

## The effect of temperature on growth and early maturation in a wild population of Atlantic salmon parr

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Atlantic salmon *Salmo salar* parr exposed to heated water effluent were larger than parr living upstream of the discharge. There was no effect, however, of temperature on the incidence of male parr maturation, despite the link between growth and maturation found in other studies. Mature parr upstream of the effluent were smaller than mature parr downstream of it, suggesting a higher size threshold for maturation in those parr exposed to the heated water. The small distance between upstream and downstream sampling sites probably precluded genetic differences between the parr, thus implying an environmental influence on the threshold size above which male parr matured.

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### INTRODUCTION

The growth and development of ectothermic animals is highly sensitive to temperature (Brett, 1979). At low temperatures metabolic rates are suppressed resulting in poor feeding and growth rates. Increasing temperatures tend to cause an increase in growth, up to an optimum temperature above which thermal stress occurs (Elliott & Hurley, 1997). The result is that growth can fluctuate with natural variation in temperature. But not all variation in temperature is natural. Human activities are altering environmental temperature at both the global scale of climate change and through the more localized effects of industry. For those animals whose growth is temperature-dependent, such human activities could cause profound changes in their growth patterns and life histories.

The River Fiddich is a tributary of the River Spey, north-east Scotland. Distilleries, situated along its length, discharge heated water into the river as a waste product of the whisky making process. This effluent can raise the mean

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monthly river temperature 8 km downstream of the distilleries by between 1.2 and 6.3° C with a mean  $\pm$  S.E. of  $2.7 \pm 0.2^\circ$  C (1996–2000 data,  $n = 45$ ), compared to sites upstream of the discharge. The temperature elevation has already been shown to increase the growth rates of juvenile Atlantic salmon *Salmo salar* L. downstream of the distilleries (Morrison, 1989). It is possible, however, that it has a more significant effect than merely altering the body size-at-age of the fish, since juvenile growth rates potentially influence subsequent life history patterns in Atlantic salmon (Metcalf, 1998).

Atlantic salmon spend their early life in fresh water. Most then migrate to richer marine feeding grounds and grow rapidly before returning to their natal river to spawn. Some Atlantic salmon, however, become sexually mature and attempt to spawn before leaving fresh water when they are still known as parr. This strategy is almost exclusively adopted by males since small male parr can fertilize a significant number of eggs by sneak mating (Thomaz *et al.*, 1997), whereas female fecundity is constrained by size.

Whether a male matures as a parr seems to depend on it exceeding a threshold size, growth rate or lipid accumulation rate within a 'decision window' that occurs up to a year before spawning (Thorpe, 1986; Thorpe *et al.*, 1998). Temperature can be a key determinant of Atlantic salmon parr growth rates (Elliott & Hurley, 1997; Forseth *et al.*, 2001). Higher growth rates should result in more parr exceeding the threshold, and such a relationship has been seen in male salmonids under hatchery conditions (Rowe & Thorpe, 1990; Berglund, 1995). In a number of studies, heating was used to accelerate growth and resulted in more mature parr or earlier maturation (Crandell & Gall, 1993; Heath *et al.*, 1994). The results of these laboratory studies may give insight into why the proportion of males that become sexually mature as parr varies within and between rivers (Myers *et al.*, 1986; Hutchings & Jones, 1998). Two recent studies of maturation rates across tributaries of the River Spey (Baum *et al.*, 2004) and in Quebec (Aubin-Horth & Dodson, 2004), however, found only a weak relationship between growth rate and the incidence of parr maturation across wild populations.

The presence in the Fiddich of a localized and consistent temperature manipulation that is known to alter parr growth rates (Morrison, 1989) allows the links between temperature and development in wild fish to be explored. The minimum distance between sampling sites upstream and downstream of the Fiddich distillery effluent is *c.* 7 km. At this spatial scale, gene flow should ensure that genetic differences between the parr are small even allowing for the natal homing abilities of spawning Atlantic salmon (Jordan *et al.*, 1992; Garant *et al.*, 2000). This offers the opportunity to test in a semi-experimental setting whether temperature does influence the incidence of sexual maturation in a wild Atlantic salmon population.

## METHODS

Atlantic salmon parr were caught by upstream backpack electrofishing at four sites along the River Fiddich (57°26' N; 3°07' W), two upstream and two downstream of the distilleries (Fig. 1). Three passes were made at each site. The area sampled ranged from 68 to 147m<sup>2</sup> between sites and years. Samples of fish were caught between late

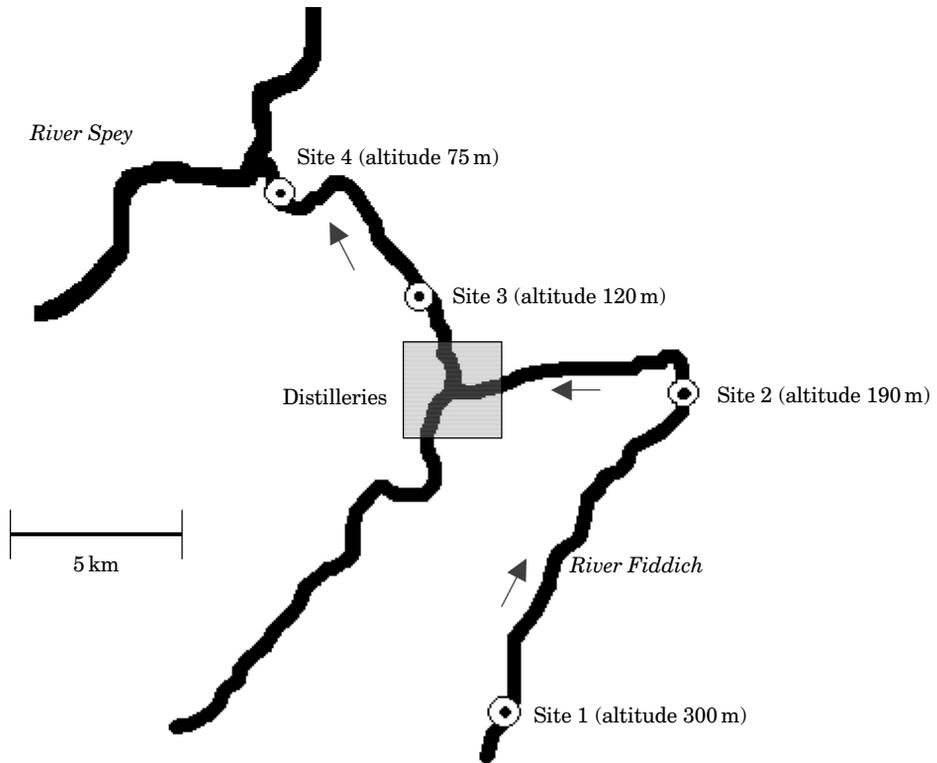


FIG. 1. Map of the River Fiddich showing the position and altitude of the sampling sites and the distilleries discharging hot water into the river.

September and early October (at the end of the growth season, but prior to spawning) in 1994, 1996, 1997 and 2003. Not all sites were sampled in each year, but in all 4 years at least one upstream site and one downstream site were sampled.

All caught parr were measured (fork length,  $L_F$ , to the nearest mm) and mature males were identified by the release of milt (sperm) when pressure was applied to the abdomen. Immature parr could be either male or female. A small sample of scales was taken from *c.* 10% of the parr and used to age the fish. Age for all parr caught was then estimated from  $L_F$  at age data from the scale-aged parr. Fish were returned alive to the capture site after measuring. Three age classes of parr were caught: 0+ (6 months old at time of capture), 1+ (18 months) and 2+ (30 months). The 0+ parr will not be considered here, since maturation at this age is unknown on the Spey. The 2+ parr were only found at sites upstream of the distilleries. This is presumably because all parr downstream of the effluent undertake the seaward smolt migration in their second spring [as a consequence of their greater growth rate (Morrison, 1989)]. Therefore the analyses mostly focus on 1+ parr, for which direct comparisons between sites above and below the distillery effluent can be made.

The altitude of each site was estimated from Ordnance Survey maps. Density measurements were calculated as the number of fish caught divided by the surface area of stream sampled.

To control for the effects on growth of differences in altitude and parr density (Baum *et al.*, 2004) between the sites, residuals were calculated from a multiple regression that predicts  $L_F$  of 1+ parr from altitude and density. The data for this calibration regression were obtained from 1135 1+ parr caught at 10 sites across the entire River Spey catchment (but not including those on the River Fiddich; Baum *et al.*, 2004). The regression equation used to calculate expected  $L_F$  was:  $L_F = 109 - 0.1a - 9.9d$

( $F_{2,1132}$ ,  $P < 0.001$ ,  $r^2 = 0.11$ ), where  $L_F$  is in mm,  $a$  is altitude in m and  $d$  is density in fish  $m^{-2}$ ).

All statistical analysis was carried out using SPSS. Factors affecting parr size were analysed using an ANOVA. Residuals from the above regression were used as the dependent variable. Position with respect to the distillery (1, downstream; 0, upstream), sampling year and maturity (1, mature male; 0, immature parr of either sex) were entered as fixed factors. Sampling site was entered as a random factor nested within position.

Predictors of maturity were identified using a binary logistic regression. Uncorrected parr  $L_F$  and the categorical variables sampling year and position (1, downstream; 0, upstream) were entered as independent factors with maturity (1, mature male; 0, immature parr of either sex) as the dependent variable.

## RESULTS

A summary of the number of mature and immature parr caught during the study is presented in Table I. Parr densities were consistently lower at sites downstream of the distilleries. Averaged across the 4 sampling years, upstream mean  $\pm$  s.e. densities for 1+ and 2+ parr combined were  $0.52 \pm 0.13$  parr  $m^{-2}$  compared to  $0.21 \pm 0.09$  parr  $m^{-2}$  downstream. This was only partly due to the presence of 2+ parr at upstream sites, since the density of 1+ parr upstream of the distilleries was  $0.45 \pm 0.12$  parr  $m^{-2}$ , more than double that at downstream sites ( $0.21 \pm 0.09$  parr  $m^{-2}$ ).

The 1+ parr at sites upstream of the effluent were close to the size expected based on the altitude and parr density at the sites. Parr downstream of the distilleries, however, were much larger than site characteristics would predict [Fig. 2(a)]. The position of the site with respect to distillery discharge (position), sampling year and maturity all significantly affected the length of parr (Table II). Mature parr were larger than their immature counterparts at the same site, independent of the effect of distillery output on growth rates [Fig. 2(a)].

Downstream of the distilleries, there was a small, but significant, difference in parr  $L_F$  between sites 3 and 4, after accounting for altitude and density. No such differences were seen between the  $L_F$  of parr at sites 1 and 2 upstream of the effluent. Mean parr  $L_F$  at both downstream sites, however, was significantly greater than that of upstream parr, and the difference in mean  $L_F$  between site 3

TABLE I. Summary of the number and age of mature male and immature Atlantic salmon parr caught upstream and down stream of heated effluent in the River Fiddich over the 4 sampling years. Immature parr include both males and females

	Upstream		Downstream	
	Site 1	Site 2	Site 3	Site 4
Number 1+ parr caught	30	148	67	63
Number 1+ mature	2	9	7	5
1+ mature (%)		6.2		9.2
Number 2+ parr caught	10	31	0	0
Number 2+ mature	0	5	0	0
2+ mature (%)		12.2		–
Overall % mature		7.3		9.2

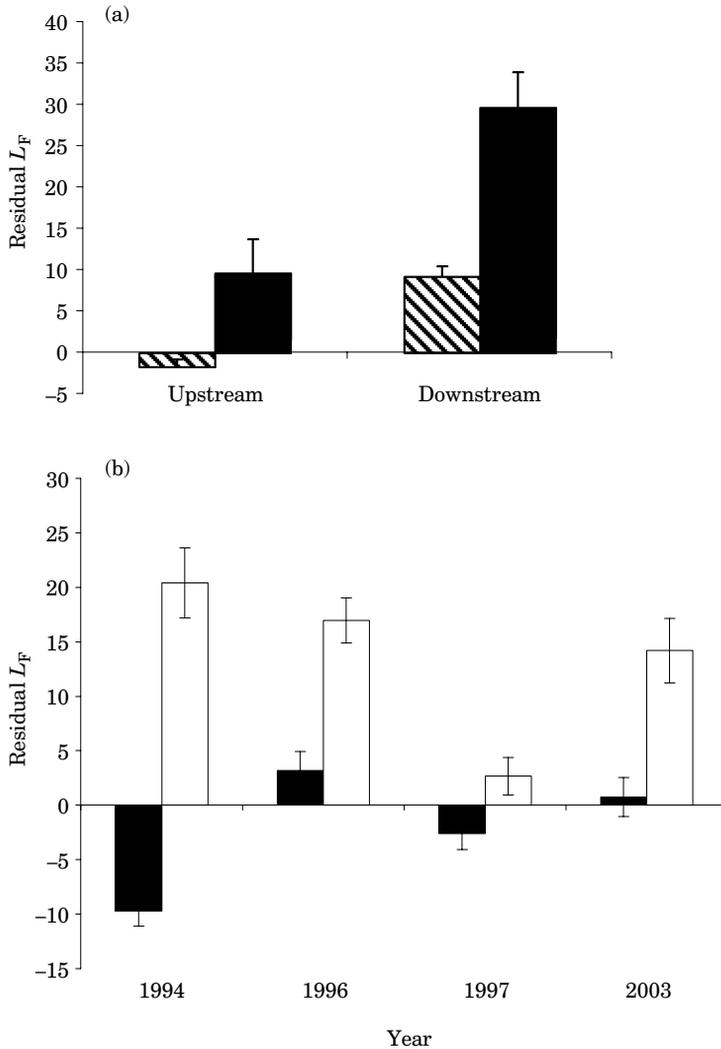


FIG. 2. (a) The effect of sexual maturity [immature (▨) and mature male (■)] and site position relative to the distilleries on body size of 1+ Atlantic salmon parr and (b) data (means  $\pm$  s.e.) presented to show year effects [upstream (■) and downstream (□)]. Body size is expressed as mean  $\pm$  s.e. fork length residuals from a multiple linear regression of parr  $L_F$  against altitude and density for 10 other sites across the whole of the Spey River catchment.

and 4 was much smaller than that between downstream and upstream parr overall. There were also year effects on parr  $L_F$ , and the difference in size between upstream and downstream fish varied between years (hence the significant position by year interaction; Table II), but in all years downstream parr were larger (after correction for altitude and density) than upstream ones [Fig. 2(b)]. To have a sufficient sample size of mature males in the following analyses of the factors influencing maturation rates, the two upstream sites were combined and pooled across years, as were the two downstream sites. There was

TABLE II. Results of an ANOVA testing the effect of position (relative to the distillery effluent), site, sampling year and maturity on the fork length of 1+ Atlantic salmon parr. Position (1, downstream; 0, upstream), year and maturity (1, mature male; 0, immature parr) were entered as fixed factors with site nested within position. Fork length is expressed as residuals from a multiple linear regression of parr  $L_F$  against altitude and density for 10 other sites across the whole of the Spey catchment. Only significant terms are listed. Overall model: ANOVA, d.f. = 10,297,  $P < 0.001$ ,  $r^2 = 0.39$

Variable	<i>F</i>	d.f.	<i>P</i>
Position	63.96	1,297	<0.001
Maturity	19.46	1,297	<0.001
Year	6.70	3,297	<0.001
Position by year	9.43	3,297	<0.001
Site nested within position	5.14	2,297	0.006

no significant difference in the proportion of 1+ parr maturing upstream and downstream of the distilleries ( $\chi^2$ , d.f. = 1,  $P > 0.1$ ). Position, however, did affect the  $L_F$  at which parr matured (Table III and Fig. 3). Downstream sites contained larger parr, but the probability of maturation was lower for a given  $L_F$  at downstream sites with the result that the proportion of 1+ parr maturing was similar above and below the distilleries (Table I).

Only a small number of 2+ parr were caught at upstream sites over the 4 years, five of which were mature (Table I). The maturation rate of 2+ parr was not significantly higher than that for 1+ upstream of the distillery ( $\chi^2$ , d.f. = 1,  $P > 0.1$ ), and the presence of 2+ parr at upstream sites did not dramatically affect the overall proportion of mature fish there.

## DISCUSSION

Atlantic salmon of a given age were larger downstream of the distillery effluent, but male maturation rates did not vary significantly between upstream and downstream areas. This contrasts with laboratory experiments that found temperature affected both growth and maturation rate (Crandell & Gall, 1993; Heath *et al.*, 1994). In this study, and that of Morrison (1989), parr density was lower downstream of the distilleries. This is unlikely, however, to be the cause of

TABLE III. Results of a stepwise logistic regression to identify predictors of maturity in 1+ Atlantic salmon parr. Fork length, year and position (1, downstream; 0, upstream of distillery effluent), together with two-way interactions between these variables, were used as the independent factors while maturity (1, mature male; 0, immature parr) was the dependent variable. Only significant terms are listed. Overall model:  $\chi^2$ , d.f. = 1,  $P < 0.001$ , Nagelkerke  $r^2 = 0.22$

Variable	Wald	d.f.	<i>P</i>
Length	23.100	1	<0.001
Position	6.244	1	.012

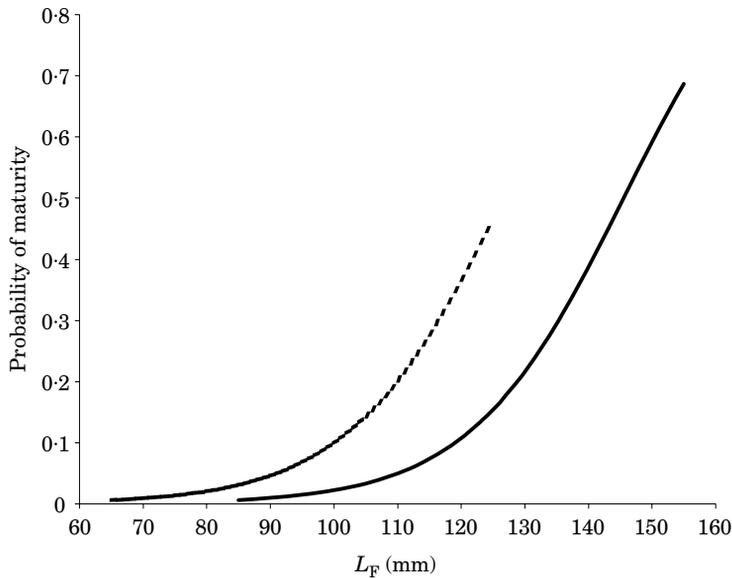


FIG. 3. The probability (taken from the logistic regression analysis presented in Table III) that a 1+ Atlantic salmon parr will be a sexually mature male based on its fork length and whether it was caught upstream or downstream of the distilleries. Regression lines are plotted over the range of  $L_F$  found at the location. Males of a given size were more likely to be mature if they were upstream (..) of the distilleries than if they were downstream (—).

the difference in growth rates since body size was adjusted for density in the present study. Moreover, Morrison (1989) found parr downstream of the distillery were larger than those caught in nearby streams with similar parr densities but not subject to distillery effluent.

Aubin-Horth & Dodson (2004) and Baum *et al.* (2004) also found that the incidence of parr maturation was not related to the mean size of fish across different rivers suggesting variability in the threshold size for maturation. Thresholds that are positively related to growth opportunity, such that males must be larger to mature where growth is fast, could be adaptive (Baum *et al.*, 2004). Parr must exceed a certain size to be physiologically capable of maturation. This creates a minimum size for maturation that would not be expected to vary greatly between rivers. Above this minimum size, however, the benefits of maturation depend on the size of the fish relative to that of other mature parr and the number of other males (both mature parr and anadromous males) with which it competes on spawning grounds. The reproductive success of mature parr declines with the number of competitors (Hutchings & Myers, 1988; Jones & Hutchings, 2001) and large male parr are able to gain better access to spawning females and hence fertilize a greater number of eggs (Myers & Hutchings, 1987; Thomaz *et al.*, 1997). Even if a male is capable of maturation, the low probability of breeding success would make maturation a costly decision for many. Higher threshold levels in areas of good growth opportunity would result in only the larger parr within a cohort, which can expect some spawning success, investing in maturation. On the River Fiddich, the probability of maturity for a

parr of given size was lower at downstream sites. This is the pattern predicted if thresholds for maturation are positively correlated with growth opportunity.

Due to negative frequency dependence in parr fertilization success, higher thresholds would also be adaptive where the number of anadromous males is greater. Male parr, however, must initiate maturation well in advance of spawning (Thorpe, 1994), before anadromous males are present in the upper reaches of a river. Therefore, only if the number of anadromous males returning to a river is highly consistent across years or correlated with environmental variables that parr experience, will the density of anadromous spawners affect the decision of male parr to mature. Anadromous males are central to ultimate models predicting male parr fertilization success (Gross, 1996), but they may not influence the proximate causes of maturation due to limited information available to parr at the time of the developmental switch.

Variable threshold rates have been assumed to have a genetic basis and rely on local adaptation to predictable differences in growth opportunity and fine scale population structuring (Aubin-Horth & Dodson, 2004; Baum *et al.*, 2004). Unlike a previous survey of maturation rates on the River Spey (Baum *et al.*, 2004), this study was confined to a single tributary where the short distance between upstream and downstream sampling sites should allow gene flow between them and prevent genetic divergence (Jordan *et al.*, 1992; Garant *et al.*, 2000), though no genetic analysis has been carried to confirm this. An alternative explanation is that there is environmental plasticity in the threshold size at which parr mature. Perhaps the growth rate or size that male parr need to exceed to mature is modified by their early experience such that males experiencing good growth conditions develop higher thresholds. Most laboratory manipulations of growth rate that affected the incidence of maturation (Rowe & Thorpe, 1990; Crandell & Gall, 1993; Berglund, 1995; Letcher & Terrick, 1998) occurred well after first feeding and so feasibly after a threshold size had been set. An adaptive explanation would be needed for the determination of the threshold size so early in ontogeny. One possibility is that individual growth in the first few months gives a good indication of the mean growth of the cohort as a whole, whereas there is less certainty in later life due to greater individual variation in growth between older parr, as a result of habitat heterogeneity. The mechanism governing which parr mature could thus have evolved to incorporate an estimate of the size of parr in a population and result in only males at the larger end of the size distribution maturing.

Another possible explanation for the larger size of mature parr downstream of the distilleries centres on growth rates during the long period of maturation. Parr below the distillery would grow more than those upstream in the year that elapses between the developmental switch governing maturation and spawning, so a uniform maturation threshold across the whole river would result in downstream mature parr being larger than those upstream by the time of spawning. Growth rates downstream, however, would also have been higher in the year preceding maturation, so more parr would have exceeded the threshold in downstream sites. This does not match the observed results, since there was no significant difference between upstream and downstream sites in the percentage of fish becoming mature.

So far the assumption has been made that parr are not moving between upstream and downstream areas. Parr have highly localized home ranges and many remain in the same small area for many months (Armstrong *et al.*, 1994). Larger scale parr migrations at particular times of the year, however, have been documented. In this study, parr were sampled in late September before any migrations associated with seaward (smolt) migration take place (Buck & Youngson, 1982). Movement of mature male parr towards spawning grounds should also not affect these results since parr were caught before this movement is initiated (Buck & Youngson, 1982) and there are established spawning grounds both above and below the distilleries.

There is a difference in the age at which parr undertake the smolt migration between areas upstream and downstream of the distilleries. The majority of Fiddich parr become smolts in the spring of their second year, but a small number above the distilleries delay smolting, hence 2+ parr were found at upstream sites in autumn. Like maturation, smolting is thought to be controlled by a growth-dependent threshold (Thorpe, 1977). The effect of heating and accelerated growth on smolting but not maturation indicates differences in the mechanisms controlling these two life-history events. Maturation rates for these remaining 2+ parr were higher than in 1+ parr, but the number of 2+ parr was small so maturation at 2+ did not greatly affect the number of mature parr above the distilleries.

The interaction between whisky making and Atlantic salmon is not a widespread problem. Human impacts on the riverine environment, however, are widespread. Jensen (2003) describes the effect of temperature changes caused by a hydroelectric scheme on Atlantic salmon growth rates and Holtby (1988) found that stream temperature and hence smolting of coho salmon *Oncorhynchus kisutch* (Walbaum) were affected by nearby logging. The presence of such human interference and the prospect of climate change make understanding the effect of environmental perturbations on salmonid life histories important to the conservation of these species. These results show that relationships between environmental conditions, growth and life-history strategy found in laboratories cannot simply be extrapolated to wild populations.

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