

Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry¹

S.P. Good, J.J. Dodson, M.G. Meekan, and D.A.J. Ryan

Abstract: We investigated the size-selective mortality of Atlantic salmon (*Salmo salar*) fry during two consecutive summers that differed markedly in weather conditions. We sampled fry shortly after emergence in June and at the end of August to compare the distributions of back-calculated body size at hatching by examining otolith microstructure. Size-selective mortality was observed in both summers; however, the direction and strength of mortality differed. During the drought conditions of 1995, selective mortality was relatively weak and directed towards the smaller fry in the population. During the flood conditions of 1996, selective mortality was relatively strong and directed towards the larger fry of the same population. Interannual variability in size-selective mortality contributed to significant differences in the mean size of fry at the end of their first summer of life. Size-selective mortality rates estimated from the shifts in fish length at hatching observed during the first summer of life were comparable with published estimates of total mortality of Atlantic salmon fry, indicating that early mortality may be largely size selective. Mortality associated with hydroclimatic events can select against either small or large fish and is a key determinant of mean size attained by the end of the first summer of life.

Résumé : Nous avons étudié la mortalité sélective, en fonction de la taille corporelle, des alevins du saumon de l'Atlantique (*Salmo salar*) durant deux étés consécutifs dont les conditions météorologiques ont été très différentes. Nous avons échantillonné des alevins après leur émergence au mois de juin et à la fin du mois d'août afin de comparer la distribution de leur taille corporelle à l'éclosion, recalculée après examen de la microstructure de leurs otolithes. L'intensité et la direction de la mortalité sélective selon la taille ont été différentes pour les deux années. Pendant les conditions de sécheresse en 1995, la mortalité sélective a été relativement faible et a affecté surtout les plus petits alevins de la population. Pendant les conditions de crue en 1996, la mortalité sélective a été plus forte et dirigée contre les alevins de plus grande taille de la même population. La variabilité inter-annuelle de la mortalité sélective a contribué aux différences significatives de la taille moyenne des alevins observée à la fin de leur premier été de vie. Les taux de mortalité sélective selon la taille, estimés à partir des changements de taille corporelle à l'éclosion entre juin et août, sont comparables aux estimations de la mortalité totale des alevins du saumon de l'Atlantique déjà publiées. Ceci suggère que la mortalité subie tôt dans la vie pourrait être sélective surtout en fonction de la taille. La mortalité associée aux événements hydroclimatiques peut être dirigée contre les petits ou les grands alevins et détermine la taille moyenne que les jeunes saumons peuvent atteindre à la fin de leur premier été de vie.

Introduction

It is generally thought that larger and faster growing juvenile fish are more likely to survive, with mortality being directed towards smaller, slower growing fish. Smaller fish are more susceptible to starvation and predation. Due to their lower social status and smaller size, they are often unable to successfully compete for food or shelter from predators (Miller et al. 1988). Predators of young fish are thought to preferentially seek out and consume smaller, more vulnera-

ble prey (Parker 1971; Juanes 1994). On the other hand, predators may preferentially choose larger juveniles, possibly due to the higher visibility and larger net energy gains associated with consuming larger prey (Pepin and Shears 1995; Gleason and Bengtson 1996a, 1996b).

In the first few weeks after hatching and emergence from the redd, young salmonids undergo size-selective mortality. Evidence for this process is derived from two sources: firstly, studies that have followed the fate of marked or known individuals (e.g., Elliott 1990), and secondly, growth

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histories that have been back-calculated from otoliths of fish where a single population or cohort has been repeatedly sampled through time (e.g., West and Larkin 1987). In all cases, the selection documented by these studies has been unidirectional, so that salmonids that were relatively small at hatching have undergone higher mortality than those that were large at hatching.

Behavioural studies of growth and size-selective mortality in salmonids have focused on the role of dominance status and competitive ability. Larger, faster growing fish occupy and defend the most profitable territories in the stream, while slower growing fish are forced into less suitable habitats and may eventually die (Elliott 1989a, 1989b). This process may not only influence mortality rates, but also the life history patterns of surviving fish. Individuals that are superior competitors and thus grow fastest may migrate to sea after only 1 year in freshwater, while slower growing fish delay migration, remaining in freshwater for at least a second year (Thorpe 1977, 1989; Wright et al. 1990).

It is unlikely, however, that behavioural traits are the sole factors influencing mortality, as the environment experienced by young fish may be an important determinant of the intensity and nature of mortality. Numerous studies have shown that meteorological and hydrological events can create environments that are unfavourable to early life history stages, so that only certain size-classes of fish survive. For example, Uphoff (1989) found that rainfall during the early postlarval stage of striped bass (*Morone saxatilis*) increased mortality among smaller individuals. Similarly, Logan (1985) found that increased flow and decreased water temperatures in the Hudson River negatively affected the growth of larval striped bass. Fish that had not yet reached a critical body size for survival under these conditions suffered high levels of mortality. In contrast, Angermeier and Karr (1984) and Pearsons et al. (1992) suggested that during flood events, size-selective mortality of stream fishes might be directed towards larger members of a cohort, as they may be unable to occupy habitats that provide physical barriers to high water velocity.

At present, few studies have examined the importance of environmental conditions in determining the extent and direction of size-selective mortality during the first year of life of Atlantic salmon (*Salmo salar*). Here, we investigate the size-selective mortality of salmon fry during two consecutive summers that differed markedly in weather conditions. In order to detect selective mortality, we back-calculated fish size at hatching from the otoliths of salmon cohorts sampled shortly after emergence at the end of June and again in late August during the summers of 1995 and 1996. Shifts in distribution of size at hatching between June and August samples were used as evidence that the cohort had undergone selective mortality (e.g., West and Larkin 1987; Meekan et al. 1998a, 1998b).

Total mortality is composed of size-selective mortality and random mortality. Random mortality is the process of removing fish from the population that is not related to size. Few studies have attempted to evaluate the relative importance of these two sources of mortality in salmon populations. We estimated the levels of size-selective mortality required to produce the shifts in the distribution of size at hatching documented in our study and compared them with

independent estimates of total mortality among salmon fry. Estimates of size-selective mortality rate comparable with independent estimates of total mortality rate would indicate that mortality was largely size selective. Such a demonstration would also refute the notion that shifts in the distribution of size at hatching between samples taken on two separate occasions may occur as a result of selection based on traits other than size (Mosegaard 1990; Metcalfe et al. 1992; but see Meekan et al. (1998a, 1998b) for an alternative view).

Materials and methods

Study site and sample collection

Atlantic salmon fry were sampled in the Ste-Marguerite River system in eastern Québec, Canada, during the summers of 1995 and 1996 (Fig. 1). Fry were collected from spawning/nursery grounds shortly after emergence and at the end of the summer. Spawning ground substrate was composed primarily of small gravel particles (diameter ranging from 20 to 30 mm) and of dispersed small boulders located mainly at the tails of pools and near the beginning of riffles. They are characterized by shallow (10–40 cm deep) and moderately fast running ($50 \text{ cm}\cdot\text{s}^{-1}$) water (reviewed in Stanley and Trial 1995). Nursery grounds are located in slower running water (end of riffles) where food is abundant and well distributed in the water column. Sampling was conducted at three spawning/nursery sites in 1995 and five such sites in 1996, two of which corresponded to sampling locations in 1995. In 1995, the three sites were located on the northeast branch at kilometre 6 (NE 06) just below a migratory fish ladder and on the principal branch at kilometre 35 (PR 35) and kilometre 58 (PR 58). In 1996, sites NE 06 and PR 58 were resampled. The spawning/nursery site located at PR 35 was abandoned in 1996, as stocking of fry produced in an in situ incubator may have confounded comparisons of fish length distributions at hatching calculated for fry sampled at emergence and again at the end of the summer. We thus sampled downstream at the next spawning/nursery area located at kilometre 27 (PR 27). New sites were added on the northeast branch at kilometre 28 (NE 28) just below the upstream limit of salmon migration and on the principal branch at kilometre 81 (PR 81). At each site, 20 fry were collected shortly after emergence at the end of June and then again at the end of August by electrofishing a 100-m^2 grid ($5 \times 20 \text{ m}$) laid out over the spawning/nursery ground to cover riffle and channel habitats. If 20 fry were not captured, a second 100-m^2 grid was laid out. In the laboratory, fish were measured using a dissecting microscope and image analysis system.

Otolith preparation

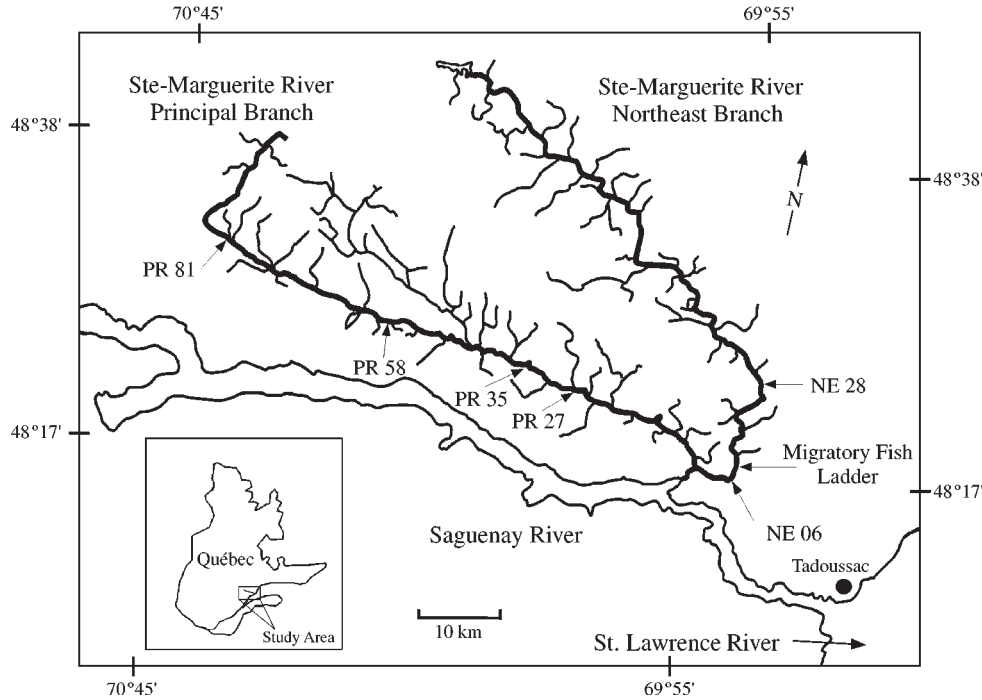
Left and right sagittal otoliths were removed from fish under a dissecting microscope equipped with a polarized light source. Otoliths were cleaned and glued to glass slides with Super Glue®. Once dry, they were ground on lapping film to the plane of the core and viewed using a compound microscope linked to an image analysis system (OPTIMAS). Growth increments were counted and measured along a constant axis from the centre to the edge of the otolith. The area within the hatch mark and the total area of the otolith were also measured.

Data analysis

Backcalculation and size-selective mortality

The standard lengths of young salmon at hatching and yolk sac absorption were back-calculated from fish collected in June and August of 1995 and 1996 using the biological intercept technique (Campana and Jones 1992). The assumptions of the back-calculation technique (daily increment formation and proportional-

Fig. 1. Location of the Ste-Marguerite River, Québec, Canada, identifying the sites sampled in the summers of 1995 and 1996.



ity between the otolith and somatic growth) have previously been validated for Atlantic salmon fry in the weeks immediately following hatching by Meekan et al. (1998a). They also demonstrated that distinctive checks are laid down on the otoliths of young salmon at hatching and then again at yolk-sac absorption, allowing the timing of these events to be determined. In young Atlantic salmon approaching the end of their first summer of life, daily increment formation and proportionality between otolith and somatic growth were validated by Wright et al. (1990). However, they also found that otolith and somatic growth might not be proportional in fish undergoing smoltification. In the Ste-Marguerite River system, no young salmon undergo smoltification at the age of 1+.

A two-factor analysis of variance (ANOVA) was used to evaluate changes in size-selective mortality between years. Site was included as a blocking effect, allowing for consistent differences in size at hatching between sites. Year (1995 or 1996), sampling period (June or August), and the interaction between year and sample period were included to test for changes in the size at hatching due to the main effects of year, sampling period, and, most importantly, the interaction between year and sampling period. The interaction is the most important term because it tests for changes in selective mortality between years adjusted for differences between sites. Comparisons of the means were carried out using the pairwise *t* tests at the 5% level of significance, only if the overall comparison of the interaction or main effects were significant at the 5% level (Steel and Torrie 1981). A residual analysis was carried out to ensure that there was no evidence that the assumptions of ANOVA were violated.

Generation of survivorship curves and mortality estimates

Frequency distributions of size at hatching of fish collected in June and August were modelled as the product of two multinomial distributions:

$$L(\pi_{01}, \dots, \pi_{0k}, \pi_{11}, \dots, \pi_{1k}) = \binom{n_0}{y_{01}, \dots, y_{0k}} \pi_{01}^{y_{01}} \dots \pi_{0k}^{y_{0k}} \cdot \binom{n_1}{y_{11}, \dots, y_{1k}} \pi_{11}^{y_{11}} \dots \pi_{1k}^{y_{1k}}$$

where π_{ij} is the probability of a fish occurring in the *j*th size-class at hatching (*j* = 1, ..., *k*), *k* is the number of size-classes in the *i*th time period (*i* = 0, prior to the period of interest, or *i* = 1, after the period of interest), *n_i* is the total number of fish captured in the *i*th period, and *y_{ij}* is the number of fish captured in the *i*th time period that were in size-class *j* at hatching. Since the same cohort was sampled in both time periods, the probability of a fish originating from hatch size-class *j* at time 1 must be related to the probability of a fish originating from hatch size-class *j* at time 0 and the probability of a fish surviving. The relationships between these variables were modelled as

$$\pi_{1j} = \frac{\pi_{0j} S_j R}{\sum_{j=1}^k \pi_{0j} S_j R}$$

where *S_j* represents the probability that a fish of hatch size *j* survives all size-selective mortality and *R* represents the probability that a fish survives all nonselective (random relative to the size of fish at hatching) mortality that occurs during the period of observation. For the purposes of this study, *S_j* was modelled as a monotonic sigmoid curve:

$$S_j = \frac{e^{\alpha + \beta x_j}}{1 + e^{\alpha + \beta x_j}}$$

where the parameters α and β corresponded to the level and rate of change of the curve, respectively. In this case, a large positive value of β indicates a severe positive size-selective process, while a zero value of β indicates that mortality is not size selective.

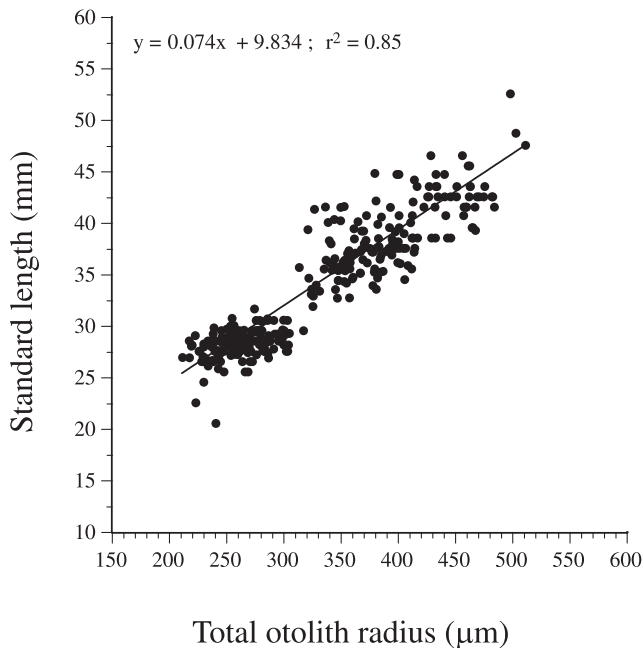
In this model, only the product of *S_j**R* can be estimated, since without knowledge of the process causing the death of an individual fish, *S_j* and *R* cannot be estimated. However, if it is assumed that *R* = 1.0 (i.e., that the cohort undergoes only size-selective mortality), then the maximum amount of selective mortality that can occur for a given size-class (*S_j⁰*) can be estimated.

Survivorship curves and estimates of size-selective mortality were modelled for the data sets from each site in both years of the study as well as for data sets pooled within years. From each of

Table 1. Average monthly precipitation, river discharge, and air temperature for the Ste-Marguerite River.

	Average precipitation (mm)			Average discharge (m ³ ·s ⁻¹)			Average temperature (°C)		
	1974–1994	1995	1996	1974–1994	1995	1996	1974–1994	1995	1996
Jan.	78.9	107.0	74.0	7.56	11.81	85.31	-10.9	-8.4	-12.4
Feb.	62.5	89.0	126.0	6.11	8.43	75.40	-8.4	-10.2	-9.7
Mar.	56.7	99.0	10.0	5.94	5.90	67.24	-5.4	-5.7	-5.0
Apr.	71.4	102.0	142.4	44.71	23.96	102.16	7.6	5.7	7.4
May	103.2	115.2	89.8	111.59	134.72	135.26	15.4	15.2	16.1
June	105.5	43.0	91.6	42.13	41.01	na	20.8	24.9	23.4
July	131.8	83.0	303.7	29.02	12.17	148.82	23.2	26.2	22.9
Aug.	112.5	160.0	29.6	22.44	6.04	29.08	21.8	25.1	24.7
Sept.	117.7	113.3	149.2	22.17	8.85	36.03	15.6	16.1	18.2
Oct.	105.9	99.7	135.0	32.95	33.54	na	8.8	12.3	9.0
Nov.	93.8	62.0	131.4	25.12	50.17	na	4.0	4.2	5.8
Dec.	99.2	43.0	114.0	14.12	87.11	na	-7.5	-7.4	-4.9

Note: May–August represent summer values. na, not available.

Fig. 2. Correlation between standard length of Atlantic salmon fry and otolith radius for 1995 and 1996.

these data sets, 1000 bootstrap samples were generated and the size-selective survivorship curve estimated using a grid search (Draper and Smith 1981) for the parameters α and β . The parameters π_{ij} were not included in this process, as this would have required a grid search of 14 parameters, which was beyond the computational resources available to the study. While alternative techniques of maximizing likelihoods were examined, (e.g., gradient methods), these were rejected because they failed to converge on estimates.

The maximum mortality (MM) undergone by a cohort was estimated from the following equation:

$$MM_j = \frac{\sum_{j=1}^k S_{ij}'' \pi_{0j}}{\sum_{j=1}^k \pi_{0j}}$$

Estimates were calculated for each of the 1000 bootstrap samples and the median, 5th, and 95th percentiles then calculated for each site and for each year averaged among sites.

Results

Environmental conditions

Weather patterns during the summers of 1995 and 1996 were among the most distinct ever recorded in the Saguenay – Lac St. Jean region of Québec (Table 1). Drought-like conditions occurred during much of the spring and summer of 1995. Air temperatures in June through August were several degrees higher than the average for the previous 20 years (1974–1994). Average monthly precipitation was low, especially during June and July, resulting in a severe reduction in river flow from mid-June until the end of September. In contrast, the largest flood event in Québec's recorded history occurred on July 20, 1996. In 1996, rainfall for the month of June was more than double that of June 1995, and July's rainfall was almost four times that of July 1995 and twice that of the previous 20-year average. As a result, river discharges for July and August 1996 were 12 times and five times more than in July and August 1995, respectively (Table 1).

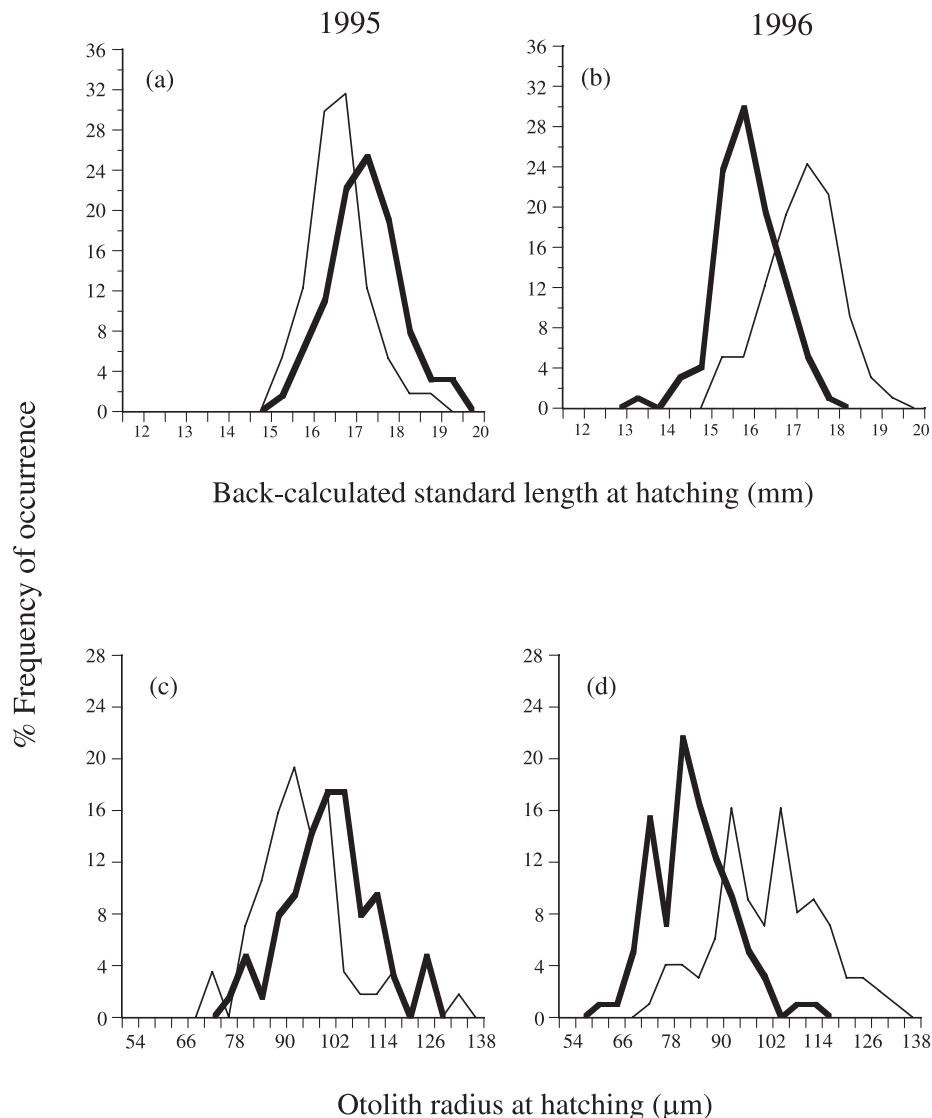
Otolith and somatic growth

There was a strong correlation between otolith radius and standard length of young salmon in both years of sampling. As an analysis of covariance found no significant differences between regression lines calculated for each year ($p = 0.35$), data sets were pooled and a single regression calculated ($r^2 = 0.85$, $n = 316$) (Fig. 2).

Variability in size-selective mortality

Standard lengths at hatching were back-calculated for fish collected in June and August for both 1995 and 1996. Back-calculation results revealed significant shifts in standard length and otolith radius at hatching between the June and August samples for both years of sampling (Fig. 3). In 1995, mean otolith radius at hatching of fish sampled in June was 93.26 μm (SE = 1.7 μm), while August fish had a larger mean otolith radius at hatching of 99.64 μm (SE = 1.7 μm). During the following summer, this pattern was reversed, with the otolith radius at hatching of fish collected in June averaging

Fig. 3. Comparisons between the size distributions of (a and b) standard length and (c and d) otolith radii at hatching for Atlantic salmon fry sampled in June (thin lines; $n = 57$ in 1995 and $n = 99$ in 1996) and August (thick lines; $n = 63$ in 1995 and $n = 97$ in 1996).



100.9 μm (SE = 1.2 μm) and of those collected in August averaging 82.3 μm (SE = 1.2 μm) at hatching. Corresponding shifts were also recorded in average standard length at hatching between these months (Fig. 3). The two-factor ANOVA revealed significant changes in back-calculated otolith radius and fish length due to the interaction between year and sampling period ($p < 0.0001$). There were thus significant changes in selective mortality between years adjusted for differences between sites. Mean size (otolith radius and standard length) at hatching for fish collected in June and August were significantly different in both years ($p < 0.001$).

The change in the direction of size-selective mortality of salmon fry from 1995 to 1996 contributed to large differences in the size distributions of fry at the end of the summer (Fig. 4). The 1995 cohort attained a significantly greater mean size by the end of their first growing season than did the 1996 cohort (ANOVA, $p < 0.0001$).

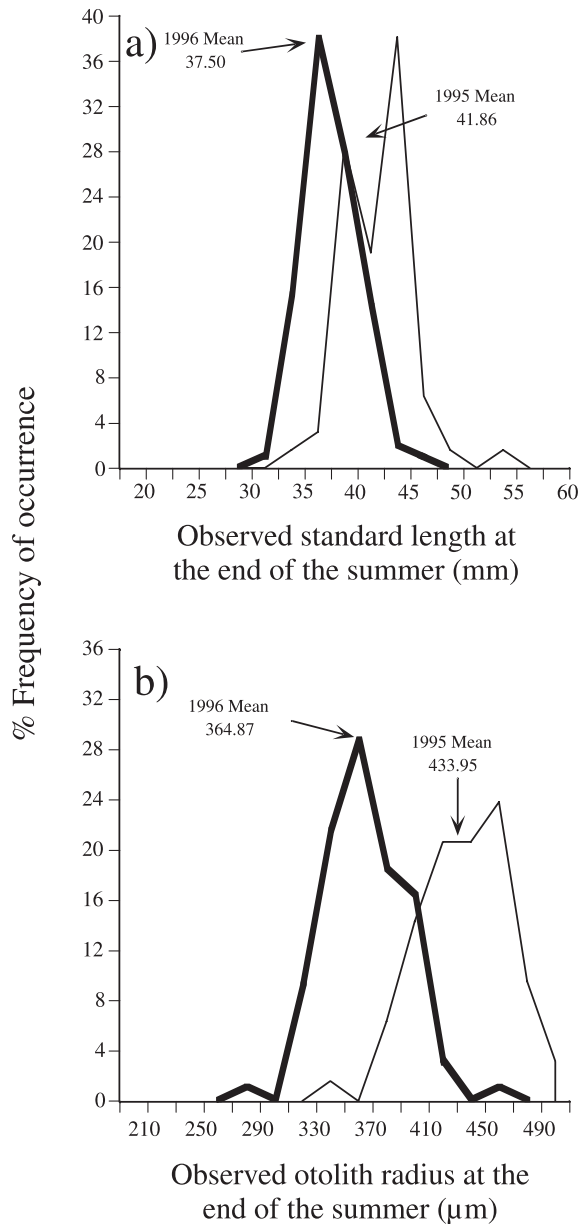
Survivorship curves and mortality rates

Patterns in survivorship were consistent among sites

within each year (Table 2; Fig. 5). The slope of survivorship curves tended to be more gentle in 1995 than in 1996, indicating that the gradient in survivorship between large and small individuals (i.e., size selectivity) was relatively weak in 1995. When size-selective mortality is weak, a small proportion of the bootstrapped estimates of size-selective mortality rates may be close to zero. As a result, the distribution of mortality estimates in 1995 was strongly bimodal for PR 35 and weakly so for NE 06, the first mode being close to zero. As a result, large error estimates for survivorship curves and mortality rates were estimated in 1995 (Table 2; Fig. 5). Therefore, although mortality rates estimated from combining all sites sampled in 1995 revealed that fry suffered a median mortality rate of 58% between June and August (Table 2), the 5th and 95th percentile limits indicated that size-selective mortality rates between 26 and 78% could have been responsible for the observed shifts in otolith size at hatching between June and August.

In contrast, the slope of survivorship curves tended to be more pronounced in 1996 than in 1995, indicating that size-

Fig. 4. Percent frequency of occurrence for Atlantic salmon (a) standard lengths and (b) otolith radii observed at the end of the summer (August) for both 1995 and 1996 sampling periods. The thin lines represent 1995 ($n = 63$) and the thick lines represent 1996 ($n = 97$).



selective mortality was relatively stronger in 1996. The distributions of bootstrapped estimates of size-selective mortality rates for individual and combined sites were unimodal and error estimates were narrower for survivorship curves and mortality rates calculated from sites sampled in 1996 (Table 2; Fig. 5). Overall estimated mortality rate in 1996 revealed that the cohort suffered a median size-selective mortality rate of 82% between June and August (Table 2). The 5th and 95th percentile limits indicated that size-selective mortality rates between 72 and 88% could have been responsible for the observed shifts in otolith size at hatching between June and August 1996.

Table 2. Estimated summer mortality rates (median, 5th, and 95th percentiles) of Atlantic salmon fry sampled at three sites in 1995 and five sites in 1996 and overall estimates within years in the Ste-Marguerite River.

Site	Year	Median	5%	95%
NE 06	1995	0.592	0.050	0.857
PR 58	1995	0.594	0.260	0.864
PR 35	1995	0.740	0.000	0.894
Overall	1995	0.581	0.266	0.789
NE 06	1996	0.732	0.470	0.906
PR 58	1996	0.814	0.608	0.948
PR 27	1996	0.979	0.951	0.994
PR 81	1996	0.818	0.629	0.954
NE 28	1996	0.802	0.395	0.949
Overall	1996	0.818	0.729	0.884

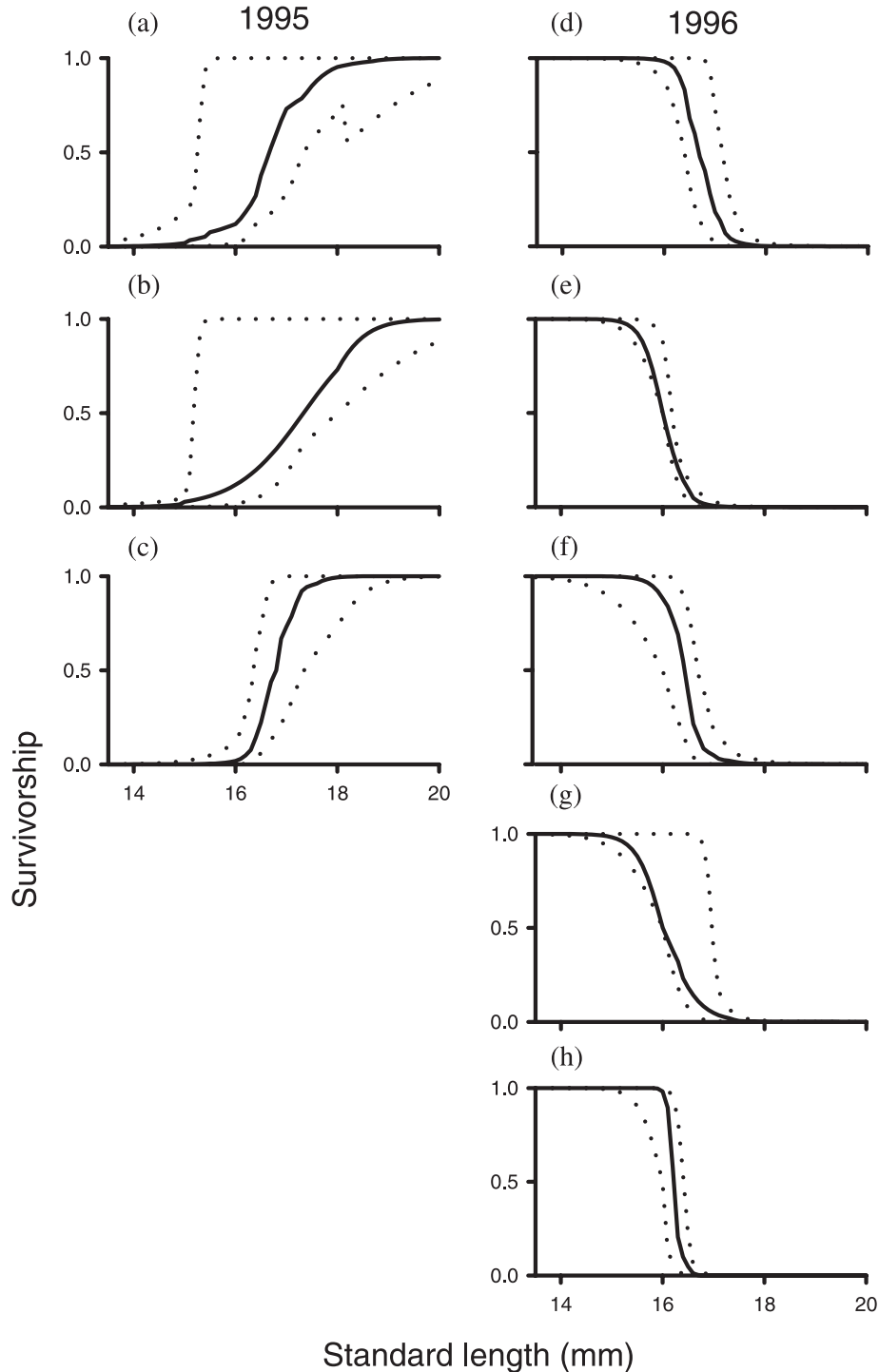
Discussion

High levels of size-selective mortality occurred among the fry of Atlantic salmon sampled in the Ste-Marguerite River during the summers of 1995 and 1996. However, the direction of size-selective mortality reversed over the two years of the study. In 1995, salmon fry sampled in August were significantly larger at hatching than those sampled in June, indicating that mortality rates were greater for the smaller individuals in the population. This observation conforms to the widely held view that large size is more advantageous to survival of young fish than small size (e.g., the bigger-is-better hypothesis; Miller et al. 1988). It is also consistent with the observation that mortality rates were greater for the smaller individuals of a cohort of sockeye salmon (*Oncorhynchus nerka*) (West and Larkin 1987; Meekan et al. 1998b). However, the bigger-is-better hypothesis was not supported by results from the summer of 1996. In that year, fish collected in August were significantly smaller at hatching than those collected in June, implying that there was relatively strong selection against larger individuals over the summer of 1996.

Gleason and Bengston (1996a) provided additional evidence that bigger is not necessarily better for the survival of young fishes. These workers found that size-selective predation by juvenile bluefish (*Pomatomus saltatrix*) was consistently directed towards the larger individuals of a population of inland silverside (*Menidia beryllina*). Their results imply that the outcomes of size-selective mortality may vary due to the identity of the prey and the foraging tactics of the predator. The results of our study are novel, however, in that they demonstrate that the direction of size-selective mortality can also differ between years for the same population.

As patterns of survivorship were consistent among sites within years, the contrasting patterns of size-selective mortality documented between 1995 and 1996 occurred at the scale of the entire river. For this reason, it seems likely that the major changes in weather and river flows that occurred between the two years were responsible for the different mortality patterns. Numerous studies have demonstrated that river flow is an important factor directly influencing the survival of the early life history stages of fluvial fishes. Crecco

Fig. 5. Estimated survivorship curves of Atlantic salmon fry sampled from the Ste. Marguerite River in 1995 and 1996. (a) NE 06; (b) PR 35; (c) PR 58); (d) NE 06; (e) PR 27; (f) PR 58; (g) NE 28; (h) PR 81. Dotted lines represent the 5th and 95th percentiles.



and Savoy (1987) showed that temporal changes in river flow and temperature coincident with early larval development regulated the feeding success of American shad (*Alosa sapidissima*). They found that 80–87% of the annual variability in recruitment over a 14-year period was explained by variability in May and June River flows and monthly rainfall. In the case of Atlantic salmon, river discharge during the weeks and months following emergence influences

fry survival and year-class strength (Frenette et al. 1984; Gibson and Myers 1988; Jensen and Johnsen 1999).

It is possible that the unusually dry conditions of 1995 may have accentuated mortality among the smallest salmon fry. Tremblay et al. (1993) studied habitat use by Atlantic salmon fry in the Trinité River on Québec’s North Shore. They found that habitat preferences were strongly size dependent. Small salmon fry (30–40 mm) occupied shallow

riffle areas, while larger fry (40–50 mm) occupied the deeper channels. In the Ste-Marguerite River, low-flow conditions in 1995 caused riffles to become shallower than normal, or even completely exposed. The smaller fry that occupied these areas may have been forced into deeper channels with the larger fry. More intense competition between salmon in these habitats may have increased the mortality rate of smaller, competitively inferior fish.

In contrast, smaller fry had the advantage during the major flood of 1996. During floods, fish may seek refuges that provide barriers to high water velocity (Angermeier and Karr 1984; Pearsons et al. 1992; Lonzarich and Quinn 1995). We know from trap net samples taken in the estuary that large numbers of 1+ and 2+ parr were swept out of the Ste-Marguerite River by the 1996 flood (J. Dodson, CIRSA, unpublished data). Large fry may have suffered a similar fate but were too small to be captured in our trap nets. As small fry may have already been associated with the shallowest riffles, these fish may have been spared the strongest currents occurring in deeper channels. Alternatively, they may have been able to exploit refuges from the current that were unavailable to larger fish due to their size.

Irrespective of the mechanism involved, it is evident that selective mortality can influence the mean length attained by young salmon at the end of the summer and thus their recruitment to later life history stages. There is evidence that this process plays a similar role in other species. Cargnelli and Gross (1996) found that overwinter survival of large-bodied young-of-the-year bluegill (*Lepomis macrochirus*) was 231% higher than for fish that were comparatively small at the end of their first summer of life. This survival translated into higher recruitment rates of large individuals to the population the following year. Similarly, Griffiths and Kirkwood (1995) found that overwinter survival of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) was highly dependent on size at age at the end of the summer.

The apparent difference in growth rate that we observed between years was a reflection of the size-selective mortality that was imposed each year. It appeared that fish sampled in 1995 had higher growth rates than fish in 1996; however, selection was against smaller fish in 1995 and larger fish in 1996. Therefore, growth rates were high in 1995 because larger, faster growing fish survived, while in 1996, growth rate was low because the small fish were the survivors. Although variables such as temperature and food availability influence growth, individual members of a cohort sampled at the end of the growing season are the survivors of size-selective mortality imposed on the population at an earlier time.

Heritability for growth rate in salmonid fishes ranges from 0.2 to 0.3, with a coefficient of variation of 20–30%, implying that it is possible to obtain large responses from selection for growth (Gjedrem 2000). The maintenance of high variance in growth rates of wild Atlantic salmon despite the potential for large responses from selection for growth may in part be related to the observation that survival advantages accrue to either faster or slower growing fish depending on environmental conditions.

The levels of size-selective mortality estimated from the shifts in otolith size and fish length at hatching observed during the first summer of life in 1995 and 1996 are compa-

table with independent estimates of total mortality rate. Direct estimates of total mortality of salmon fry are available for fry that have been stocked as part of restoration and enhancement programs for Atlantic salmon. In a tributary stream of the Connecticut River, fry measuring between 25 and 32 mm released in May at densities of between 100 and 150 fry·100 m⁻² experienced summer mortalities of 65% in 1982, 98% in 1983, 82% in 1984, and 72% in 1985 (Orciari et al. 1994). Excluding the very high mortality of 1983 associated with the stocking of fry from an Icelandic stock, the mean summer mortality of stocked Penobscot-strain fry measured over a period of 3 years was 73% (SD = 8.5%). In the West River, Vermont, fry measuring 25–30 mm were released during May in successive years at densities ranging from approximately 50 to 150 fry·100 m⁻². These cohorts experienced summer mortalities of 85% in 1984, 94% in 1985, and 83% in 1986 (McMenemy 1995). Stocking at much lower densities (approximately 30 fry·100 m⁻²) resulted in a mean summer mortality of 58% (SD = 8.1%) over a 5-year period. It is obvious that comparisons between these measurements and our estimated mortality rates are confounded by various factors (e.g., differences in years of observation and environmental conditions, the use of hatchery-reared as opposed to naturally produced fry, and different dates of sampling and release). Nevertheless, in the absence of more appropriate in situ measurements of fry mortality, size-selective mortality rates estimated from the shifts in otolith and fish size distributions at hatching documented in the present study were within the range of total mortalities measured in the field. The approximate agreement between observed total mortalities and our estimates of maximum size-selective mortality indicates that total mortality rates of salmon fry may be largely size selective.

Our results show that the prevailing view that size at age in young salmon is largely controlled by competitive ability acting on growth rate is overly simplistic. Regardless of inherent superiority, mortality associated with hydroclimatic events may select against either small or large fish and is a key determinant of mean size attained by the end of the first summer of life and subsequent recruitment to the older life history stages of Atlantic salmon.

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