Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*

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Abstract: Based upon published and unpublished data compiled for 275 populations, we describe large-scale spatial and temporal patterns in Atlantic salmon, *Salmo salar*, life history and model these data to evaluate how changes to life history influence optimal growth rate thresholds for sea age at maturity. Population means (ranges in parentheses) describe the following for salmon throughout its range: smolt length = 14.8 cm (10.5–21.5 cm); smolt age = 2.91 years (1.04–5.85 years); egg-to-smolt survival = 1.5% (0.2–3.2%); grilse length = 56.8 cm (48.5–70.0 cm); sea age at maturity = 1.60 years (1.00–2.64 years); smolt-to-grilse survival = 7.4% (1.3–17.5%). Growth rate thresholds specify the length increase between the smolt and grilse stages above which reproduction after one winter at sea is favoured over later maturity. Our simulations indicated that increased growth generally favours earlier, but never delayed, maturity. Optimal growth rate thresholds for sea age at maturity are highly sensitive to survival but only moderately sensitive to fecundity, smolt size, and smolt age. Depending on an individual's growth rate at sea, early maturity is favoured by decreased smolt age or by increased smolt length, fecundity, or survival (freshwater or marine). We suggest that future Atlantic salmon life history research focus upon reaction norms and growth rate thresholds for age at maturity, demographic and genetic consequences of male parr maturation, and the origin and maintenance of coexisting anadromous and nonanadromous life history polymorphisms.

Résumé : À partir de données publiées et non publiées relatives à 275 populations, nous décrivons des profils spatiaux et temporels à grande échelle du cycle vital du saumon de l'Atlantique, *Salmo salar*, et modélisons ces données pour évaluer comment les changements dans le cycle vital influent sur les seuils de taux de croissance optimaux relatifs à la durée du séjour en mer avant la maturité. Les moyennes (fourchettes entre parenthèses) de divers paramètres des populations du saumon dans l'ensemble de son aire de répartition sont les suivantes : longueur des smolts = 14,8 cm (10,5-21,5 cm); âge des smolts = 2,91 ans (1,04–5,85 ans); taux de survie de l'oeuf au stade de smolt = 1,5 % (0,2–3,2 %); longueur des grilses = 56,8 m (48,5–70,0 cm); durée du séjour en mer avant la maturité = 1,60 an (1,00–2,64 an); taux de survie du smolt au grilse = 7,4 % (1,3–17,5 %). Les seuils de taux de croissance indiquent l'accroissement de longueur du stade de smolt au stade de grils au-delà duquel la reproduction après un hiver en mer est favorisée par rapport à une maturité plus tardive. Nos simluations ont indiqué qu'une croissance accrue donne généralement lieu à une maturité hâtive, et jamais à une maturité retardée. Les seuils de croissance optimaux relatifs à la durée du séjour en mer avant la maturité sont hautement sensibles à la survie, mais seulement modérément sensibles à la fécondité, à la taille des smolts et à l'âge des smolts. Selon le taux de croissance individuel en mer, la maturité sera atteinte plus rapidement plus l'âge des smolts est bas et plus la longueur, la fécondité et le taux de survie (eau douce ou eau salée) de ces derniers sont élevés. Nous proposons de concentrer les recherches futures concernant le cycle vital du saumon atlantique sur les normes de réaction et les seuils de taux de croissance relatifs à la durée du séjour en mer avant la maturité, sur la démographie et les conséquences génétiques de la maturation des tacons mâles, et sur l'origine et le maintien des polymorphismes coexistants dans les cycles vitaux anadromes et non anadromes.

[Traduit par la Rédaction]

Introduction

Life history variation in Atlantic salmon, *Salmo salar*, is matched by few vertebrates. Age at maturity ranges one order of magnitude from 1 year for male parr in France (Baglinière and Maisse 1985) to 10 years for some anadromous salmon in northern Québec (Power 1969; Robitaille et al. 1986). Size at maturity varies 14-fold from less than 7 cm for males in Newfoundland rivers (Hutchings 1986; Gibson et al. 1996) to more than 100 cm for females in Norway's River Vosso (Huitfeldt-Kaas 1946). Fecundity can vary 500-fold from fewer than 40 eggs per female in wholly freshwater populations (Gibson et al. 1996) to 18 000 eggs per female in anadromous populations (e.g., Margaree River, Nova Scotia; Canadian Department of Fisheries and Oceans (DFO) unpublished data). Offspring size, measured as egg volume, varies more than three-fold from 48 mm^3 for landlocked salmon, or ouananiche, (4.5 mm egg diameter; Gibson et al. 1996) to 171 mm^3 in anadromous individuals (6.9 mm diameter for salmon in Restigouche River, New Brunswick/Québec; DFO unpublished data).

Since the early experimental (e.g., Shaw 1836) and descriptive work on Atlantic salmon life histories in Europe (e.g., Brown 1862; Miescher-Rusch 1883; Calderwood 1906; Dahl 1910) and in North America (Atkins 1884;

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Chambers 1896; Huntsman 1931), considerable research has been directed to identifying the causal basis for population differences in the ages at which salmon migrate to and return from the sea (e.g., Schaffer and Elson 1975; Power 1981; Myers and Hutchings 1987; Metcalfe and Thorpe 1990; see also the review by Gardner (1976) and the papers contained in Meerburg (1986)), and for population differences in the incidence of early maturity among males (e.g., Jones 1959; Thorpe 1975; Thorpe et al. 1983; Myers 1984; Myers et al. 1986; Hutchings and Myers 1988, 1994; see review by Fleming 1996). Within this research milieu, our objectives were to describe spatial and temporal life history variation throughout the geographical range of Atlantic salmon and, using the life history trait associations that emerged, to predict optimal responses in sea age at maturity effected by changes to growth rate and survival.

Naturally reproducing Atlantic salmon exist throughout the North Atlantic coasts from Maine to northern Labrador in North America, throughout Iceland, Ireland, and Great Britain, and in mainland Europe from northern Spain to the Kara River, Russia (Berg 1948; Nielson 1961; Scott and Crossman 1973). Anadromous individuals typically spend 20–50% of their life at sea; nonanadromous populations spend their entire life in fresh water. Females bury fertilized eggs in the substrate of freshwater rivers and streams in autumn. After hatching, the young obtain nourishment from a yolk sac before emerging from the substrate in spring. After periods of usually 1 to 5 years in fresh water as parr, anadromous individuals emigrate as smolts and generally spend 1 or 2 (rarely 3 or 4) years at sea before returning to fresh water to spawn. In populations for which migration to sea is not prevented by physical barriers, females are usually anadromous, although there are numerous exceptions in Newfoundland (Hutchings 1986) and some elsewhere (Baglinière and Masse 1985; also see Fleming 1996). In contrast, males often reproduce after 1 to 4 years in fresh water, after which they may or may not migrate to sea. Estimates of post-reproductive, overwinter survival for mature male parr range from less than 15% (calculated from Hutchings 1985, 1986) to 40% (Myers 1984; Hutchings and Myers 1994); those for anadromous males and females are often less than 15% (Bley and Moring 1988).

There are several means by which one can practically assess the adaptive significance of life history variation in fish, each with its limitations and advantages. These include field (e.g., Reznick et al. 1990; Fleming and Gross 1993) or laboratory manipulation experiments (e.g., Metcalfe et al. 1989; Hutchings 1991), within- (e.g., Riddell and Leggett 1981; Sandlund et al. 1992) and among-population comparisons in the field (e.g., Leggett and Carscadden 1978; Hutchings 1993; Fox 1994), and analyses of data from the literature on life history differences within and among species (e.g., Beverton and Holt 1959; Schaffer and Elson 1975; Roff 1984; Hutchings and Morris 1985). We adopt the last of these to describe and analyse Atlantic salmon life history variation throughout the species' geographical range.

An extensive among-population study allows one to examine life history differences throughout the entire range of variation expressed by a species, thus encompassing the boundaries or potential limits of phenotypic variation. As a consequence, among-population correlations between life history traits can delineate phenotypic patterns to which any general life history model of Atlantic salmon should ascribe (Marschall et al. 1998). Limitations to analyzing data from the literature include practical issues such as (1) an inability to quantify measurement errors, (2) unknown sample sizes, and (3) varying numbers of years and time periods over which population means are estimated. There is also the theoretical caveat that associations between life history traits at the population level need not reflect natural selection. This is why we supplemented our analyses with empirically based simulations to predict optimal life history responses within populations.

Data analysis

Published and unpublished data were compiled for 13 life history-related variables for 275 Atlantic salmon populations (Table 1; Appendices 1–2) and grouped by region: U.S.A., Québec, Newfoundland, Canadian Maritimes, Iceland, Ireland, Great Britain, mainland Europe, Norway, Sweden, Russia. Naturally, there are a number of means by which populations could be classified. One could argue, for example, that latitudinal groupings might be appropriate. However, given the extraordinary life history variation in salmonids that can exist within narrow ranges of latitude, e.g., incidence of male parr maturity in Atlantic salmon (Myers et al. 1986), survival and egg size in brook trout, *Salvelinus fontinalis* (Hutchings 1991, 1993), and age and size at maturity in Arctic char, *S. alpinus*, (Skúlason et al. 1998), even traditional latitudinal classifications can be problematic. The geographical categories in which we have grouped salmon populations approximate those used by national (e.g., Canada's DFO) and international (e.g., ICES) management agencies.

Rather than depicting the current status of specific populations, the data presented in Appendix 1 are intended to reflect the range of natural variation in Atlantic salmon life history. For many populations, data have been obtained from comparatively recent statistics (e.g., Newfoundland populations, 1950s to 1990s), for others they have not (e.g., England, 1920s to 1950s). With few exceptions (e.g., the American populations), data were collated for populations that are maintained by naturally reproducing salmon. Our data compilation should not be considered exhaustive; there are assuredly data in the secondary literature that we have overlooked. It might be advantageous to use the present initiative as a basis for constructing a web site devoted to Atlantic salmon population data worldwide.

Box-and-whisker plots were used to illustrate geographical differences in life history. These plots are particularly useful for such a comparison because they allow for simple visual inspection of medians (indicated by a bar in each box; Figs. 1–6), data composition (the lower and upper ends of each box represent the 25% and 75% quartiles, respectively), skewness (the position of the median relative to the ends of each box), and data range (the "whiskers" represent lines extending from the top and bottom of each box to adjacent data no more than 1.5 times the inter-quartile range; values beyond this range are indicated by solid circles).

Table 1. Geographical areas and number of populations included in the among-population life history analyses.

Region	Number of populations	Subregion	Number of populations by subregion
Iceland	78		
Newfoundland (Canada)	51	Newfoundland	47
		Labrador	4
Norway	37		
Québec (Canada)	36		
Maritimes (Canada)	19	Nova Scotia	10
		New Brunswick	9
Great Britain	18	Scotland	13
		England and Wales	5
Europe	15	France	11
		Spain	4
United States	8		
Ireland	6		
Sweden	5		
Russia	2		
Finland	1		
Total	275		

One-way analysis of variance was used to assess the significance of regional differences in life history trait means, calculated as the average of population means within a given region (Table 2). The regions included in each analysis depended upon data availability. Statistical significance was based upon 1000 randomizations of the data (Manly 1991).

Smolt-to-grilse survival estimates were modified to reflect population differences in sea age at maturity. Unless a population is composed entirely of grilse (i.e., 1SW salmon), survival estimates based upon the numbers of returning grilse relative to the number of smolts that emigrated the previous year will underestimate smolt-to-grilse survival. This is because some proportion of smolts are “pre-determined” to return as multi-sea-winter fish. To account for this bias, we divided reported smolt-to-grilse survival estimates by the percentage of grilse in the population. It should be noted, however, that our estimates of percent grilse (i.e., (*n* grilse) / (*n* grilse + *n* multi-sea-winter salmon)) will be overestimated with the degree of overestimation declining with the true percentage of grilse in a population. The reason for this overestimation is the absence of data on the number of multi-sea-winter salmon that died prior to returning to their natal river. In addition to these caveats, survival estimates for salmon at sea include natural and fishing mortality. Thus, the smolt-to-grilse survival data used here probably underestimate true survival at sea.

To examine how various life history traits and growth rate at sea combine to influence optimal sea age at maturity, we estimated fitness, *r*, from the discrete-time version of the Euler-Lotka equation,

$$(1)\qquad 1 = \sum_{x=\alpha}^{x=\omega} l_x m_x e^{-rx}$$

where, for ages x between maturity α and death ω, l_x represents the survival probability from birth to the beginning of the spawning season at age x, and m_x represents the number of zygotes produced by an individual spawning at age x. Given the paucity of fecundity and survival data for the same population, we examined how changes to single life history traits influence optimal sea age at maturity by holding the remaining traits constant at values equal to the grand means across all populations. These grand means, and their respective population minima and maxima, are given in Table 3.

Age-specific fecundities, m_x, were calculated using the fecundity–length relationship intermediate among those reported in Fleming’s (1996) review, i.e., the relationship between fecundity (F) and length (L, cm) reported for Scotland’s River Dee: $F = 0.4667\ (L^{2.2018})$. The length of fish remaining two winters at sea was assumed to be 20 cm longer than the length of grilse (20 cm being the average difference in length between grilse and 2SW fish among all populations in the present data set). To generate differences in fecundity in our simulations, we held the exponent of the fecundity–length regression model constant at 2.2 and varied the intercept (there was no appreciable difference in the results when holding the intercept constant and varying the exponent).

In our model, survival of 2SW salmon from the smolt stage was set at 55% the survival from the smolt to the grilse stages (55% being the average survival difference reported for a tributary of the Miramichi River; Cunjak and Therrien 1998). Optimal associations between growth rate at sea (approximated by the difference between smolt and grilse lengths) and sea age at maturity were calculated for the minimum (0.013), average (0.074), and maximum (0.175) smolt-to-grilse survival probabilities reported in Appendix 1. The sensitivity of our simulations to our parameter estimates is evident from the model’s graphical results.

To normalize the data and to remove any effect of the mean on the variance, we transformed original data before

Fig. 1. Box-and-whisker plots of parr growth rate (A) and smolt age (B) for Atlantic salmon throughout its geographical range. Explanation of plots: medians are represented by the white bar in each box; the lower and upper ends of each box represent the 25% and 75% quartiles, respectively; skewness is reflected by the position of the median relative to the ends of each box; the "whiskers" represent lines extending from the top and bottom of each box to adjacent data no more than 1.5 times the inter-quartile range with values beyond this range indicated by solid circles; the width of each box is proportional to the square root of the number of populations represented in each sample. Sample sizes for each region are given in Table 2.

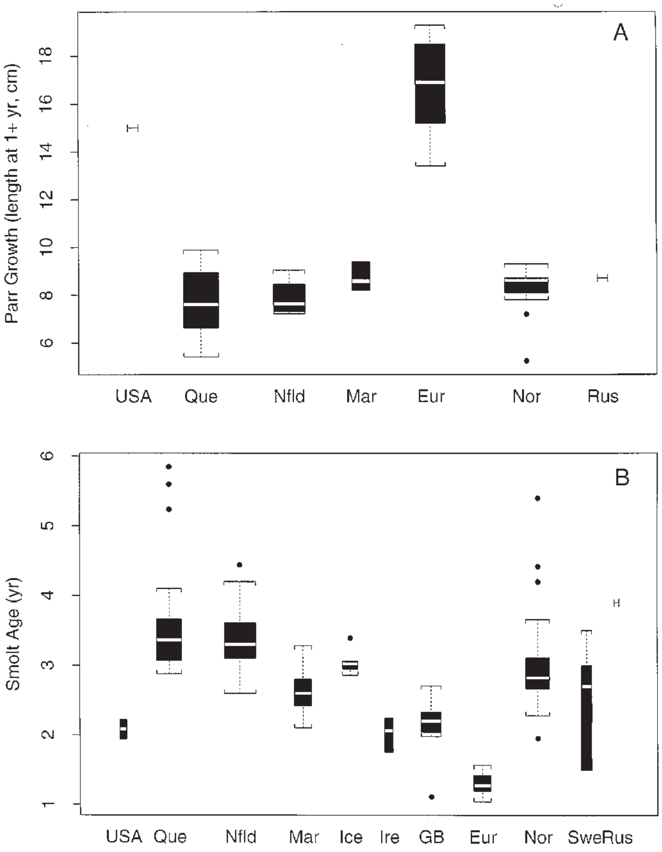
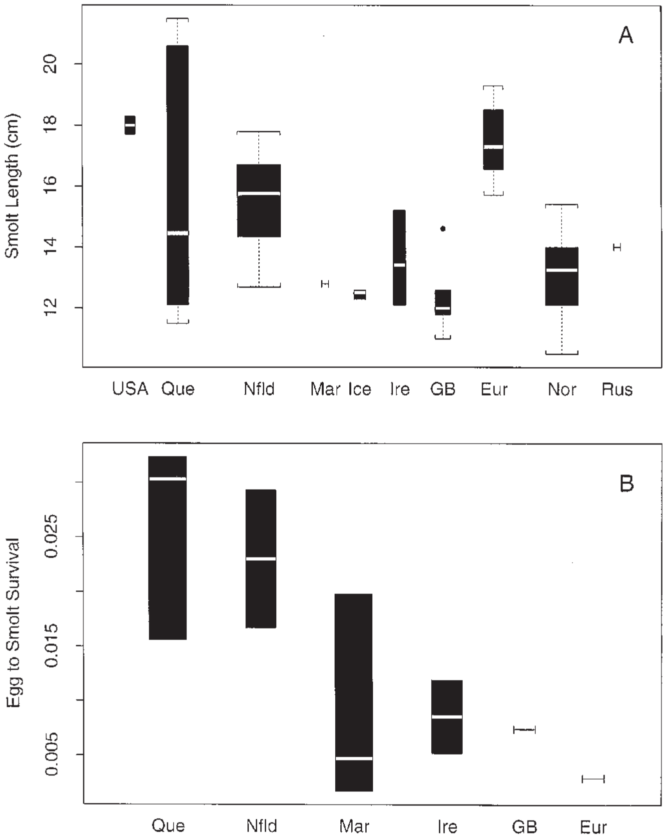


Fig. 2. Box-and-whisker plots of smolt length (A) and survival from the egg to smolt stages (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.



estimating temporal variation in life history traits (Sokal and Rohlf 1981; Appendix 2). The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) were calculated from original proportions, *p*, transformed as $\arcsin(p^{1/2})$; variances of non-proportional data were calculated from $\log_e$-transformations of the original data.

Results

Regional differences in Atlantic salmon life history

Regional differences in age-specific parr length were accentuated by the rapid growth experienced by mainland European populations (Fig. 1A) in which parr aged 1+ year averaged 17.2 cm in length compared to the non-significant differences among Canadian and Norwegian populations for which regional differences in 1+ year parr length ranged, on average, between 7.8 and 8.8 cm (Table 2). The minimum and maximum parr lengths at age 1+ year for single populations were documented for Norway's Beiarelva (5.2 cm) and France's Adour (19.3 cm), respectively (Appendix 1).

Smolt age differed significantly among regions (Fig. 1B), ranging from a mean of 1.29 years for European populations to 3.36 and 3.60 years for Newfoundland and Québec populations, respectively (Table 2). Population mean smolt age ranged from 1.04 years (Nivelle, France) to 5.85 years (George, Québec) (Appendix 1). Among the 94 populations for which data were available, smolt age was uncorrelated with smolt length ($r = -0.13$, $p = 0.24$), the latter varying among regions from an average 12.4 and 12.5 cm for British and Icelandic populations, respectively, to 17.6 and 18.0 cm for European and American populations, respectively (Table 2, Fig. 2A). Among populations, smolt length ranged from 10.5 cm (Nummedals, Norway) to 21.5 cm (George, Québec) (Appendix 1).

Survival during the freshwater stage is usually estimated as the proportion of eggs in a cohort that survive to migrate to sea. The uncertainty associated with this estimate may be considerably greater than that associated with other life history variables. This is because of the numerous parameters, each with an associated measurement error, and many assumed invariant among years, used to estimate egg deposition (e.g., number of females, number of eggs per female, sex ratio of anadromous adults, female weight). Notwithstanding these caveats, there was no significant difference in

Fig. 3. Box-and-whisker plots of length of 1SW salmon (A) and growth rate at sea (the differences between lengths of smolts and 1SW salmon) (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.

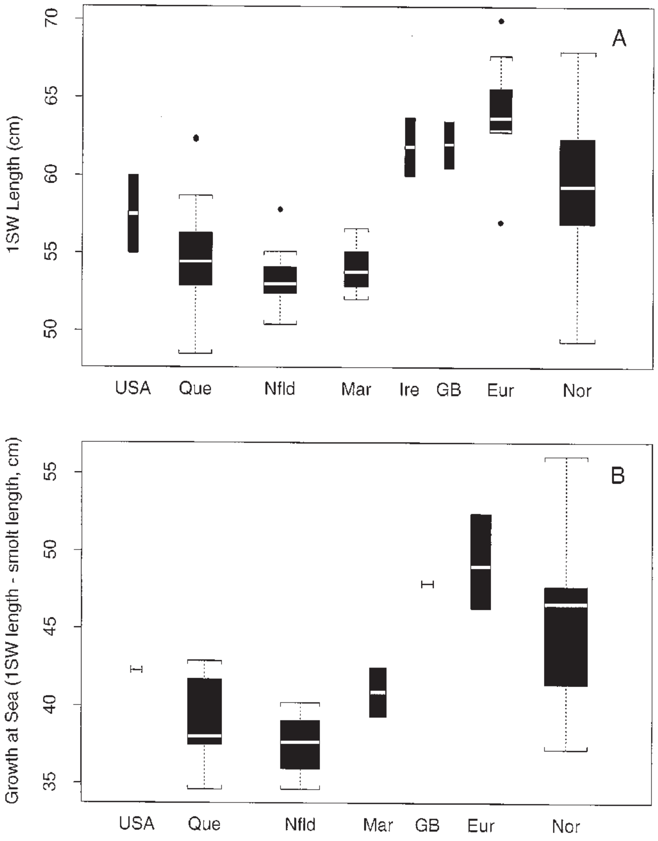
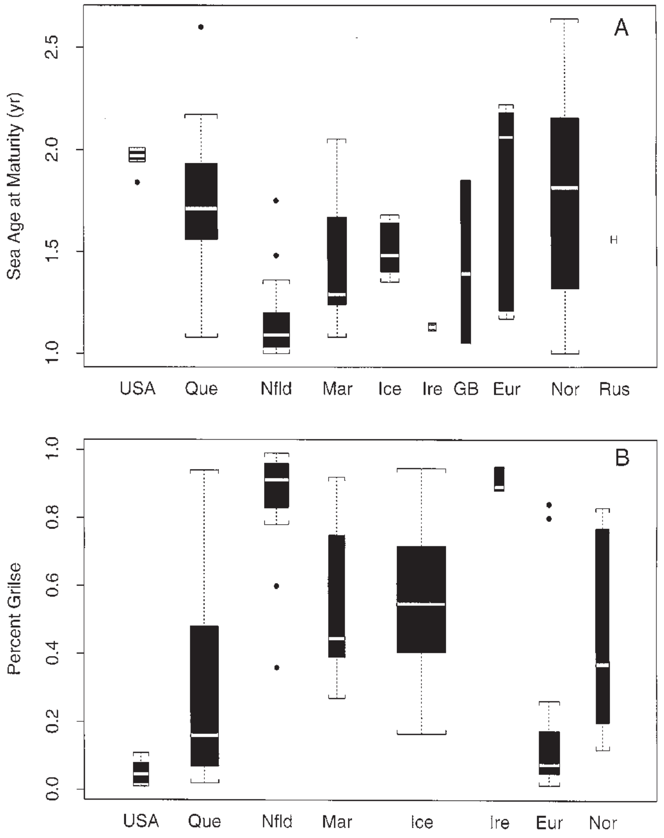


Fig. 4. Box-and-whisker plots of sea age at maturity (A) and percentage of grilse (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.



egg-to-smolt survival among regions (Table 2, Fig. 2B). Although sample sizes were small and the range in estimates within regions large, data indicate that mean freshwater survival is highest in Newfoundland and Québec (0.023 and 0.026, respectively) and lowest among Northeast Atlantic populations, ranging from 0.003 to 0.009. Accounting for regional differences in mean smolt age, annual survival probabilities in fresh water ranged from 0.01 in Europe to 0.33 in Newfoundland and Québec (other estimates include 0.15 (Maritimes), 0.10 (Great Britain), and 0.09 (Ireland)).

Growth rate at sea can be approximated as the difference between the lengths of smolts and grilse. The latter differed by 20% among regions (Fig. 3A, Table 2) being lowest in the western North Atlantic (regional averages of 53.2, 54.3, and 54.7 cm for Newfoundland, Maritime, and Québec populations, respectively) and highest in the eastern North Atlantic (e.g., 62.0 and 64.1 cm for British and European populations, respectively). On average, the smallest grilse were those in Québec's Jupiter (48.5 cm) with the largest being those in Spain's Narcea (70.0 cm) (Appendix 1). Average length gained at sea between the smolt and grilse stages differed significantly among Newfoundland (37.4 cm), Québec (38.8 cm), Maritimes (40.9 cm), Norway (45.9 cm), and Europe (49.2 cm) (Fig. 3B).

Mean sea age at maturity differed significantly among regions (Fig. 4A). Comparing the extremes (Table 2), American (1.96 years), Norwegian (1.83 years), and mainland European (1.81 years) salmon spend 60 to 70% more time at sea than those in Newfoundland (1.15 years) and Ireland (1.13 years). Among populations, the youngest average sea ages were those for Newfoundland's Wings Brook (1.00 year) and Western Arm Brook (1.01 years) and the oldest for Norway's Vosso (2.58 years) and Årøelva (2.64 years) (Appendix 1). Among regions, the average incidence of grilse ranged from 5% for American populations to 86 and 91% for Newfoundland and Ireland populations, respectively (Table 2, Fig. 4B). The female sex ratio of returning grilse, varying from 5% (Québec) to 67% (Newfoundland), also differed significantly among regions (Fig. 5A, Table 2). Average smolt-to-grilse survival, highest in the Maritimes (0.130) and lowest in Iceland (0.010), did not differ significantly among regions, although sample sizes were low and the range in population estimates within regions high (Table 2, Fig. 5B).

Salmon age at maturity (smolt age plus sea age plus 1 year, to ensure that total age represented absolute time between an individual's fertilization and spawning) differed significantly among regions ($p < 0.001$) (Table 2, Fig. 6). The oldest average ages at maturity were found in Québec (6.27 years; species' population maximum of 8.80 years in George), Norway (5.71 years), and Newfoundland (5.58 years) with the youngest observed in Great Britain (4.58 years), mainland Europe (4.08 years; species' popula-

Fig. 5. Box-and-whisker plots of the percentage of grilse that are females (A) and adjusted survival between the smolt and grilse stages (B) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.

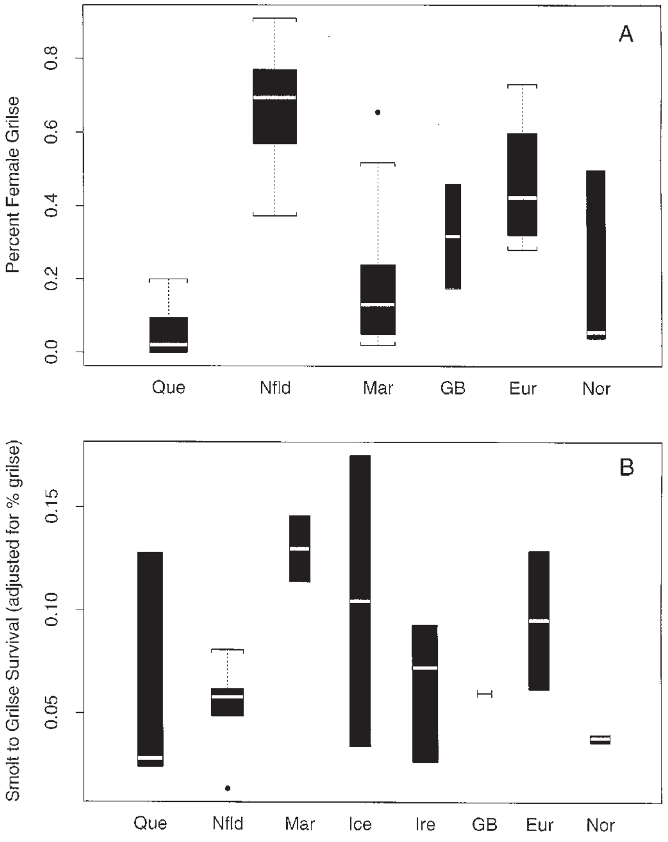


Fig. 6. Box-and-whisker plot of age at maturity (smolt age plus sea age plus 1, see text for further details) for Atlantic salmon throughout its geographical range. See Fig. 1 for description of box-and-whisker plots.

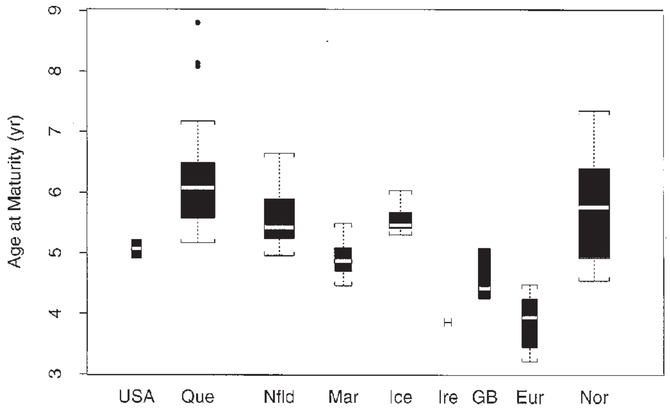
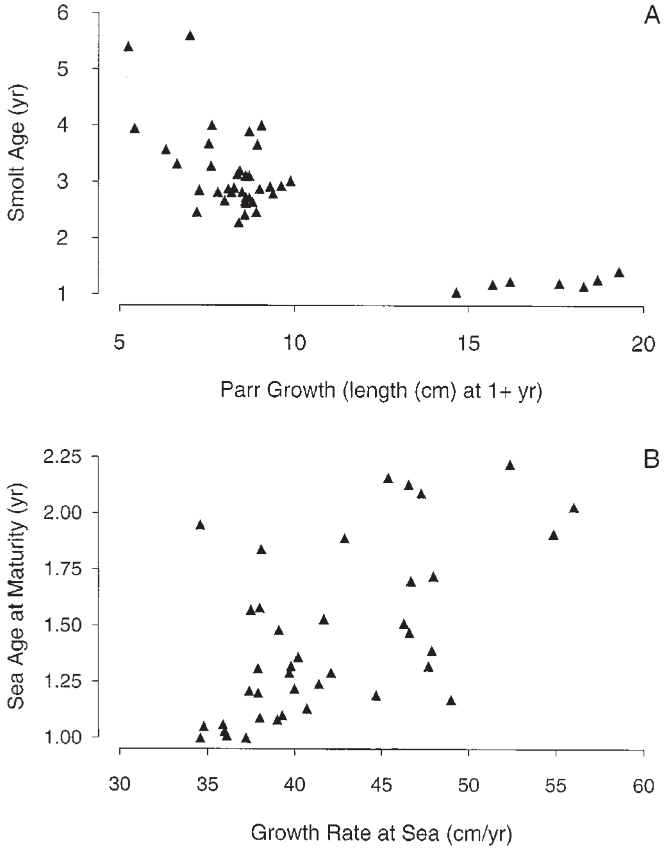


Fig. 7. Scatterplots between smolt age and parr growth (length at age 1+ year) (A) and between sea age at maturity and growth rate at sea (B) for Atlantic salmon populations throughout the species' range.



tion minimum of 3.21 years in Nivelle), and Ireland (3.86 years).

The freshwater residence period of anadromous salmon declined with increasing parr growth at the population level ($r = -0.79$, $p < 0.001$; Fig. 7A). In addition to being the primary determinant of smolt age, previous work suggests that parr growth rate is also positively associated with the incidence of male parr maturity (Myers et al. 1986; Thorpe 1986) which differs significantly among Canadian populations, ranging from an average of 22% for Québec populations to 57% in Newfoundland (Appendix 1, Table 2).

Time spent at sea, a major component of age at maturity for anadromous salmon, was positively associated with growth rate at sea among populations ($r = 0.47$, $p = 0.002$; Fig 7B). Sea age at maturity was not correlated with post-smolt survival at the population level ($r = -0.17$, $p = 0.254$).

Predicted optimal associations among growth rate, survival, and sea age at maturity

Empirically based model simulations provide one means of identifying optimal associations among growth rate, survival, and sea age at maturity. A primary feature of the results of these analyses (Figs. 8–10) is the characterization of growth rate thresholds for sea age at maturity, i.e., the 1-year increase in length between the smolt and grilse stages that favours reproduction after one rather than two winters at sea.

Age and length at smoltification appear to have comparatively small influence on optimal growth rate thresholds for sea age at maturity (Fig. 8A–F). The primary effects of increases in smolt age and smolt length are increases and declines in growth rate thresholds, respectively, over comparatively small ranges of 5 to 10 cm·year^{-1}. Increased 1SW survival (i.e., smolt-to-grilse survival) reduces growth

Table 2. Regional means of Atlantic salmon life history traits and associated ANOVA results. Means represent averages among populations (*n*) within regions; standard deviations are those for the regional means; population averages represent means across years of available data.

Trait	Region	Mean	SD	*n*	*p*
Parr length at 1+ year (cm)	Europe	16.7	2.1	8	<0.001
	U.S.A.	15.0	—	1	
	Maritimes	8.8	0.6	3	
	Russia	8.7	—	1	
	Norway	8.3	0.9	17	
	Newfoundland	7.9	0.7	9	
	Québec	7.8	1.4	11	
Smolt age (years)	Russia	3.90	—	1	<0.001
	Québec	3.60	0.79	27	
	Newfoundland	3.36	0.45	45	
	Iceland	3.03	0.13	11	
	Norway	3.01	0.74	25	
	Finland	2.70	—	1	
	Maritimes	2.59	0.33	13	
	Sweden	2.44	0.90	5	
	Great Britain	2.18	0.35	17	
	U.S.A.	2.08	0.20	2	
	Ireland	2.02	0.25	3	
	Europe	1.29	0.15	13	
Smolt length (cm)	U.S.A.	18.0	0.4	2	<0.001
	Europe	17.6	1.4	6	
	Newfoundland	15.5	1.4	38	
	Québec	15.5	3.9	10	
	Russia	14.0	—	1	
	Ireland	13.6	1.6	3	
	Maritimes	13.4	0.8	2	
	Norway	13.1	1.2	22	
	Iceland	12.5	0.2	3	
	Great Britain	12.4	1.4	5	
Egg-to-smolt survival	Québec	0.026	0.010	3	0.25
	Newfoundland	0.023	0.009	2	
	Maritimes	0.009	0.010	3	
	Ireland	0.009	0.005	2	
	Great Britain	0.007	—	1	
	Europe	0.003	—	1	
Grilse length (cm)	Europe	64.1	3.4	10	<0.001
	Great Britain	62.0	2.1	2	
	Ireland	61.8	2.6	2	
	Norway	59.5	4.3	25	
	U.S.A.	57.5	3.5	2	
	Québec	54.7	3.5	22	
	Maritimes	54.3	1.5	12	
	Newfoundland	53.2	1.6	22	
Sea age (years)	U.S.A.	1.96	0.50	8	<0.001
	Norway	1.83	0.51	24	
	Europe	1.81	0.44	8	
	Québec	1.72	0.33	33	
	Russia	1.56	—	1	
	Iceland	1.50	0.12	11	
	Maritimes	1.43	0.33	11	
	Great Britain	1.43	0.40	3	
	Newfoundland	1.15	0.17	23	
	Ireland	1.13	0.03	2	
% Grilse	Ireland	0.91	0.04	3	<0.001
	Newfoundland	0.86	0.15	20	

Table 2. (*Concluded*).

Trait	Region	Mean	SD	*n*	*p*
	Great Britain	0.80	—	1	
	Iceland	0.58	0.19	78	
	Russia	0.53	—	1	
	Maritimes	0.52	0.24	12	
	Norway	0.44	0.27	7	
	Québec	0.32	0.28	27	
	Europe	0.20	0.27	14	
	USA	0.05	0.04	8	
% Female grilse	Newfoundland	0.67	0.15	16	<0.001
	Europe	0.47	0.16	7	
	Great Britain	0.32	0.20	2	
	Maritimes	0.21	0.21	10	
	Norway	0.20	0.26	3	
	Québec	0.05	0.07	12	
Smolt-to-grilse survival	Maritimes	0.130	0.02	2	0.354
	Europe	0.095	0.047	2	
	Newfoundland	0.073	0.027	5	
	Québec	0.060	0.059	3	
	Ireland	0.060	0.047	2	
	Great Britain	0.060	—	1	
	Norway	0.038	0.003	2	
	Iceland	0.010	0.010	2	
Age at maturity (yr)	Québec	6.27	0.95	24	<0.001
	Norway	5.71	0.81	20	
	Newfoundland	5.58	0.46	19	
	Iceland	5.54	0.21	11	
	USA	5.07	0.21	2	
	Maritimes	4.91	0.36	6	
	Great Britain	4.58	0.44	3	
	Europe	4.08	0.51	8	
	Ireland	3.86	—	1	
% Mature male 1+ parr	Newfoundland	0.57	0.31	9	0.024
	Maritimes	0.53	0.27	3	
	Québec	0.22	0.22	10	
	Russia	0.10	—	1	

Table 3. Age (yr)-specific schedules of survival and fecundity used to estimate optimal sea age at maturity in Atlantic salmon.

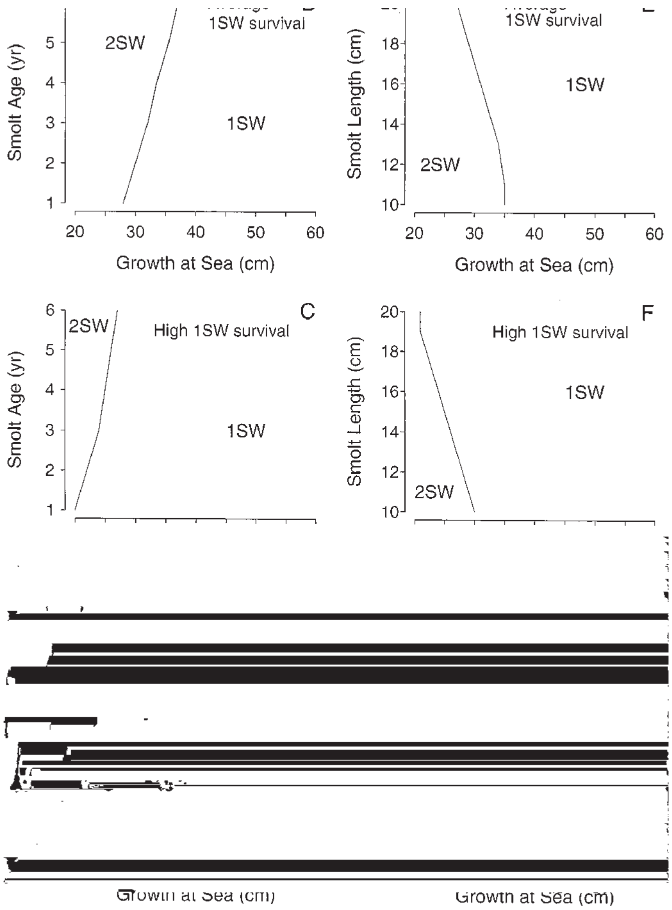
		Population	
Trait	Average	Minimum	Maximum
Smolt length (cm)	14.8	10.5	21.5
Smolt age (yr)	3.5	1.0	5.8
Egg-to-smolt survival	1.5%	0.2%	3.2%
Smolt-to-grilse survival	7.4%	1.3%	17.4%

rate thresholds for maturation as grilse, irrespective of smolt age or length.

In contrast to smolt age and size, survival in fresh water (i.e., egg-to-smolt survival) has a strong influence on optimal growth rate thresholds for maturity (Figs. 9A–C). A decline in freshwater survival is associated with an increase in the growth rate required for maturity after 1 sea winter to be favoured over maturity after 2 winters at sea. If survival in both fresh water and the sea is low (Fig. 9A), females are favoured to mature as 2SW fish, independent of growth rate. Similarly, if survival in both fresh water and the sea is high, maturation as grilse is favoured (Fig. 9C).

The effect of a decline in smolt-to-grilse survival on growth rate thresholds is similar to that produced by a decline in freshwater survival — increased survival at sea reduces the growth rate at which early maturity is favoured over delayed maturity (Figs. 9D–F). The main effect of an increase in the sea survival of grilse relative to that of 2SW salmon is also a decline in the growth rate threshold for maturity.

Fig. 8. Effect of smolt age (A–C) and smolt length (D–F) on growth rate thresholds for sea age at maturity in female Atlantic salmon at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival. Growth rate thresholds, identified by continuous lines in each bivariate plot, identify the growth rate at sea, approximated here as the difference in length between smolts and grilse, that must be exceeded for maturity after one winter at sea (1SW) to be favoured (i.e., have a higher fitness, *r*) over the strategy of maturing after two winters at sea (2SW). Thus, combinations of smolt age or smolt length and growth at sea that lie to the right of each line are those that favour maturity after one winter at sea; those to the left of each line favour maturity after two winters at sea.

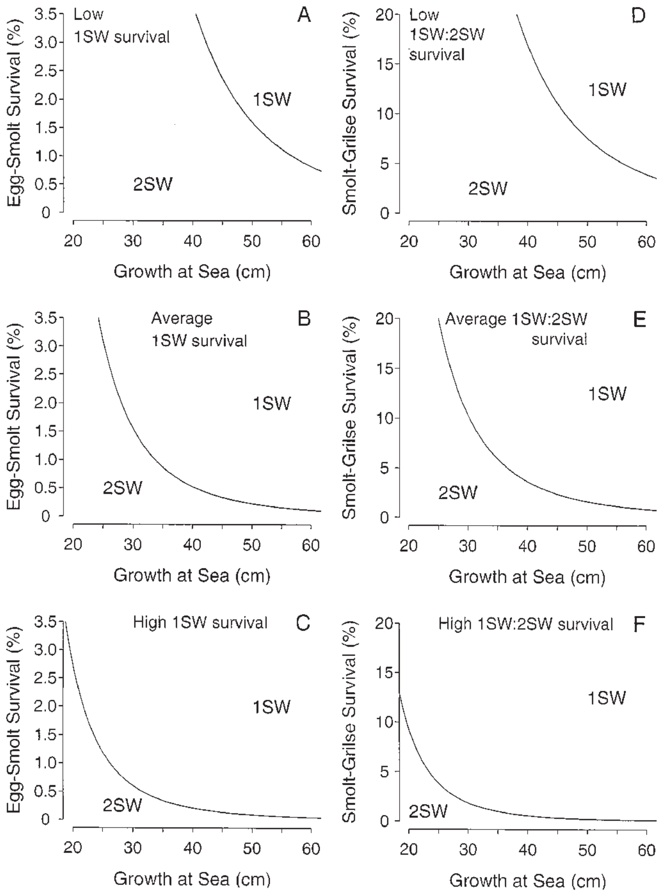


Within the two-fold range of 1500 to 3000 eggs per 50-cm female, as calculated for Atlantic salmon from the regressions given by Fleming (1996), fecundity appears to have comparably little effect on growth rate thresholds for sea age at maturity, being of import within growth rates of 10 cm yr^{-1} or less (Fig. 10). Again, an increase in 1SW survival is predicted to favour earlier maturity, the reduction in growth rate threshold being largely independent of fecundity.

Temporal variation in life history

To illustrate temporal variation in salmon life history characters, we plotted time series of seven traits in populations for which the log$_e$- or arcsin-transformed variances represented the among-population means, minima, and maxima (Fig. 11; Appendix 2).

Fig. 9. Effect of survival in fresh water and at sea on growth rate thresholds for sea age at maturity in female Atlantic salmon. Figures A–C illustrate changes in thresholds effected by changes in egg-to-smolt survival at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival. Figures D–E illustrate changes in thresholds effected by changes in smolt-to-grilse survival at low (0.25), average (0.55), and high (0.75) ratios of survival between the sea survival of 1SW versus 2SW salmon. Growth rate thresholds are defined further in the caption for Fig. 8.



The longest continuous time series of estimates of percent grilse (24 years; Western Arm Brook; Fig. 11A) exhibits remarkably low variation with estimates ranging between 95 and 100% although annual fluctuations of 20 to 30% appear to be not uncommon in other populations. Smolt-to-grilse survival, adjusted for grilse percentage as described previously, ranged from 2.1 to 12.2% for Western Arm Brook, the population for which interannual variance in survival represented the among-population average (Fig. 11B). Annual fluctuations in grilse sex ratio ranged from a low of 5% (NE Placentia River) to as much as 50% (Lomond River) with 10 to 20% being typical (Fig. 11C). For the only time series of fecundity extending more than 3 years, annual changes of 500 to 1000 eggs per female appear to be not uncommon (Fig. 11D).

Smolt age fluctuated comparatively little within populations, varying by less than 0.5 year annually within populations (Fig. 11E). Annual changes in grilse length of 2 to 3 cm appear to be typical (e.g., Western Arm Brook;

Fig. 10. Effect of fecundity on growth rate thresholds for sea age at maturity in female Atlantic salmon at low (0.0135), average (0.0740), and high (0.1740) rates of smolt-to-grilse survival (A–C). Growth rate thresholds are defined further in the caption for Fig. 8.

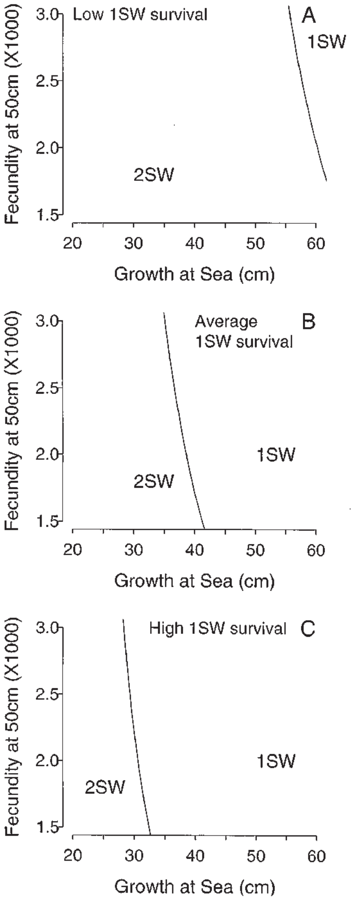


Fig. 11F) although for some populations (e.g., Conne River) this variable is remarkably constant. Annual fluctuations in smolt length are typically less than 1 cm, as indicated by salmon from Norway's River Alta (Fig. 11G).

Temporal variation in life history characters was generally uncorrelated with life history trait means of other characters. A notable exception was a negative association between sea age at maturity and temporal variance in survival at sea for 15 populations throughout the species' geographical range ($r = -0.51$, $p = 0.025$).

Discussion

Our initial postulate that life history variation in Atlantic salmon is matched by few vertebrates seems an appropriate characterization of the life history data available for this species. There are sufficient data on Atlantic salmon to construct an empirical framework against which life history responses to changes in growth rate and mortality can be predicted. What cannot as yet be predicted with confidence is the rate at which such changes might occur. This is a question of quantitative genetics and phenotypic plasticity, and the answer(s) depend upon the amount of heritable variation in life history traits, the sign and magnitude of genetic correlations among traits, the existence of reaction norms, and temporal variation in the environment (Charlesworth 1990; Roff 1997). Based on previous research (see also Fleming 1998; Marschall et al. 1998; Metcalfe 1998), the spatial and temporal data presented here, and our optimality modelling of sea age at maturity, there are sufficient data from which some general conclusions regarding the effects of growth and survival on Atlantic life history can be drawn. Following a discussion of these below, we suggest areas of research, for which there is comparatively little information, upon which future work on Atlantic salmon life history might focus.

Influence of growth rate on seaward migration and maturity as parr

The negative association between parr growth rate and smolt age (Fig. 7A) is consistent with individual and population studies in the wild and in the laboratory. The hypothesis that increased growth rate in fresh water leads to decreased age at smoltification was first proposed by Dahl (1910). He postulated that the reduction in length of growing season was responsible for the increase in smolt age with latitude in Norwegian populations. Power (1981) also found smolt age in Québec, Newfoundland, and Labrador populations to be negatively associated with length of growing season. Metcalfe and Thorpe (1990) have shown that this negative association persists throughout the geographical range of Atlantic salmon and that more than 82% of the among-population variation in smolt age can be explained by a temperature- and photoperiod-based metric of growth rate in freshwater. At the individual level, Menzies (1927) observed that the oldest smolts in two Scottish populations tended to be those having the slowest growth rates as parr. This negative association between parr growth rate and smolt age, further noted by Jones (1959) and Shearer (1972), has been documented repeatedly in the laboratory (e.g., Thorpe 1977; Thorpe and Morgan 1980; Saunders et al. 1982; see Thorpe 1986 and Saunders 1986).

How might increased growth rate be related to the fitness benefits of early maturity? Rapid growth during pre-reproductive ages reduces the time required to attain a size at which reproduction is possible. By shortening this period of time, an individual increases its probability of surviving to reproduce. For anadromous salmon, the sooner an individual migrates to sea, the sooner it reaches a size at which it can reproduce. This provides one explanation for the negative association between parr growth rate and smolt age among Atlantic salmon populations. Similarly, increased incidence of maturity with increased growth rate can be interpreted as an adaptive response by male parr (Hutchings and Myers 1994; Thorpe et al. 1997; Metcalfe 1998). Such a maturation response appears not to be adaptive for female parr, presumably because the fitness benefit of increased pre-reproductive survival does not outweigh the fitness cost of the low fecundity effected by small body size.

Fitness trade-offs between early and delayed maturity at sea

Previous support for the hypothesis that growth rate at sea influences sea age at maturity has been equivocal. In his review, Gardner (1976) found evidence of both positive and

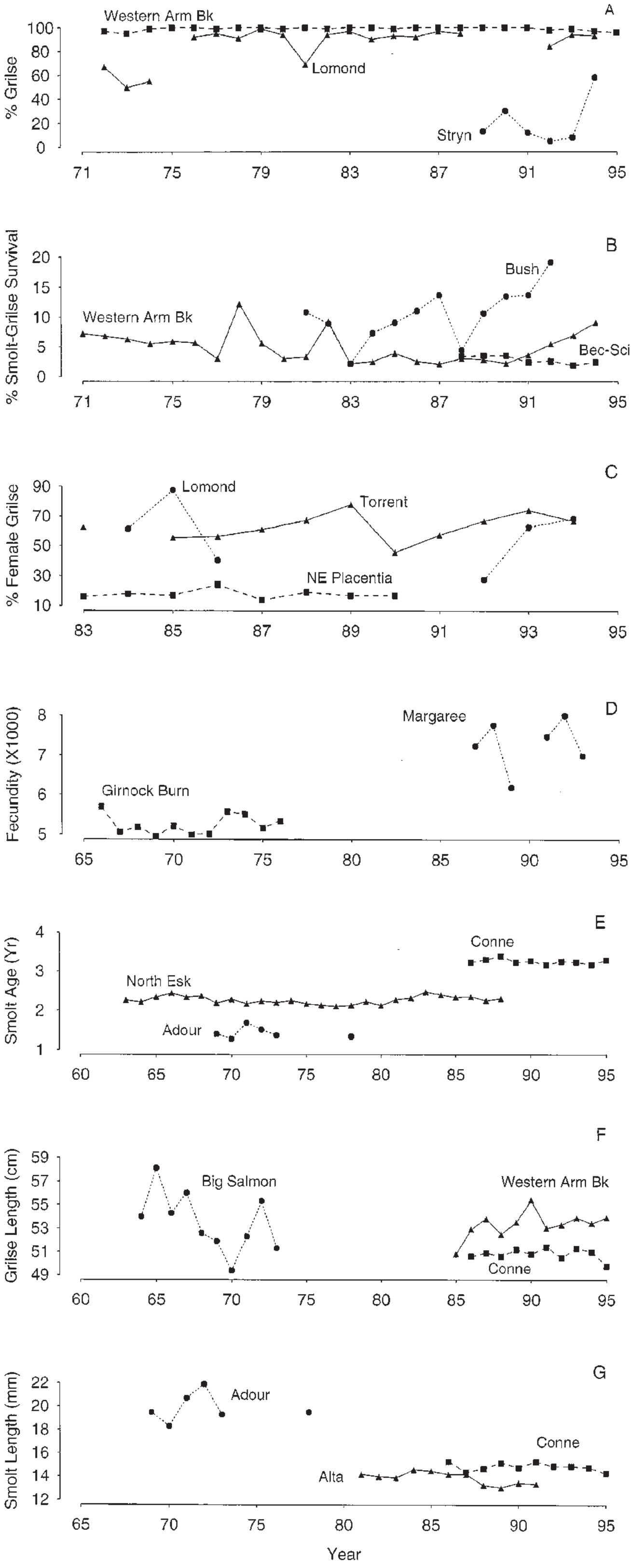


Fig. 11. Temporal variation in Atlantic salmon life history characters. The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) have been calculated from original proportions, *p*, transformed as arcsin($p^{1/2}$). Variances of non-proportional data have been calculated from $\log_e$-transformations of the original data. Plotted time series are those that approximate the among-population means (▲—▲), minima (■ – – – ■), and maxima (● - - - ●).

negative associations between growth at sea and time spent at sea, concluding that, "it is certain there is no causal or universal relationship between growth rate … in the sea, and the age at eventual return to fresh water" (Gardner 1976:320). Similar to our pattern (Fig. 7B), Schaffer and Elson (1975) previously documented a positive association between growth at sea and age at maturity for 14 North American populations, although their observation was supported neither by a re-analysis of the same data nor by an analysis of an expanded population data set (Myers and Hutchings 1987).

Our modelling of growth rate thresholds provides an empirical framework against which changes in sea age at maturity effected by changes in growth rate at sea can be predicted. For a given age-specific schedule of survival and fecundity, i.e., within a single population, optimal sea age at maturity is predicted to either decline or remain constant with increases in growth rate at sea (Figs. 8–10); delayed maturity appears not to be favoured by increased growth rate, all else being equal. The conclusion that earlier age at maturity is an adaptive response to increased growth rate at sea is consistent with theory (Roff 1992; Stearns 1992; Hutchings 1993, 1996) and with life history patterns observed in Atlantic salmon (e.g., Friedland and Haas 1996) and other salmonids (e.g., Hutchings 1996, 1997).

For a given growth rate at sea, our modelling suggests that uncorrelated changes to single life history characters will often have no effect on sea age at maturity. However, when an individual's growth at sea is encompassed by the range of growth rates within which changes to sea age at maturity are predicted to be favoured by selection, uncorrelated changes to single traits influence optimal age at maturity. Early maturity (i.e., maturation as a 1SW rather than a 2SW salmon) is favoured by increases in smolt length, fecundity, survival in fresh water or at sea, and survival of grilse relative to that of 2SW salmon (Figs. 8–10). Delayed maturity is favoured by reductions in smolt size, fecundity, and survival, but by increases in smolt age.

The fitness simulations may provide some insight into the causal basis for regional differences in Atlantic salmon life history. For example, compared to Newfoundland populations, European salmon grow rapidly at sea but spend almost twice as much time in the marine environment before spawning. According to the life history simulations, such an association between growth rate and sea age at maturity is adaptive only when smolt-to-grilse survival at sea, and secondarily egg-to-smolt survival, is low. At the other extreme, the observed associations among smolt age, smolt length, growth at sea, and sea age at maturity for Newfoundland populations suggest that survival at sea, and secondarily survival in freshwater, is comparatively high.

Does age at maturity covary with temporal variation in survival?

We documented a negative association between sea age at maturity and temporal variance in smolt-to-grilse survival at sea. One implicit assumption of our analysis was that variation in survival from the smolt to the grilse stages accurately reflected variation in survival after the grilse stage. This assumption appears reasonable, given the significantly positive correlation that exists between the variances in smolt-to-grilse and smolt-to-2SW survival probabilities for salmon in the Rivers Vesturdalsa, Bush, Imsa, and North Esk ($r = 0.99$, $p = 0.003$; ICES 1994*a*).

Although life history theory provides no clear prediction of how variation in survival at potentially reproductive ages should influence age at maturity (Charlesworth 1994), we suggest that as variation in smolt-to-grilse survival increases, so does the uncertainty associated with the probability of surviving two or more winters at sea. In environments where this uncertainty is high, selection may act against genotypes that delay maturity by prolonging the time spent at sea. This might account for the negative association between sea age at maturity and variance in smolt-to-grilse survival observed here.

Future research

Although addressed indirectly by the fitness simulations, we did not examine genotype-by-environment interactions in Atlantic salmon life history. Adaptive phenotypic plasticity, via selection for norms of reaction, provides one means by which genetically based life history responses to environmental change can be effected (Bradshaw 1965; Via and Lande 1985; Stearns and Koella 1986; Hutchings 1996; Roff 1998). Herein lies one of the gaps in Atlantic salmon research. There is a need for studies that focus on the underlying basis for life history change in Atlantic salmon. Are population changes in life history, e.g., sea age at maturity, or incidence of male parr maturity, generally effected by changes in gene frequencies, a comparatively slow process occurring across generations, or by phenotypic alteration along norms of reaction, a comparatively rapid response occurring within a single generation? Questions that future research might address include: Do reaction norms, such as the predicted growth rate thresholds for male parr maturity and female sea age at maturity, exist in Atlantic salmon? If so, how do the shapes of the reaction norms differ among populations and at different spatial scales? How much additive genetic variance, and thus potential for selection, exists for the shapes of such norms of reaction? Answers to these questions would provide guidance in predicting the rate and direction of life history responses to environmental influences on growth rate and survival.

A second deficiency in our knowledge of Atlantic salmon life history concerns male age at maturity, specifically the demographic and genetic consequences of male parr reproduction. Despite the considerable laboratory (see Metcalfe 1998) and theoretical (Leonardsson and Lundberg 1986; Myers 1986; Hutchings and Myers 1994) interest in proximate and evolutionary mechanisms of male parr maturity, the demographic consequences of early male reproduction has received remarkably little attention, being limited to Myers' (1994) estimate that the increased mortality and delayed age at smoltification experienced by post-reproductive male parr may be responsible for the loss of 60% of the anadromous male salmon production in some populations. How do changes in survival and growth rate at sea influence the incidence of male parr maturity (see also Marschall et al. 1998)? What are the consequences of male parr maturity to estimates of spawning requirements in Atlantic salmon populations? And, to address an issue that has received no attention in the literature, what are the genetic and ecological consequences of male parr maturity to estimates of effective and minimum viable population sizes?

A third area of life history research that merits study concerns the ecological and evolutionary mechanisms permitting the maintenance of anadromous and nonanadromous populations of Atlantic salmon in systems in which physical barriers to seaward migration are absent. Although it has received comparatively little attention (e.g., Hutchings 1986), the study of coexisting life history polymorphisms in Atlantic salmon seems likely to bear the informative fruits borne by research on resource-based polymorphisms in threespine sticklebacks, *Gasterosteus aculeatus*, (Schluter 1996) and Arctic char (Skúlason et al. 1998).

Thus, be it from an ecological, evolutionary, conservation, or harvesting perspective, we anticipate significant contributions to science from Atlantic salmon life history research that focuses upon reaction norms for age at maturity, demographic and genetic consequences of male parr maturation, and the evolutionary and ecological mechanisms that permit coexistence of anadromous and nonanadromous life history polymorphisms.

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Appendix 1.

Table A1. Atlantic salmon life history data from unpublished and published sources used in the present study.

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg– smolt survival	Smolt– grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
England	Avon	11.8	1.11											Harris (1973)
England	Dart		2.04											Nott (1973)
England	Tees	14.6	2.07											Harris (1973)
England	Wye		2.01											Harris (1973)
Finland	Simojoki		2.7											Toivonen and Jutila (1982)
France	Adour	19.3	1.42	1.51	65.6	79.9	94.2	0.063					193	Bousquet and Marty (1987)
France	Aulne		1.45		57	77		0.015						Baglinière et al. (1987)
France	Blavet				63	75		0.174	0.42					Baglinière et al. (1987); Prévost and Porcher (1996)
France	Bresle	16.2	1.23	1.21				0.8			0.1287		162	Fournel et al. (1987); ICES (1994*b*)
France	Ellé		1.42		65	75.7		0.091	0.42					Prévost and Porcher (1996); Baglinière et al. (1987)
France	Elorn		1.57		64	75		0.087	0.466					Prévost and Porcher (1996); Prouzet and Gaignon (1982, 1985); Baglinière et al. (1987)
France	Léguer		1.27		63.4	78.7		0.032					187	Baglinière et al. (1987)
France	Nivelle	18.7	1.04	1.17	67.7			0.84	0.54		0.0617		146.6	Bousquet and Marty (1987); Dumas (1979); ICES (1994*a*)
France	Oir								0.32	0.00292				Baglinière et al. (1993); ICES (1994*a*,*b*); Prévost and Porcher (1996)
France	Scorff		1.31		62.8	77.4		0.166	0.422			0.65		Baglinière and Champigneulle (1986); Baglinière et al. (1987, 1994); Prévost and Porcher (1996)
France	Selune		1.22		63	76.4		0.263	0.28					Baglinière et al. (1987, 1993)
Iceland	Álftá							0.74						Scarnecchia (1983)
Iceland	Andakílsá							0.84						Scarnecchia (1983)
Iceland	Austurá							0.39						Scarnecchia (1983)
Iceland	Bakkaá							0.465						Scarnecchia (1983)
Iceland	Blanda							0.255						Scarnecchia (1983)
Iceland	Breiddalsá							0.81						Scarnecchia (1983)
Iceland	Bruará							0.375						Scarnecchia (1983)
Iceland	Brynjudalsá							0.88						Scarnecchia (1983)
Iceland	Bugda							0.81						Scarnecchia (1983)
Iceland	Deildará							0.425						Scarnecchia (1983)
Iceland	Eldvatn							0.875						Scarnecchia (1983)
Iceland	Ellidaár	12.5	3.05	1.39				0.61			0.1754			Scarnecchia (1983); Gudjónsson (1978); ICES (1994*a*)
Iceland	Fáskrúd							0.705						Scarnecchia (1983)
Iceland	Fljótaá							0.54						Scarnecchia (1983)
Iceland	Flekkudalsá							0.785						Scarnecchia (1983)
Iceland	Flókadalsá							0.895						Scarnecchia (1983)
Iceland	Fnjóská							0.35						Scarnecchia (1983)
Iceland	Fossá í Laxárdal							0.455						Scarnecchia (1983)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Iceland	Fródá							0.72						Scarnecchia (1983)
Iceland	Geirlandsá							0.71						Scarnecchia (1983)
Iceland	Gljúfurá							0.945						Scarnecchia (1983)
Iceland	Grímsá		2.94	1.5				0.5						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Hafralónsá							0.285						Scarnecchia (1983)
Iceland	Haffjardará							0.63						Scarnecchia (1983)
Iceland	Haukadalsá							0.645						Scarnecchia (1983)
Iceland	Hítará							0.67						Scarnecchia (1983)
Iceland	Hofsá í Vesturdal							0.43						Scarnecchia (1983)
Iceland	Hölkná							0.38						Scarnecchia (1983)
Iceland	Hördudalsá							0.745						Scarnecchia (1983)
Iceland	Hrófá							0.515						Scarnecchia (1983)
Iceland	Hrútafjardará/Siká							0.44						Scarnecchia (1983)
Iceland	Húseyjarkvísl							0.835						Scarnecchia (1983)
Iceland	Hvannadalsá							0.515						Scarnecchia (1983)
Iceland	Hvítá í Borgarf		3.03	1.62				0.41						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Hvolsá/Stadarh							0.79						Scarnecchia (1983)
Iceland	Ísafjardadá							0.625						Scarnecchia (1983)
Iceland	Krossá á Skardsst							0.795						Scarnecchia (1983)
Iceland	Langá							0.84						Scarnecchia (1983)
Iceland	Langadalsá							0.415						Scarnecchia (1983)
Iceland	Laugardalsá							0.645						Scarnecchia (1983)
Iceland	Laxá á Ásum							0.705						Scarnecchia (1983)
Iceland	Laxá á Skögst							0.71						Scarnecchia (1983)
Iceland	Laxá á Hrútafirdi							0.51						Scarnecchia (1983)
Iceland	Laxá í Adaldal							0.29						Scarnecchia (1983)
Iceland	Laxá í Adaldalur		3.05	1.64				0.368						Gudjónsson (1978)
Iceland	Laxá í Kjós		2.99	1.68				0.319						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Laxá í Lsveit							0.745						Scarnecchia (1983)
Iceland	Laxá-Ytri							0.58						Scarnecchia (1983)
Iceland	Leirá							0.93						Scarnecchia (1983)
Iceland	Leirvogsá							0.855						Scarnecchia (1983)
Iceland	Midá í Dölum							0.715						Scarnecchia (1983)
Iceland	Midfjardará		3.39	1.64				0.356						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Midfjardará/Kverká							0.43						Scarnecchia (1983)
Iceland	Nordurá		3	1.41				0.594						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Núpsá							0.48						Scarnecchia (1983)
Iceland	Olfusá	12.3	2.95	1.35				0.653						Gudjónsson (1978)
Iceland	Ormarsá							0.4						Scarnecchia (1983)
Iceland	Reykjadalsá							0.77						Scarnecchia (1983)
Iceland	Sæmundará							0.33						Scarnecchia (1983)
Iceland	Sandá							0.38						Scarnecchia (1983)
Iceland	Selá. Stfirdi							0.595						Scarnecchia (1983)
Iceland	Selá í Vopnafirdi							0.5						Scarnecchia (1983)
Iceland	Skjálfandafljót							0.44						Scarnecchia (1983)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Iceland	Sog		2.86	1.44				0.591						Gudjónsson (1978)
Iceland	Sogid							0.66						Scarnecchia (1983)
Iceland	Stóra-Laxá							0.385						Scarnecchia (1983)
Iceland	Straumfjardará							0.585						Scarnecchia (1983)
Iceland	Svalbardsá							0.365						Scarnecchia (1983)
Iceland	Svartá							0.41						Scarnecchia (1983)
Iceland	Thjórsá							0.34						Scarnecchia (1983)
Iceland	Thverá		3.06	1.4				0.597						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Úlfarsá	12.6						0.93						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Vatnsdalsá							0.445						Scarnecchia (1983)
Iceland	Vesturá							0.49						Scarnecchia (1983)
Iceland	Vesturdalsá							0.555			0.0342			Scarnecchia (1983); ICES !994*a*)
Iceland	Vídidalsá		3.04	1.48				0.518						Scarnecchia (1983); Gudjónsson (1978)
Iceland	Vididalsá/Fitjaá							0.345						Scarnecchia (1983)
Iceland	Vikurá							0.375						Scarnecchia (1983)
Ireland	Burrishoole	12.1	2.24							0.0052	0.0724			ICES (1994*a*,*b*); Harris (1973); Kennedy and Crozier (1993)
Ireland	Bush	15.2		1.15				0.88		0.0119	0.0932			ICES (1994*a*,*b*); Kennedy and Crozier (1993)
Ireland	Corrib	13.4	1.75	1.11				0.89			0.0266			Brown (1988)
Ireland	Foyle				63.7									Went and Twomey (1971)
Ireland	Moy				60									Went and Twomey (1971)
Ireland	Owenduff		2.06											Harris (1973)
Labrador	Forteau		4.09	1.03	54.2	72.9		0.97	0.645					Lowe and Mullins (1996); Myers and Hutchings (1987)
Labrador	Pinware		4.2	1.16	53.2	74.3		0.84	0.372					Myers and Hutchings (1987)
Labrador	Eagle			1.03	54.4	74.7		0.97						Myers and Hutchings (1987)
Labrador	Sandhill	16	4.44	1.2	53.9	73.4	79.2	0.89			0.0815			Myers and Hutchings (1987); Power (1981); Reddin et al. (1996); Chadwick (1988)
Maritimes	Big Salmon	13.9	2.6	1.1	53.2	70.8		0.445	0.654	0.0017	0.1461			Jessop (1986); Ritter (1989)
Maritimes	Bouctouche		2.69						0.12					Atkinson and Chaput (1996)
Maritimes	East (Pictou)				55.6			0.27	0.05					Claytor et al. (1995*a*)
Maritimes	LaHave		2.17	1.29	53.6	72.5		0.71						Amiro et al. (1996, 1998); Cutting and Jefferson (1986); Myers and Hutchings (1987)
Maritimes	Liscomb			1.08	52.3	72.4	91.7	0.92						Myers and Hutchings (1987)
Maritimes	Margaree		2.42	1.36	53.5	71.1	81.7	0.59	0.11			0.75	85.8	Claytor et al. (1995*b*); Myers et al. (1986); Myers and Hutchings (1987)
Maritimes	Medway		2.58	1.24										Ritter (1974)
Maritimes	Miramichi	12.8	2.8	1.29	55.3	73.4	86.9	0.75	0.24	0.0047	0.1410	0.605	93.9	Chaput et al. (1996, 1998); Cunjak and Therrien (1998); Moore et al. (1995); Myers et al. (1986)
Maritimes	Nepisiguit		2.15						0.178					Locke and Mowbray (1996)
Maritimes	North		3.28	1.95	54.6	72.3		0.05						Myers and Hutchings (1987); Ritter (1974)
Maritimes	Philip			2.05	56.6	74.4	86.7	0.39						Claytor et al. (1995*a*); Myers and Hutchings (1987)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg–smolt survival	Smolt–grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Maritimes	Pollett		2.1							0.0198				Elson (1975)
Maritimes	Restigouche		2.82	1.67	52	76	92	0.39	0.02			0.22	82	Locke et al. (1996); Myers et al. (1986); Myers and Hutchings (1987)
Maritimes	Richibucto		2.74											Atkinson et al. (1995)
Maritimes	Saint John		2.54	1.42	56.3	78		0.55	0.144					Marshall and Jones (1996); Myers and Hutchings (1987)
Maritimes	South (Antig)				54.4				0.03					Claytor et al. (1995*a*)
Maritimes	St. Marys			1.24	54	74.9	91.1	0.76						Myers and Hutchings (1987)
Maritimes	Tabusintac		2.8											Atkinson and Hooper (1995)
Maritimes	West (Antig)							0.38						Claytor et al. (1995)
Newfoundland	Bay de l’Eau											0.724	73.1	Myers et al. (1986)
Newfoundland	Beaver	13.2	3											O’Connell and Ash (1993)
Newfoundland	Biscay Bay		3.1	1.05	52.9				0.75					O’Connell et al. (1996*a*)
Newfoundland	Branch	15.8	3.1											Chadwick et al. (1986)
Newfoundland	Burlington	15.1	3.6											Chadwick et al. (1986)
Newfoundland	Cambellton	17.7	3.5	1.05	52.5			0.95	0.763					Dempson et al. (1998*a*); O’Connell et al. (1996*a*)
Newfoundland	Champney’s	15.5	3.4											Chadwick et al. (1986)
Newfoundland	Come-By-Chance											0.786	72.2	Myers et al. (1986)
Newfoundland	Conne	14.8	3.28	1.06	50.7	68.3		0.94	0.78		0.0578			Dempson et al. (1998*a*,*b*)
Newfoundland	East	13.6	4											Chadwick et al. (1986)
Newfoundland	Exploits			1.1	52	75.6		0.9						Bourgeois et al. (1996); Myers and Hutchings (1987)
Newfoundland	Farmers	16.6	3.1											Chadwick et al. (1986)
Newfoundland	Fischells	14	2.6						0.587					O’Connell and Ash (1993)
Newfoundland	Gambo	16.7	3											Chadwick et al. (1986)
Newfoundland	Gander	15.7	3.7	1.09	53.7			0.9	0.76					Dempson et al. (1998*a*); O’Connell et al. (1996*b*)
Newfoundland	Garia	15.7	2.9											Chadwick et al. (1986)
Newfoundland	Harry’s		3.4	1.02	50.4	71.4		0.98	0.621					Mullins et al. (1996)
Newfoundland	Highlands	13.1	2.9	1.36	53.3	73.4		0.36				0.55	82.7	Myers et al. (1986); Myers and Hutchings (1987); O’Connell et al. (1996*a*)
Newfoundland	Humber		3.8	1.13	55	73.5	86.5	0.92						Mullins and Reddin (1996); Myers and Hutchings (1987); Power (1981)
Newfoundland	Hunt			1.75	57.8	76.6								Myers and Hutchings (1987)
Newfoundland	Indian Bay	16.7	3.3											O’Connell and Ash (1993)
Newfoundland	Little Bk Pds	17.4	3.1											Chadwick et al. (1986)
Newfoundland	Little Codroy	15	2.66	1.48	54.1	75.1	89.6	0.6	0.411	0.0293	0.0135	0.715	85.9	Murray (1968); Myers et al. (1986); Myers and Hutchings (1987)
Newfoundland	Lomond		2.86	1.14	52.4	70.7		0.86	0.55			0.486	72.7	Myers et al. (1986); Myers and Hutchings (1987); O’Connell et al. (1996*a*)
Newfoundland	Middle Bk	17.1	3.47	1.03	53.1			0.97	0.79					Dempson et al. (1998*a*); O’Connell and Ash (1993); O’Connell et al. (1996*a*)
Newfoundland	NE Placentia	13.9	2.88	1.08	52.9			0.92	0.91					Dempson et al. (1998*a*); O’Connell and Ash 1993); O’Connell et al. (1996*a*)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg– smolt survival	Smolt– grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Newfoundland	NE Trepassey	15.4	3.67	1.18				0.82			0.0622			Dempson et al. (1998*a*)
Newfoundland	North Hr	15.1	3.2	1.22	55.1	76.3		0.78				0.118	84.3	Myers et al. (1986); Myers and Hutchings (1987); O'Connell and Ash (1993)
Newfoundland	Northwest	17.2	4									0.952	90.5	Chadwick et al. (1986); Myers et al. (1986)
Newfoundland	Pipers Hole	16.4	3.4											Chadwick et al. (1986)
Newfoundland	Ragged Hr	17.6	3.5											O'Connell and Ash (1993)
Newfoundland	Red Harbour	14.7	3.2											Chadwick et al. (1986)
Newfoundland	Renews	17.8	2.7											Chadwick et al. (1986)
Newfoundland	River of Pds	16.2	3.3											O'Connell and Ash (1993)
Newfoundland	Riverhead	16	3.4											Chadwick et al. (1986)
Newfoundland	Robinsons	13.5	2.9						0.551					Mullins et al. (1996); O'Connell and Ash (1993)
Newfoundland	Salmonier	16	3.1											Chadwick et al. (1986)
Newfoundland	Sops Arm	13	4.1											Chadwick et al. (1986)
Newfoundland	Southwest	13.4	3											Chadwick et al. (1986)
Newfoundland	St. Geneviev	17	4.2											Chadwick et al. (1986)
Newfoundland	Taylor Bay	17.5	3.3											Chadwick et al. (1986)
Newfoundland	Terra Nova	14.9	3.44	1.21	52.3			0.79	0.74					Dempson et al. (1998*a*); O'Connell et al. (1996*a*);
Newfoundland	Terrenceville	13.9	3.3											Chadwick et al. (1986)
Newfoundland	Torrent		3.17	1.07	52.7			0.93	0.647					O'Connell et al. (1996*a*)
Newfoundland	Trouty	16.7	3.2											Chadwick et al. (1986)
Newfoundland	Wst Arm Bk	16.8	3.68	1.01	52.9			0.99	0.778	0.0167	0.0489	0.039	75.4	Myers et al. (1986); O'Connell et al. (1996*a*)
Newfoundland	Wings Bk	16.4	4	1	51							0.793	76.3	Hutchings (1985, 1986); Myers et al. (1986)
Norway	Altaelva	13.5	4.2	2.15				0.423	0.056					Lund et al. (1989); Saksgård et al. (1992)
Norway	Årøelva	14.8	3.1	2.64		89.3	104.8						86.3	Huitfeldt-Kaas (1946)
Norway	Beiarelva	13.6	5.4										52.4	Jensen and Johnsen (1985); Økland et al. (1993)
Norway	Blomo		3.16	1.69										Dahl (1937)
Norway	Bondalselv				57.54	80.25								Jonsson et al. (1991)
Norway	Drammenselv				66.27	90.32								Jonnson et al. (1991)
Norway	Eira	12.1	2.88	2.53		83.2	104.1						81	Huitfeldt-Kaas (1946)
Norway	Etneelv				62.36	77.83								Jonsson et al. (1991)
Norway	Figgenelva	11.7	2.28	1.47	58.3	77.1							84	Huitfeldt-Kaas (1946)
Norway	Figgjo				59.31	75.95					0.0399			Jonsson et al. (1991); Friedland et al. (unpublished data)
Norway	Håelva	12.5	2.47	1.32	60.2	80							89	Huitfeldt-Kaas (1946); Jonsson et al. (1991)
Norway	Imsa	15.4	1.95	1.19	61.29	82.36	90.6	0.83			0.0357			ICES (1994*a*); Jonsson et al. (1991, 1998)
Norway	Kristiansand		2.96	1.63										Dahl (1937)
Norway	Lærdalselva	11.9	2.82	2.03	67.96	89.26	98.7	0.12					82	Huitfeldt-Kaas (1946); Jonsson et al. (1991); Lund et al. (1989); Økland et al. (1993)
Norway	Loneelv				55.41									Jonsson et al. (1991)
Norway	Målselva	14.5	3.66	1.72	62.5			0.47	0.039					Kristoffersen and Staldvik (1996)
Norway	Mandalselva	13.3	2.82	1.13	54	79.3							85	Huitfeldt-Kaas (1946)
Norway	Moltuen		3.66	1.72										Dahl (1937)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg– smolt survival	Smolt– grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Norway	Namsen	11.9	2.67	2.13	58.49	86.75	100.24	0.27	0.497				80	Huitfeldt-Kaas (1946); Jonsson et al. (1991); Lund et al. (1989)
Norway	Nummedals	10.5	2.47	1.91	65.4	84.5	101.7						72	Huitfeldt-Kaas (1946); Jonsson et al. (1991)
Norway	Ogna	13.2	2.65	1.24	54.6	78.6							88	Huitfeldt-Kaas (1946)
Norway	Opo				59.04	81.69	99.12							Jonsson et al. (1991)
Norway	Orkla	11.4	2.82	2.16	56.8	81.6	98.7						78	Huitfeldt-Kaas (1946)
Norway	Ørstaelv				56.92									Jonsson et al. (1991)
Norway	Otra	12.8	2.63	2.09	60.1	86.8	107.8						86	Huitfeldt-Kaas (1946)
Norway	Ranaelv				60.85	80.04								Jonsson et al. (1991)
Norway	Repparfjord			1.32				0.77						Lund et al. (1989)
Norway	Sandvikselv				64.21	83.49								Jonsson et al. (1991); Økland et al. (1993)
Norway	Saltdalselva	14.3	4.42											Jensen (1995); Økland et al. (1993)
Norway	Stjørdalselv				63.24	86.15								Jonsson et al. (1991)
Norway	Stryneelva	13.7	2.77	2.48				0.2						Jensen (1995); Lund et al. (1989)
Norway	Tana	13.3	3.11	2.53		78.7	94.5						87	Huitfeldt-Kaas (1946)
Norway	Tengselva	14.1	2.92	1.7	60.8	75.8							93	Huitfeldt-Kaas (1946)
Norway	Tovdalselva	13	2.72	1.32	52.8	76.1							87	Huitfeldt-Kaas (1946)
Norway	Varhaugelva	12.1	2.73	1	49.3								86	Huitfeldt-Kaas (1946)
Norway	Vefsna				59.34	85.48	94.31							Jonsson et al. (1991)
Norway	Vosso	14	2.88	2.54			107.3						90	Huitfeldt-Kaas (1946)
Québec	Bec-Scie		2.97	1.52						0.0156	0.0283			Caron (1992, 1996); Caron and Bolduc (1991)
Québec	Bouleau	13.1	3.14	1.57	50.6	74.6		0.43				0.13	83.6	Randall and Power (1979)
Québec	Cap-Chat			2.16	56.3	78.9	93.4	0.13						Myers and Hutchings (1987)
Québec	Cascapédia	13.9	3.30			77.7								Power (1981)
Québec	Corneille		3.02	1.71	53.3	70.0		0.13	0			0.383	98.9	Bielak and Power (1986). Myers et al. (1986); Myers and Hutchings (1987); Power (1981)
Québec	Etamamiou		3.66	1.23										Bielak and Power (1986)
Québec	George	21.5	5.85	1.95	56.1	78.7		0.05	0.20					Power (1969)
Québec	Godbout		3.36	1.67				0.82	0.02					Bielak and Power (1986)
Québec	Grande Rivière			1.97	54.9	74.4	90.9	0.12						Myers and Hutchings (1987)
Québec	Grand Trinite		3.07	1.1										Bielak and Power (1986)
Québec	Gros Mecatina		3.43	1.08										Bielak and Power (1986)
Québec	Jupiter		4.10		48.5	70.2								Power (1981)
Québec	Koksoak	20.6	5.60	1.53	62.3	80.3		0.47	0				70.0	Power (1969); Robitaille et al. (1984, 1986)
Québec	Laval		2.88	1.77										Bielak and Power (1986)
Québec	Leaf			1.88	62.4	79.7		0.12						Lee and Power (1976)
Québec	Madeleine			1.79	51.5	75.2	92.1	0.31						Myers and Hutchings (1987)
Québec	Matamek	15	3.11	1.31	52.9	72.9		0.68	0.06			0.626	85.9	Bielak and Power (1986); Gibson (1978); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Matane			1.67	54.8	71.9	90.3	0.48						Myers and Hutchings (1987)
Québec	Matapédia			2.17	56.8	80	94.6	0.11						Myers and Hutchings (1987)
Québec	Mingan		3.48	1.64				0.07	0					Bielak and Power (1986)
Québec	Mistassini		3.28	1.69				0.64	0.14			0.097	76.1	Bielak and Power (1986); Myers et al. (1986)
Québec	Mitis			1.74				0.38						Côté and Beaulieu (1987)

Table A1. (*Continued*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg– smolt survival	Smolt– grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Québec	Moisie	12	3.57	2.6	48.7	74.6	90.7	0.05	0			0	63.1	Bielak and Power (1986); Myers et al. (1986); Power (1981)
Québec	Nabisipi		4.07	1.98	54.5	77.4	87.6	0.05						Bielak and Power (1986); Myers and Hutchings (1987)
Québec	Natashquan		3.95	1.33										Bielak and Power (1986)
Québec	Olomane		3.62	1.93										Bielak and Power (1986)
Québec	Pigou	15.1	2.93	1.58	53.1	72.7						0.375	96.2	Randall and Power (1979); Myers et al. (1986)
Québec	Pt. Saguenay			1.67	56.7	79.1	92.3	0.6						Myers and Hutchings (1987)
Québec	Puyjalon											0	71.3	Myers et al. (1986)
Québec	Romaine		3.1	2.08				0.02	0					Bielak and Power (1986)
Québec	Ste. Anne			2.12	56.1	80.8	95.8	0.12						Myers and Hutchings (1987)
Québec	Ste. Marguerite		3.32	1.86	52.8	75.2	90.1	0.07	0			0.167	66.3	Bielak and Power (1986); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Saint-Jean	11.5	3.52	1.89	54.4	73.3	90.7	0.23	0.02	0.303	0.1282	0	54.2	Caron (1996); Caron and Bolduc (1991); Caron and Fontaine (1998); Myers et al. (1986); Myers and Hutchings (1987)
Québec	Trinité	12.1	3.00	1.29	54.2	74.7		0.59	0.08	0.0324	0.0237		80.6	Caron (1992, 1996); Caron and Bolduc (1991);Caron and Fontaine (1998); Myers and Hutchings (1987)
Québec	Grand Watchichou		3.66	1.56	53.3	70.4		0.43				0.408	89.3	Bielak and Power (1986); Myers and Hutchings (1986); Riley et al. (1984)
Québec	Whale	20.6	5.24	1.84	58.7	77.4		0.16	0.11					Power (1969)
Russia	Pizhma	14	3.9									0.1	87	Martynov et al. (1994)
Russia	Tuloma							0.53						Sharov et al. (1990)
Scotland	Almond				63.5	81.9								Thorpe et al. (1984)
Scotland	Bran	11.0	2.43											Harris (1973)
Scotland	Conon		2.62											Harris (1973)
Scotland	Dee		2.23	1.85			0.15		0.174	0.0074				Buck and Hay (1984); Harris (1973)
Scotland	Ewe		2.53											Harris (1973)
Scotland	Grimersta		2.71											Harris (1973)
Scotland	Nith		2.03											Harris (1973)
Scotland	North Esk	12.6	2.33	1.39	60.5	74.2	88.1	0.8	0.46		0.0601			ICES (1994*a*); Shearer (1992)
Scotland	Shelligan Burn		2.2	1.05										Egglishaw and Shackley (1977)
Scotland	Spey		2.30											Harris (1973)
Scotland	Tay		2.19											Harris (1973)
Scotland	Thurso	12.0	2.04											Harris (1973)
Scotland	Tweed		2.20											Mills (1989)
Spain	Cares	18.3	1.15	2.18				0.05					183	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Esva	15.7	1.18	2.06				0.06					157	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Narcea	17.6	1.2	2.22	70			0.05					176	Nicieza and Braña (1993*a*,*b*); Nicieza et al. (1991); Ventura (1987)
Spain	Sella		1.36	2.12				0.04						Ventura (1987)
Sweden	Eman		1.5											Karlström (1977)

Table A1. (*Concluded*).

Country/ Region	River	Smolt length (cm)	Smolt age (yr)	Sea age (yr)	Grilse length (cm)	2SW length (cm)	3SW length (cm)	% Grilse	% fem grilse	Egg– smolt survival	Smolt– grilse survival	% 1+ Male parr maturity	1+ Parr length (mm)	References
Sweden	Kalix Alv		3											Karlström (1977)
Sweden	Mörrumsån		1.5											Lindroth (1977)
Sweden	Ricklean		2.7											Osterdahl (1964)
Sweden	Torne Alv		3.5											Karlström (1977)
U.S.A.	Connecticut	18.3	1.94	1.98				0.02					150	Friedland et al. (1996); Orciari et al. (1994)
U.S.A.	Dennys			2.01				0.01						Baum (1997)
U.S.A.	East Machias			1.96				0.05						Baum (1997)
U.S.A.	Machias			1.97				0.04						Baum (1997)
U.S.A.	Penobscot			1.84	55.0	72.5	87.0	0.11						Baum (1997); Friedland et al. (1996)
U.S.A.	Pleasant			1.97				0.07						Baum (1997)
U.S.A.	Narraguagus	17.7	2.22	2.00	60.0	76.0	89.0	0.02						Baum (1997)
U.S.A.	Sheepscot			1.94				0.09						Baum (1997)
U.S.A.	Dee		1.98											Harris (1973)

Appendix 2.

Table A2. Temporal variation in Atlantic salmon life history characters. The variances of proportional data (i.e., survival, percentage grilse, grilse sex ratio) have been calculated from original proportions, *p*, transformed as arcsin($p^{1/2}$). Variances of non-proportional data have been calculated from $\log_e$- transformations of the original data.

Trait	Region	River	Number of years	Years	Variance
Smolt-to-grilse survival	Québec	St. Jean	6	89–94	0.0026
		Trinité	11	84–94	0.0020
		Bec-Scie	7	88–94	0.0004
	Newfoundland	Sandhill	4	69–72	0.0056
		NE Trepassey	8	86–93	0.0020
		Conne	8	87–94	0.0031
		Western Arm Brook	24	71–95	0.0033
		Little Codroy	7	54–61	0.0004
	Canadian Maritimes	Miramichi	4	90–93	0.0051
		Big Salmon	5	66–71	0.0204
	Iceland	Elidaar	7	75–92	0.0103
		Vesturdalsa	5	83–92	0.0036
	Ireland	Burrishoole	14	79–92	0.0030
		Bush	12	81–92	0.0066
	Scotland	North Esk	8	81–91	0.0008
	Europe	Nivelle	5	86–90	0.0122
		Bresle	4	83–86	0.0042
	Norway	Imsa	12	81–92	0.0045
Percent grilse	Québec	Trinité	13	80–92	0.0187
		Bec-Scie	9	84–92	0.0222
	Newfoundland	NE Trepassey	8	86–93	0.0052
		Conne	9	87–95	0.0012
		Western Arm Brook	24	71–95	0.0001
		Exploits	26	60–94	0.0250
		Salmon Brook	25	57–94	0.0412
		Gander	6	89–94	0.0061
		Middle Brook	17	72–94	0.0042
		Terra Nova	34	56–94	0.0306
		Biscay Bay	12	83–94	0.0037
		NE Placentia	21	71–94	0.0137
		Highlands	5	80–94	0.0156
		Humber	5	90–94	0.0066
		Lomond	19	72–94	0.0369
		Torrent	24	71–94	0.0085
	Labrador	Sandhill	5	69–94	0.0154
	Canadian Maritimes	Miramichi	25	71–95	0.0310
		Liscomb	15	80–94	0.0114
		Saint John	29	67–95	0.0222
		Magaguadavic	8	83–95	0.0119
		St. Croix	13	82–95	0.0502
	Norway	Strynelva	6	89–94	0.0534
Percent female grilse	Newfoundland	Western Arm Brook	10	85–94	0.0092
		Gander	3	92–94	0.0046
		Middle Brook	5	83–87	0.0388
		Terra Nova	5	83–87	0.0028
		NE Placentia	9	78–86	0.0017
		Lomond	6	84–94	0.0524
		Torrent	11	83–94	0.0090
	Labrador	Forteau	9	75–94	0.0204
		Pinware	8	74–93	0.0164
	Canadian Maritimes	Nepisiquit	8	83–90	0.0014
		Big Salmon	5	68–73	0.0026

Table A2. (*Concluded*).

Trait	Region	River	Number of years	Years	Variance
Fecundity	Newfoundland	Terra Nova	3	84–86	0.0006
		Middle Brook	3	84–86	0.0006
	Canadian Maritimes	Margaree	6	87–93	0.0086
	Scotland	Girnock Burn	11	66–76	0.0022
Smolt age	Québec	Bec-Scie	9	84–92	0.0018
		Trinité	9	84–92	0.0005
	Newfoundland	Middle Brook	5	83–87	0.0014
		Terra Nova	5	83–87	0.0004
		NE Placentia	9	78–86	0.0056
		Lomond	13	78–95	0.0046
		Torrent	15	75–95	0.0017
		Western Arm Brook	25	71–95	0.0032
		Conne	10	86–95	0.0004
	Labrador	Forteau	8	78–94	0.0009
	Scotland	North Esk	26	63–88	0.0019
	Europe	Adour	6	69–78	0.0100
	Norway	Stryneelva	6	89–94	0.0018
		Saltdalselva	5	90–94	0.0010
		Altaelva	11	81–91	0.0010
Grilse length	Newfoundland	Terra Nova	5	83–87	0.0003
		NE Placentia	8	78–86	0.0003
		Torrent	11	83–94	0.0002
		Western Arm Brook	10	85–94	0.0005
		Conne	10	86–95	0.0001
	Labrador	Forteau	9	79–94	0.0002
	Canadian Maritimes	Big Salmon	10	64–73	0.0022
		LaHave	13	85–97	0.0003
		Miramichi	27	71–97	0.0009
Smolt length	Québec	St-Jean	10	88–97	0.0006
		Trinité	10	88–97	0.0005
	Newfoundland	Conne	10	86–95	0.0005
	Europe	Adour	9	69–82	0.0040
	Norway	Altaelva	11	81–91	0.0013