School of Fisheries, University of Washington, Seattle

Behavioral Tactics of Male Sockeye Salmon (*Oncorhynchus nerka*) under Varying Operational Sex Ratios

THOMAS P. QUINN, MILO D. ADKISON & MICHAEL B. WARD

Abstract

Previous studies have demonstrated several reproductive-behavior patterns in male salmon, including competitive and sneaking tactics, the formation of hierarchies, and non-hierarchical aggregations around ripe females. Through behavioral observations at varying spatial and temporal scales, we examined the hypothesis that operational sex ratio (OSR) determines male sockeye salmon (*Oncorhynchus nerka*) distribution and breeding tactics. Patterns of male distribution and behavior varied over both coarse and fine scales, associated with apparent shifts in reproductive opportunities, the physical characteristics of the breeding sites, and the deterioration of the fish as they approached death. Females spawned completely within a few days of arriving on the spawning grounds, whereas males courted the available ripe females from the date of their arrival on the spawning ground until their death. This difference in reproductive lifespans tended to elevate late-season OSRs but was partially counterbalanced by male departures and the arrival of other ripe females. The proportion of males able to dominate access to ripe females decreased and the number of large courting groups increased over the course of the season, apparently related to both increasing OSR and the deteriorating physical condition of males. However, great variation in OSR was observed within the spawning sites on a given day. OSRs were generally higher in shallow than in deep water, perhaps because larger females or more desirable breeding sites were concentrated in shallow water. The aggregations of males courting females were not stable (i.e. many arrivals and departures took place) and male aggression varied with group size. Aggression was most frequent at low OSRs and in groups of intermediate size (2–4 males per female), and much less frequent in larger groups, consistent with the needs of maximizing reproductive opportunities while minimizing unproductive energy expenditure. These results indicate that, while OSR strongly influences male distribution and behavior, other factors such as physical condition, limited movement and habitat choice may also affect male reproductive opportunities.

Introduction

The operational sex ratio (OSR: ratio of sexually active males to sexually active females) influences the intensity of sexual selection and the expected variance in reproductive success in males and females (EMLEN & ORING 1977; WADE & ARNOLD...
The OSR is affected by differences between males and females in mortality, spatial distribution and parental care (ANDERSSON 1994). High (i.e. male-biased) OSRs result in competition and are often associated with sexual dimorphism and large variation in reproductive success among males (e.g. elephant seals: LE BOEUF 1974) whereas low (female-biased) OSRs may result in female competition for mates (BERGLUND et al. 1993). Varying levels of male competition may affect the overall mating system (e.g. anurans: ARAK 1983) and such aspects of male behavior as dispersal tendency (milkweed beetles: LAWRENCE 1987), courtship mode (salamanders: VERRELL 1983), frequency and duration of aggression (guppies: WARREN 1973; spider mites: ENDERS 1993; medaka: GRANT et al. 1995), nest building (sticklebacks: WARD & FITZGERALD 1988), duration of copulation (water striders: CLARK 1988) and selection on dimorphic features (water striders: ARNQUIST 1992). High levels of male competition are often associated with conditional or alternative male mating tactics (e.g. anurans: SULLIVAN 1982).

While OSR can influence male tactics, it is by no means the only factor. Variation in the physical characteristics of the breeding area (KODRIC-BROWN 1986), density (PETERSEN 1990) and the size and vigor of individual males and females may also be important (e.g. in fish, reviewed by KODRIC-BROWN 1990). Predation risk often affects male tactics (e.g. guppies: GODIN 1995; review: MAGNHAGEN 1991). Additionally, in some species male tactics vary among developmentally or genetically discrete morphotypes (e.g. RA’ANAN & SAGI 1985; SHUSTER 1989).

Salmonid fish (e.g. genera *Oncorhynchus*, *Salmo* and *Salvelinus*) present excellent opportunities to examine the relative importance of OSR in male tactics. Their reproductive lives are generally limited to a few weeks, followed by death (in the semelparous Pacific salmon, *Oncorhynchus* spp.) or emigration from the spawning grounds. Females compete for access to spawning sites, generally spawn within a few days of arrival on the spawning grounds, and then defend their nests from being dug-up and re-used by other females (SCHRODER 1981; VAN DEN BERGHE & GROSS 1986, 1989; FOOTE 1990). Males compete for access to females and are reproductively active during their entire life on the spawning ground (SCHRODER 1981). Consequently, the OSR often becomes skewed towards the end of the spawning period and male competition is intense. In addition to changes in OSR related to differences in reproduction and nest guarding between the sexes, it has long been known that male salmon tend to migrate upriver and arrive on spawning grounds before females (e.g. STONE 1896; KILLICK 1955; LORZ & NORTHCOATE 1965; QUINN & UNWIN 1953). This phenomenon has not been analysed with respect to patterns of breeding opportunity in salmon, although early emergence of male insects (protandry) has been hypothesized to be a reproductive strategy resulting from competition for females (WIKLUND & FAGERSTROM 1977), and the synchrony of female availability affects male aggression and variation in reproductive success in medaka (GRANT et al. 1995).

The results of many investigations, and our own observations, indicate considerable variation in male tactics among and within salmon populations. Large males generally dominate access to females. Unsuccessful combatants may take up positions farther from the female ("satellites") or avoid competition and try to dart in and fertilize eggs at the moment of spawning ("sneakers": CHEBANOV 1980; SCHRODER 1981;...
Sneaking behavior is generally restricted to small males, often those that returned from the ocean at an earlier age than most males (Gross 1985), non-anadromous individuals sympatric with anadromous populations (Montgomery et al. 1987; Foote & Larkin 1988) or smaller freshwater resident males competing with larger residents (Sigurjonsdottir & Gunnarsson 1989; Hino et al. 1990). The prevalence and success of these behavior patterns is related to the size distribution of males in the population (e.g. Maekawa et al. 1994). Large males may be able to dominate access to females only at low and intermediate OSRs; sneaking behavior seems to be favored at high OSRs (Fleming & Gross 1994).

Previous work with sockeye salmon (O. nerka) on island beaches in Iliamna Lake, Alaska, revealed extreme sexual dimorphism (Blair et al. 1993), a brief (ca. 3 wk) spawning season, spatially discrete spawning areas with high densities of salmon and a tendency for larger females to construct their nests in shallower water than smaller females (Quinn & Foote 1994). In addition, the absence of predation by bears (a common event in nearby shallow streams) simplifies the system for the study of male behavior (Crowley et al. 1991; Sih & Krupa 1995). These populations are thus both convenient for field studies and ideal for testing hypotheses regarding male competition. Although satellite and sneaker males are common in salmonid mating systems, precociously mature males were rare (Blair et al. 1993) in this population and Quinn & Foote (1994) observed few satellites and sneakers. Rather, most males were either dominant, were actively competing for access to the female but not in a secondary or satellite position, or were alone. Towards the end of the breeding season, the few ripe females were often courted by large groups of males, though a few males were able to dominate access to ripe females.

The behavior of males might vary as the OSR on the spawning ground changes over time. However, the physical deterioration of male salmon as they approach death may also affect their ability to compete for access to females, hence their behavior. Finally, male distribution might also vary over the spawning ground, reflecting spatial variation in the quality of spawning sites and/or females. High OSRs might occur where nesting-site quality is higher and/or females are larger (hence more fecund: Blair et al. 1993). Sargent et al. (1986) concluded that the distribution of male coho salmon tended to be ideal free (Fretwell & Lucas 1970), in response to female size, under low levels of male competition, but tended to be despotic under more intense competition.

The purpose of this study was to determine the extent to which OSR (reflecting the intensity of competition) influences male sockeye salmon distribution and behavior. We collected data to test this hypothesis using three spatial and temporal scales of observation: 1. Daily transect surveys to determine the number, distribution and reproductive status of males and females; 2. Observations of the number of males courting each ripe female and the number alone throughout the season; and 3. Observations of the behavior of males in these groups over short time intervals. Specifically, we evaluated the following predictions, based on principles of reproductive ecology: 1. The abundance of males in the spawning area will increase with the arrival of females and decrease in response to high OSR (i.e. either a low abundance of ripe females or high competition for access to them); 2. OSR will vary over the spawning
grounds in a manner related to the quality of the spawning sites or females; 3. Increased competition (i.e. OSR) and the declining strength of most males will result in larger courting groups and an increase in the number of lone males late in the season; 4. The size of courting groups around individual ripe females will vary over short time scales as males move among females to assess the females’ readiness to spawn; and 5. Levels of male aggression will show a dome-shaped relationship to competition: low at low OSRs (reflecting high availability of females), high at intermediate OSRs reflecting battles among males, and low at high OSRs as it becomes impossible to control access to a female.

Methods

Data Collection

Sockeye salmon spawning behavior was studied with population surveys along transects, assessment of the social status of males along the transects, and detailed observations of males courting ripe females. Transects were established on 12 Aug. 1991 at spawning beaches on three islands in the eastern end of Iliamna Lake, Alaska: a bay in the northwest side of Woody Island, a bay in the eastern side of Fuel Dump Island, and a section of Porcupine Island known as Painted Rock. Surveys were continued up to and including 28 Aug., when the total population had declined by over 80% from the peak and there were few ripe females remaining. These sites are spatially discrete and previous studies (BLAIR & QUINN 1991; QUINN & FOOTE 1994; HENDRY et al. 1995) have revealed that movement among the sites by tagged salmon is rare. The transects consisted of 50-m lengths of weighted rope along the 0.5-, 1.5-, 2.5- and 3.5-m isobaths. Each day, divers with snorkeling equipment swam along the transects, recording all sockeye salmon within 1 m of each side of the rope (i.e. 2 m x 50 m for each of four transects). Water clarity (ca. 10 m) facilitated observations and the salmon did not flee or react when approached.

Females were classified as ‘green’ (unspawned fish not holding territories, usually near the surface, moving throughout the area), ‘ripe’ (unspawned, territorial fish), ‘spent’ (territorial fish that had apparently completed spawning, based on gaunt appearance), or ‘dying’ (spent fish not holding territories). Unspawned females are easy to distinguish from spent females on the basis of their rotund appearance. We excluded green and dying females from the analysis as they were transient in the area. Males were classified according to social status: ‘alone’ (not courting any female) or ‘courting’ females. Courtship was characterized by repeated circular movements around the female, nosing and other direct contact with her, and aggression towards nearby males. For courting males, we recorded the number of other males (if any) courting the female.

Surveys were conducted at Woody Island in the same manner in 1992 as in 1991, except that data were collected from 9 to 31 Aug. In 1993, surveys were only conducted at a depth of 1.5 m (this depth was selected because it had the highest density of salmon and seemed to best typify the habitat). We did not survey the other sites in 1992 or 1993, as densities and distribution patterns of salmon made them less suitable for study than Woody Island. In addition to the surveys, in 1992 and 1993, we also observed aggregations of males around ripe females at Woody Island to quantify the stability of mating aggregations and the levels of aggression in them. We observed a ripe female and the males around her for 10 min, recording male lateral displays, chases and bites (HANSON & SMITH 1967). We also recorded the number of males courting the female at each 1-min interval. The number of males monitored on any given day was a small fraction of the number of males present on the spawning ground, and repeat observations of males were probably rare.

Data Analysis

To examine temporal patterns in OSR, we used $\chi^2$ tests to compare the ratio of males to ripe females (pooled over all depths) during early and late periods of the spawning seasons (before and after 20 Aug. in each year). We examined spatial patterns in OSR by comparing the ratio of males to ripe females (pooled over all dates) at each transect. In an observational study such as this, variables are often confounded (for example, OSR covaries with date). We therefore employed multivariate logit regression linear models.
Table 1: Frequency of per capita aggression (counts per 10–min observation period) by male sockeye salmon at Woody Island as a function of the number of males courting a ripe female (‘group size’) and the ambient operational sex ratio (OSR: ratio of sexually active males to ripe females)

<table>
<thead>
<tr>
<th>Group size</th>
<th>0–1.99</th>
<th>2–3.99</th>
<th>≥ 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X</td>
<td>SD</td>
<td>n</td>
</tr>
<tr>
<td>0–1.99</td>
<td>4.50</td>
<td>3.69</td>
<td>35</td>
</tr>
<tr>
<td>2–3.99</td>
<td>6.26</td>
<td>2.38</td>
<td>10</td>
</tr>
<tr>
<td>&gt; 4</td>
<td>5.22</td>
<td>NA</td>
<td>1</td>
</tr>
</tbody>
</table>

(CHRISTENSEN 1990) to properly analyse the influence of various factors on male social status. Male status was divided into four categories: alone, dominant (only male courting a female), competitor (one of two or three males courting a female), group (one of four or more males courting a female). We examined four factors that might influence male status: OSR, depth, date and year. OSRs were categorized as low (< 2), intermediate (2–3.99), high (4–7.99) and extreme (> 8). Depth was categorized by the three transects (0.5, 1.5 and 2.5) where large numbers of fish were observed. Date was categorized as early (before Aug 20) and late (Aug 20 and later), and year as 1991 and 1992.

Parameter estimates and goodness-of-fit statistics were calculated for each logit model by fitting the equivalent log-linear model using the SPSS procedure LOGLINEAR (SPSS 1990). All models included an intercept, the main effect of reproductive tactic, and all possible interactions among the explanatory variables; any effects of explanatory variables were included as interactions between the explanatory factor or a combination of factors and reproductive tactics (CHRISTENSEN 1990, p. 238). Models were constructed using hierarchical stepwise procedures, both backwards from a saturated model (unique frequencies of reproductive tactics for each combination of explanatory variable levels) and forward from the minimal model (no effect of the explanatory variables on reproductive tactics).

The significance level for inclusion of an explanatory factor was defined as a decrease in the log-likelihood of at least 1% per degree of freedom lost by including the factor in the model. The criterion, much stricter than the conventional $\chi^2$ test, was employed for two reasons. First, with a sample size of 2840 males, slight differences in frequencies could be statistically significant but biologically insignificant (REYNOLDS 1977, p. 176; SANTNER & DUFFY 1989; p. 170). Second, the observations were not completely independent for a variety of reasons (e.g. males occurred in groups, weather patterns may have affected males simultaneously, etc.), violating the assumptions of the conventional test.

Initially, we used analysis of variance (ANOVA) to select a model for male aggression using a backwards step-wise procedure, deleting an explanatory factor if its deletion did not result in an F-statistic significant at the 0.05 level. In model selection, only the size of the courting group and ambient OSR were considered as potential explanatory factors. Depth, data and year were excluded from this analysis as the sampling design was unbalanced with respect to these factors. Only one of the male groups monitored for aggression levels was at a depth greater than 2.0 m, OSR was highly correlated with date (always low or intermediate before Aug 20 and high or extreme after that date), and the observations in 1992 were towards the end of the season when OSRs were relatively high.

For the ANOVA, observations of aggressive behavior were classified into nine cells delimited by ranges of values for OSR (low, medium, and high or extreme, as defined above) and the average number of males in the courting group (small: < 2.0, intermediate: 2–3.9, large: > 4). As only the 1.5 m transect was surveyed in 1993, 1992 OSR from a depth of 1.5 m was also used in this analysis. In the five instances when no ripe females were present (four with five males present and once with 15 males), OSR was categorized as...
OSR and Male Sockeye Salmon Reproductive Tactics

As an index of per capita aggression within each male group, we used the total number of lateral displays, chases, and bites over a 10-min observation period divided by the average number of males present during that period.

Although ANOVA was initially used to investigate hypotheses about factors underlying male aggression, several assumptions of the F tests used in ANOVA were violated by these data. Cells differed greatly in the number and variance of observations (Table 1). No transformation of the aggression index was found to equalize the variances. Accordingly, in addition to ANOVA, we also used bootstrap tests (EFRON & GONG 1983) to assess the significance of including the average number of males, OSR, and their interaction in the model of aggressive behavior. The aim of the bootstrap test was to approximate the distribution of the residual sum of squares if the factor under consideration had no influence, to get a better estimate of the p-value for including the factor.

The bootstrap procedure for calculating the significance of including a factor in the model was as follows. First, a model that did not include the factor being tested was fit to the data. Second, the differences (residuals) between the aggression index observations and their cell-specific means under this model were standardized by dividing by their cell-specific standard deviations. Third, 300 pseudo data sets were generated assuming that the cell means of the simpler model (i.e. without the selected factor) were correct. Each pseudo data set was constructed by replacing each true observation with a pseudo observation that was generated by adding to the cell mean a randomly selected residual (drawn from the set of residuals of all cells), multiplied by the cell-specific standard deviation. That is, the cells of the pseudo data sets had the same number of observations and, on average, the same means and standard deviations as the model. Fourth, both a model which did and a model which did not contain the factor being tested were fit to each pseudo data set. For each data set, the ratio of the residual sums of squares from these two model fits (SSQ0/SSQA) was preserved. The significance level of the tested factor was the fraction of times this ratio from the 300 pseudo data sets was larger than this ratio from the true data set.

Results

In 1991, daily counts of all sockeye salmon at Woody Island (WI) declined from 242 on 12 Aug. to 66 by 28 Aug., when the study was terminated. The number of ripe females fluctuated considerably but was highest on the first day of the surveys, then declined as those females spawned. The number of ripe females increased when a second group arrived around 17–22 Aug. and then declined as they spawned. The number of ripe females was generally paralleled by the number of males, though male density did not change as rapidly as did ripe-female density (Fig. 1). The OSR varied from 1.0 to 4.9 but only exceeded 3.0 on 3 of 17 d, reflecting the arrival of the second group of females and the apparent departure of some males from the spawning area (Fig. 2). Overall, OSR did not differ between early and late periods in 1991 ($\chi^2 = 1.77$, p > 0.10; Table 2).

Observations at the two other sites were generally consistent with those at WI, although several differences were noted. Densities of salmon at the Fuel Dump (FD) site were lower than those at WI (total counts of ripe females at WI were 825 in 1991; 710 in 1992 vs. 555 at FD; Table 3). Arrivals of females and males occurred several days later at FD and spawning occurred farther offshore than at WI (as shown by the large number of salmon observed on the 3.5-m transect; Table 3). OSR was lower in the early than the later period of the season ($\chi^2 = 4.28$, p < 0.05, Table 2). The salmon at the Painted Rock (PR) site were essentially restricted to the 1.5-m transect and their density was much lower than at the WI or FD sites (Table 3). OSRs did not differ between early and late periods ($\chi^2 = 2.07$, p > 0.10) but the large day-to-day changes in the number of territorial females indicated that some females may have initiated nest construction there but then departed.
In 1992, surveys were initiated earlier at WI and a rapid rise in density was observed (Fig. 1). No females had settled on 8 Aug., but on 9 Aug. 42 ripe, territorial females were observed. Additional ripe females settled over the next few days, and by 12 Aug. there were 93 territorial females, all ripe. The total number of females continued to increase (to 141 on 17 Aug.), but females were spawning at a higher rate than new females were settling, thus, 12 Aug. represented the peak abundance of ripe females. The male population generally declined with the reduction in the number of ripe females (Fig. 1b). Unlike 1991, OSRs exceeded 3.0 on 9 of the last 10 days, and were much higher in the late than in the early period ($\chi^2 = 106.79$, $p < 0.001$, Table 2; Fig. 2). Overall, OSRs were also higher in 1992 than 1991, whether analysed as the sum of observations (2.10 vs. 1.66, $\chi^2 = 14.06$, $p < 0.001$) or a comparison of the daily estimates (6.38 vs. 2.08, $t = 2.55$, $p = 0.02$).

While general trends were revealed by summing the data over all transects, additional patterns emerged when each transect's data were examined separately. Females colonized the shallower transects sooner than the deeper ones at WI. For each depth, we summed all of the observations of ripe females and calculated the date by which 50% of the observations had occurred. In 1991, the 50% dates were Aug. 17, 18, 20 and 22 for the 0.5-, 1.5-, 2.5- and 3.5-m transects, respectively, and the dates in 1992
were Aug. 14, 14 and 15 (no females settled at the 3.5 m transect in 1992). This pattern was not evident at FD (50% dates were 22, 23 and 22 Aug.). Because ripe females did not arrive synchronously on the transects, very high OSRs were occasionally observed (e.g. at WI: 27: 0, 23: 1 & 41: 3 in 1991; 27: 0, 18: 1, 20: 1 & 29: 2 in 1992) on one transect when much lower OSRs prevailed elsewhere. Males thus failed to match the spatial distribution of ripe females on a day-by-day basis. In addition, the overall OSRs on the WI transects differed, being more male-biased in shallower water ($\chi^2 = 21.35$, p < 0.001 in 1991; $\chi^2 = 19.02$, p < 0.001 in 1992; Table 3), indicating an absence of adjustment of male density to that of ripe females. A similar pattern was observed at FD but the difference was not significant ($\chi^2 = 1.83$, p > 0.10).

Of the 1366 observations of male salmon at WI in 1991, 31% were alone, 31% were courting without a competitor, and 37% were courting the female in groups of 2–12 (Table 3). Very similar overall patterns of male status were seen at WI in 1992 and FD in 1991; the pattern at PR differed slightly but there were fewer observations. The proportion of males in the different categories varied widely (e.g. at WI in 1991: dominant: 5–47%, competitor: 18–74% and alone: 9–59%; Fig. 3). There were consistently fewer males courting females without competitors and more males in large groups towards the end of the season, even though OSRs were slightly lower late in the season at PR and WI in 1991.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Dates</th>
<th>Males</th>
<th>Male group size (% of all males)</th>
<th>Alone</th>
<th>Ripe females</th>
<th>OSR</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2–3</td>
<td>4 +</td>
<td></td>
</tr>
<tr>
<td>WI</td>
<td>1991</td>
<td>early</td>
<td>798</td>
<td>35.8</td>
<td>26.3</td>
<td>9.7</td>
<td>28.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>568</td>
<td>25.0</td>
<td>19.7</td>
<td>19.7</td>
<td>35.6</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>early</td>
<td>1041</td>
<td>42.2</td>
<td>29.9</td>
<td>2.9</td>
<td>25.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>450</td>
<td>6.2</td>
<td>9.3</td>
<td>45.8</td>
<td>38.7</td>
</tr>
<tr>
<td>FD</td>
<td>1991</td>
<td>early</td>
<td>186</td>
<td>46.8</td>
<td>21.5</td>
<td>5.4</td>
<td>26.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>778</td>
<td>27.1</td>
<td>26.2</td>
<td>17.1</td>
<td>29.6</td>
</tr>
<tr>
<td>PR</td>
<td>1991</td>
<td>early</td>
<td>145</td>
<td>31.7</td>
<td>13.1</td>
<td>2.8</td>
<td>52.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>81</td>
<td>8.6</td>
<td>35.8</td>
<td>11.1</td>
<td>44.4</td>
</tr>
</tbody>
</table>
Table 3: Reproductive status of sockeye salmon observed along four transects at the Woody Island (WI), Fuel Dump Island (FD) and Painted Rock (PR) study sites. Dominant males were those with uncontested access to ripe females and competitors were males in groups of two or more around ripe females.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Depth (m)</th>
<th>Ripe females</th>
<th>Males</th>
<th>OSR</th>
<th>Dominant</th>
<th>Competitor</th>
<th>Alone</th>
</tr>
</thead>
<tbody>
<tr>
<td>WI</td>
<td>1991</td>
<td>0.5</td>
<td>176</td>
<td>346</td>
<td>1.97</td>
<td>24.6</td>
<td>37.3</td>
<td>38.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>287</td>
<td>557</td>
<td>1.94</td>
<td>32.9</td>
<td>40.1</td>
<td>27.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.5</td>
<td>319</td>
<td>407</td>
<td>1.28</td>
<td>33.9</td>
<td>35.4</td>
<td>30.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.5</td>
<td>43</td>
<td>56</td>
<td>1.30</td>
<td>41.1</td>
<td>23.2</td>
<td>35.7</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.5</td>
<td>219</td>
<td>600</td>
<td>2.74</td>
<td>27.3</td>
<td>41.8</td>
<td>30.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>358</td>
<td>649</td>
<td>1.81</td>
<td>35.6</td>
<td>42.1</td>
<td>22.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.5</td>
<td>133</td>
<td>234</td>
<td>1.76</td>
<td>30.3</td>
<td>27.8</td>
<td>41.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.5</td>
<td>0</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>total</td>
<td>825</td>
<td>1366</td>
<td></td>
<td></td>
<td>1.66</td>
<td>31.4</td>
<td>37.3</td>
</tr>
<tr>
<td>FD</td>
<td>1991</td>
<td>0.5</td>
<td>2</td>
<td>3</td>
<td>1.50</td>
<td>31.3</td>
<td>39.5</td>
<td>29.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>90</td>
<td>168</td>
<td>1.87</td>
<td>20.8</td>
<td>50.6</td>
<td>28.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.5</td>
<td>312</td>
<td>561</td>
<td>1.80</td>
<td>29.2</td>
<td>43.0</td>
<td>27.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.5</td>
<td>151</td>
<td>233</td>
<td>1.54</td>
<td>42.1</td>
<td>26.2</td>
<td>31.8</td>
</tr>
<tr>
<td></td>
<td>total</td>
<td>555</td>
<td>965</td>
<td></td>
<td></td>
<td>1.74</td>
<td>30.9</td>
<td>40.1</td>
</tr>
<tr>
<td>PR</td>
<td>1991</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5</td>
<td>108</td>
<td>214</td>
<td>1.98</td>
<td>24.8</td>
<td>27.6</td>
<td>47.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.5</td>
<td>1</td>
<td>7</td>
<td>7.00</td>
<td>0.0</td>
<td>28.6</td>
<td>71.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.5</td>
<td>0</td>
<td>5</td>
<td>-</td>
<td>0.0</td>
<td>0.0</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>total</td>
<td>109</td>
<td>266</td>
<td>2.07</td>
<td></td>
<td>23.4</td>
<td>27.0</td>
<td>49.6</td>
</tr>
</tbody>
</table>
Fig 3: The proportions of male sockeye salmon categorized as dominant (having uncontested access to ripe females, designated by solid bars), competitor (one of two or more males competing for access to ripe females, designated by cross-hatched bars) or alone (not associated with any ripe female, designated by open bars) at Woody Island during the spawning seasons in 1991 (above) and 1992 (below). No surveys were conducted on 19 and 30 Aug., 1992.

Forward model selection suggested that male status was affected by both OSR and date. Inclusion of these two factors resulted in a $R^2$ (the fraction of the likelihood of the minimal model explained by the more complex model; Christensen 1990, p. 150) of 0.65. The frequency of males in dominant or competitive status declined with increasing OSR. There was an additional decline in frequency, independent of OSR, late in the season. Backwards model selection also suggested that male status was affected by date, but that this effect differed between years. The frequency of males in the dominant and competitive classes declined with date, but the magnitude of this decline was much greater in 1992 than in 1991. In this model, depth had a weak effect; there was a tendency for a higher frequency of competitive males at 0.5 m, groups at 1.5 m and dominant males at 2.5 m. The $R^2$ for this model was 0.68. OSR was not included in the backwards model; however, OSR was the last factor to be removed and was close to significant (0.92% reduction in likelihood per degree of freedom lost, $R^2 = 0.76$). When included, its estimated effect was similar to that in the model constructed by forward selection.
Observations of spawning groups revealed several patterns. First, the groups were not stable. Males frequently left the focal ripe female, moving to other females, and then back to the focal female. Only 6 of the 107 groups experienced no change in group number over the 10-min observation period, and 25% of the groups experienced changes of at least four males (maximum = 15). Second, levels of aggression were correlated with group size. Our statistical analysis pooled lateral displays with rams and bites but the relationships with group size were similar for these behaviors (Fig. 4). The conclusions based on ANOVA and bootstrap procedures were virtually identical (Table 4): both group size and OSR affected the per capita aggression displayed by males (Table 1) and these influences were independent. That is, the effect of OSR on aggression did not depend on the group size, and vice versa. Per capita aggression declined with increasing OSR, and was highest at intermediate group sizes (2–3.99 males per group; Table 1).

**Discussion**

We studied sockeye salmon under natural conditions to examine the relationships between OSR and male behavior at different scales of space and time. The overall
Table 4: Statistical analyses of the importance of the number of males courting a ripe female ('group size') and the ambient operational sex ratio (OSR) on per capita aggression by male sockeye salmon, using ANOVA and the ambient operational and bootstrap tests (see text for details)

<table>
<thead>
<tr>
<th>Factors</th>
<th>Residual SSq (SE)</th>
<th>Ratio SSqO/SSqA</th>
<th>F-statistic p</th>
<th>Bootstrap p</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>1071 (10.11)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group size</td>
<td>897 (8.62)</td>
<td>1.19</td>
<td>&lt; 0.001</td>
<td>0</td>
</tr>
<tr>
<td>OSR</td>
<td>833 (8.01)</td>
<td>1.29</td>
<td>&lt; 0.001</td>
<td>0</td>
</tr>
<tr>
<td>Group size, OSR</td>
<td>771 (7.56)</td>
<td>1.08 (vs. size)</td>
<td>0.019</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.16 (vs. OSR)</td>
<td>&lt; 0.001</td>
<td>0</td>
</tr>
<tr>
<td>Group size interaction × OSR</td>
<td>767 (7.83)</td>
<td>1.01</td>
<td>0.980</td>
<td>0.917</td>
</tr>
</tbody>
</table>

results indicated that, while OSR was strongly correlated with male distribution and behavior, other factors such as variation in the physical condition of the male, and preference for certain habitats and/or large females may also have been involved. It is important to note that the patterns of male behavior ('tactics') examined here were much less varied than have been described in other mating systems (review: ANDERSSON 1994). Unlike species with distinct male morphotypes (e.g. crustaceans: RA'ANAN & SAGI 1985; SHUSTER 1989), those in which the presence or absence of male parental care is closely linked to size (e.g. sunfish: GROSS 1982), or species in which environmental factors can influence the functional sex of simultaneous hermaphrodites (PETERSEN 1990), male sockeye salmon in this population displayed a more limited repertoire of behavior. They attempted to monopolize access to females, courted them in groups of 2–10 or more, moved through the spawning site, or departed from it temporarily (QUINN & FOOTE 1994).

Our first prediction was that the abundance of males in the spawning area would reflect the number of ripe females and would rise and fall with their availability. In general, this was the case; the number of males observed on the entire spawning ground generally tracked the number of ripe females rather than the total number of females. This was especially obvious at WI in 1991, when male abundance declined but then rose again when a second wave of females arrived later in the season. Some males may have left the spawning ground when ripe females were scarce, perhaps to seek opportunities in other spawning areas. These demographic results are consistent with tagging studies at this site (BLAIR & QUINN 1991; QUINN & FOOTE 1994) that showed some males leaving the area one or more times during the spawning season. The hypothesis that males move among spawning sites in response to variation in breeding opportunities is reminiscent of the ideal-free distribution theory (FRETWELL & LUCAS 1970). However, two lines of evidence argue against the hypothesis that salmon distribution fits this model. First, very high OSRs (i.e. unfavorable for males) were sometimes observed in localized areas. Second, males tagged at these sites have generally been observed at that spawning site or not observed at all (BLAIR & QUINN 1991; QUINN & FOOTE 1994; HENDRY et al. 1995). We have only rarely observed tagged males moving between nearby, physically similar, sites occupied by ripe sockeye salmon, even if the OSRs vary greatly between sites (HENDRY et al. 1995). It is unclear why males leave their 'primary'
breeding site; perhaps they move into open water where we could not observe them and where they can rest.

FOOTE (1990) found that male sockeye salmon in a stream do not establish exclusive territories but restrict their movements to a small area. We hypothesize that a male salmon that establishes dominant status with a female may be more likely to dominate access to another female in the vicinity after the first female has spawned completely than would be the case elsewhere. However, this benefit of dominance might come with the cost of waiting for another female to arrive. On the other hand, males roving the spawning ground might have more opportunities to locate ripe females but might also have more difficulty establishing dominance. QUINN & FOOTE’S (1994) study at WI found no relationship between size or dominance status and the tendency to move or remain in a limited area. However, tagged males moved less in shallow than deep water. The mean distances between twice-daily observations were 2.1, 4.7, 5.0 and 5.3 m for salmon observed between depths of 0–1, 1–2, 2–3 and 3–4 m, respectively (n = 630 observations of 101 males, F = 2.62, 3 df, p < 0.001, T. P. Quinn & C. J. Foote, unpubl. data). These data were consistent with the hypotheses that male behavior varies among individuals and among habitats (see below), and that factors other than OSR affect male distribution over the spawning area.

Our second hypothesis was that OSR might vary over the spawning grounds in a manner related to the quality of the spawning sites or females. We observed significantly higher OSRs in shallow water than deeper water in both years at WI, indicating that breeding competition did not fully explain male distribution. Presumably, males spawning in shallow water accrue benefits commensurate with the additional cost of competing there. Male distribution may have reflected variation in the quality (i.e. size) of females or in breeding-site quality. Mate-quality variation can influence breeding competition in other animals (review: CLUTTON-BROCK & PARKER 1992). Larger female salmon have larger and more numerous eggs than smaller females (e.g. BLAIR et al. 1993), and dig deeper nests that are less vulnerable to scouring or excavation by other females (CRISP & CARLING 1989), hence males might be expected to compete for larger females. Evidence from a previous study at this site indicated that females spawning near shore tended to be larger than those settling in deeper water, but the relationship was quite variable (QUINN & FOOTE 1994). Regarding habitat quality, we have no direct evidence that eggs spawned in shallow water have higher survival rates than those deposited deeper, but several lines of evidence indicate that shallow sites are most desirable. First, the earliest arriving females tended to settle in shallow water at WI, even though temperatures do not vary over these spatial scales. Second, larger (presumably competitively superior) females tended to settle near shore (QUINN & FOOTE 1994). Third, salmon embryos rely on circulation of oxygenated water during incubation and wind-driven surface currents and wave action at WI produce more water circulation in shallow water (F. Leonetti & T. P. Quinn, unpubl. data). Fourth, female aggression is greater in shallow than deeper water, indicating intense competition for space there (ADKISON 1994).

Interestingly, the relationship between OSR and depth was weaker at FD than WI and females did not arrive later in deep water at FD. This site drops steeply to about 1 m depth and the shallowest water is exposed to such high wave action that the gravel is
unstable, explaining the scarcity of females at the 0.5-m transect. The bottom is then relatively level and suitable for spawning for about 50 m offshore, unlike WI which changes sharply after about 3 m depth into substrate unsuitable for spawning.

Our third hypothesis was that the proportion of males in courting groups of different sizes would be affected by OSR. We expected that increased competition would result in larger courting groups around ripe females as OSR became more male-biased towards the end of the season. As predicted, the estimated effect of increased competition (increasing OSR) was a decrease in the fraction of males dominant or in small courting groups. However, two lines of evidence indicated that OSR was not the only factor affecting group size. First, considerable variation in group size was observed, even along a single transect, on a given day. This may have resulted from variation in female size (i.e. perceived female quality: SARGENT et al. 1986) and the readiness of the female to spawn (SCHRODER 1981). Second, late date was also associated with increased group size, indicating that declining strength may have reduced males’ ability to monopolize access to females. However, a few ‘fresh’ males, distinguished by the absence of scars and fungus, arrived late in the season and were sometimes able to monopolize access to ripe females, even under very unfavorable OSRs. Towards the end of the season, males that had arrived early may have been unable to compete with the recently arrived males, and formed unaggressive groups around some females. Consistent with this hypothesis, males tagged at this site at the beginning of the season exhibited decreased dominance over time (QUINN & FOOTE 1994). The late season reduction in the fraction of males dominant or in small groups was less pronounced in 1991 than 1992, likely because the second group of females that arrived in 1991 (but not in 1992) kept the OSR lower late in the season.

With regard to our fourth hypothesis, individual courting groups were not stable but varied in size and composition. It was our general observation that a few males would remain with a female but many others might leave and return several times during the 10-min observation period. These transient males seemed to be attracted to the digging of other females or to the aggregation of males around another female. In some cases virtually the entire group of males (e.g. 8–15) temporarily abandoned a ripe female. This is consistent with SCHRODER’S (1981) observation that female readiness to spawn is more important than size in determining attractiveness to males. Volatile group sizes such as those we observed would hinder reliable comparisons between the observed distribution of salmon and that predicted by the ideal-free distribution theory (FRETWELL & LUCAS 1970; SARGENT et al. 1986).

Our fifth hypothesis was that aggression would be related to group size (i.e. local OSR). Most lateral displays and attacks took place in groups of 2–4 males per female, consistent with the ‘dome-shaped’ relationship between density and aggression observed in guppies by WARREN (1973). In these small groups, several males actively attempted to limit access by the others to the female. Male salmon that had dominated access to a female (i.e. mean male group size near 1) had to expend relatively little effort in displacing competitors, and males in large groups were very unaggressive. We believe that the lack of aggression in large groups resulted from the absence of any male able to dominate access to the female and from the low reproductive payoff for efforts expended in aggression in such large groups (FLEMING & GROSS 1994). We anticipated
that male aggression would decrease towards the end of the season, at high OSR, as males might no longer be able to deny the many competitors access to a ripe female. This reduction in aggression was observed at all levels of group size (Table 1). However, because OSR increased with date over the period of these observations, this decrease in aggression might also reflect decreasing energy reserves of males. The males in small groups towards the end of the season appeared relatively healthy and were probably late-arriving. Perhaps only very healthy males can dominate access to females or battle with one or two other males for access, whereas weaker males may form larger and less aggressive groups.

To summarize, our overall hypothesis that OSR determines male distribution and behavior was examined through five sub-hypotheses at varying spatial and temporal scales. Our results supported the conclusion of Grant et al. (1995) that the value of OSR in predicting the patterns and results of mating competition depends on the scales over which it is measured. At the broadest scale, male density on the spawning ground as a whole generally reflected the availability of ripe females and OSR did not become very high until the end of the season. However, within the spawning ground on a given date, great variation in OSR was observed among transects and, in general, OSRs were higher in shallow than in deep water. We conclude that the skewed OSRs resulted from the limited movement of many males and the preference of males for some features of shallow water (quality of females or nesting sites). Group size generally increased at high OSRs, as predicted, but there was also a pronounced effect of date. Large aggregations of males around females were not stable. Males in these aggregations displayed remarkably little aggression, consistent with the needs of maximizing reproductive opportunities while minimizing energy expenditure at a time when breeding opportunities and energy are both severely limited.

Our results shed light on the observation that male salmon generally arrive on the spawning grounds before females (Killick 1955; Lorz & Northcote 1965; Quinn & Unwin 1993). This is consistent with the general tendency for the sex with higher levels of intrasexual competition to arrive on breeding grounds first (Myers 1981; Clutton-Brock & Parker 1992), even if the early arriving sex does not establish territories (Reynolds et al. 1986). Female salmon construct the nests without assistance from males, hence one might expect them to arrive first. However, a male arriving before the first ripe female is ready to spawn will only lose breeding opportunities in proportion to his expected life on the spawning grounds (e.g. 1 d out of 10) but a male arriving 1 d after females arrive will lose breeding opportunities in proportion to the rate at which they spawn. Females often spawn within 1–2 d of settling (e.g. Schroder 1981; Quinn & Foote 1994), hence late arriving males will lose much more of their reproductive opportunities than those arriving early, especially if female arrival is highly synchronous. Similar arguments have been advanced to explain early male emergence (protandry) in insects (Wiklund & Fagerström 1977). However, many factors affect realized reproductive success in salmon and arrival date may not always be the most important (see also Baughman 1991).

Previous studies have demonstrated competitive and sneaking tactics and the development of hierarchies or aggregations of male salmon around ripe females. Our study provides insights into this variety of reproductive tactics of male salmon and the
flexibility of individual males attempting to maximize their breeding success under the wide range of conditions experienced during their brief reproductive lifetime. We have shown that male distribution and aggressive behavior varies over both coarse and fine spatial and temporal scales and is driven by shifts in reproductive opportunities and intrasexual competition. The changes in OSR during the spawning season are a fundamental aspect of salmon breeding systems, as they result from the fact that females devote most of their time on the spawning grounds to parental care rather than breeding, unlike males. However, OSR is only one index of reproductive opportunities; male behavior apparently also reflects habitat quality and the individual's physical condition.

Acknowledgements

We thank Chris Foote and Ian Fleming for constructive criticism, Rebecca Bernard, Andrew Hendry, Frank Leonetti, Sandra O'Neill and Tom Rogers for assistance with the field work, and the Pacific Seafood Processors' Association for their financial support for the Bristol Bay Sockeye Salmon Program.

Literature Cited


QUINN et al., OSR and Male Sockeye Salmon Reproductive Tactics


Received: June 27, 1995
Accepted November 6, 1995 (J. Brockmann)