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Maturation of male age-0 Atlantic salmon following a massive, localized flood

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Maturation of male age-0 Atlantic salmon *Salmo salar* parr in New England, U.S.A. streams is rare (~5%), but age-0 parr maturation was high (74%) by autumn in the Sawmill River following a massive, localized flood. Maturation was low in two other study streams (3, 7%) in the same year as the flood, and in the Sawmill River (6%) and the other rivers (5%) in the subsequent year, suggesting that high maturation rates were related to the flood. The high age-0 maturation rates appear to have been the result of greater growth opportunity following the flood. Masses of fish in October were two-fold greater in the Sawmill River (13·2 g) than in the other rivers (6·5, 6·9 g). Mechanisms contributing to the fast growth may include community reorganization following the flood and water temperature differences among rivers. The flood caused an age-0 year-class failure for brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* and a large reduction (69%) in the number of salmon compared to the other rivers, possibly reducing competition or agonistic interactions among remaining fish. Average water temperatures were slightly warmer in the Sawmill River (17·0° C) than in the other rivers (15·5, 14·9° C). By influencing community structure and growth of remaining fish, it appears that a strong environmental disturbance can also alter the direction and timing of life histories in Atlantic salmon.

Key words: Atlantic salmon; parr maturation; growth; flood; relative condition factor; disturbance.

INTRODUCTION

Parr maturation is common in male Atlantic salmon *Salmo salar* L. (Dalley *et al*., 1983; Saunders & Schom, 1985) and may have a significant impact on population dynamics (Myers, 1984; Lundqvist *et al*., 1988). Parr maturation can reduce subsequent growth (Myers *et al*., 1986) and the timing and magnitude of smolt production (Myers, 1984; Hansen *et al*., 1989; Berglund, 1992). Most maturing parr are age-1 or older fish, but the occurrence of maturation appears to depend on early growth rates and lipid accumulation (Thorpe, 1986; Rowe *et al*., 1991), so fast-growing fish in very productive environments could mature at age 0. Although large numbers of fast-growing age-0 fish can mature in the laboratory (Bailey *et al*., 1980; Duston & Saunders, 1997), age-0 maturation is rare in nature [~5% in France; (Baglinière & Maisse, 1985)] and unobserved outside the southern extent of the range of Atlantic salmon. The potential for fast growth of juvenile Atlantic salmon could result from a variety of mechanisms, including variations in prey base (Wankowski, 1979; Holm & Møller,

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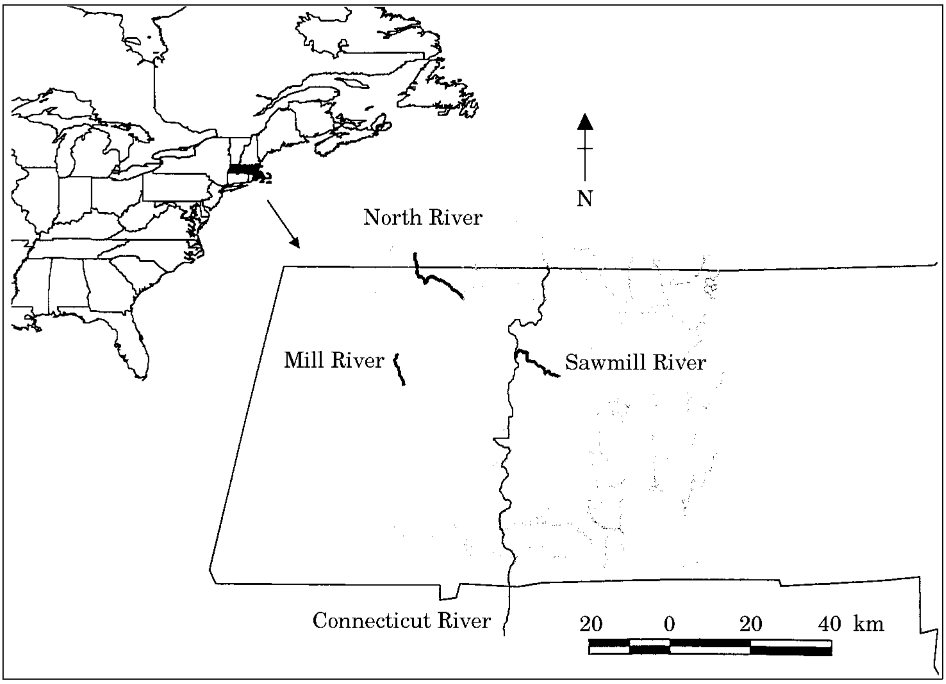

FIG. 1. Geographical location of the three study streams in Massachusetts, U.S.A.

1984; Browman & Marcotte, 1987), temperature (Siemien & Carline, 1991), flow rates (Rimmer & Power, 1978) and fish community changes following a disturbance (Elwood & Waters, 1969; Matthews, 1986; Harvey, 1987). Differences in these environmental variables among streams or years could influence growth rates and age-0 maturation rates. We report a high incidence of parr maturation of age-0 male Atlantic salmon in a single study stream following a highly-localized, massive flood.

MATERIALS AND METHODS

Studies were conducted in three tributaries of the Connecticut River in Massachusetts, U.S.A., the Sawmill River, the West Branch of the North River (North River hereafter) and the Mill River in Plainfield, MA (Fig. 1). Average (± S.D.) stream width was 6·9 ± 1·5 m (Sawmill), 6·6 ± 1·4 m (Mill), 11·9 ± 2·5 m (North) and water depths were 19·7 ± 5·2 cm (Sawmill), 13·4 ± 2·1 cm (Mill), and 18·9 ± 3·2 cm (North). Substrate was predominantly cobble with occasional bedrock and boulders (<5%). Each stream was divided into three 2000-m^2 study sections with at least 1 km between sections. Atlantic salmon fry were stocked between 24 April and 9 May 1996 at a density of 50 fish 100 m^{-2} both within and outside sections for a total of 1000 fish per section. Stocked fry are the only source of salmon in these rivers. Hatchery (White River National Salmon Station, Bethel, VT, U.S.A.) fry were stocked outside sections and fry that had been marked with thermal bands on their otoliths (Volk *et al.*, 1994; Letcher & Terrick, 1998) for a separate study were stocked inside the sections. Otolith band patterns allowed us to identify fish unambiguously as age-0 fish that had been stocked in the study sections. Unmarked hatchery fish were assigned to the age-0 year class based on size (<95 mm).

Study sections were sampled between 29 August and 17 October 1996 (Fig. 2) using three-pass removal (Zippin, 1958) with block nets and a backpack electroshocker set at

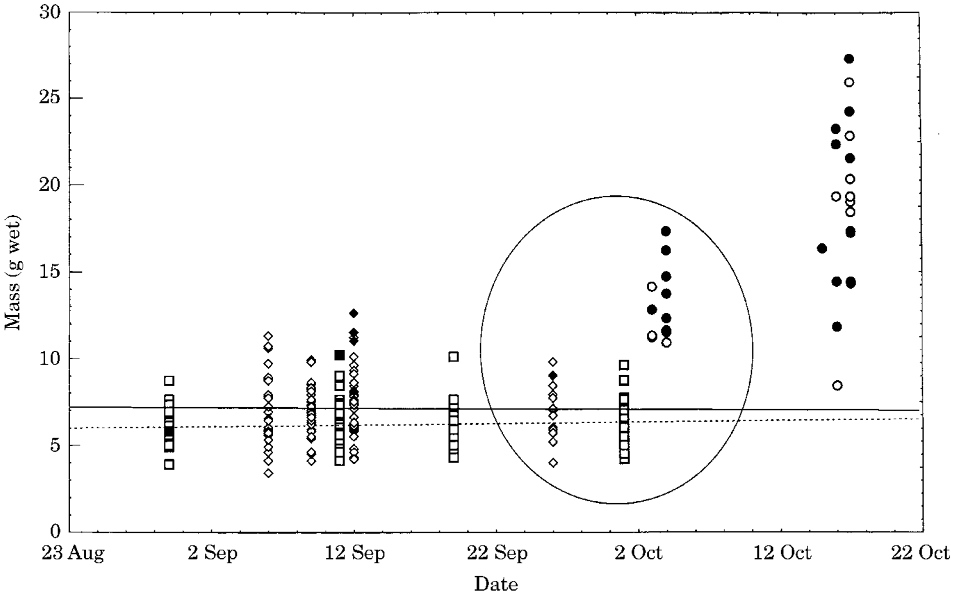

FIG. 2. Masses of individual fish sampled in the three rivers during the 1996 experimental period. Closed symbols represent mature males and open symbols represent either immature males or females. Circled fish were used for comparisons of size and growth among rivers. Lines are linear regressions. ○, Sawmill River; □, North River; ◇, Mill River.

500–600 V unpulsed d.c. current. In addition to the study sections, samples were also taken 50 m up and downstream of the sections. All salmonids were retained and measured for fork length (± 1 mm) and wet weight (± 0·1 g) after anaesthetizing with MS-222 (100 mg l^{-1}). Automatic temperature recorders placed in the middle of the study sections in each river measured temperatures every 2 h. Instantaneous growth rates (G) were calculated as $G = \log_{10}(W_2\ W_1^{-1})\ (t_2 - t_1)^{-1}$ where W_1 was initial mass at time t_1, and W_2 was final mass at time t_2. Growth rates were calculated in length as $(l_2 - l_1)\ (t_2 - t_1)^{-1}$, where l_1 was initial length and l_2 was final length. Average initial masses were measured on the day of stocking. Brown trout *Salmo trutta* L., and brook trout *Salvelinus fontinalis* (Mitchill), and age-1 salmon were returned to the river and age-0 salmon were brought to the laboratory for otolith analysis. The expression of milt was used as evidence of parr maturation in the field. Gonads of all fish were examined in the laboratory to determine sex and maturity. Gonads from a random subsample of 20% of males and all males estimated to be mature in the field were removed and weighed to determine gonadosomatic index, $I_G = 100\ W_G\ W^{-1}$ where W_G was gonad mass and W was fish mass. Relative condition factor (F_R) was calculated as $10^6\ W\ L_F^{-3{\cdot}079}$, where L_F was fork length and 3·079 was the exponent of the length–weight relationship of all fish used in the analysis. Gonad-free relative condition factor was calculated as $10^6\ (W - W_G)\ L_F^{-3{\cdot}079}$ and gonad-free growth rates were calculated as $(\log_{10}(W_2 - W_G) - \log_{10}(W_1))/(t_2 - t_1)^{-1}$.

On 13 June 1996 the Sawmill River experienced a massive flood resulting from a localized rainstorm (>15 cm in 3 h). There is no gauging station on the Sawmill River, so we have no estimate of the highest flows during the flood. The impact of the flood on the physical characteristics of the river was dramatic and included the destruction of most of the bridges over the river, and severe gouging of the river bed and bank. Sections of adjacent roads collapsed into the river and up to 4 m vertical sections of the bank were exposed. Based on the height of the bridges that were washed away, the water level was at a minimum 3 m above typical.

Mean values of arcsin-square root transformed per cent mature for each of the three sites were used as replicates in ANOVAs to test for differences in maturity among rivers.

Because samples among rivers were not evenly distributed in time (Sawmill River samples follow other rivers, Fig. 2), data are presented for comparisons (ANOVA) of size and growth among rivers for the subset of samples collected for all three rivers within 8 days (circled samples in Fig. 2). Comparisons of I_G and F_R for fish with different sex/maturity status (female, male-immature, male-mature) within a river were made using all of the samples for each river. Mean values of I_G and F_R were used for each of the three sites as replicates in ANOVAs to test for river effects. For comparisons of I_G, gonad-free F_R and gonad-free G between immature and mature males we used only the fish that had been examined for gonad mass.

RESULTS

Age-0 male maturation rate was elevated in the Sawmill River in the year of the flood compared with those in the other rivers or in the following year. The Sawmill River contained a substantially higher percentage of age-0 mature males (74·3%) in 1996 than did the North (2·8%) or the Mill (6·7%) [P=0·005, F(2,6)=14·55; Fig. 2] rivers. Per cent mature age-0 Sawmill River parr in 1997, the year following the flood, was similar to 1996 levels in the North and the Mill rivers, indicating that the high levels of maturity were probably related to effects of the flood. In 1997, 5·9% (n=152) of the age-0 males in the Sawmill, 7·4% (n=136) in the Mill and 5·3% (n=131) in the North rivers were identified as mature based on gonad evaluation. Among rivers, 78% of the age-1 males were mature (assuming a 50 : 50 sex ratio; sex ratios of age-0 fish in the three rivers were approximately 50 : 50) in 1996.

In 1996, fish masses for fish collected between 26 September and 4 October (Fig. 2) were more than two-fold heavier in the Sawmill River (13·2 ± 2·1) than in the Mill (6·9 ± 1·6) or in the North (6·5 ± 1·6) rivers. Masses varied significantly among rivers [P<0·00001, F(2,45)=68·8] and were significantly higher in the Sawmill River compared to the Mill (P=0·00013) or the North (P=0·00013) rivers. Masses were not different between the Mill and the North rivers (P=0·81). G for the same fish was also significantly higher [P<0·00001, F(2,45)=39·4] for the Sawmill River fish (0·013 ± 0·00086) than for the Mill (0·012 ± 0·00080) or the North (0·011 ± 0·00083) river fish. Growth in length also varied among rivers [P<0·00001, F(2,45)=38·4], with the fastest growth in the Sawmill (0·49 ± 0·039 mm day^{-1}) and slower growth rates in the Mill (0·42 ± 0·041) and the North (0·37 ± 0·042) rivers. Mean 1996 water temperature was warmer in the Sawmill River (17·0° C) than in the North (15·5° C) or in the Mill (14·9° C) rivers (Fig. 3).

Although no data were collected on the Mill and North rivers in the second half of October, it appears unlikely that fish in these rivers would have attained the sizes found in the Sawmill River in October (Fig. 2). Extension of the mass trajectories of the Mill and the North river fish into October suggests that fish in these rivers would have required unrealistically high growth rates in October to match sizes in the Sawmill River. In contrast to the proposed trajectories in the Mill and North rivers, masses in the Sawmill appear to increase through October, suggesting that the Sawmill River fish, both mature and immature, were still growing in October.

All fish in the Sawmill River grew rapidly, but maturation appeared restricted mainly to larger, faster-growing fish in the other rivers. The few fish that were

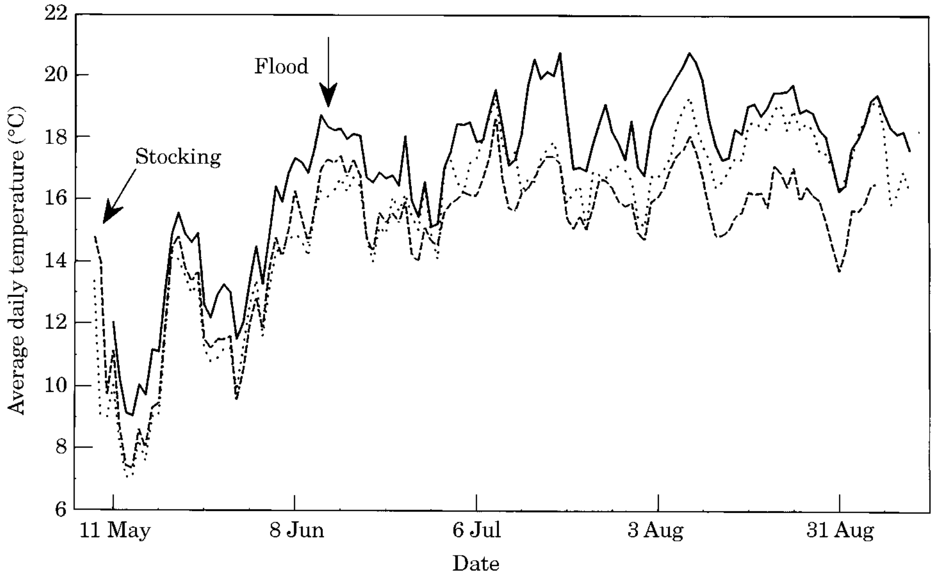

FIG. 3. Mean daily temperature during the 1996 experimental period in the three rivers. ——, Sawmill River; · · · ·, North River; – – – –, Mill River.

TABLE I. Gonadosomatic index (I_G) and gonad-free relative condition factor (F_R) (mean ± S.D.) for the age-0 males sampled for gonad mass from the three rivers in 1996; gonad-free F_R was calculated using (total mass − gonad mass) for final mass

River	Status	n	I_G (g g^{-1} fish^{-1} 100)	Gonad-free F_R
Sawmill	Male-immature	2	0·113 ± 0·128	7·02 ± 0·18
	Male-mature	26	9·524 ± 3·275	7·54 ± 0·54
North	Male-immature	12	0·0578 ± 0·0561	7·31 ± 0·41
	Male-mature	2	7·028 ± 8·695	7·57 ± 0·52
Mill	Male-immature	16	0·237 ± 0·320	7·70 ± 0·36
	Male-mature	5	12·061 ± 2·942	7·52 ± 0·32

mature in the Mill and North rivers were generally the larger fish at any one sample (Fig. 2), but there was no significant difference in mass among mature males, immature males, and females in the Sawmill River [P=0·49, F(2,32)=0·72].

In 1996, mature age-0 fish had significantly higher mean I_Gs (9·86) than did immature fish [0·13, P=0·0006, F(1,9)=27·0] and there was no difference in I_Gs of mature males among rivers [P=0·38, F(2,9)=1·1] (Table I). Relative condition factor was significantly higher for mature males (8·48 ± 0·72) than for immature males (7·58 ± 0·50) [P<0·00001, F(2,15)=40·10]. In contrast to total-mass relative condition factor, gonad-free relative condition factor did not vary between mature and immature males (average mature=7·50, average immature=7·54; Table I).

The flood also appears to have altered the fish community in the Sawmill River compared to the following year and to the other rivers. In the autumn following the flood, age-0 salmon densities in the Sawmill were about 30% of those in the other rivers (mean ± S.E. 0·60 ± 0·25 fish 100 m^{-2} in the Sawmill *v.* 2·0 ± 0·36 fish 100 m^{-2} in the Mill and 1·8 ± 0·32 fish 100 m^{-2} in the North). In the year after the flood, age-0 Sawmill River salmon densities were over six-fold greater (3·9 ± 1·0 fish 100 m^{-2}) than the flood year. In the flood year, there was an age-0 class failure for brook trout and brown trout (both 0 fish 100 m^{-2}) in the Sawmill River and in the next year (1997) age-0 brown trout (0·42 ± 0·36 fish 100 m^{-2}) and brook trout (0·03 ± 0·18 fish 100 m^{-2}) densities were higher.

DISCUSSION

Male Atlantic salmon age-0 maturation is reported rarely and its occasional occurrence appears to depend on unusual circumstances. In the laboratory, fish growing to 100–150 mm by their first November can mature (Bailey *et al.*, 1980), but these growth rates are high compared to most field growth rates. In the field, age-0 maturation has been reported only in the southern end of the geographical range [France (Baglinière & Maisse, 1985); Spain (Ritchie, 1998); and Massachusetts, U.S.A., this study] where growth is generally faster than in the northern part of the range. In most of these cases, age-0 maturation rates are fairly low (around 5%). Our very high (74%) age-0 maturation rate in the Sawmill River in 1996 appears to have resulted from the combination of the catastrophic, localized flood, which reorganized the fish community, and the location of the river in the southern extent of the range, which permits growth sufficiently fast for age-0 maturation. Age-0 maturation rates were low in our two other study rivers in the year of the flood, and in the Sawmill River and the two other rivers in the subsequent year, providing support for the hypothesis that high maturation rates were facilitated by the flood.

It is hypothesized that the flood provided greater growth opportunity for the few fish that remained in the Sawmill River by sharply reducing competitors and that this fast growth (~0·5 mm day^{-1}) resulted in high maturation rates. The few fish that did mature in the Mill and the North rivers were relatively larger than immature fish and grew as fast (0·5 mm day^{-1}) as the fish in the Sawmill River, indicating a clear and possibly general link between age-0 growth rate and maturation. Differences in growth and parr maturation rates among rivers cannot be attributed to genetic differences among rivers because the fish in the three study rivers derived from randomly mixed hatchery fry.

Age-1 Atlantic salmon males that mature are commonly larger in the spring than fish that do not mature in freshwater (Lundqvist, 1980; Herbinger & Friars, 1992; Simpson, 1992; Berglund, 1995), suggesting a relationship between growth rate and maturation (Myers *et al.*, 1986; Thorpe, 1986). Early lipid accumulation also appears related to the incidence of maturation (Rowe *et al.*, 1991) and age-0 maturing fish in our rivers were probably able to store sufficient levels of lipid in the first few weeks after first feeding and following the flood to avoid inhibition of maturation (Thorpe, 1994). Because only a single sample for each fish was available, the interaction of the timing of rapid growth and maturation cannot be evaluated, but our field results showing a link between growth rate variability among rivers and maturation indicate clearly that rapid growth during the first year of life is directly related to age-0 maturation.

Effects of floods on movement (Valentin *et al*., 1994), mortality (Elwood & Waters, 1969; Lobón-Cerviá, 1996; Unwin, 1997) and community composition (Seegrist & Gard, 1972; Harrell, 1978; Matthews, 1986; Dolloff *et al*., 1994) of stream fishes have been documented, but less is known about the interaction between flood events and the direction and timing of life histories. Our results indicate a clear effect of the flood on movement/mortality and on community composition in the Sawmill River; the flood caused a brown and brook trout year-class failure and reduced the number of age-0 Atlantic salmon substantially. These survival and community composition changes also appear to have altered the direction of a crucial life history decision (parr maturation) in age-0 Atlantic salmon probably through their interactions with individual salmon growth rates.

The impact of floods on fish survival and community composition appears to vary widely and may depend on habitat complexity (Lobón-Cerviá, 1996), flood severity (Seegrist & Gard, 1972), flood timing and the relative susceptibility of different life stages (Seegrist & Gard, 1972; Hansen *et al*., 1989) and the species involved (Harrell, 1978). Habitat complexity can shield fish from displacement by floods (Pearsons *et al*., 1992). Some Atlantic salmon found refuge during the flood in the Sawmill River, where the substrate is dominated by large cobble and boulders. Age-0 brown and brook trout, however, were absent in the study sections following the flood. In the Sawmill River, trout sizes (mm ± S.D.) in a non-flood year (1997) for which data were available were not significantly different from salmon sizes in the autumn (brown = 65·4 ± 6·0, brook = 74·5 ± 7·0, salmon = 71·6 ± 5·4), suggesting that differences in fish sizes alone cannot account for retention differences between salmon and trout. In enclosure studies, dispersal rates of salmon were negatively related to water velocities but brown trout dispersal rates were positively related (Ottaway & Clarke, 1981; Crisp & Hurley, 1991), providing a possible species-dependent behavioural explanation for the differences we observed in the field. The mechanism resulting in differences between salmon and trout may be related to choice of station; the trout tend to hold station in the water column in typically slower water, potentially making them more susceptible to floods than salmon which are often in contact with the substrate in riffles (Heggenes & Saltveit, 1990; Gibson *et al*., 1993; Heggenes *et al*., 1995).

Lobón-Cerviá (1996) examined the impact of a severe flood on brown trout and Atlantic salmon populations in northern Spain. The severity of the two floods appears similar; the one in Spain was the most severe on record for the river. Lobón-Cerviá's results indicate that the flood had no effect on fish sizes or population numbers, which contrasts markedly with our results. Differences between the two studies may be due to the timing of the flood relative to fish life stages; the flood we describe occurred in June when the fish were approximately 35–50 mm, while the flood in Spain was in December when the fish were 70–100 mm. The smaller age-0 fish in our study, except for some salmon, apparently were not able to maintain position in the very high flows of the flood, whereas the larger fish in Spain could. Differences in response between our study and Lobón-Cerviá's study were also probably not due to habitat complexity; based on simple visual observation (B. H. Letcher, pers. obs.) our site appears more complex, with a wider variety of rock sizes than in the Spanish river. It is this complexity combined with salmon behaviour that may have allowed a small portion of the age-0 salmon to remain in the Sawmill River despite the high flows of the flood.

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