Balancing selection on size: effects on the incidence of an alternative reproductive tactic

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ABSTRACT

Question: Does fluctuating natural selection on body size of fish among years (balancing selection) influence the frequency of an alternative male reproductive tactic?

Hypothesis: When the surviving juveniles of a cohort are larger because of selection, a higher proportion of the population will develop as mature 'sneaker' males than expected in the absence of selection. In the case where selection favours smaller individuals, a lower proportion will develop as mature 'sneaker' males.

Organisms: Juvenile Atlantic salmon (*Salmo salar*) from a naturally sustained population in the Ste-Marguerite River, Centre Interuniversitaire de Recherche sur le Saumon Atlantique, Province of Québec, Canada.

Methods: The presence of balancing size-selection was examined by measuring the proportional shift of the mean size and variance of juvenile salmon sampled in the autumn and following spring at multiple sites for each of three annual cohorts. The proportional shift in mean size of individuals over winter was then correlated with the incidence of early male maturity (sneakers) observed at the same sites for each cohort the following fall.

Conclusions: Winter mortality decreased the size of surviving fish in one cohort by 7.8% on average, increased size by 2.7% on average in another and had little effect on the third. Proportionally more juvenile males adopted the sneaker tactic when juveniles surviving winter were larger, whereas fewer juvenile males adopted the sneaker tactic when surviving juveniles were smaller. The fluctuating nature of selection on body size indirectly maintains life-cycle divergence through a direct effect on size frequencies within a cohort.

Keywords: alternative reproductive tactics, body size, development, fitness, natural selection, phenotypic plasticity, salmonid, survival, threshold trait.

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INTRODUCTION

A paradox in life-history evolution concerns the maintenance of genetic variability for life-history traits in natural populations (Price and Schluter, 1991). For example, body size plays a key role in determining various characteristics that ultimately affect the lifetime reproductive success of a vast array of organisms (Johnson, 1982; Peters, 1983; Stearns, 1992; Janzen, 1993; Cutts *et al.*, 1999; Iyengar and Eisner, 1999; Frankino and Pfennig, 2001; Bekkevold *et al.*, 2002). In spite of this central role, body size can be highly variable and heritable in individuals of the same population. If large size is favourable for fitness, this variation is not what would be expected (Mousseau and Roff, 1987; Weigensberg and Roff, 1996; Blanckenhorn, 2000). In an attempt to resolve this paradox, Hedrick *et al.* (1976) proposed that fluctuating natural selection on body size among years, populations or habitats, termed 'balancing selection', could favour different genotypes on a temporal or spatial scale and thus maintain variability. Balancing selection has been shown to explain among-population variability on a spatial scale (Reznick *et al.*, 1990). However, evidence that temporal fluctuation in selection of a trait in animals could maintain variation within a natural population has rarely been obtained (Grant and Grant, 1989). Furthermore, evidence that balancing selection is acting to maintain genetic variability within a population has dealt mainly with Mendelian traits, such as immune defence gene complexes (Hedrick and Thomson, 1983) and allozymes (Schmidt *et al.*, 2000), and rarely with polygenic quantitative traits.

Several phenotypic variations within a population result from developmental plasticity. These include variation in feeding and reproduction phenotypes found both in invertebrates and vertebrates (Wimberger, 1991; Gross, 1996; Moczek and Emlen, 1999; Frankino and Pfennig, 2001; Taborsky, 2001; Brockmann, 2002). Many of these phenotypes show condition-dependent development, whereby the developmental pathway depends upon an underlying trait termed the 'liability' trait. If the value for the trait exceeds a threshold, an individual will follow a different developmental pathway than if the value of the trait does not exceed the threshold (Hazel *et al.*, 1990; Roff, 1996). Therefore, if selection is acting on the frequency distribution of a liability trait (e.g. body size) and if selection is strong enough, this could be reflected in the frequency of individuals developing each phenotype. Hence, balancing selection could indirectly affect dynamics of life-cycle divergence through its direct effect on a liability trait.

Salmonid fishes (salmons, trouts and charrs) are particularly susceptible to balancing size selection for several reasons and thus they form an ideal study system. Size is positively related to many aspects affecting lifetime reproductive success, such as competition, mating access and survival. Juvenile size is often highly variable and heritable in individuals of the same population, with a high potential for selection response on fast growth (Gjerde and Gjedrem, 1984). High heritability of size has been demonstrated directly in the wild for juveniles in their first year of life for the natural population of Atlantic salmon reported herein [$H^2 = 0.27$–0.57 (Garant *et al.*, 2003)]. Salmonids live in highly variable environments both at the temporal and spatial scale, making it more likely that selection is variable.

Developmental plasticity is another key feature of the Atlantic salmon life cycle. Following several years of freshwater residence as juveniles, males migrate to the ocean, and upon their return to their natal river 1–3 years later, compete to mate with females. This tactic is referred to as the anadromous fighter tactic. In contrast, other males employ a 'sneaker' reproductive tactic by maturing during the freshwater phase of the life cycle and fertilizing eggs by sneaking into the nests of mating anadromous pairs. The development of these tactics depends upon body size and growth at a certain time in life (Saunders *et al.*, 1982; Rowe and

Thorpe, 1990a; Hutchings and Myers, 1994; Berglund, 1995; Aubin-Horth and Dodson, 2004). Males may maximize their lifetime reproductive success by becoming sneaker males only if their body size (the liability trait) is above a threshold value (Hutchings and Myers, 1994; Gross, 1996). If their body size is below the threshold, males do not mature but continue to grow and eventually migrate to the sea to become anadromous males. The threshold is a complex trait that is presumably genetically influenced and heritable. It has been shown that the same genotype can express both the sneaker reproductive tactic and the anadromous fighter tactic depending on the environment that affects growth (Rowe and Thorpe, 1990b). The incidence of the sneaker tactic varies among populations and among cohorts in a river, and more than one threshold has been found within a population (Hutchings and Myers, 1994; Aubin-Horth and Dodson, 2004).

In this study, a natural population of Atlantic salmon was examined over a 4 year period for evidence of balancing selection on size and its influence on the incidence of divergent life cycles. We sought evidence that when selection is acting on the frequency distribution of size, it also influences the frequency of mature 'sneaker' males, as development of this reproduction tactic is condition (size)-dependent. We predicted that when the surviving juveniles of a cohort are larger because selection favours larger individuals during their first winter, a higher proportion of the population will then develop as mature sneaker males the following fall than expected in the absence of selection. Conversely, in the case where selection favours small individuals, a lower proportion of the population will develop as sneaker males than expected. To achieve these objectives, we examined the relationship between size and winter survival of age-0 juvenile salmon found in a naturally sustained population located in the middle of the species range (48°20′N, 70°00′W) in North America. Our study also accounted for possible spatial variability of selection within the population by sampling multiple sites for each cohort. We used the variability in incidence of sneaker males of the same population over the different cohorts to address the prediction that the presence of balancing selection on size will indirectly affect the incidence of divergent life cycles.

MATERIALS AND METHODS

Sampling

We sampled three cohorts of Atlantic salmon juveniles (fish hatched in 1995, 1996 and 1997) in the Ste-Marguerite River (Québec, Canada). Three sites were sampled for the 1995, 1996 and 1997 cohorts. An additional site was sampled for the 1996 and 1997 cohorts. We chose the sampling sites to represent sub-populations in the river, as they exhibit differences at neutral genetic markers and for functional genes such as MHC (Landry and Bernatchez, 2001), and to represent a large physical portion of the river system. These sites were located on two branches of the river [Principal (PR) and Nord-Est (NE)], distributed over 30–60 km on each branch, and separated by an average of 30 km. At each site, we sampled about 20 individuals at age-0 (2–3 months old) in late August and 40–80 individuals of the same cohort, now aged 1, in the following July at these same sites (Table 1). Fish were measured and sacrificed to obtain otoliths. Hatch marks on the otoliths were used to back-calculate length frequency at hatching for each cohort of fish sampled in August (reference population) and the same cohort of fish that survived the winter (survivor population) (Meekan et al., 1998; Aubin-Horth and Dodson, 2002). This analysis reveals patterns of size-dependent survival when the same population is sampled on both occasions (no emigration or immigration). Earlier

Table 1. Sample size for each cohort of Atlantic salmon, sampling site and time of sampling, before selection (BS) and after selection (AS)

| | | Sampling site | | | | | | | |
| | | PR27 | | PR58 | | NE06 | | NE28 | |
Cohort	Total	BS	AS	BS	AS	BS	AS	BS	AS
1995	106	23	10	20	13	20	20	–	–
1996	150	20	21	19	12	19	30	19	10
1997	185	20	24	19	33	20	34	20	15

Note: Total is for a given cohort.

studies attest to the high territoriality and low movement rate of juvenile Atlantic salmon (Armstrong *et al.*, 1994; Keeley and Grant, 1995). This is corroborated by a parallel mark–recapture study in the same river system (N. Aubin-Horth and J.J. Dodson, unpublished), which shows that almost all (92%) juvenile salmon marked in autumn and recovered 9 months later were recaptured within 100 m of their original marking location, and 100% within 1.6 km.

Selection on size

Selection is most often examined using longitudinal data. For example, a set of characteristics is measured on a number of individuals. These individuals are then exposed to a period of selective pressure and the survival or other measures of fitness are measured on each individual. A variety of regression techniques can then be used to relate the measure of fitness to the measured characteristics of the individuals. These estimates are then expressed as linear and quadratic selection differentials (Brodie *et al.*, 1995). In this study, independent samples of a population were taken at two different times, resulting in two snapshots: one of the population before a period of selection (reference population) and a second of individuals surviving the period of selection (survivor population). Since the effect of selection on the individuals in the reference population is unknown, as they were removed from the population before the period of selective pressure, standard regression models are not appropriate. For this reason, we concentrated on examining changes in the moments of the survivor population distribution relative to the reference population. One standard technique is the phenotypic selection differential, which is the ratio of the difference between the survivor and reference means to the standard deviation of the reference population. Our concern about this measure is that selective pressures affect both the mean and the variability of the survivor distribution and should really be represented by a bivariate measure. For this reason, we propose an alternative measure of the selective pressures and use a randomization test to examine the significance of these pressures. The major advantage of the proposed technique is that assumptions required for this approach to be valid are minimal: simply a representative sample from the two populations of interest [it should be noted that some authors claim this technique is valid in certain situations even without this assumption (Manly, 1997)].

Our proposed method measures linear and quadratic selection differentials using direct comparisons of the means and standard deviations of the two populations. Referred to

as selection ratios, there are two ratios of interest. The first measures the proportional shift of the mean size of the surviving population relative to that of the reference population. The second ratio measures the proportional shift of the standard deviation of the surviving population relative to the reference population. Essentially: SR_m = mean size of survivors/mean size of the reference population and SR_v = standard deviation in size of survivors/standard deviation in size of the reference population. Selective pressures (as described by Brodie *et al.*, 1995) indicate that positive directional selection will result in a positive proportional increase in SR_m and a corresponding decrease in SR_v (i.e. the mean increases in the surviving population while the variance decreases). A corresponding proportional decrease in SR_m occurs under negative directional selection together with a proportional decrease in SR_v. Both ratios are relevant in the discussion of selective pressures as selection can act upon both the mean and variability of the selected characteristic. To compare our results with those of other studies (Kingsolver *et al.*, 2001), the phenotypic standardized linear selection differentials (Brodie *et al.*, 1995) were also estimated. These differentials are expressed as multiples of standard deviations of the original phenotypic mean.

The selection ratios can best be illustrated by use of a bivariate plot of the ratios (Fig. 1). Populations undergoing positive directional selection will occur in the upper left-hand quadrant, negative directional selection will occur in the lower left-hand quadrant, positive disruptive selection will occur in the upper right-hand quadrant, and negative disruptive selection will occur in the lower right-hand quadrant. A population that has not undergone any selection will fall at the origin.
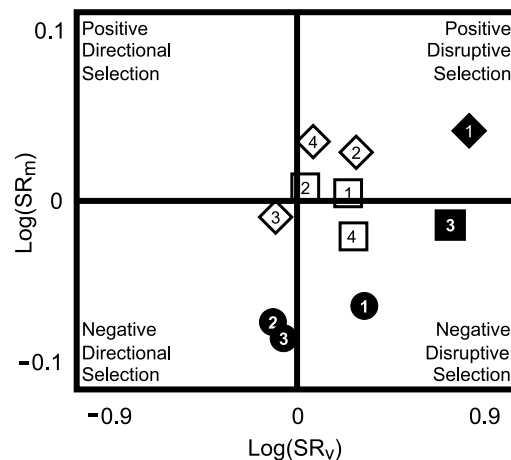

Fig. 1. Scatter plot of the log selection ratios for each site and cohort. The circles represent the 1995 cohort, the squares the 1996 cohort and the diamonds the 1997 cohort, while the numbers within represent a site (PR27 = 1, PR58 = 2, NE06 = 3, NE28 = 4). Solid symbols indicate that selection is significant at the 5% level. Linear and quadratic selection ratios are measured using direct comparisons of the means and standard deviations of the before and after samples. SR_m measures the proportional shift of the mean size of the surviving population relative to that of the reference population. SR_v measures the proportional shift of the standard deviations of the surviving population relative to the reference population. Positive directional selection will result in a positive proportional increase in SR_m and a corresponding decrease in SR_v, while a decrease in SR_m occurs under negative directional selection together with a proportional decrease in SR_v. If SR_v is positive, it shows disruptive selection (variance increase).

Percentile confidence limits of the log(selection ratios) under the assumption of no selection were calculated for each site/cohort combination based upon a randomization procedure (Manly, 1997). Observations from the survivor and reference populations were randomly sub-sampled and the corresponding selection ratios were calculated. This was repeated 1000 times to create the randomization distribution of the selection ratios under the null hypothesis that there was no selection. A 95% percentile envelope was created using a bivariate kernel density estimator (SAS, 2000). If the observed selection ratio fell outside this envelope, the site was identified as undergoing significant selection. This was repeated for each site.

An overall test for changes in the log(size) of the fish over the winter period was carried out (SAS, 2000) using a mixed linear model where cohort, time and the interaction of the two were included as fixed effects and site(cohort) was included as a random effect.

Balancing selection and the incidence of the sneaker tactic

The relationship between size-selective selection and changes in the incidence of early male maturity involved the calculation of two variables. First, the mean size at hatching of individuals captured during the autumn (reference population) and following spring (surviving population) was compared to detect the amount and direction of size-selective pressures during the selection period, at each site and for each cohort. This value was then divided by the mean size at hatching before the selection episode. Second, an adjusted estimate of sneaker male incidence was calculated as follows: the difference between the incidence of sneaker males at a site in a given cohort and the average incidence for that sub-population calculated over all cohorts was divided by the average and multiplied by 100. The incidence of parr maturity was calculated as the number of males exhibiting ripe testes in the fall divided by the total number of males in the sample from a given site (full details on sampling is presented in Aubin-Horth, Bourque, Hedger, Daigle and Dodson, in prep.). The correlation between selection on size and relative shift in sneaker male incidence was assessed using a weighted product–moment correlation, where the weights were proportional to the total number of males used to calculate each estimate of sneaker male incidence. We also estimated the relationship between the relative shift in sneaker male incidence and the standardized linear selection differentials, as defined in Brodie *et al.* (1995).

RESULTS

Selection on size

Significant differences in the mean back-calculated size at hatching as measured in the spring versus the previous fall were found between cohorts ($P = 0.0002$), while no significant differences were found in the standard deviation of the back-calculated size ($P = 0.1055$). The percentage changes in the mean for two of the three cohorts indicate that significant selection pressure was exerted upon those populations (Table 2). Smaller fish were selected for in the 1995 cohort, decreasing the size of the fish by 7.8% on average ($P < 0.0001$), while larger fish were selected for in the 1997 cohort, increasing the size of fish by 2.7% on average ($P = 0.0150$). The effect of selective pressure was not evident in the 1996 cohort, where no significant selection was observed ($P = 0.3447$). Plotting the log of the site-level selection ratios (Fig. 1), there is a clear trend for the 1995 cohort ratios to suggest negative directional

Table 2. Percentage change of the mean body size and its standard deviation: the estimates, the *P*-values (% change significantly different from zero) and the 95% confidence intervals for each cohort of Atlantic salmon

Cohort	% change in mean	*P*-value change in mean	95% CI (% change in mean)	% change in standard deviation	*P*-value change in standard deviation	95% CI (% change in standard deviation)
1995	−7.8	<0.0001	(−9.9, −5.7)	6.8	0.6725	(−24.5, 51.0)
1996	−0.9	0.3447	(−2.8, 1.1)	33.7	0.0703	(−3.0, 84.2)
1997	2.7	0.0150	(0.7, 4.8)	32.7	0.0766	(−3.7, 82.8)

selection. The 1996 cohort, despite there being no significant difference in the log SR_m, displayed one site with significant selection (suggesting negative disruptive selection), while the others clearly displayed a lack of selection. The 1997 cohort displayed a single site which was by itself significant, with two of the remaining three sites not being significant but suggesting positive disruptive selection. As a standardized linear selection differential (95% confidence intervals in brackets), these shifts represented changes of −1.69 (−1.83, −1.56), −0.22 (−0.80, 0.36) and 0.76 (−0.33, 1.85) for the 1995, 1996 and 1997 cohorts respectively.

Balancing selection and the incidence of early male maturity

A positive correlation was found between the mean selection ratios and the relative shifts in sneaker male incidence ($r = 0.66$, $P = 0.0263$, $n = 11$). A similar result was found when using the standardized linear selection differentials, as shown in Fig. 2 ($r = 0.67$, $P = 0.0234$). The relationship between the mean selection ratios and the relative shifts in sneaker male incidence was negative for one sub-population due to the 1995 cohort (site 3, NE06, see Fig. 2), which was not consistent with our prediction. When the analysis was restricted to the other three sub-populations, the significance of the correlation between selection ratios and sneaker male incidence was stronger ($r = 0.85$, $P = 0.0081$).

DISCUSSION

Balancing selection on size

We provide evidence for the presence of balancing selection on body size over years in a natural population of Atlantic salmon. The probability of surviving winter was unequal among juveniles of Atlantic salmon of different body sizes in certain cohorts and the size classes with the highest survival probability fluctuated among cohorts. Indeed, in a given cohort, being large in winter was positively linked to survival. In another cohort, a large size was associated with an equal or lower chance of surviving. As heritability of body size is high in this population (Garant *et al.*, 2003), we propose that the fluctuating nature of selection on body size that occurs during winter may contribute to maintaining the genetic variance that underlies body size. Intermittent selective advantage of large size-classes has been shown in species from different taxonomic groups, while studies that illustrate significantly higher probability of survival of small size-classes are scarce (see reviews in Sogard, 1997; Blanckenhorn,
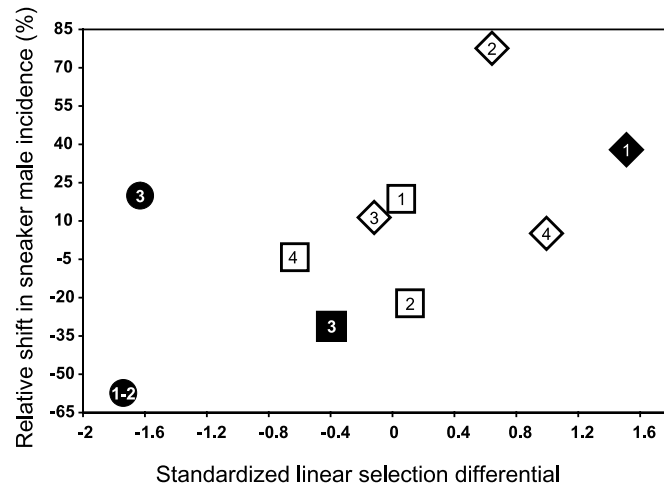
Fig. 2. Relative shift in sneaker male incidence for a sub-population (in percentage) in relation to the direction and magnitude of the standardized linear selection differential, expressed as multiples of standard deviations of the original phenotypic mean, estimated for the same site during the preceding winter. Each sub-population sampled–year combination is represented by the same symbol as in Fig. 1. Note that sites 1 and 2 of the 1995 cohort overlap completely.

2000). For example, almost all studies of juvenile salmonids suggest that size-dependent survival either favours large individuals or is absent (Sogard, 1997). Only a few recent studies have documented lower survival of the largest juvenile Atlantic salmon. A lower survival of large size-classes of age-0 juveniles was demonstrated during an extraordinary summer flood (Good *et al.*, 2001). A study of three consecutive cohorts of Atlantic salmon found no significant variation in survival with morphological traits in the second winter of life, but lower survival of large size-classes in two of the three cohorts in the third winter of life (Hendry *et al.*, 2003). However, Hendry *et al.* (2003) did not find evidence of balancing selection on a temporal scale.

In the present study, the observed selection was 'strong' in 1995 and 1997, based upon the standardized linear selection differentials (−1.69 and 0.76), when compared with other studies. Kingsolver *et al.* (2001) reported that 87% of the published absolute values of the linear selection gradients were less than 0.50, while 95% were less than 0.75. The overall consistency of direction of selection observed in the sub-populations within a cohort suggests that the changes in selective pressures experienced by this population are system-wide in nature, although local deviations occur. For example, the 1995 cohort exhibited consistent and strong negative selection, while the 1997 cohort exhibited weaker positive selection. This suggests phenotypic changes are due to broad-scale environmental factors which influenced survival in some winters but not in others (e.g. no overall detectable selection on size in the 1996 cohort). The fact that both negative and positive selection was observed within the same system at different times indicates the presence of strong, balancing selection acting upon the population. Thus a single genotype will not be successful in all years, and this mechanism may be a major factor contributing to the maintenance of genetic variation for body size. Our findings are in accordance with theoretical arguments stating that more than one growth rate can provide optimal fitness because of different selection pressures acting on these phenotypes (Schluter *et al.*, 1991; Mangel and Stamps, 2001).

Balancing selection and plastic life-cycle divergence

We present evidence supporting the prediction that when survival is higher for large individuals, a higher incidence than average of sneaker males is found than when survival probability is better or equal for small individuals (Fig. 2). Although the observed relationship must be viewed as an indirect proof through correlation and hence exploratory in nature, this study is the first to reveal direct selection on a liability trait that in turn indirectly affects the frequency of divergent life cycles in nature. Future research must involve direct artificial manipulation of size frequencies to measure its impact on sneaker incidence and reproductive success.

Based on these results, we propose a mechanism by which balancing body-size selection may contribute to the maintenance of genetic variation in the threshold that must be reached for the development of early male maturity. The threshold is assumed to be genetically determined for a given genotype, but with genetic variation in the population [for a discussion in Atlantic salmon, see Hutchings and Myers (1994), Roff (1996); for examples of a genetically determined threshold and its evolution in different populations of insects, see Moczek and Nijhout (2003), Tomkins and Brown (2004)]. Fertilization success of sneaker males is in some instances size- and frequency-dependent (Thomaz *et al.*, 1997; Garant *et al.*, 2002), such that larger individuals have higher fertilization success. Therefore, by removing different sizes from the population in different cohorts, body size selection affects the competition intensity among males and the fitness obtained by a sneaker of a given size. When smaller-sized fish enjoy preferential survival relative to larger-sized juveniles, competition usually imposed by the largest sneaker males is relaxed, and smaller individuals may obtain higher reproductive success than in a year where no selection on size occurs and competition is severe. We speculate that for a small fish to develop into a sneaker, its threshold value must be low, while large sneakers may have low or high thresholds. It follows from this that the lower thresholds of small sneaker males are in higher proportion among reproducing males in the cohorts when selection favoured small size. The mean threshold value that is transmitted to the next generation could therefore be lower than in years where directional selection on size favoured large individuals. This may act to maintain variability in threshold genotypes in the population. Although speculative, we propose that balancing selection may be indirectly favouring the presence of several thresholds for maturation in a population. The ultimate consequence of favouring threshold variation is the maintenance of the two divergent male life cycles. This study provides empirical support for the prediction that balancing selection on size acting on a temporal scale is present and that it indirectly affects life-cycle divergence resulting from developmental plasticity within a natural population.

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