Size-assortative mating in salmonids: negative evidence for pink salmon in natural conditions

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Driven by competition and mate choice, size-assortative mating has been seen in many organisms. The breeding system of salmonid fish, *Oncorhynchus* spp., has been extensively investigated and many examples of size-assortative mating have been found. However, assortative mating is not always observed and many reported examples involved cases with a large dichotomy in size classes or were conducted in artificial arenas where other factors influencing mate choice and competition were controlled. This study investigated size-assortative mating in a population of naturally reproducing pink salmon, *O. gorbuscha*. We made direct observations of courtship behaviour over 3 years on fish of known sizes. To determine the extent to which these observations corresponded to reproductive success, we assessed the parentage of the offspring produced by the fish in the first 2 years of the study using DNA fingerprinting. Size-assortative mating was not seen in the behavioural observations. Parentage results showed that our measure of dominance (proximity of males to ripe females) corresponded with successful matings, suggesting that the fish that we observed as dominant were in fact involved in more matings or more successful matings. We also saw no size-assortative mating in male and female pairs that produced adult offspring. We are not suggesting that the processes that can lead to size-assortative mating are not occurring, but that many other factors, such as female ripeness, male availability, predation threat and changing environmental conditions, may minimize the importance or mask the occurrence of size-assortative mating under natural conditions.

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The mating systems of many fish are strongly affected by male and female body size. Larger males often have a competitive advantage over smaller males and thus have a greater ability to select females in mating systems dominated by male competition (Kodric-Brown 1990). Larger females produce more numerous and larger offspring (Dickerson et al. 2002), and may acquire higher-quality breeding or nesting sites (Fleming & Gross 1994). These female traits would be expected to result in higher offspring survival, hence large males should both choose large females when possible (e.g. Grant et al. 1995) and be able to dominate access to them (Morris et al. 1992).

In some species, females have been shown to be more receptive to large males (e.g. Schroder 1981), perhaps because size is often heritable and females that mate with larger males may have larger offspring. Females mating with large males may gain direct advantages in the quality of the male's territory or parental care (e.g. Downhower & Brown 1980), although this has not been demonstrated in semelparous salmon, or indirect benefits in the male's successful genotype (Kirkpatrick 1996).

In some cases, competition and choice combine to produce size-assortative mating (the tendency for individuals of similar relative sizes to mate together; e.g. lampreys, *Lampetra planeri*: Malmqvist 1983), and this can be an important aspect of the evolutionary and behavioural ecology of the species. Size-assortative mating has been studied closely in salmonid fish, and it has been reported in natural populations of Japanese char, *Salvelinus leucomaenis* (Maekawa et al. 1994), sockeye salmon, *Oncorhynchus nerka* (Hanson & Smith 1967), and coho salmon, *O. kisutch* (Chebanov 1990), and in experimental...
arenas in sockeye (Foote 1988, 1989), chum, O. keta (Chebanov 1979) and pink salmon, O. gorbuscha (Chebanov 1980, 1989). Such nonrandom mating not only affects patterns of reproductive success within populations but may also contribute to isolation between anadromous and nonanadromous forms because they differ greatly in body size (e.g. Taylor et al. 1996). However, assortative mating is not always observed (Schroder 1981; Quinn & Foote 1994), and many reported examples of size-assortative mating involved a large dichotomy in size classes or were conducted in artificial areas where other factors influencing mate choice and competition were controlled (e.g. Foote 1988, 1989; Maekawa et al. 1994). Under natural conditions, choice and competition may be influenced by the ripeness of available females, vigour of the males, threat of predation, and other factors that might reduce the importance of size.

In addition to the diverse factors that influence mate pairings under natural conditions, the study of size-assortative mating in salmonids is complicated by methodological issues. Male dominance is often assessed by the number of observations or length of time that the male is in closest proximity to a ripe female (e.g. Gross 1985; Quinn & Foote 1994; Dickerson et al. 2002). However, one of the main mechanisms of female choice is to delay spawning when courted by a small or otherwise undesirable male (Foote 1989; Berejikian et al. 2000; de Gaudemar et al. 2000). Thus, one might question whether a male seen in an apparently dominant position with a female is favoured by her or is actually being subjected to this delaying tactic and so more likely to be observed with her.

This study tested the hypothesis that mating is size assortative with 3 years of observations in a naturally reproducing population of pink salmon, a species with normal rather than bimodal distributions of male and female body sizes. The reproductive behaviour of pink salmon is similar to that of other salmon species (Quinn 1999) except that males do not display alternative life history patterns based on age at maturity and all individuals are anadromous. Despite the uniform age distribution and the absence of nonanadromous individuals, male pink salmon show great variation in size (Beacham & Murray 1985), which could increase the potential for size-assortative mating to occur, as has been shown in arena experiments (Chebanov 1980, 1989). We also determined the extent to which apparent dominance based on observations corresponded to reproductive success, assessed by parentage analysis of the offspring produced by the matings in the first 2 years of the study.

**METHODS**

The study was conducted on adult pink salmon in the summers of 1997–2000 at a small, unnamed stream (named Himmel Creek for the purposes of this study) on Chichagof Island in Port Frederick, southeastern Alaska, U.S.A. A logjam limited pink salmon to the lower 330 m of the creek in 1997 and 1998 but the fish were able to use 800 m of creek in subsequent years. The creek varied from 3.7 to 11.8 m wide, depending on location and discharge. Pink salmon densities were high in the creek; peak daily counts of live fish were 797 in 1997, 367 in 1998, and 792 in 1999. Within the reach of stream used by the fish, local densities varied depending on habitat type. Chum salmon (O. keta) co-occur in this creek during the early part of the pink salmon run. Bear predation is a threat to the fish throughout the run; between five and 12 brown bears, Ursus arctos, were seen feeding on salmon in the creek.

We used a beach seine, dip nets and stick seines to capture as many of the salmon in the creek as possible (1255 fish in 1997, 1092 in 1998, 1382 in 1999, and 758 in 2000). We anaesthetized the fish in MS-222 and recorded the body length (mid-eye to hypural plate) and sex of each individual. All fish were tagged with white, lettered, plastic disc tags, allowing us to identify and observe individuals from the bank without disturbing them. The behaviour of tagged fish was observed in two approximately 100-m-long sections of the creek in 1997 and in the entire reach in 1998 and 1999. Once daily, observations were taken from the bank with binoculars to avoid disturbing fish behaviour. Starting downstream, we identified all tagged fish in the visible area and recorded the courtship status of the males and the identity of the female being courted. We categorized each male's courtship status as ‘1’ if he was dominant (closest to the female in proximity or the sole male courting a ripe female), ‘2’ if he was in a subdominant position, or ‘1’ if he was not involved in courting. When a male courted an untagged female, we recorded the male’s status for analysis of dominance/size relationships, but did not include these data in our analysis of size-assortative mating. The status of untagged males was not recorded but was taken into account when assigning the status of tagged males courting the same female. When all tagged fish in the visible area were recorded we moved upstream to the next reach and began again.

As part of a larger study of reproductive success, fin clips were taken from all fish when tagged during 1997–2000 for use in an analysis of parentage. DNA was extracted from these clips using ammonium acetate protocol. PCR was used to amplify six microsatellite loci (Ogo1a, Ogo4, Ots101, Omy1001UW, Omy 1212 and Oki23) and the resulting product was visualized using the MegaBACE 1000 capillary electrophoresis system (Amersham Pharmacia Biotech Limited, Piscataway, New Jersey). Using a combination of CERVUS, exclusion software (Marshall et al. 1998) and PAPA, maximum likelihood software (Duchesne et al. 2002), we matched the adult offspring (fish from 1999 and 2000) with their parents (fish from 1997 and 1998). All pink salmon mature at 2 years of age, so sampling in 1999 and 2000 was sufficient to obtain all adult offspring produced in 1997 and 1998, respectively.

We examined possible size-assortative mating from both female and male perspectives, because salmonid mating systems involve male competition and female choice. Univariate linear regressions were used to investigate the following relationships (SPSS v7.5). From the female perspective, we looked for a relationship between the body size of a given female and (1) the average body size of the males in closest proximity to her across all observations, (2) the average body size of all of the males courting her, regardless of their status, and (3) the average body size...
of all males with whom she produced identified offspring. From the male perspective, we looked for a relationship between the body size of a given male and (1) the average length of all females he courted, (2) the average size of the females he was in closest proximity to, and (3) the average body size of all females with whom he produced identified offspring. We analysed each of the 3 years separately because fish from different years were physically separated and the average body size of both females and males differed between years. An analysis of variance (ANOVA) blocked by year to remove year-to-year variation was used to investigate the relationship between the male’s average dominance score and the number of identified offspring produced. Very few families were represented by many offspring, so for purposes of analysis, we placed male parents into one of three categories: no offspring, one offspring, and greater than one offspring.

RESULTS

There was no relation between the average length of males courting a given female and her length in any year (regression: 1997: $F_{1,44} = 0.557$, $P = 0.50$, $r^2 = -0.01$; 1998: $F_{1,25} = 0.173$, $P = 0.68$, $r^2 = -0.042$; 1999: $F_{1,71} = 0.395$, $P = 0.53$, $r^2 = -0.009$), nor was female length related to the length of the primary male courting her (regression: 1997: $F_{1,38} = 2.086$, $P = 0.16$, $r^2 = 0.028$; 1998: $F_{1,25} = 0.713$, $P = 0.41$, $r^2 = -0.03$; 1999: $F_{1,59} = 1.267$, $P = 0.27$, $r^2 = 0.005$; Fig. 1). There was also no relation between the length of a female and the average length of the males that sired her offspring (regression: 1997: $F_{1,10} = 2.209$, $P = 0.15$, $r^2 = 0.039$; 1998: $F_{1,32} = 0.022$, $P = 0.88$, $r^2 = 0.032$; Fig. 2).

The length of a given male was unrelated to the average length of females that he courted in any year (regression: 1997: $F_{1,38} = 0.85$, $P = 0.36$, $r^2 = -0.004$; 1998: $F_{1,30} = 0.005$, $P = 0.94$, $r^2 = 0.034$; 1999: $F_{1,121} = 0.284$, $P = 0.60$, $r^2 = -0.006$; Fig. 1), and was unrelated to the average length of the females with whom he was in closest proximity (regression: 1997: $F_{1,30} = 0.361$, $P = 0.55$, $r^2 = -0.012$; 1998: $F_{1,22} = 1.427$, $P = 0.25$, $r^2 = 0.019$; 1999: $F_{1,67} = 0.524$, $P = 0.47$, $r^2 = -0.007$). There was also no relation between the length of a male and the average length of the females with whom he produced adult offspring (regression: 1997: $F_{1,31} = 1.69$, $P = 0.20$, $r^2 = 0.022$; 1998: $F_{1,35} = 0.016$, $P = 0.90$, $r^2 = 0.029$; Fig. 2).

Not only were there no linear relationships but there were

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Figure 1. (a) Relation between the body length (mm) of female pink salmon and both the average body size of all male pink salmon observed courting her and the average body size of the primary male pink salmon (male closest to her in the courtship hierarchy) observed courting her. (b) Relation between body length of male pink salmon and the average length of the female pink salmon he was observed courting.
no significant parabolic relationships in any of the above comparisons for either sex in any year (NS in all cases).

To assess the validity of our observational data on dominance, we compared our measure of dominance with the number of offspring produced. Males that produced two or more detected adult offspring had the highest average dominance scores, followed by males that produced one offspring, and males that produced no detected adult offspring had the lowest average scores (ANOVA: $F_{1,179} = 5.223$, $P = 0.023$).

**DISCUSSION**

Within this population, larger males are more often found in closest proximity to spawning females (Dickerson et al. 2002), suggesting that larger males have a competitive advantage over smaller males when it comes to mate choice. Because larger females produce larger and more numerous eggs than smaller females (Dickerson et al. 2002), large males should choose large females when possible. Large females should also be more receptive to large males because size is heritable and females that mate with larger males may have larger offspring (Beacham & Murray 1988; Smoker et al. 1994). Despite this logic, there was no evidence of size-assortative mating for either sex, in any year, with any index of mating.

In any study reporting negative evidence, one must consider the power of the study to falsify the null hypothesis of no effect. Given the levels of variation we observed, only unrealistically large sample sizes ($\sim 700,000$–$560$ million) could have detected significant effects. There was also no evidence of parabolic relationships (large males courting large and small females rather than females of intermediate sizes) as was seen in pink salmon tested in experimental arenas (Chebanov 1980). Thus, the parsimonious conclusion is that the hypothesized patterns simply were not present, rather than that we were unable to detect them.

Pairings may not be determined by body size or mate choice as much as arrival timing, ripeness of available females, and availability of males. Schroder (1981) found that male chum salmon choose females based on nest-digging activity, an indicator of a female’s readiness to spawn, rather than size. Thus, males may try to minimize the time delay between spawnings (hence maximize the number of possible mating events) rather than maximize the number of potential eggs fertilized (i.e. by female size) in any given event.

Schroder (1981) also found that females prefer males of their own size or larger and that they express choice by delaying nest construction when courted by inferior (smaller) males. When a female delays the release of her eggs (presumably to maximize the chances that a higher-quality male will arrive), an observer might mistakenly categorize the attending male as dominant because of his proximity to the female. In this case, apparent dominance and realized reproductive success might be uncorrelated or even inversely related if females breed so quickly with desirable mates that they are seldom seen together. However, our parentage analysis revealed that males with high observer-based dominance scores indeed produced more offspring than those with lower observer-based
dominance scores. This result suggests that the males we categorized as dominant were in fact dominant, and participated in more spawning events or more successful spawning events than those with lower scores. Because we did not identify offspring as juveniles, our conclusion may be biased by selection on traits at sea, such as body size or growth rate, which could decrease the apparent successful matings of other males by weeding out their offspring. However, the most convincing evidence that size-assortative mating does not occur in this population was the lack of a relationship between male and female body size in pairs that produced adult offspring.

It is not our view that the processes that can lead to size-assortative mating are not occurring on the spawning grounds, but that other factors such as female ripeness, male availability, predation threat and changing environmental conditions may minimize or mask the occurrence of size-assortative mating in natural situations.

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