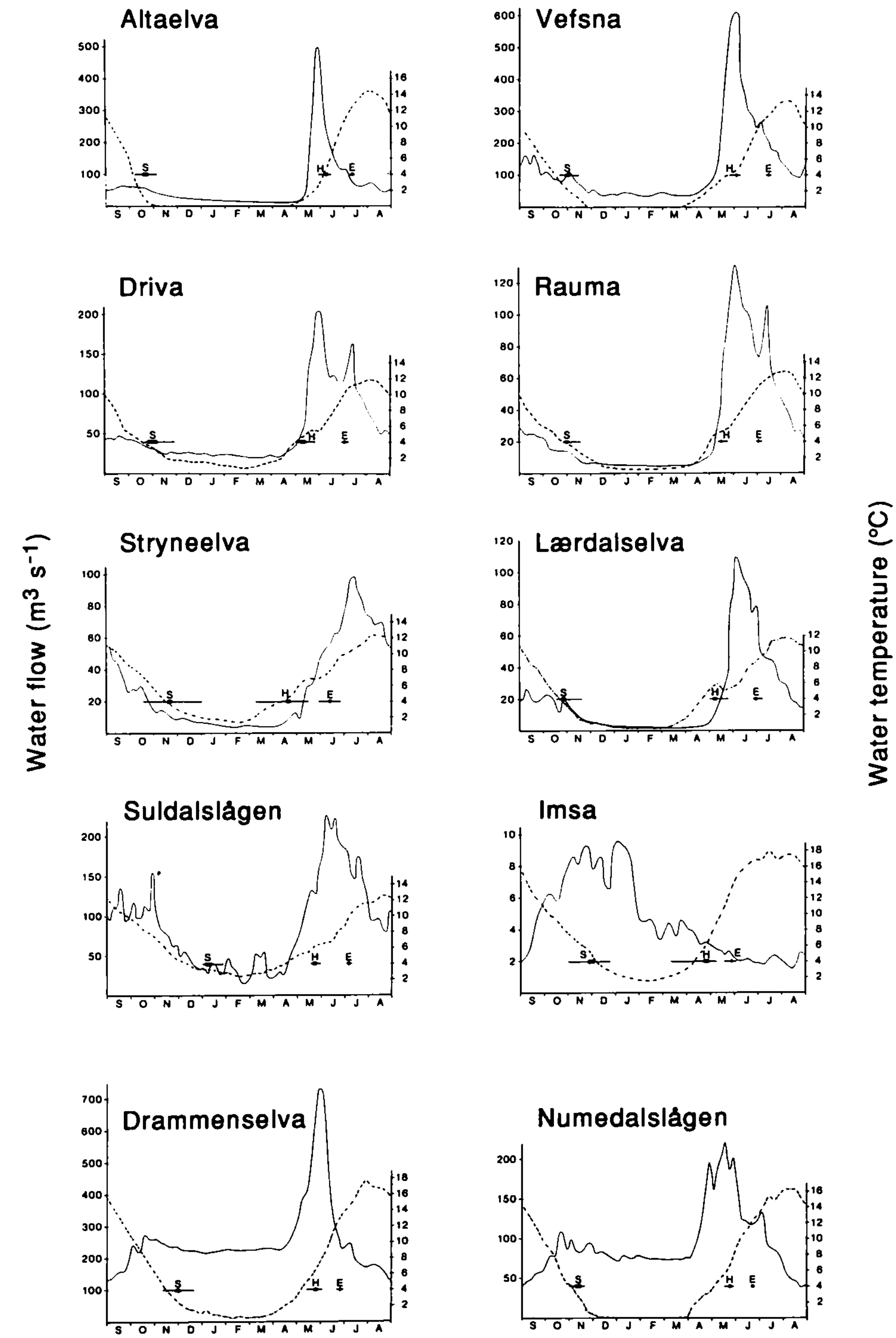

Fig. 2. Median water flow (——) and mean water temperature (----) in the ten streams studied, as well as time for spawning (S), hatching (H), and initial feeding (E) of Atlantic salmon in each stream. The thick part of the bars represents the peak (50 percent) of spawning, hatching and initial feeding.

Brunswick (Rimmer et al. 1983), is 9–10° C. Power (1969) and Lee & Power (1976), on the other hand, used 5.6 to 6° C as the lowest temperature for growth in the Ungava Bay region in northern Canada. Hence, the lowest temperature for growth varies with temperature conditions in the nursery stream. The lower limit for growth in Norwegian rivers seems to be about 7° C (Jensen & Johnsen 1986), the same as found in some British rivers by Allen (1940, 1941) and Gardiner & Geddes (1980). Experiences from Norwegian salmon farming have demonstrated that for successful initial feeding of Atlantic salmon, temperature should be above 8° C (Refstie 1979). This indicates that the ideal time for emergence and initial feeding of alevins should be when water temperature exceeds 7–8° C in spring, unless other factors are unfavourable for survival at that time.

Alevins avoid initial feeding at peak flow, regardless of the temperature conditions. Two different strategies are traced. In the river Stryneelva initial feeding takes place before peak flow, while in the other rivers initial feeding takes place afterwards. In eight of these rivers (except the river Imsa) the river flow rises to a high level before the water temperature exceeds 7–8° C, and initial feeding is thereby delayed until the river flow decreases again. In three rivers two peaks in river flow are observed; first the main peak and then a smaller one. In these rivers initial feeding seems to occur in the period between the two peaks. The alevins seem to be less tolerant to high water flow during initial feeding, supposing that swimming capacity increases soon after emergence.

In the river Stryneelva, where initial feeding takes place before peak flow, water temperature also exceeds 7–8° C before peak flow. Hence, the alevins start feeding at rising flow. It is, therefore, important to do this as early as possible to avoid unfavourably high water flow during the first critical days, but not before the river temperature exceeds the limit of 7–8° C for initial feeding.

In the river Imsa, the flow regime is quite different from the nine other rivers. Imsa is the smallest river, with a median peak flow of only $10\,m^3\,s^{-1}$. It is located in southwestern Norway, an area with particularly mild winters, and peak flow occurs in autumn and winter. Therefore, water flow at initial feeding is never crucial. Under such conditions we expected initial feeding to take place as soon as the water temperature had exceeded 7–8° C, i.e. about three weeks earlier than the computed date. If so, peak spawning had to take place as early as the first days of October. One may speculate that in dry years the flow may be too low for adult salmon to ascend to the spawning areas at that time. For this reason salmon adapted to spawning later probably have the highest reproductive success.

Nickelson et al. (1986) suggested that spring freshets reduced survival of early emerging coho salmon, and Cramer et al. (1985) found a negative relationship between survival of spring chinook, *Oncorhynchus tshawytscha,* from eggs to juveniles and winter flows. High summer flows increased survival of coho salmon (Neave & Wickett 1948, Neave 1949, Wickett 1951). These observations indicate that water flow is essential for survival of early juveniles, while increased water flow some time after initial feeding does not affect survival negatively.

We conclude that river flow and water temperatur are important environmental factors influencing selection for optimal initial feeding time. In northern streams alevins seem to avoid initial feeding at peak spring flow, and also before water temperature exceeds 8° C. Two different strategies were indicated; (1) initial feeding may take place before or (2) after the spring flow has culminated. Choice of strategy depends on temperature and flow regimes in each river.

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