# Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success

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## SUMMARY

In Atlantic salmon, as in most salmonids, males can mature early in the life cycle, as small freshwater fish, termed parr, and/or undergo a sea migration before maturing as full-size adults. The alternative life histories are contingent on environmental and social circumstances, such as growth rate, territory quality or any other factor that affects the individual's state. In order to model the choice of life history in this group of commercially valuable species, it is necessary to understand not only the relative contribution of the different male types to subsequent generations, but also to know the factors that affect reproductive success in each type.

In this paper we present the results of a study designed to investigate the factors that affect the reproductive success of mature parr. We used highly polymorphic minisatellite DNA markers to analyse paternity in a series of mating experiments where the number and body size of parr were manipulated. The fraction of eggs fertilized by mature parr ranged from 26 to 40%, with individual parr fertilizing up to 26% of the eggs. A strong positive correlation was found between parr size and reproductive success. The relative success of parr decreased with increasing parr number. Data from this and other studies on variation in the timing and degree of parr reproductive success are discussed in relation to the evolution of male mating strategies and life history in salmonids.

## 1. INTRODUCTION

Understanding the mechanisms involved in directing the individual choice of life history is a major goal of current research in behavioural ecology (McNamara & Houston 1996). Age and size at first maturation, the frequency of reproductive episodes, and offspring survival are all life-history variables that help to define an organism's breeding system, timing and pattern of migrations, and ultimately its life-time fitness.

In species with complex breeding systems individual reproductive success is often difficult to measure. The advent of techniques for detecting highly polymorphic genetic markers has made it possible to quantify individual reproductive success in wild populations (Burke & Bruford 1987; Wetton *et al*. 1987; Burke 1989). One remarkable observation made in many bird species is that the degree of cuckoldry is often far greater than traditional observational studies suggest (Birkhead & Møller 1992). These findings are changing our views on animal mating behaviour and the role of sperm competition.

In Atlantic salmon (*Salmo salar*), as in other species of salmonids, males are known to mature after a sometimes long sea migration, or else whilst still in the river as juvenile-like fish called mature parr (Jones 1959). This polymorphism in the timing of first maturation has been interpreted in many different ways. Jones (1959) believed that mature parr acted to ensure that all eggs were fertilized, and Myers (1986) regarded them as being the product of a mixed evolutionarily stable strategy (ESS) in which two genetically encoded behaviours coexist because of some frequency-dependent mechanism affecting reproductive success. Alternative male reproductive phenotypes are a common feature in many animal species (Gross 1996) and can be status-dependent, when for example a younger male is smaller and therefore incapable of matching a larger one (e.g. red deer, *Cervus elaphus*, Clutton-Brock *et al*. 1979), or genetically determined, when the behavioural phenotype is simply the product of the genotype (e.g. ruff, *Philomachus pugnax*, Lank *et al*. 1995). In status-dependent tactics the fitness of the different types will not necessarily be equal, one type having higher success than the other(s) at evolutionary equilibrium. In genetically determined cases life-time fitness should be equal in all behavioural types. Although there are many examples of status-dependent tactics, there are very few accepted genetically determined cases (Andersson 1994; Gross 1996).

There is evidence that the sperm of mature parr males is as good as that of migrant males for fertilizing eggs and that mature parr take part in the spawning (Jones 1959). Enzyme polymorphisms have been used

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Table 1. *Total length and body weight of the* (a) *parr and* (b) *migrant adults used in the experiments carried out in the Lapitxuri artificial spawning channel*

(a)

| channel section | trial date start | end | number of parr | parr size length (cm) | weight (g) |
|---|---|---|---|---|---|
| 8 | 17/12/92 | 18/12/92 | 6 | 9.8 | 11.0 |
| | | | | 17.5 | 54.0 |
| | | | | 18.0 | 65.0 |
| | | | | 13.4 | 27.0 |
| | | | | 10.8 | 14.0 |
| | | | | 13.4 | 27.0 |
| 8 | 18/12/92 | 23/12/92 | 6 | 9.7 | 9.5 |
| | | | | 9.3 | 9.0 |
| | | | | 10.7 | 13.0 |
| | | | | 17.5 | 56.0 |
| | | | | 16.8 | 46.0 |
| | | | | 17.4 | 53.0 |
| 9 | 11/12/92 | 18/12/92 | 1 | 12.8 | 21.0 |
| 10 | 22/12/92 | 02/01/93 | 3 | 18.4 | 65.0 |
| | | | | 14.2 | 30.0 |
| | | | | 11.5 | 17.0 |
| 12 | 30/12/92 | 02/01/93 | 12 | 17.0 | 51.0 |
| | | | | 9.7 | 12.0 |
| | | | | 9.8 | 12.0 |
| | | | | 11.0 | 14.0 |
| | | | | 12.0 | 19.2 |
| | | | | 9.7 | 10.2 |
| | | | | 12.5 | 22.7 |
| | | | | 10.6 | 12.3 |
| | | | | 10.0 | 11.3 |
| | | | | 11.3 | 15.9 |
| | | | | 11.0 | 13.1 |
| | | | | 9.8 | 10.4 |

(b)

| channel section | sex | river of origin | body size length (cm) | weight (kg) |
|---|---|---|---|---|
| 8 | male | Nivelle | 68 | 2.610 |
| 8 | female | Nivelle | 60 | 1.620 |
| 9 | male | Nivelle | 64 | 2.115 |
| 9 | female | Nivelle | 62 | 1.665 |
| 10 | male | Nivelle | 65 | 2.030 |
| 10 | female | Nivelle | 61 | 1.840 |
| 12 | male | Nivelle | 60 | 1.870 |
| 12 | female | Nivelle | 60 | 1.750 |

as markers for estimating the contribution of mature parr in matings where there was competition from anadromous males (Hutchings & Myers 1988; Jordan & Youngson 1992). In this way, mature parr were found to fertilize a significant proportion of the eggs deposited. This proportion (5–30 %) varied with the number of parr present at each spawning and with the order of egg nest construction (Hutchings & Myers 1988), and averaged around 15 % of the eggs spawned (Jordan & Youngson 1992). With data from these experiments and demographic parameters estimated from the field, Hutchings & Myers (1994) proposed a threshold model of parr maturation in which frequency-dependent reproductive success defines an evolutionarily stable continuum of strategy frequencies along which the fitnesses of mature parr and anadromous males are equal. However, the available data

do not include the effect of parr size on individual parr success. Size has been shown to be important in determining a parr's position in the social (and spawning) dominance hierarchy (Myers & Hutchings 1987; Huntingford *et al.* 1990; Metcalfe & Huntingford 1990), and its role should be investigated to discover if size is an important variable that should be included in life-history models.

The role of mature parr in salmonid life histories is potentially of major demographic significance in the Atlantic salmon, and is of importance to the industrial production of salmon for commercial and sports markets and the management of wild salmon stocks, including understanding the impact of human activity on wild populations. Myers (1984) has estimated the cost of parr maturation as representing a 60 % reduction in anadromous male salmon in some

Newfoundland populations, and has also predicted that increasing fishing pressure could lead to all males maturing as parr and never leaving the river.

The aim of this study was to identify the factors determining the choice of reproductive tactics in Atlantic salmon by quantifying the contribution of body size and parr number to the reproductive success of mature parr. This was achieved by using hypervariable minisatellite DNA markers to assign paternity in matings where mature parr were allowed to compete with anadromous males. An important advantage of using minisatellite markers was that we were able to carry out the experiments with minimum intervention and genetically tag the individuals to measure their success *a posteriori*. In this way we show that parr body size is a significant predictor of parr reproductive success, and that negative frequency-dependent success plays some role in the maintenance of these alternative reproductive behaviours. A framework for the decision processes involved in the choice of life history in male salmonids is proposed on the basis of these results.

## 2. MATERIALS AND METHODS

In the winter of 1992–93 a series of mating experiments was carried out at the Lapitxuri field station of the INRA (National Institute for Agricultural Research) hydrobiological station at St-Pée-sur-Nivelle, south-west France. At the station there is an artificial spawning channel 130 m long × 3 m wide, divided into thirteen 10 m-long sections with controllable water depth and flow. Water is supplied by the Lapitxuri, a tributary stream of the River Nivelle. In one of the sections it is possible to make underwater observations via a viewing room equipped with a glass window at the level of the stream bed (for further information on the characteristics of the channel refer to Beall & Marty 1983). The channel has been used for many previous experiments concerning salmon and trout reproduction and the early stages of fry development and behaviour (Beall & Marty 1983; Rene *et al.* 1987; Marty & Beall 1989). During the months of December 1992–January 1993, five sections of the channel were each stocked with a pair of migrant salmon originating from the River Nivelle. In each of the sections a number of mature male parr were released with the anadromous salmon. All parr used belonged to the wild Nivelle stock. Table 1 shows the numbers and size distributions of the fish in each section and gives details of the migrant males and females used.

In each section the fish were allowed to spawn and the progress of the redds was monitored daily. Sections 8 and 10 were the only two sections where spawning was closely monitored, and after three or four egg pockets had been made all the parr were fished out of the section and replaced by a new set of parr. In all the others spawning was either completed within one night or else spawning was characterized by irregular bursts of activity that made it difficult to assess progression.

When all the females had finished spawning the channel was cleared of fish by electrofishing and the eggs were left in the gravel over winter. Each parr used in the experiment was measured (total body length and weight) and sampled for a piece of muscle. The size of the gonad was estimated by eye as small, medium or large. The number of salmon eggs found in the stomach of each parr was also recorded.

The incubation period is relatively short in the mild winter of the French Pyrenees and by the beginning of February a sample of around 50 eggs from each egg pocket was collected and preserved in absolute ethanol. The eggs had developed to the eyed egg stage.

The methods used to extract the DNA from the eggs and tissue samples and for subsequent typing of each individual with a series of hypervariable minisatellite single-locus probes are described elsewhere (Thomaz (1995) and in preparation; Bruford *et al.* 1992). The analysis of the correlation between body size and parr reproductive success was made using a linear regression model. For the analysis of heterogeneity in parr fertilization success among egg pockets and between trials we used either Fisher's exact test (in $2 \times 2$ tables, Engels 1988*a*) or a Monte Carlo test for $2 \times n$ contingency tables (Engels 1988*b*) using 10 000 randomizations of the data.

## 3. RESULTS

### (a) *Reproductive success of mature male parr in relation to body size*

When in competition, mature male parr of larger body size achieved higher reproductive success than smaller parr. The only experiment in which more than one parr competed for spawning and in which parr success was assigned unequivocally to individuals was the trial in section 8 (see table 1). The relationship is clearly demonstrated in figure 1, where parr reproductive success (as the percentage of eggs fertilized) is plotted as a function of body size. Body size explains a significant proportion of the variation in reproductive success ($n = 12$, $r^2 = 0.948$, $p < 0.001$).

The relationship between reproductive success and parr size, although strong when data from all egg pockets within each trial ($p_{8.1}$ and $p_{8.2}$, figure 2) or from both trials together in section 8 were pooled ($p_{ALL}$ in figure 2), was not so evident when each egg pocket was analysed separately. Regression coefficients for the seven successive egg pockets collected in section 8 are only significant in egg pockets 1 and 5 (figure 2). The significant result obtained in the fifth egg pocket coincides with the removal of the initial set of six male parr and the introduction of a new set of six parr. Also, when data from both trials are pooled for each successive egg pocket, only in the first is the relationship
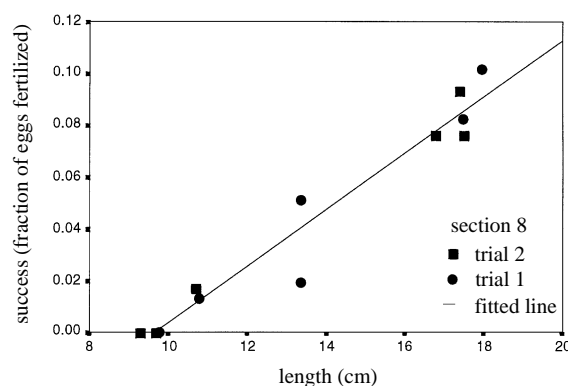


Figure 1. Relationship between reproductive success (measured as the percentage of eggs fertilized) and body length in parr used in experimental matings in section 8. The regression of reproductive success on body length (success = $-0.105393 + \text{length} \times 0.010914$) is highly significant ($n = 12$, $r^2 = 0.948$, $p < 0.001$).
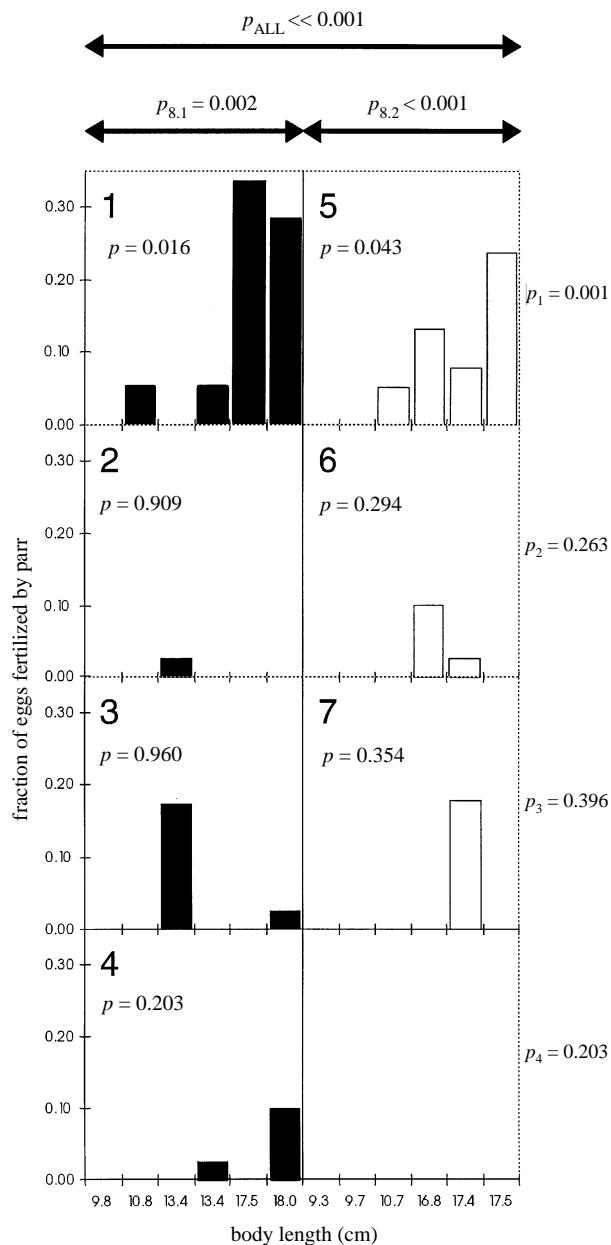
Figure 2. Individual male parr reproductive success in both trials in section 8 in relation to body size; plots are for individual egg pockets. Probability values were calculated for the regression of reproductive success on body length. $p_1$ to $p_4$, pool data from both trials for each egg pocket, $p_{8.1}$ and $p_{8.2}$ treat each trial separately and $p_{ALL}$ uses data pooled for all egg pockets and both trials. Probability values in each plot refer to that egg pocket alone.

between reproductive success and body length significant ($p_1$–$p_4$ in figure 2).

In sections 8 and 9 we were able to determine the temporal sequence of the sampled egg pockets. There was a decrease in the success of parr as the redds progressed (figures 2 and 3). Figure 3 shows the proportion of eggs fertilized by parr in each of the egg pockets sampled in these sections. In both sections the order of the egg pockets goes from first to last. In both trials in section 8 and in the trial in section 9 there was a higher parr contribution in the first egg pocket than in the later ones ($p < 0.001$), and, interestingly, a recovery in success in the third egg pockets (two-tailed

probability using Fisher's exact test on the pooled success of parr and anadromous males in pockets 2 and 3, $p = 0.016$, figure 3).

## (b) The effects of varying parr density

Figure 4 shows the observed total parr success, average parr reproductive success and average parr success relative to the success of the anadromous male for each of the experiments conducted in the Lapitxuri. There was a decrease of parr success relative to the success of the anadromous male as parr number increased (Spearman's rank correlation coefficient $R_s = 0.98, p = 0.05$, two-tailed). The parr accounted for a substantial proportion of the fertilizations in each case, with at least 26% being achieved even when only a single parr was present (figure 4).

## 4. DISCUSSION AND CONCLUSIONS

### (a) Parr body size and reproductive success

Large mature male parr were more successful than small parr in fertilizing eggs ($n = 12$, $r^2 = 0.948$, $p < 0.001$). This result is fundamental to our understanding of life history choices in Atlantic salmon and other salmonids. The precise nature of this relationship seems likely to vary between spawning events and between populations. Nevertheless, the trend of increasing reproductive success with body size will probably hold, and might be explained by field observations that larger parr are usually dominant and position themselves closer to the spawning female than do smaller parr (John Webb, personal communication, Huntingford *et al.* 1990; Metcalfe & Huntingford 1990).

In the matings in sections 8 and 9, where the progression of the redd was followed more closely, it was repeatedly found that parr fertilization declines in the second egg pocket made, and recovers again in the third (figure 3). Two possible explanations for this are the exhaustion of the gonads, with immediate reduction in fertilizing capacity (and a subsequent recovery), or a development of the capacity of migrant males and females to better fight the small parr. The fact that, in section 8, where two sets of six parr were allowed to spawn consecutively with the anadromous pair, parr success increased when new parr were added, can be taken as evidence that the decrease in success in the second egg pocket was not due to an increase in the aggressiveness of the anadromous male or female, as the same migrant pair experienced an increase in parr success when new parr replaced the old. Unfortunately, there is a scarcity of data on spermatogenesis in mature male parr, although there is some evidence that sperm production is enhanced during the spawning period (Kazacov 1981).

Another possible factor is the mortality associated with energetic costs of maturation and sneaking. If smaller parr were to suffer higher mortality costs when mature then it would be expected that larger size would be favoured. Unfortunately, information on differential mature parr mortality is difficult to obtain. Nevertheless, there are two facts that favour a view
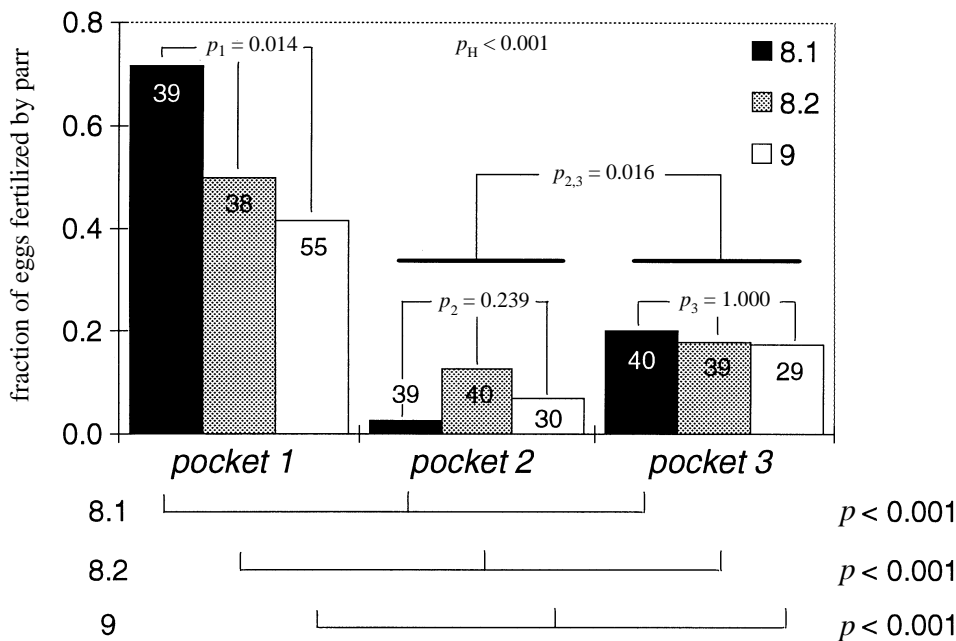
Figure 3. Variation in total parr reproductive success in the first three egg pockets of both trials of section 8 and in section 9. Abscissa represents the fraction of eggs fertilized by parr, and the numbers shown in the columns are the numbers of eggs analysed. The probability values shown are for heterogeneity tests for all the data ($p_H$) or for the subsets indicated (see Materials and Methods).
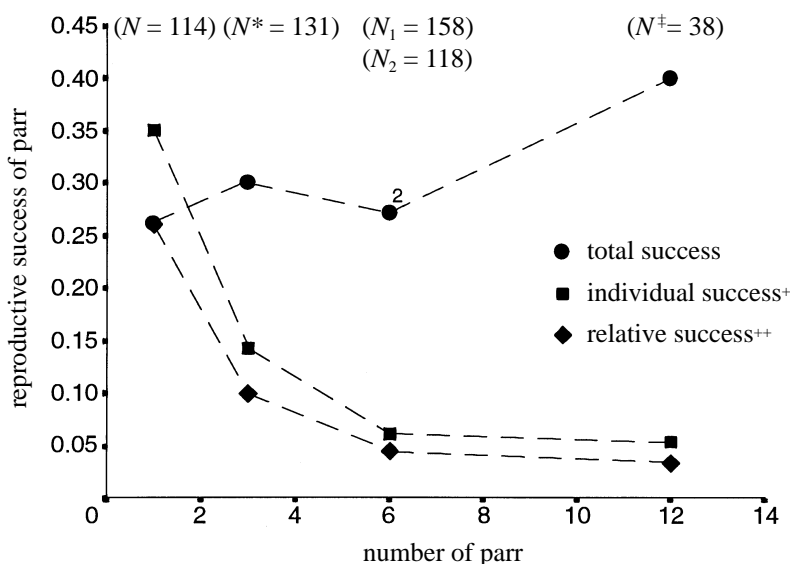


Figure 4. Variation of total, relative and mean parr success in relation to number of parr in the experiments conducted in the Lapitxuri channel. $N$ values indicated in parentheses are the number of eggs typed; there are two replicates of the six parr density experiment (section 8). There was no difference in the sizes of the parr used at each density (ANOVA, $F_{4,23} = 1.402$, n.s. *In all but one (the first) of the egg pockets in this section there was an abnormally high egg mortality, possibly due to algal growth in the gravel or over-maturation of the female; therefore only one egg pocket was used in the analysis. ++Proportion of eggs fertilized. +Parr success relative to anadromous male success ($= 100 \times$ (mean parr success)/(1−total parr success)). ‡This section suffered very high mortality and only 38 eggs were recovered. The mean number of fertilizations per parr was too small to justify more detailed analysis.

that differential mortality is not a major factor in determining reproductive choice in parr. First, only a small fraction of the mature parr probably sneak into redds, where they are subject to attack by anadromous males and females, probably the main added cause of mortality in parr that mature (D.T. personal observation; Garcia de Léaniz 1990). This view is supported by estimates (C. Garcia-Leaniz, personal communication) and direct counts (L'Abée-Lund 1989) of the ratio of mature parr to anadromous females in typical salmon rivers. These estimates show ratios of the order of 100–200, and it therefore seems unlikely that all mature parr participate in spawning. Secondly, in rivers where a high percentage of parr become sexually mature, the ratio of returning migrant males to females is usually close to 1:1 (L'Abée-Lund

1989), which would not be expected if mature male parr (often > 80 % of all male parr, Myers *et al.* 1986) suffered high mortality rates.

It therefore seems likely that male–male competition among mature parr is the main factor leading to an advantage of large body size, and this is probably counterbalanced by the need to be small, to avoid being detected by migrant males and females during spawning. It is hence reasonable to infer that there will be a size threshold above which the advantages of being a large parr (i.e. mating success) are offset by the disadvantages of parr versus anadromous male competition. Previous threshold models were based either on empirical observations (Thorpe 1989) or on ESS theory (Hutchings & Myers 1994) but only now, with the knowledge of the effect of parr size on reproductive success, can we appreciate fully the factors determining the threshold decision.

When considering approximately constant growth phases (i.e. when the whole life cycle happens either in the river, as in some *Salvelinus* species or some brown trout, *Salmo trutta*, populations, or in the sea, as in species of *Oncorhynchus* where the sea phase begins very early in the life cycle) it is expected that a situation of the type described in Coho salmon (*Oncorhynchus kisutch*, Gross 1985) will evolve, where disruptive selection is believed to be responsible for the discreteness of two male reproductive forms. In Atlantic salmon, as in other salmonids, smoltification and sea migration provide a way of rapidly increasing body size halfway through the individual's life cycle, and this ultimately gives individuals an advantage when competing for mating with the much smaller mature parr. This produces a large discrepancy in size between migrant and parr males, with no intermediate sized males. As it has been shown that smaller smolts have a reduced rate of survival during sea migration (Berglund *et al.* 1992), parr should not smoltify at small sizes. It is this balance between reproductive chance, survival during sea migration, and body size (which influences both), that determines the best life history for Atlantic salmon males.

Sexual selection theory predicts that in situations of strong male–male competition subdominant males should invest more heavily in gonad production and thus compensate for their limited access to females (Møller 1991; Birkhead & Møller 1992). Mechanisms for competition range from multiple copulation to larger ejaculates, depending on the capacity to store sperm, but in species with external fertilization sperm placement can also be optimized, and this is probably the main challenge to mature parr. Studies on the characteristics of ejaculates from parr and migrant males (Kazacov 1981) found that sperm concentration and activity did not differ between these male types and that the average ejaculate size of migrant males is 20–30 times as large as the ejaculate volume of parr, larger than the parr's total gonad weight. Furthermore, parr allocate a larger fraction of their energies to reproduction (Gage *et al.* 1995), having gonadosomatic indexes (gonad weight/total body weight) of around 4.65 % compared with only 2.33 % in migrant males. The advantages of this higher allocation are not marked in the face of the huge disparity in absolute gonad sizes.

Parr have been known to eat eggs (either directly in the redd or eggs floating downstream) (Jones 1959) but the behaviour has never been linked with any particular group of parr. One of us (E.B. unpublished data) has observed that when mature and immature parr are kept with spawning migrants it is the immature parr (males and females) that eat more eggs. This, together with the results presented here, suggests that smaller parr are less preoccupied with sneaking and successful spawning than they are in profiting from the energetic meals provided by the eggs.

### (b) Frequency-dependent parr success

Our data, although limited, are consistent with negative frequency dependence of the relative reproductive success of parr *versus* anadromous males ($R_s = 0.98$, $p = 0.05$, two-tailed, figure 4). It should be noted that there was no difference in the sizes of the parr used at each density (ANOVA, $F_{4, 23} = 1.402$, n.s.). However, the result was not robust when reproductive success, with smaller sample sizes, was taken only from the first egg pocket. The observation of frequency dependence, which was also made by Hutchings & Myers (1988), suggests a role for this mechanism in the evolution of salmon life histories, so leading to the maintenance of both mating phenotypes (Gross 1996). It is also interesting to observe that the five-fold higher success of parr in these experiments compared with the experiments in Canada has not modified the general effect of frequency dependence.

The higher success of parr observed in these experiments compared with those of Hutchings & Myers (1988) could result from an adaptation of the females to an environment where the number of anadromous males is reduced and the probability of finding one on the spawning grounds is close to zero. This is speculative but, in southern rivers, due to increased mortality caused by temperature stress, the densities of spawners are often very low, and females could become more tolerant to spawning with mature parr males. There have been reports (E. Garcia-Varquez, personal communication) of females from rivers in northern Spain cutting redds and spawning in the presence of parr only.

### (c) Female mating preferences

Female mate choice has been observed in many salmonid species. Pacific salmon species usually spawn in large aggregations where densities can be very high and, therefore, competition for good spawning sites and redd guarding could provide a reason for females to choose large (dominant) males. In fact, in Chum salmon it was found that females prefer to mate with large males with stripes along their flanks (Schroder 1981). This was also shown in other species of Pacific salmon (for a review of published data see Groot & Margolis 1991).

In the dolly varden (*Salvelinus malma*, another Salmonid), mature parr are also present in spawning

events and females have also been reported to attack and avoid spawning with them (Maekawa & Hino 1986). A similar observation was made in *Symphodus tinca*, a Mediterranean labrid fish. In this species, males can be territorial and fight to protect a good spawning ground or adopt a series of tactics ranging from sneaking and female mimicry to intercepting females. In a series of elegant manipulations it was found that in the presence of satellite (sneaker) males (usually younger and smaller than territorials), females delayed spawning and spawned less often (and released fewer eggs) than they did if they were alone with the territorial male. This reduction in mating opportunity for territorials was three and a half times more costly to these males than the number of eggs lost to the sneakers (Van den Berghe *et al.* 1989).

The apparent female preference for older territorial males and dislike of sneaker males is of particular interest. As there is no component of parental care, this implies that females may obtain an indirect genetic benefit for their offspring ('good genes', Andersson 1994). There is evidence in Atlantic salmon that faster juvenile growth rates translate into a higher incidence of maturation in the parr stage, and slower growth occurs in parr that undergo smoltification and sea migration without previous maturation (Myers *et al.* 1986; Rowe & Thorpe 1990; Berglund 1992). It seems unlikely therefore that old returning males indicate a genetically determined, faster growth rate. The main difference between the two behavioural tactics is that anadromous males have survived the sea migration and on their return will achieve a greater reproductive success (and possibly a higher lifetime fitness) than the average mature parr. The overall benefits of being an anadromous male are questionable, however, as surviving a sea migration is thought to be subject to strong stochastic factors, with mortality varying from 50 to $> 90\%$ (Shearer 1992). Smolt body size and smoltification age have been shown to affect this survival (Berglund 1992) and probably sexual selection through female preference for anadromous males contributes to determining the optima for these parameters.

In summary, the study suggests that body size is the main determinant of reproductive success in mature parr. Other factors such as differential mortality and dominance behaviour will probably affect parr success, but since they are correlated with body size their effects will be confounded. Gonad size is a limiting factor for mature parr as the number of successful spawnings is limited to one or two; this fact puts pressure on the optimal use of sperm as it is a limiting resource. Subdominant mature parr and immature parr probably concentrate their efforts into eating eggs and less into spawning (either because they cannot spawn or because larger parr do not let them spawn). In the wild, there will be a continuous supply of large parr (as it appears to be common, the number of mature parr vastly exceeds the number of migrants) and this will have two consequences. First, the success of smaller parr will be even more reduced and, secondly, the overall success of parr will be higher than estimated in the experiments described here. Another inference that

we can make is that when carrying out this type of experiment it would be better to restrict sampling (and analysing the outcome of the matings) to the first egg pocket made by the female. Alternatively, one could follow closely each spawning and replace the parr after each spawning act, thus increasing the number of significant trials per set of migrants.

## REFERENCES

Andersson, M. 1994 *Sexual selection*. New Jersey: Princeton University Press.

Beall, E. & Marty, C. 1983 Reproduction du Saumon Atlantique, *Salmo salar* L., en millieu semi-naturel contrôlé. *Bull. fr. Piscic.* **289**, 77–93.

Berglund, I. 1992 Growth and early sexual maturation in Baltic salmon (*Salmo salar*) parr. *Can. J. Zool.* **70**, 205–211.

Berglund, I., Schmitz, M. & Lundqvist, H. 1992 Seawater adaptability in Baltic salmon (*Salmo salar*): a bimodal smoltification pattern in previously mature males. *Can. J. Fish. Aquat. Sci.* **49**, 1097–1106.

Birkhead, T. R. & Møller, A. P. 1992 *Sperm competition in birds: evolutionary causes and consequences*. London: Academic Press.

Bruford, M. W., Hanotte, O., Brookfield, J. F. Y. & Burke, T. 1992 Single-locus and multilocus DNA fingerprinting. In *Molecular genetic analysis of populations: a practical approach* (ed. A. R. Hoelzel), pp. 225–269. Oxford: IRL Press.

Burke, T. 1989 DNA fingerprinting and other methods for the study of mating success. *Trends Ecol. Evol.* **4**, 139–144.

Burke, T. & Bruford, M. W. 1987 DNA fingerprinting in birds. *Nature, Lond.* **327**, 149–152.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–225.

Engels, B. 1988*a* *Fish* 6. Madison: Bill Engels.

Engels, B. 1988*b* *Monte Carlo $2 \times N$ contingency tables*. Madison: Bill Engels.

Gage, M. J. G., Stockley, P. & Parker, G. A. 1995 Effects of alternative male mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): theoretical and empirical investigations. *Phil. Trans. R. Soc. Lond.* B **350**, 391–399.

Garcia de Leaniz, C. 1990 Distribution, growth, movements and homing behaviour of juvenile Atlantic salmon and brown trout in the Girnock burn, Aberdeenshire. Ph.D. thesis, University of Aberdeen.

Groot, C. & Margolis, L. 1991 *Pacific salmon life histories*. Vancouver: UBC Press.

Gross, M. R. 1985 Disruptive selection for alternative life histories in salmon. *Nature, Lond.* **313**, 47–48.

Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98.

Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D. & Adams, C. E. 1990 Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *J. Fish Biol.* **36**, 877–881.

Hutchings, J. A. & Myers, R. A. 1988 Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. *Oecologia* **75**, 169–174.

Hutchings, J. A. & Myers, R. A.  1994  The evolution of alternative mating strategies in variable environments. *Evol. Ecol.* **8**, 256–268.

Jones, J. W.  1959  *The salmon*. London: Collins.

Jordan, W. C. & Youngson, A. F.  1992  The use of genetic marking to assess the reproductive success of mature male Atlantic salmon parr (*Salmo salar* L.) under natural spawning conditions. *J. Fish Biol.* **41**, 613–618.

Kazacov, R. V.  1981  Peculiarities of sperm production by anadromous and parr Atlantic salmon, (*Salmo salar* L.) and fish cultural characteristics of such sperm. *J. Fish Biol.* **18**, 1–8.

L'Abée-Lund, J. H.  1989  Significance of mature male parr in a small population of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **46**, 928–931.

Lank, D. B., Smith, C. M., Hanotte, O., Burke, T. & Cooke, F.  1995  Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature, Lond.* **378**, 59–62.

Maekawa, K. & Hino, T.  1986  Spawning behaviour of dolly varden in south-eastern Alaska, with special reference to mature male parr. *Japan. J. Ichthyol.* **32**, 454–458.

Marty, C. & Beall, E.  1989  Modalités spatio-temporelles de la dispersion d'alevins de saumon Atlantique (*Salmo salar* L.) à l'emergence. *Revue des Sciences de l'Eau* **2**, 831–846.

McNamara, J. M. & Houston, A. I.  1996  State-dependent life histories. *Nature, Lond.* **380**, 215–221.

Metcalfe, N. B. & Huntingford, F. A.  1990  The effects of social status on life-history variation in juvenile salmon. *Can. J. Zool.* **68**, 2630–2636.

Møller, A. P.  1991  Sperm competition, sperm depletion, paternal care and relative testis size in birds. *Am. Nat.* **137**, 882–906.

Myers, R. A.  1984  Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **41**, 1349–1353.

Myers, R. A.  1986  Game theory and the evolution of Atlantic salmon (*Salmo salar*) age at maturation. *Can. Spec. Publ. Fish Aquat. Sci.* **89**, 53–61.

Myers, R. A., Hutchings, J. A. & Gibson, R. J.  1986  Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* **43**, 1242–1248.

Myers, R. A. & Hutchings, J. A.  1987  Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr. *J. Fish Biol.* **31**, 143–146.

Rene, F., Beall, E. & Marty, C.  1987  Analyse sequentielle du comportement de reproduction du saumon atlantique *Salmo salar* L. dans des conditions variables de sex-ratio. *Bull. SFECA* **2**, 119–128.

Rowe, D. K. & Thorpe, J. E.  1990  Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L. parr. *J. Fish Biol.* **36**, 643–658.

Schroder, S. L.  1981  The role of sexual selection in determining overall mating patterns and mate choice in Chum salmon. Ph.D. thesis, University of Washington.

Shearer, W. M.  1992  *The Atlantic salmon*. Fishing News Books. Oxford: Blackwell Scientific Publications Ltd.

Thomaz, D.  1995  Alternative life-history strategies in male Atlantic salmon (*Salmo salar* L.). Ph.D. Thesis, University of Leicester.

Thorpe, J. E.  1989  Developmental variation in salmonid populations. *J. Fish Biol.* **35**, 295–303.

Van den Berghe, E. P., Wernerus, F. & Warner, R. R.  1989  Female choice and the mating cost of peripheral males. *Anim. Behav.* **38**, 875–884.

Wetton, J. H., Carter, R. E., Parkin, D. T. & Walters, D. T.  1987  Demographic study of a wild house sparrow population by DNA fingerprinting. *Nature, Lond.* **327**, 147–149.