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The influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*)

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ABSTRACT

We found that young salmon fathered by precocious males grew faster than those fathered by anadromous males in Atlantic salmon (*Salmo salar* L.) during the time from hatching to yolk sac absorption, when the young are completely dependent on endogenous food resources. We first compared growth rate of artificially reared progeny of precocious and anadromous fish harvested as embryos directly on spawning grounds after reproduction. In a second experiment, we compared fish lengths and growth rate of offspring of precocious and anadromous fish that were caught before reproduction, artificially bred and reared *in situ*. The first experiment revealed that the progeny of precocious males had a significantly higher growth rate between hatching and yolk sac absorption, resulting in a larger body size, than anadromous offspring. In the second study, we found no significant differences in size between the two groups at any time during the experiment, which could be explained by the artificially enhanced reproductive success of potential subordinate males. Indeed, in the second experiment, the microsatellite analysis of paternal identity revealed that precocious males who fathered the most progeny had offspring with a larger mean size throughout the experiment, resulting in a marginally significant difference in length between precocious offspring and anadromous offspring. A higher but not significantly different mortality rate was also observed in anadromous than in precocious offspring throughout the second experiment. Our results indicate an inherent fitness advantage in some offspring fathered by precocious males, which may ultimately favour the development of precocious sexual maturity in Atlantic salmon.

Keywords: alternative reproductive tactics, conditional strategy, fertilization success, growth rate, Salmonidae.

INTRODUCTION

There is an amazing diversity of mating patterns within and across species of fish (for reviews, see Breder and Rosen, 1966; Gross, 1984; Henson and Warner, 1997). Among many externally fertilizing fishes, males must compete for access to females and defend breeding

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territories to maximize fertilization success. However, maintaining such a defence while striving to maximize fertilization success may result in an inability to conserve exclusivity to female eggs. Thus, in combination with the differential competitive abilities of males, these circumstances favour the evolution of alternative reproductive strategies in which smaller males 'sneak' fertilizations rather than defend breeding sites. Indeed, there is evidence of 'simultaneous parasitic spawning' in 140 fish species with external fertilization belonging to 28 different families. More specifically, this phenomenon is present in 13 salmonid species, including Atlantic salmon (*Salmo salar* L.) (see Taborsky, 1998).

Atlantic salmon show the greatest within-population variability in size at maturity of all salmonid fishes (Fleming, 1996). In this species, two extremely distinct male phenotypes co-exist on most spawning grounds. First, large anadromous males require a minimum of 3–4 years, including an oceanic phase, to mature. Generally, anadromous males compete among themselves for the opportunity to guard females (Belding, 1934; Jones and Ball, 1954; for a review, see Fleming, 1998). Second, precocious males reach maturity in fresh water as early as the second summer of life. These males attempt to sneak fertilizations and can be very efficient in doing so (Hutchings and Myers, 1988; Jordan and Youngson, 1992; Thomaz *et al.*, 1997), fertilizing up to 89% of eggs within redds in some cases (Morán *et al.*, 1996).

The most likely explanation for the co-existence of these two phenotypes in the same population is a combination of frequency- and status-dependent selection within the framework of the conditional strategy (see Gross, 1996). The main prediction of this model is that frequency-dependent selection should operate when the relative success of the tactic used by an individual is influenced by the tactics adopted by other members of the same population. If the success of the individual tactic relies on competitive ability (or state) relative to other individuals in the population, then status-dependent selection should operate. Alternative tactics of a conditional strategy have unequal fitness but can remain in equilibrium even with inheritance (Gross and Repka, 1998a; but see also Hazel *et al.*, 1990; Hazel and Smock, 2000). Therefore, the conditional strategy requires that juveniles are able to switch to the tactic that will provide them with the highest fitness, and that this choice is made as a function of their individual status (Gross, 1996), which, in turn, is mainly influenced by their growth rate.

This is presumably the case in Atlantic salmon, as it has been shown that growth rate is one of the most important factors contributing to the development of precocity (Lundqvist, 1980; Whalen and Parrish, 1999). Indeed, it has been shown that both a heritable component (Naevdal *et al.*, 1976; Thorpe *et al.*, 1983; Glebe and Saunders, 1986) and an environmental component (Bohlin *et al.*, 1990; Berglund, 1992) determine whether an individual reaches a threshold size beyond which it is possible for salmon to mature (see Hutchings and Myers, 1994). What are less clear are the respective roles that the genetic and the environmental components play in determining precocity. In fact, no study has attempted to isolate the heritable component from environmental influences and, in this way, estimate the importance of male phenotypic identity on the subsequent development of sexual maturity in this species.

The main aim of this study was to isolate the influence of the precocious and anadromous male genotypes on the growth of offspring. We achieved this by establishing if offspring fathered by precocious males grew faster than those of anadromous males during the time from hatching to yolk sac absorption, when the young are completely dependent on endogenous food resources, thus eventually increasing the probability of precocious

maturity. Two experiments were conducted over 4 years. In the first experiment, we compared otolith size (see 'Materials and methods') and thus growth rate of artificially reared progeny of precocious and anadromous fish harvested as embryos directly on spawning grounds after reproduction. In the second experiment, we compared fish lengths and growth rate of offspring reared *in situ* of precocious and anadromous fish that were caught before reproduction and artificially bred. We also used DNA analyses to establish fertilization success of all males in both experiments.

MATERIALS AND METHODS

Naturally bred progeny

In the fall of 1995, open corridors (5 m wide) built with nets and poles were established in known spawning grounds on the northeast branch of the Sainte-Marguerite River (48°20′N, 70°00′W), Québec, Canada. To maintain as best as possible natural conditions, these corridors were closed after 4–6 h observation of extensive courtship. After reproduction occurred and nests had been covered with gravel, we captured all individuals that took part in reproductive activities at three nest sites. These fish were aged, measured and their tissues were sampled for further DNA analysis. Embryos were recovered from the nests by divers and were then transported to the Station Piscicole of Tadoussac, a local government hatchery. Upon hatching, progeny were held and fed *ad libitum* for 2 months before being sacrificed for DNA analyses.

To determine growth rate of offspring after hatching, the sagittal otoliths of an equal number of progeny fathered by precocious and anadromous males from each nest were removed and mounted on microscope slides (see Meekan *et al.*, 1998, for methods). The otoliths were measured using a compound microscope with a high-resolution video camera connected to a personal computer as described by Meekan *et al.* (1998). Otolith size was used in this part of the study as a surrogate measure of body size at successive ages during the development of fry that were sacrificed after approximately 2 months of rearing. It has been reported that variation in otolith size accounts for 98% of the variation in length of young Atlantic salmon (Meekan *et al.*, 1998).

Analysis of variance (ANOVA) for repeated measures was used to detect differences in otolith radius at age zero, 10, 20, 30, 40 and 50 days between the two groups. This model takes into account two types of dependency in an attempt to avoid potential bias from pseudoreplication of data. First, the dependency between some offspring who shared the same mother and father was taken into account to avoid bias due to different levels of inheritance or the maternal effect of egg size on alevin size. The second type of dependency was between the observations made at different times on a specific individual (time structural dependency). Multiple comparisons were then made *a posteriori* in cases where a significant effect was observed in the ANOVA table using Fisher's least significant differences method to identify differences in length between precociously and anadromously fathered offspring.

Artificially bred progeny

In the fall of 1997, precocious males of the same cohort were sampled on the Sainte-Marguerite River and were transported to the Station Piscicole of Tadoussac where

fertilization crosses were made with anadromous individuals that had been previously caught on the same river for a supportive breeding programme. The eggs of a single female were split into four equal batches, each of which was fertilized with the sperm of two males of the following identity: (1) two precocious males P1 and P2 (batch PREC1); (2) another two precocious males P3 and P4 (PREC2); (3) two anadromous males A1 and A2 (ANAD1); and (4) another two anadromous males A3 and A4 (ANAD2). Anadromous males were all multi-sea winter fish (which spend more than one winter at sea before returning to spawn). We then transported the eggs to a flow-through incubator that drew water directly from a tributary of the Sainte-Marguerite River. The eggs were left to incubate and develop naturally from October to May. Tissues from all parents were preserved in 95% ethanol for genetic identification.

At hatching in May 1998, 90 eggs of each batch were transferred to individual rearing cups. We then filmed the young, using a video camera with a 12× zoom, to establish the individual growth rate and the survival rate of each family. We filmed two batches per day including one batch of each parental identity. Specifically, batch PREC1 was compared with batch ANAD2 and batch PREC2 with batch ANAD1. Offspring were filmed for 30 days for a total of 15 observations per batch. Data from this video monitoring were then analysed using image analyser software (Sigmascan pro v.2). This allowed us to determine the length and the daily growth rate of each alevin as described by Meekan *et al.* (1998). Furthermore, as growth increments are formed on a daily basis on the sagittal otolith of these fish (Meekan *et al.*, 1998), we used these structures to establish if all offspring were of the same age. We counted growth increments from the hatching mark to the margin using a compound microscope as described in the previous subsection. Mortality was established by counting living offspring at each observation period.

We tested homogeneity of survival curves in time (Lawless, 1982) using the LIFETEST procedure (SAS v.8) for each of the following: (1) between paternal identity, (2) within paternal identity and (3) between batches. A mixed-model analysis of variance was used to detect differences in length at each observation period between PREC1 and ANAD2 offspring and between PREC2 and ANAD1 offspring. This model takes into account dependency between the observations made at different times on a specific subject (time structural dependency). Multiple comparisons were made in cases where a significant effect was observed in the ANOVA table using Fisher's least significant differences method (LSD) to identify differences in length between precocious and anadromous offspring.

Differences in the number of offspring sired was tested for each batch using the chi-square test (SAS v.8). Finally, we also tested for possible differences in progeny length between males within batches using repeated-measures analysis of variance and a model taking into account both dependency between observations at different times and also dependency of offspring who shared the same father.

Genetic identification

DNA analyses were used in both experiments to establish parental identity of all offspring. In all cases, total DNA extraction was performed from approximately 30 mg of tissue according to Bernatchez *et al.* (1992). In the first experiment, we used five microsatellite loci (*Ssa171*, *Ssa197*, *Ssa202*, O'Reilly *et al.*, 1996; *SSOSL85*, *SSOSL417*, Slettan *et al.*, 1995) and, in the second experiment, we used three microsatellite loci (*Ssa171*, *Ssa197*, *Ssa202*, O'Reilly *et al.*, 1996). Microsatellite polymorphism analysis using radioactive labelling was

performed as detailed in Fontaine and Dodson (1999) and Garant *et al.* (2000). Paternal identity (and thus fertilization success of males) for all offspring could unambiguously be established simply by comparing the allelic identity of the potential parents with that of their offspring.

RESULTS

Naturally bred progeny

Fertilization success

There was a variable number of precocious males (12, 7, 23) and anadromous males (2, 6, 1) within each nest (Table 1). However, in each case, most eggs were fertilized by a single anadromous male (Table 1). Other anadromous males present in nests were unsuccessful at fertilization, except for nest 1 where a second anadromous male fertilized 5% of the eggs. Precocious males were more efficient in sneaking fertilizations as two, one and four of them participated in reproduction depending on nest, fertilizing between 6% and 15% of the eggs (Table 1). Older precocious males were most successful in taking part in reproduction, as six of seven males involved in fertilizations were 2+ fish (more than 2 years of growth in fresh water), representing 89% of total precocious fertilization success. There was also a marginally significant effect of size, as precocious individuals that fertilized eggs were larger than unsuccessful ones ($P = 0.0524$; Fontaine, 1998, results not shown).

Growth

Of a total 266 fry analysed from the three isolated nests, 28 were related to a specific precocious male. The analysis of the otolith growth increments revealed that the progeny of the precocious males had significantly larger otolith size, and thus a larger body size, than anadromous offspring at each period from hatching (day zero) to 50 days of age (Table 2),

Table 1. Number of precocious and anadromous males present in the three sampling areas in Experiment 1 (top) and their individual relative fertilization success (%) (bottom)

	Nest 1	Nest 2	Nest 3
Number of anadromous males	2	6	1
Number of precocious males	12	7	23
Number of eggs analysed	99	85	82
Anadromous #1	84 (75)	94 (91)	85 (84)
Anadromous #2	5 (68)	—	—
Precocious #1	8 (2+, 11.7)	6 (2+, 10.4)	8 (2+, 10.7)
Precocious #2	4 (1+, 7.5)	—	5 (2+, 11.3)
Precocious #3	—	—	1 (2+, 11.7)
Precocious #4	—	—	1 (2+, 10.4)
Total fertilization by precocious males (%)	12	6	15

Note: Age (for precocious males) and size (cm) are shown in parentheses.

resulting in a significant effect of male identity on otolith size ($P = 0.0055$) and on growth curves through time ($P = 0.0008$) (Table 3). This was also demonstrated by the non-parallel growth curves resulting from significantly different growth rates from day 0 to day 10 ($P < 0.0001$) and from day 10 to day 20 ($P = 0.0145$) (Fig. 1). However, growth rate was not significantly different during the remaining days (from day 20 to day 50, $P > 0.05$) (Fig. 1).

Artificially bred progeny

Mortality rate

There was a higher mortality for anadromous than precocious offspring on day 1, the first day of observation following the transfer of embryos from the incubator to rearing cups (anadromous offspring 26.7%; precocious offspring 20.5%; $P = 0.1722$, chi-square test, SAS v.8). Total mortality throughout the experiment was also higher in anadromous progeny

Table 2. Fisher's least significant differences method of multiple comparisons of growth patterns of the otolith between the progeny of the precocious and anadromous fathers in Experiment 1

	Mean size of otolith radius (μm)				
Age (days)	Anadromous	Precocious	d.f.	*F*	*P*
0	115.08 ± 0.72	119.32 ± 0.79	1,2.30	16.01	0.045
10	165.30 ± 0.41	180.96 ± 0.41	1,4.57	541.54	<0.0001
20	213.64 ± 0.52	234.05 ± 0.57	1,3.72	522.29	<0.0001
30	252.76 ± 1.99	274.51 ± 2.20	1,2.06	53.84	0.0167
40	285.06 ± 2.40	308.32 ± 2.66	1,2.04	42.49	0.0217
50	317.05 ± 2.74	340.62 ± 3.04	1,2.04	33.20	0.0276

Table 3. Results of split-plot in time design with fixed and random factors

Source of variation	d.f.	MS	*F*	*P*
Nest sites	2	2 028.25	8.43	0.0299
Type of male	1	22 225.41	147.6	0.0055
Nest sites*type of male	2	146.69	23.19	0.9987
Male*(nest sites*type of male)	4	393.07	0.52	0.7239
Error 1	44	767.28		
Time	5	261 147.39	4 026.00	0.0001
Time*nest sites	10	65.31	1.24	0.3627
Time*type of male	5	574.90	10.98	0.0008
Time*nest sites*type of male	10	52.31	10.98	0.2514
Time*male*(nest sites*type of male)	20	27.28	2.49	0.6986
Error 2	220	33.62		

Note: Otolith sizes and growth curves between type of male (precocious and anadromous) were significantly different in Experiment 1 ($P = 0.0055$ and $P = 0.0008$, respectively).

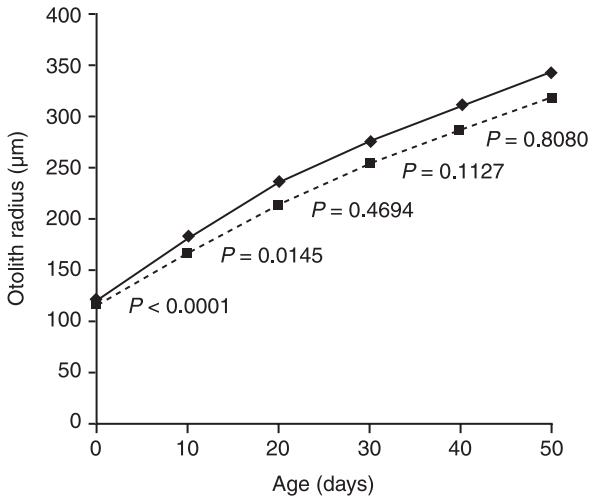

Fig. 1. Growth curves of precocious (continuous) and anadromous (dashed) offspring in Experiment 1. *P*-values indicate significance of difference between slopes for each segment of 10 days. Values are significantly different at each point (see Table 2).

(5.2%) than in precocious progeny (4.5%). Thus, mortality rate at day 30 was greater for anadromous progeny (32.2%) than for precocious progeny (25.0%). However, the difference in mortality was not significantly different throughout the experiment ($P = 0.1326$, Wilcoxon test, SAS v.8).

Age

A distinct mark was formed on day seven (the seventh increment, which corresponded to a rise in temperature in the incubator) for all offspring. That this occurred on the same day for all fish indicated that all fish hatched on the same day. As a result, all subsequent comparisons were made by day of observation rather than ageing all offspring according to the total number of otolith increments.

Growth and influence of paternal identity

The mixed-model analysis of variance of fry length revealed no significant differences in size between the progeny of precocious and anadromous fathers through time ($P = 0.6430$) (Table 4). Specifically, multiple comparisons from day 1 to day 30 revealed no significant differences between batches PREC2 and ANAD1 at any time. In comparisons of batches PREC1 and ANAD2, we found significant differences at observation periods 1 ($P = 0.029$), 3 ($P = 0.033$) and 9 ($P = 0.033$), with precocious offspring being larger in each case (results not shown). To estimate the error on each measure, we randomly sampled 25 fish and measured them again. We found, on average, an error of 0.67% (0.17 mm). We found significant differences in the proportion of progeny sired between precocious males within their batch ($P = 0.0299$; results not shown). In the first precocious batch (PREC1), we found that male P1 (11.9 cm) fathered only 27.8% of the progeny compared with 72.2% for male P2 (9.6 cm) ($P < 0.001$; chi-square test for specified proportions, SAS v.8). The same phenomenon was observed in the other precocious batch (PREC2), where male P3

Table 4. Results of the mixed procedure analysis (SAS v.8) in Experiment 2 for length through time of precocious and anadromous offspring

Source of variation	n.d.f.	d.d.f.	*F*	*P*
Group (PREC1-ANAD2 *vs* PREC2-ANAD1)	1	271	7.96	0.0051
Type of male	1	271	1.99	0.1595
Group*type of male	1	271	0.78	0.3791
Time	14	3509	9 878.43	0.0001
Type of male*time	14	3509	0.82	0.6430
Group*type of male*time	28	3509	4.68	0.0001

Table 5. Precocious males' relative fertilization success and offspring mean length throughout Experiment 2

Male identity	Fertilization success (%)	Offspring size (mm)
PREC1		
P1	27.8	25.95
P2	72.2	**26.24**
PREC2		
P3	30.9	25.69
P4	69.1	26.00

Note: **Bold** value indicates a marginally significant difference in length between precious and anadromous progenies ($P = 0.0552$).

(10.1 cm) fathered 30.9% of offspring, which was significantly lower than the 69.1% for male P4 (9.7 cm) ($P < 0.001$) (Table 5). However, a different pattern was observed among anadromous males. In batch ANAD1, all offspring (100%) were fathered by the same male (A1); in batch ANAD2, the A3 male sired most of the progeny (93.3%), with the other male (A4) having only 6.7% of the offspring matching his allelic identity. Mortality rate between fathers within each batch was not significantly different (results not shown).

We found a significant effect of the father's identity on offspring length within batch through time in precocious males ($P = 0.0355$; results not shown). Specifically, the male who had offspring with a larger mean size throughout the experiment also fathered the most progeny. Within batch PREC1, P2 offspring measured 26.24 mm and P1 offspring 25.95 mm; within batch PREC2, P4 progeny averaged 26.00 mm compared with 25.69 mm for P3 offspring (Table 5). Also, when comparing these most successful precocious males with anadromous males of their corresponding batches (P2 *vs* ANAD2; P4 *vs* ANAD1), we found a marginally significant difference in length between P2 offspring and offspring of ANAD2 ($P = 0.0552$) (Table 5).

DISCUSSION

The main aim of this study was to isolate the influence of the precocious and anadromous male genotypes from that of the environment on the growth of offspring in Atlantic

salmon. We achieved this by establishing if offspring fathered by precocious males grew faster than offspring fathered by anadromous males during the time from hatching to yolk sac absorption, the period when offspring are completely dependent on endogenous food resources. We also established relative fertilization success of precocious and anadromous males in wild conditions.

Higher growth rate in the offspring of precocious males

The results of the experiment conducted with embryos harvested directly on spawning grounds after reproduction revealed that precocious offspring had a significantly higher growth rate during the time from hatching to yolk sac absorption (day 1 to day 20) than anadromous males. However, two potential confounding factors have to be considered. First, we assume a strong relation between otolith growth and somatic growth in young Atlantic salmon, as shown by Meekan *et al.* (1998). Secondly, embryonic development time was accelerated in the first experiment, as these fish were reared at higher temperatures in hatchery conditions. Although there is no apparent reason to believe that this could have created the significant differences observed, it remains a potentially confounding factor. For these reasons, we conducted a second experiment to measure directly the growth of fish during their development so as to eliminate the potential error associated with otolith back-calculation and to eliminate any possible bias associated with accelerated development rates. This meant that fish had to be captured before reproduction to establish known batches of the progeny of anadromous and precocious fathers to be subsequently raised under natural conditions in an incubator.

In the second experiment, we initially found no obvious evidence of a potential growth rate advantage of precocious offspring over anadromous offspring with only sporadic differences at certain times in the comparisons involving batches PREC 1 and ANAD 2. However, we found a significant difference in the length of progeny fathered by precocious males fertilizing the same female ($P = 0.0355$). This resulted in a marginally significant difference between the length of the progeny of one of these males and that of the offspring of the anadromous males (P2 *vs* ANAD2). Thus, this indicates a possible advantage in growth rate of 'best-male' offspring within the precocious tactic.

In controlling the potential shortcomings of the first experiment, we introduced what we consider to be yet another confounding factor in the second experiment. In fact, the less significant results observed in the second experiment may be largely explained by the artificially enhanced reproductive success of potentially subordinate precocious males. In the first experiment, the precocious males competed actively for mates on the spawning grounds. In Experiment 2, precocious males were captured 1 month before the spawning season. The choice of males to fertilize eggs under controlled hatchery conditions was entirely arbitrary. Thus, in the second experiment, we may have enhanced the reproductive success of subordinate precocious males that may not have reproduced under natural conditions. This is supported by the marginally significant difference found between the length of the progeny of one of the males and that of the offspring of the anadromous males when the two most unsuccessful precocious males were removed. This possibility is also illustrated by the results of the first experiment, which showed variable individual fertilization success (from 0 to 8%) depending on individuals within each nest. This result is also concordant with previous estimates (Hutchings and Myers, 1988; Jordan and Youngson, 1992; Morán *et al.*, 1996, Thomaz *et al.*, 1997) where fertilization success ranged from

0.9 to 35% among individuals within nests. We also observed a marginally significant effect of precocious male size on fertilization success in the first experiment, which is also concordant with previous literature (Thomaz *et al.*, 1997). Older precocious males (2+) were more efficient in fertilizing eggs than younger individuals (1+). Together, these findings suggest a high variability in reproductive success among precocious males and support the presence of subordinate individuals with inferior fitness, which could account for the less significant results observed in the second experiment.

Possible explanations for the presence of 'inferior' precocious males

The high variability in reproductive success among precocious individuals was also observed among anadromous males. The results of the first experiment illustrate such variability between anadromous males, as dominant males fertilized 84% or more of the eggs, whereas only one of the six subordinate anadromous males participated in fertilizing the eggs (Table 1). A high variabilty between males was also demonstrated by Mjølnerød *et al.* (1998), where one male fathered more than 80% of the embryos in each spawning analysed. Furthermore, in a previous experiment in which we estimated reproductive success of anadromous salmon in the wild, we found a high variability in reproductive success between males with a significant correlation between male size and reproductive success (see Garant *et al.*, 2001). Such high individual variance in reproductive success was in part a result of the presence of smaller anadromous males called 'grilse'. These males, which spend only one winter at sea before returning to spawn, are known to avoid confrontation with larger multi-sea winter males (Webb and Hawkins, 1989; personal observations) and to act like subordinate males (Fleming, 1996), resulting in lower reproductive success (for a review, see Fleming, 1998). However, a higher proportion of grilse than multi-sea winter fish survive to their first reproductive event and can potentially reproduce again in the future (Jonsson *et al.*, 1991), thus increasing their lifetime reproductive success. Therefore, the higher survival rate of these subordinates to reproduce the following year may offset their low reproductive success during their first year of spawning. We believe that this could also be the case for subordinate precocious males. In fact, as these individuals are less involved in reproduction, they should have higher survival (Hutchings, 1994) and thus a greater probability of migrating to sea, as is the case for immature males (Whalen and Parrish, 1999).

Within the framework of the conditional strategy, the adoption of a tactic by an individual involves a choice at a given stage of life as a function of his relative 'status' (Gross, 1996). However, the status of a male at a given reproductive event might be lower than that predicted by its choice made at a previous time (status evaluation time). Indeed, this is very likely in cases where the environmental conditions vary stochastically through time (see Hofmann *et al.*, 1999) and, as a consequence, males are unable to assess correctly their status relative to others. Very few experiments conducted under natural conditions have tried to identify the moment of life when males decide whether or not to mature. Whalen and Parrish (1999) showed that variation in the incidence of maturation was largely explained by body size and that the choice of the tactic seemed to be related to size early in the summer preceding reproduction. Also, others have shown in experimental conditions that early spring is a critical period for maturation (Rowe and Thorpe, 1990; Rowe *et al.*, 1991). Together, the results of these experiments suggest that there is a significant gap between the decision to become sexually mature and reproductive activity. This may

provide opportunities for environmental conditions to alter the relative status of males in the population. This implies that the 'status evaluation' process might not be perfect, given the likelihood that the assessment of individual status at a given stage might not always be the best at a later stage. Indeed, this may promote the production of subordinate precocious males.

We propose that the significantly different growth rates found before emergence in Experiment 1 are the result of an inherent fitness advantage in offspring fathered by dominant precocious males, and that the less significant results observed in Experiment 2 can be explained by the artificially enhanced reproductive success of subordinate males. Higher growth rates may increase the probability that the progeny of these dominant precocious males reach the threshold size required for early maturation (Hutchings and Myers, 1994), as a higher growth rate is associated with competitive advantage for territorial defence (Elliott, 1990; Johnson *et al.*, 1999), protection against starvation (Einum and Fleming, 1999) and higher survival (Meekan *et al.*, 1998; Einum and Fleming, 2000). To our knowledge, this study provides the first evidence of higher growth rates of precociously fathered offspring relative to offspring fathered by anadromous males, which is in agreement with the predictions of the conditional strategy hypothesis (Gross and Repka, 1998a,b).

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