



Patterns of Aggression and Operational Sex Ratio Within Alternative Male Phenotypes in Atlantic Salmon

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Received: July 1, 2009

Initial acceptance: August 3, 2009

Final acceptance: November 13, 2009

(Editor: L. Ebensperger)

doi: 10.1111/j.1439-0310.2009.01723.x

Abstract

The intensity of male–male aggression during mating is predicted to increase with the operational sex ratio (OSR) (the ratio of sexually active males to females). We observed aggressive behaviour in relation to OSR within alternative phenotypes (large anadromous males and small ‘sneaker’ mature male parr) of Atlantic salmon, *Salmo salar*, as they competed for access to anadromous females in large outdoor arenas immediately prior to spawning events as well as throughout the spawning season. Anadromous males were primarily aggressive outside of spawning events, and their aggression increased with OSR over a narrow range of 0.08–4. By contrast, mature male parr were aggressive just prior to spawning, with a decrease in aggression over a broad range of OSRs from 1 to 7.4. Similarly, literature data for three other salmonid species indicated a decrease in aggression with increasing OSRs over a range of 1–6.33. These observations suggest that there is considerable variability in competitive behaviour, even within alternative phenotypes. Because our data are derived from repeated observations on the same individuals of different genetic origin, further confirmation of these findings is desirable. Nevertheless, our study underscores the importance of measuring competitive behaviour and OSR at ecologically relevant spatial and temporal scales, both of which may differ between alternative maturation phenotypes.

Introduction

The ability of some individuals within a population to monopolize mates is a key concept structuring classical mating systems theory (Emlen & Oring 1977; Davies 1991; Reynolds 1996). The environmental potential for monopolization may be quantified using the operational sex ratio (OSR; Emlen 1976), the ratio of males to females in a population that are ready to mate at a particular time and place (Emlen & Oring 1977). OSR is often considered a proxy for the opportunity for sexual selection (Kvarnemo & Ahnesjö 1996), and can be used to

predict the intensity and form of competition for mates. As predicted by Emlen & Oring (1977), males switch from courting females to fighting with other males as OSR increases (Enders 1993; Jirotkul 1999).

At high OSRs, however, resource defense theory predicts that males cannot effectively defend females and switch from interference to scramble competition (Brown 1964; Grant 1993). Although some researchers have documented a decrease in aggression at extremely high OSRs (Davis & Murie 1985; Michener & McLean 1996), few studies have documented a dome-shaped relationship (Grant et al.

2000), almost certainly because most studies encompass a relatively narrow range in OSR. Most empirical studies conclude that the relationship between the intensity of aggression and OSR is linear and increasing (e.g. Tejado 1988; Kvarnemo & Ahnesjö 1996; but see Quinn et al. 1996; Grant et al. 2000).

In addition to OSR, the occurrence of alternative mating strategies and tactics (sensu Gross 1996) affects the level of aggression within populations. Alternative male phenotypes often adopt non-aggressive behaviour in order to 'sneak' fertilizations (e.g. Gross 1984; Sinervo & Lively 1996; Dubois et al. 2004), and hence lower the per-capita rate of aggression in the population. However, the categorization of males as either fighters or sneakers has tended to obscure the degree of behavioural plasticity within alternative phenotypes. For example, hooknose and jacks in coho salmon (*Oncorhynchus kisutch*) engage in both fighting and sneaking behaviour (Gross 1984).

A classic example of alternative male phenotypes occurs in Atlantic salmon, whereby sneakers mature as freshwater parr and can be more than an order of magnitude smaller than large migratory, or anadromous, males (e.g. Hutchings & Myers 1994; Hutchings & Jones 1998). These two strategies are presumed to have equal lifetime fitness, and parr maturation is likely genetically influenced (e.g. Garant et al. 2003; Piché et al. 2008), but also depends upon favourable environmental conditions for growth (Hutchings & Myers 1994). In Atlantic salmon, females usually spawn asynchronously, and anadromous males compete for access to females using a range of agonistic behaviour from subtle displays to intense fighting involving physical contact (Fleming 1996). By contrast, smaller sneaker males are considered largely opportunistic and compete for fertilizations with the larger males by darting in and fertilizing eggs simultaneously with the release of gametes from the anadromous fish (Fleming 1998). Qualitative evidence suggests that sneakers engage in aggressive interactions to defend favourable positions behind females prior to spawning (Jones 1959; Myers & Hutchings 1987), although quantitative data in this regard are lacking. Classic 'fighter' and 'sneaker' designations predict that large anadromous males are more aggressive than small mature male parr. However, given that male aggression occurs primarily within strategy, OSR theory predicts similar patterns of aggression for the two phenotypes, albeit at a lower rate for parr than for anadromous males. The purpose of our study was to investigate the pattern of aggression over a broad range of OSR

within alternative male phenotypes. Specifically, we tested the predictions that: (1) the rate of male-male aggression either increases monotonically with increasing OSR, or increases and then decreases as OSR becomes more biased; (2) the patterns of male-male aggression vs. OSR are similar for both phenotypes and (3) the overall rates of per-capita aggression are higher for anadromous males than for mature male parr at a given OSR. In addition, we compared our data with those available in the salmonid literature to describe general patterns of male-male aggression vs. OSR.

Methods

The experiment was conducted at the Norwegian Institute for Nature Research (NINA) field station in Ims, Norway, from 6 November 2001 to 14 December 2001 in four outdoor arenas ($l \times w \times h = 21.0 \text{ m} \times 2.2 \text{ m} \times 1.0 \text{ m}$; described in Fleming et al. 1996), during the natural spawning period for Atlantic salmon (Fleming 1996). We created four replicate spawning populations by placing 12 anadromous females, 12 anadromous males and 30 mature male parr in each arena (see below). Each arena contained 47 m² of cobble substrate suitable for spawning, providing 4 m² per female, which is similar to an average redd size for anadromous female salmon (e.g. Heggberget et al. 1988). Arenas were also uncovered such that fish were exposed to ambient weather and provided with water from a nearby lake system with water velocities between 4 and 32 cm/s. As such, these arenas are representative of the densities of adults that are attracted to natural spawning sites in rivers (Fleming 1996).

Prior to the experiment, we selected mature males from groups of mature and immature parr by squeezing gently until milt was expressed. Parr were raised at the research station and were of three different origins: wild, farmed and F₁ hybrids between the two pure populations. Mature males were distributed such that each of the four arenas contained 30 parr with 10 of each type (see Weir et al. 2005 for details). Anadromous females were either wild or farmed fish raised at the research station. Six females of each origin were placed in each spawning arena. Two arenas held 12 mature anadromous, wild males, while the other two arenas held only mature farmed anadromous males. For analyses and further discussion, we did not include data for anadromous farmed males because of inherent differences in behaviour between the anadromous farmed and wild males in this experiment (see Weir et al. 2004).

Farmed males do not successfully establish dominance hierarchies and do not consistently spawn successfully (see Weir et al. 2004 for a more detailed analysis). Hence, we had only two replicate arenas (arenas 1 and 2) for anadromous male behaviour. To increase our sample size, we obtained data from a previous experiment conducted at the same facility with wild fish from the same population and at the same anadromous fish density (Fleming et al. 1996). Live observations similar to those made in the 2001 study recorded male and female aggressive and spawning behaviour over a 38-day period. Although Fleming et al. (1996) compared farmed and wild fish in direct competition with one another, we included in our analysis only those data obtained from the arena that contained wild fish from the Imsa River.

Parr aggression was not obviously affected by the type of anadromous males present (Weir et al. 2005) and thus behaviour in all four arenas was analysed. In each arena, parr were tagged with white plastic beads in a unique location below the dorsal fin to identify genetic origin and anadromous fish were tagged with 3.5 cm disk tags enabling individual identification.

Behavioural Observations

Our results for the two male phenotypes focus upon large-scale observations for anadromous males and small-scale observations for mature male parr. These are the scales at which competition occurs most frequently within phenotypes, and have also been used in other studies (anadromous males: Webb & Hawkins 1989; Økland et al. 1995; mature male parr: Jones & King 1952; Myers & Hutchings 1987).

Interactions between male phenotypes were rare (i.e. a total of only 12 acts by anadromous males towards parr were observed over 38 days, when compared with 199 and 161 aggressive acts among anadromous males in arenas 1 and 2, respectively) and thus were not analysed.

Large-Scale Observations

Definition of OSR

For each arena, we conducted live observations of behaviour at a relatively large spatial scale (i.e. 47 m²) each day within the entire experimental arena over time periods that included both day and night (i.e. 0800 to 0000 hours). At the large spatial scale, our operational definition of OSR, following Emlen (1976), was the number of active males to unspawned females in an arena on a given day.

Unspawned females were ripe (i.e. soft bellied with running eggs) prior to being placed in the experiment tanks but had not yet started to construct nests or release eggs. We defined males as active if they were observed being aggressive, receiving aggression or courting females during at least one of the four daily observation periods (see definitions below). This measure of OSR reflected the level of competition experienced by males because they act aggressively and court females even when females are not actively spawning or building nests. Because studies on other salmonid species have defined OSR as the ratio of active males to active females, we also calculated this measure each day, to correspond with methods used by some other authors (e.g. Healey & Prince 1998; Quinn 1999; see Appendix S1 for a preliminary comparison of the two methods). A female was considered active, if she had started digging, was at her nest, or was aggressive towards other fish.

Observation of aggressive behaviour

Our large-scale observations focused on daily activity at the spatial scale of the entire arena. Each day, four 5-min periods of live observations of interactions among males were recorded at least 3 h apart between 0800 and 0000 hours. During these observation periods, behaviour was recorded by scanning the arenas for activity. We recorded the origin of the mature male parr or the identity of anadromous fish initiating and receiving aggression. Overt aggressive behaviour that was common included: chases, whereby one individual swam rapidly towards another causing the latter to change direction; charges, which differ from chases in that the receiver of aggression did not flee; and bites, when one individual contacted the other. Anadromous males also exhibited display behaviour, classified into three different types: lateral display, whereby an anadromous male presented his lateral side with dorsal and anal fins extended; parallel swimming, whereby fish swam beside each other with dorsal fins erect; and head-down display, whereby a male raised his tail and lowered his head towards the substrate (Fleming 1996). Total aggression was defined as the sum of the number of aggressive acts and displays on a day.

Statistical analyses

We examined the patterns of aggression vs. OSR within each arena during the reproductive period. This approach is analogous to an observational field study in which the patterns of behaviour are related

to OSR over the reproductive season at a particular lek or spawning site (e.g. Quinn et al. 1996). Because we have data for each individual anadromous male, we incorporated this into a mixed-effects model, with male identity as a random factor, day of experiment and both linear and quadratic values of OSR as continuous fixed factors. Models were fit using a Poisson distribution because data were counts, and weighted by the number of observations per day. The best model was evaluated by AIC, and the significance of model reduction, beginning with random factors, was analysed by chi-square tests. However, for the purpose of comparison with other studies, we also treated each arena as a spawning shoal to examine the overall patterns of aggression vs. OSR. For analyses of the relationship between aggression and OSR, we only included days on which at least two males were active, such that there was a possibility of male aggression. The response variable for male aggression was the per-capita rate of aggression among active males. This calculation removes the influence that the total number of aggressive males will have on the relationship between aggression and OSR, as our definition of active males included males that were not behaving aggressively.

Small-Scale Observations

Definition of OSR

We obtained data on behavioural interactions among males at a considerably smaller scale (about 1 m²) during discrete spawning events from video recordings of behaviour prior to spawning. At the scale of single spawning events, OSR was defined as the average number of males of each type present during the observation period; there was always one female. This method of estimating OSR is similar to that applied in other studies of salmonid fish (e.g. Blanchfield & Ridgway 1999).

Observation of aggressive behaviour

Small-scale observations involved recording behaviour in a 1-m² area around a female over short time periods just prior to spawning. Behaviour at nests was videotaped from the time a female started digging until a few minutes after the time of egg release (*t*). We took samples of parr and anadromous male aggression beginning at *t*-10 min and ending at *t*+5 min. Competitive interactions among mature male parr were most frequent before spawning when unimpeded by female behaviour signalling egg

release, such as crouching in the nest, which corresponds with parr ceasing aggressive behaviour (Jones 1959). During these sampling periods, we counted the number of chases, charges and bites that occurred among mature male parr present at the nest. In contrast with anadromous males, mature male parr did not display to one another. Because the number of parr at the nest during the 5-min period changed frequently, we also recorded the number of parr present during scan samples taken every 30 s to estimate the mean number of parr present for the observation period.

Statistical analyses

Each spawning was treated as a datum for the small-scale observations. The per-capita aggression among either anadromous or parr males was calculated by dividing the total number of chases, charges and bites observed by the average number of males in the 5-min time period prior to spawning. We binned OSR at this scale in the same categories as for the large-scale observations. Unlike for the anadromous males, we did not have individually identifiable mature male parr in this study. Thus, it is possible that we observed the same individuals interacting in more than one spawning event because individual mature male parr fertilize eggs in an average of 1.5 nests (Jones & Hutchings 2002). Thus, we attempted to minimize the problem of pseudoreplication by also analysing data on a per female basis, as individual parr often spawn in sequential nests constructed by a given female (Thomaz et al. 1997; Jones & Hutchings 2002). Average aggression and OSR per female for which data were suitable (i.e. more than one parr was present at the nest) were also analysed by regression. Relationships between aggression and OSR were analysed using linear and non-linear regression analyses.

Comparison Between Male Phenotypes

To compare rates of aggression between anadromous males and mature male parr, we binned our data into six categories of OSR (0–0.4, 0.4–0.8, 0.8–1.6, 1.6–4.0, 4.0–7.0, >7.0) for each phenotype, chosen such that approximately equal numbers of data points were in each category, and then calculated the average rate of male aggression for each category of OSR in each arena as a datum in this analysis (*n* = 2 for anadromous males and *n* = 4 for parr males). Rates of aggression within categories for which anadromous males and parr overlapped (i.e.

0.8–1.6 and 1.6–4.0) were compared using a generalized linear model.

Literature Data

In addition to our observational data, we also obtained aggression and OSR data from five studies of three other salmonid species: *Salvelinus fontinalis* (Blanchfield & Ridgway 1999), *Oncorhynchus kisutch* (Fleming & Gross 1993, 1994; Healey & Prince 1998) and *O. nerka* (Quinn et al. 1996; Quinn 1999) for which data on changes in behaviour with respect to OSR similar to those in the present study were available. The OSRs in these other studies were calculated either by investigating the number of active males and active females on a given day (Fleming & Gross 1993, 1994), or by quantifying the number of active males competing for a female on her nest (Quinn et al. 1996; Healey & Prince 1998; Blanchfield & Ridgway 1999; Quinn 1999). Thus, the present study and our literature data used true OSRs, as opposed to adult sex ratios that may be inappropriate measures when investigating sexual selection and behaviour (Kokko & Jennions 2008). To remove some among-study variance, we ranked average aggression within a given OSR value in ascending order within studies before parametric analyses (see Green 1976), such that the highest rate of aggression had the highest rank value. Relationships between aggression and OSR in these studies were investigated using regression analyses. All statistical analyses were carried out using R 2.6.2.

Results

Large-Scale Observations

Daily non-zero OSR for anadromous males ranged from 0.09 to 2.25 in arena 1 and 0.08 to 1.60 in arena 2. OSR increased over time in both arenas

(Pearson's correlation, arena 1: $r = 0.789$, $n = 30$, $p < 0.001$; arena 2: $r = 0.746$, $n = 33$, $p < 0.001$) because of a decrease in the number of spawning females as the season progressed (arena 1: $r = -0.939$, $n = 38$, $p < 0.001$; arena 2: $r = -0.937$, $n = 38$, $p < 0.001$) and an increase in male activity throughout the experiment (Pearson's correlation: arena 1: $r = 0.464$, $n = 38$, $p < 0.01$; arena 2: $r = 0.481$, $n = 38$, $p < 0.01$).

Mixed effects modelling suggested strong effects of OSR and day of experiment on the rate of male aggression (Table 1). However, because many males in a group are rarely aggressive, the data should be fit with a zero-inflated model, which is not a readily tractable statistical analysis at present (Zuur et al. 2009). Thus, we also analysed the data using only the dominant male (i.e. the male performing the majority of aggressive acts in an arena), with arena as the random factor in the analysis. Results of this more appropriate analysis given available models suggests similar patterns with significant linear and quadratic OSR values (Table 1). In both cases, removal of the quadratic term from the random effect of male resulted in significant change to the model (all males: $\chi^2 = 64.2$, $df = 3$, $p < 0.001$; dominant males only: $\chi^2 = 18.17$, $df = 3$, $p < 0.001$) and an increase in AIC (all males: full model: 3401; reduced model: 3460; dominant males: full model: 465.4; reduced model: 477.5). Full models, including separate slopes for males, were preferred over reduced models. Thus, these results indicate that both linear and quadratic terms may affect OSR, supporting a dome-shaped relationship between anadromous male aggression and OSR. When we included the data from Fleming et al. (1996), the overall results did not change, except there was now a significant effect of arena in the model (Table 1).

Because of inherent problems with mixed effects modelling with our data, we also treated each arena as a spawning shoal and did not include data for

Table 1: Variable estimates for fixed continuous factors in a mixed-model analysis

All males				Dominant males only			
Variable	Estimate	AIC	Log likelihood	Variable	Estimate	AIC	Log likelihood
Intercept	-3.54* (-2.68*)			Intercept	-1.42* (-0.603)		
OSR ²	-2.31* (-1.14*)	3401 (1552)	-1690 (-764.8)	OSR ²	-1.24* (-1.03*)	465.4 (881.4)	-222.7 (-430.7)
OSR	5.95* (4.07*)			OSR	4.35* (3.50*)		
Day	-0.025* (-0.02*)			Day	-0.007 (0.001)		
Arena	0.098 (-0.001*)						

Results are for the model of best fit, including separate slopes among males with respect to OSR.

Data in parentheses include the arena from a previous study (Fleming et al. 1996).

*Significant contributions to model fit ($p < 0.01$).

individual males. This analysis was performed such that we could make more appropriate comparisons among salmonid species. The per-capita rate of aggression among anadromous males increased with OSR over the relatively narrow range of OSR observed in arena 1 (linear regression: $r^2 = 0.51$, $F_{1,21} = 21.69$, $p < 0.001$) and in arena 2 ($r^2 = 0.20$, $F_{1,18} = 4.60$, $p = 0.046$; Fig. 1). There was no evidence of a dome-shaped relationship between male-male aggression and OSR in either arena when the linear term was included in the model (partial F -tests for the quadratic term: arena 1, $F_{1,20} = 0.069$, $p = 0.795$; arena 2, $F_{1,17} = 0.53$, $p = 0.477$; Fig. 1). The data from Fleming et al. (1996), which included OSRs of up to 6, indicated a dome-shaped pattern between male aggression and OSR ($r^2 = 0.48$, $F_{2,17} = 7.12$, $p = 0.007$; Fig. 1). However, the quadratic regression was non-significant ($r^2 = 0.32$, $F_{2,16} = 3.22$, $p = 0.071$), and the data followed a significant positive linear trend ($r^2 = 0.26$, $F_{2,16} = 5.31$, $p = 0.036$) when an influential datum at a high OSR value was excluded.

Small-Scale Observations

We obtained data for mature male parr behaviour prior to spawning for 22, 25, 36 and 39 spawnings in arenas 1 through 4, respectively. Of these, 14, 14, 16 and 14 observations had at least two parr present during the observation period in each of the four arenas, respectively. In recordings in which more than one parr was present at the nest, the average number of parr decreased over the course of the

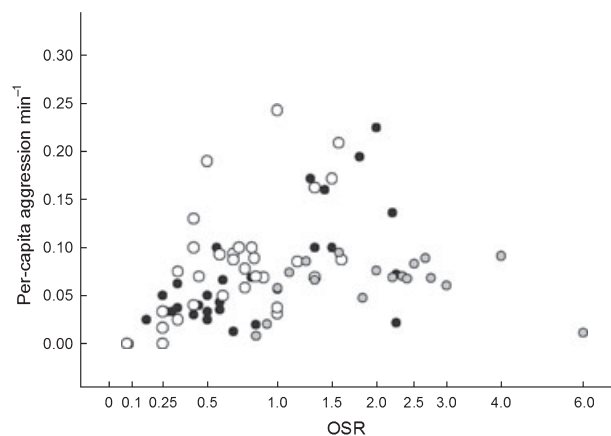


Fig. 1: Per-capita rate of aggression among active anadromous males as a function of OSR over the course of the experiment in arenas 1 (closed symbols, $n = 23$), 2 (open symbols, $n = 20$) and from the 1996 study (grey symbols, $n = 17$). OSR is on a \log_{10} scale.

experiment in three of the four arenas (Pearson's correlation: arena 1: $r = -0.737$, $n = 14$, $p = 0.003$; arena 2: $r = -0.660$, $n = 14$, $p = 0.01$; arena 3: $r = -0.717$, $n = 14$, $p = 0.004$; arena 4: $r = -0.296$, $n = 16$, $p = 0.266$).

We first analysed the data on a per female basis, whereby we calculated the average aggression and OSR for spawnings for each female when encounters occurred ($n = 20$ females). There was a significant decrease in aggression as average OSR increased from 1.4 to 7.4 as well as over time (multiple linear regression: $r^2 = 0.49$, $F_{2,17} = 8.33$, $p = 0.003$; day: partial F -test: $F_{1,18} = 6.64$, $p = 0.02$; OSR: partial F -test: $F_{1,18} = 16.25$, $p < 0.001$; Fig. 2). The ranges of OSR were similar across arenas (arena 1: 0.73–8.45; arena 2: 1.45–8; arena 3: 1.0–9.0; arena 4: 1–7.18). However, the average OSR within arenas differed, such that a comparison using arenas as replicates was possible. Our data suggested a negative trend (linear regression: $r^2 = 0.80$, $F_{1,2} = 7.82$, $p = 0.108$; data not shown) as OSR increased from 2.33 to 4.05, but this result was not significant.

Comparison Between Male Phenotypes

Parr and anadromous males exhibited similar rates of aggression within the two categories of OSR for which they overlapped (i.e. 0.8–1.6 and 1.6–4.0; $F_{1,10} = 1.47$, $p = 0.252$).

Literature Data

For a given OSR, the rates of aggression between anadromous males differed widely between studies (Fig. 3a). For the ranked data, there was a significant

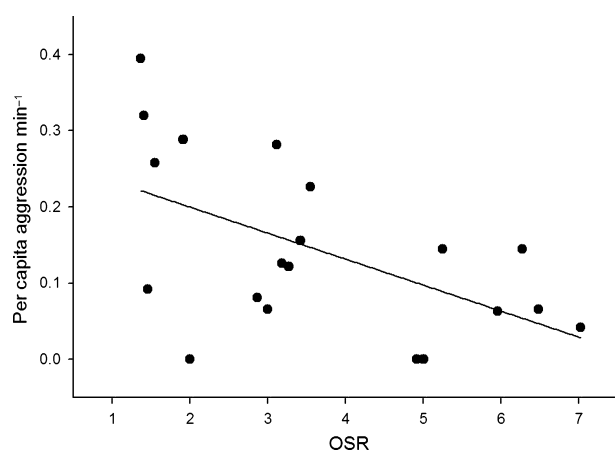


Fig. 2: Per-capita aggression by parr males as a function of parr OSR averaged across nests of individual females ($n = 20$).

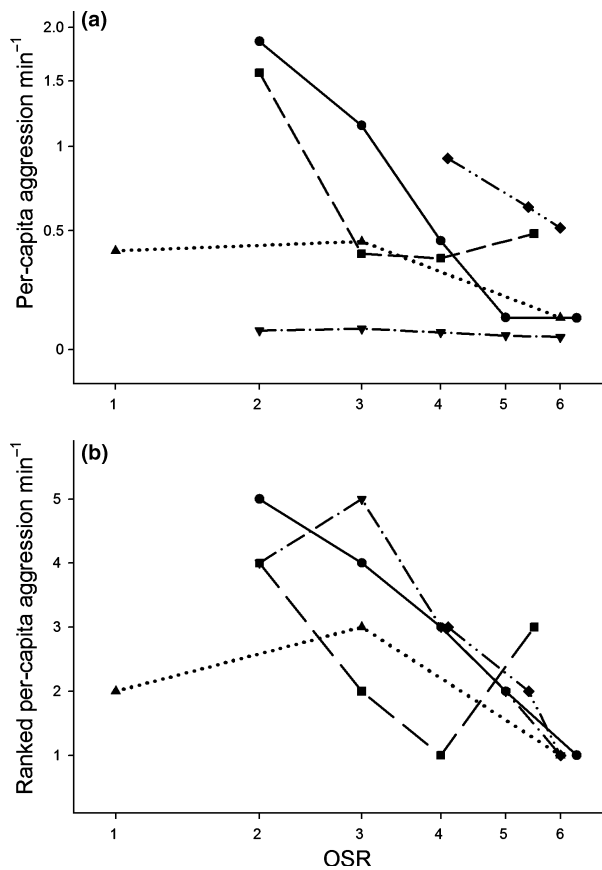


Fig. 3: (a) Literature data for per-capita male salmonid aggression vs. OSR. Both OSR and per-capita aggression are on a log₁₀ scale. (b) Per-capita aggression ranked within studies vs. OSR. Literature data are from Blanchfield & Ridgway (1999) (circles), Healey & Prince (1998) (squares), Quinn et al. (1996) (triangles), Fleming & Gross (1993, 1994) (diamonds) and Quinn (1999) (inverted triangles).

overall linear decrease in per-capita aggression as OSR increased (linear regression: $r^2 = 0.45$, $F_{1,18} = 15.00$, $p < 0.001$; Fig. 3b), and no evidence of a quadratic effect when the linear term was included in the model (partial F -test for the quadratic term: $F_{1,17} = 2.12$; $p = 0.16$).

Discussion

Our results underscore the importance of measuring behaviour, like other ecological variables, at scales relevant to the organisms involved (e.g. Ray & Hastings 1996). Male aggression was only significantly related to OSR when both were measured at temporal scales relevant for each phenotype, i.e., throughout the spawning season for anadromous males (e.g. Webb & Hawkins 1989; Økland et al. 1995) and just prior to spawning for mature male parr (e.g. Jones & King 1952; Myers & Hutchings 1987).

Our study indicated that the per-capita rates of male–male aggression: (1) increased with OSR for anadromous males; (2) decreased with OSR for mature male parr and (3) were similar for mature male parr and anadromous males when measured at the appropriate temporal scale for each phenotype. While we recognize the limitations of our study, the large-scale observations in three arenas may be quite representative of field conditions. Anadromous males rarely fought just prior to spawning events, likely because males had established dominance relationships long before the female had finished constructing her nest (Fleming 1998). This observation is in contrast with data for other salmonids (e.g. *S. fontinalis*; Blanchfield & Ridgway 1999; *O. nerka*, Quinn et al. 1996; *O. kisutch*, Healey & Prince 1998), in which OSR can predict aggression by males during single spawning events. This difference may be related to the closed mating system in our arenas, in which anadromous males were familiar with the eleven other males and their relative dominance ranks.

Anadromous male aggression, as shown by data for all males as well as for the most successful male, increased as OSR increased. However, results of our mixed-effects models suggest that there was a significant negative quadratic relationship between aggression and OSR. While this result supports the prediction of a dome-shaped relationship, we interpret this result with caution because of the lack of mixed-models that can properly accommodate zero-inflated count data (Zuur et al. 2009). For our simpler regression analyses, there was an increase in aggression up to an OSR of 2.25 in the present study and an OSR of 4 for the data from Fleming et al. (1996). Recall, however, the suggestion of a quadratic relationship in the data of Fleming et al. (1996). The increase in aggression among anadromous males over the relatively narrow range of OSR in our study was consistent with predictions of mating systems theory (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996) and previous research (Enders 1993; Jirotkul 1999).

We used a slightly different measure of OSR for the large-scale observations, but one that closely follows Emlen (1976), for two reasons. First, we knew the total number of females in the area and their spawning history, which is not the typical case for field studies. In addition, male aggression occurred during lapses in female activity, suggesting that they fight for access to inactive females and to maintain dominance for subsequent periods of female activity. In contrast with *Oncorhynchus* species, Atlantic salmon females do not guard or stay on their nests

when not actively constructing them. Thus, males may compete for ripe females even when they are not active on the nest. Nevertheless, the two measures of OSR were correlated, as both include active males. However, our measure of OSR was only weakly correlated with day of experiment, such that the effect of OSR is independent of season in our analyses.

Mature male parr were rarely aggressive outside of actual spawning events. Presumably, it was not cost-effective for male parr to establish a dominance hierarchy prior to spawning, given the large numbers in each arena and congregating at each spawning event. Despite being characterized as 'sneaker' males, aggression among mature male parr was not unexpected; parr defend feeding territories (Kalleberg 1958) and compete for positions close to spawning females (Jones 1959; Myers & Hutchings 1987). Considerable variability in the fertilization success of mature male parr (Jones & Hutchings 2001) suggests that some parr are competitively superior to others under experimental conditions. However, because of the high abundance of mature male parr in some rivers (Hutchings & Jones 1998), densities of individuals at spawning time may encourage scramble competition by mature male parr in the wild, notwithstanding the observation that they engage in aggressive defense of females at low densities. The rate of aggression by male parr decreased with increasing OSRs greater than one.

For OSR values that overlapped between anadromous males and mature male parr, per-capita rates of aggression were similar. While this may be somewhat surprising because parr are often considered non-aggressive 'sneakers', parr compete aggressively for favourable positions during spawning (Jones 1959; Myers & Hutchings 1987). The similarity of the intensity of competition within male phenotypes deserves further study in Atlantic salmon and in other mating systems.

While many studies have documented increases in aggression with OSR, few have identified a decrease in aggression at higher OSRs (see Grant et al. 2000; Mills & Reynolds 2003; Reichard et al. 2004; data in Fig. 3a). Interestingly, our parr data and those for other salmonid species indicate that aggression among males, regardless of strategy, decreases as OSR increases above two. This likely reflects similar changes in behavioural tactics within strategies as a consequence of increasing OSR. Given that the data for parr were collected similarly to data in most other studies (i.e. male aggression around a given female prior to spawning), this decrease in aggression

appears to be common across salmonid species. Other studies have also indicated that male behavioural tactics begin to change after the ratio of competitors to resources increases above two (Grant et al. 2000; Noël et al. 2005).

Results for the mature male parr in this study had to be interpreted with caution, because of the different genetic backgrounds of the individuals and the potential for repeated observations of some individuals. While there were no obvious differences in aggression among groups (Weir et al. 2005), subtle differences in behaviour may exist between farmed and wild fish that could not be detected in our results. Similarly, our analyses for parr may have been affected in an undetected way by the genetic background of the anadromous males in the four arenas.

In closing, because the experiment was not originally designed to test how aggression changes with OSR, we would ideally have manipulated the OSR of fish of the same genetic origin in separate, replicated arenas. Such replicated experiments are routinely conducted on smaller fish species in static-water conditions (e.g. medaka: Grant et al. 2000; guppies: Jirotkul 1999), but rarely on large, anadromous salmonids in flowing-water conditions. Our data may be analogous to those obtained in a field study of a single population in a given stream, such that the results may not always be representative of other situations. Acknowledging this potential difficulty, we were conservative in our analyses by averaging data within females or OSRs. Regardless of the analysis used, there was a decreasing trend of aggression with OSR when using arenas as true replicates. Our comparison with other studies suggests that this may represent a general overlying trend among salmonid species, such that the results of the present study might encourage further investigation of the relationship between male aggression and OSR under more controlled settings.

Acknowledgements

We thank Ian Fleming, Sigurd Einum and the research staff at the Norwegian Institute for Nature Research for their involvement in the experiment, as well as Ian Fleming, Mart Gross, Bror Jonsson and Anders Lamberg for allowing us to incorporate their data from a previous study. The work was supported by an AquaNet Network Centre of Excellence Grant to Jeffrey Hutchings and Ian Fleming, the Norwegian Research Council and the Norwegian Directorate for Nature Management funding to Sigurd Einum and

Ian Fleming, and a Natural Sciences and Engineering Research Council (Canada) Graduate Scholarship to Laura Weir. We are grateful to Ian Fleming, Dylan Fraser, Mark Johnston, Bror Jonsson, Marty Leonard and anonymous referees for providing comments on earlier versions of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comparison of different measures of OSR.

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