Promoting the Science of Ecology

Relative Importance of Salmon Body Size and Arrival Time at Breeding Grounds to
Reproductive Success
Author(s): B. R. Dickerson, K. W. Brinck, M. F. Willson, P. Bentzen, T. P. Quinn
Source: *Ecology*, Vol. 86, No. 2 (Feb., 2005), pp. 347-352
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/3450954
Accessed: 21/10/2008 10:10

http://www.jstor.org

# RELATIVE IMPORTANCE OF SALMON BODY SIZE AND ARRIVAL TIME AT BREEDING GROUNDS TO REPRODUCTIVE SUCCESS

B. R. Dickerson,[1,6] K. W. Brinck,[2] M. F. Willson,[3] P. Bentzen,[4] and T. P. Quinn[5]

[1]University of Washington, School of Aquatic and Fishery Sciences, P.O. Box 355020, Seattle, Washington 98195 USA
[2]University of Washington, Quantitative Ecology and Resource Management, P.O. Box 355020,
Seattle, Washington 98195 USA
[3]5230 Terrace Place, Juneau, Alaska 99801 USA
[4]Dalhousie University, Department of Biology, Halifax, Nova Scotia B3H 4J1, Canada
[5]University of Washington, School of Aquatic and Fishery Sciences, P.O. Box 355020, Seattle, Washington 98195 USA

*Abstract.* The importance of body size to reproductive success has often been emphasized, but timing of arrival to the breeding grounds may also be important. To assess the relative roles of size and timing, we investigated the influence of life history and of behavioral and morphological traits on realized reproductive success in wild pink salmon, *Oncorhynchus gorbuscha*, during the 1997 and 1998 spawning seasons. Reproductive success was quantified by the number of adult offspring returning to spawn (1999 and 2000; parentage determined via DNA microsatellite genotyping). Males that arrived earlier, lived longer in the stream, and were more often observed in dominant courtship positions had significantly more offspring, although the importance of dominance was overshadowed by timing. Female reproductive success was not closely linked to any measured trait, but stabilizing selection on arrival timing and length is possible, as 1998 fish showing intermediate values of these traits were the most productive. Bear predation accounted for up to 50% of the mortality on the spawning grounds, yet did not have detectable effects on reproductive success. The absence of strong linear relationships between reproductive success and such traits as body size and fecundity may indicate that selection has driven the population to equilibrium values.

*Key words: adult progeny; body size; breeding timing; DNA microsatellites;* Oncorhynchus gorbuscha; *parentage analysis; reproductive success; southeast Alaska; spawning grounds; wild pink salmon.*

## INTRODUCTION

Understanding the factors affecting variation in reproductive success among individuals is key to understanding the selective pressures driving adaptation and evolution (Stearns 1992). Reproduction has been well studied in salmonid fishes (Fleming 1998); their breeding system, especially that of Pacific salmon, *Oncorhynchus* spp., makes them ideal for examining reproductive success. These anadromous, semelparous fishes achieve most of their adult body size while feeding at sea, do not feed or grow during the breeding season, home to their natal stream to breed at very discrete times of the year, and die upon completion of spawning, allowing an individual's lifetime reproductive output to be estimated in one season (reviewed by several authors in Groot and Margolis [1991]).

Most research on reproductive success in salmonids has emphasized the importance of adult body size. Females can benefit from large size by producing larger

and more numerous eggs (Beacham and Murray 1993, Dickerson et al. 2002), obtaining and defending high-quality breeding sites (Foote 1990), and burying their eggs deeper (hence safer; Steen and Quinn 1999). Large males may have advantages in intrasexual competition and mate choice (Quinn and Foote 1994, Fleming 1998, Dickerson et al. 2002). However, the timing of arrival on the spawning grounds may have at least as much influence on reproductive success as body size. Early, arriving males are more likely to obtain mates because later in the season the females are nest guarding and no longer reproductively active (Quinn et al. 1996, Dickerson et al. 2002). Earlier-arriving fish also typically, though not always (Smoker et al. 2000), live longer than later arrivals, allowing males more time to participate in spawning events and females a longer nest-guarding period (McPhee and Quinn 1998, Dickerson et al. 2002). Countering these advantages, large size and early arrival may increase vulnerability to bear predation (Quinn and Buck 2001, Quinn et al. 2003).

Reproductive success in salmon has typically been estimated by using surrogate traits such as observations of courtship, spawning events, or body size or shape (e.g., Fleming and Gross 1994). However, several males may participate in each spawning event, females

spawn more than once, and the survival of the offspring cannot be inferred from observations on the adults. Thus reproductive success of individual salmon cannot be accurately determined by indirect methods. Molecular biology provides powerful tools for parentage analysis and the direct measurement of reproductive success (Wright and Bentzen 1994). However, most studies have examined the fertilization success of males (e.g., Foote et al. 1997), neglecting variation in reproductive success among females, and most have sampled offspring as embryos or juveniles, neglecting important events that may occur later in life. In contrast, we determined reproductive success using a more appropriate measure, the number of mature progeny.

The objective of this study was to examine the relationship between arrival timing, body size, and other associated traits (fecundity, egg size, dominance, and longevity) and the number of adult progeny produced by pink salmon (*Oncorhynchus gorbuscha*). We hypothesized that the number of offspring would be positively correlated with (1) large size, high fecundity, and large eggs in females, (2) long duration of nest defense in females, (3) large size and behavioral dominance in males, and (4) early arrival and protracted breeding life in males. Finally, we predicted greater variation in reproductive success among males than among females in this competitive breeding system.

## MATERIALS AND METHODS

This study was carried out in 1997–2000 on a natural population of pink salmon in a small, unnamed stream located in Port Frederick, Chichagof Island, southeastern Alaska. All pink salmon mature at age two, so the adults sampled in 1999 and 2000 were the offspring of the 1997 and 1998 adults. The stream had an accessible length of 330 m in 1997 and 1998, and the range of the bank-full width was 3.7–11.8 m. The early part of the pink salmon spawning period overlapped with spawning by chum salmon (*Oncorhynchus keta*), and both species were subjected to predation by 5–12 brown bears (*Ursus arctos*).

Our goal was to sample all adult pink salmon entering the creek but logistic constraints prevented 100% sampling. We estimated based on tag recovery rates that ~75% of the fishes that died before sampling were washed out of the creek or carried away by bears. Over the course of the four years we sampled a total of 2348 males and 2139 females while alive and an additional 1025 DNA samples taken from fish found dead (see Appendix A for details).

A beach seine was used at the mouth of the creek to capture fish prior to entry, and dip nets were used to opportunistically capture untagged fishes after entry. Fish were tagged with white Floy disk tags (Floy Tag, Seattle, Washington, USA) each with a unique identification letter and/or number combination, allowing identification from the bank without disturbing behavior. Before release, we recorded the fish's sex, body length (mid-eye to hypural plate, a measurement unbiased by jaw development), body shape (depth of the dorsal hump [lateral line to highest point on the hump], and snout length [tip of the upper jaw to mid-eye]), and removed a small fin clip from the pectoral fin for DNA analysis. Individual egg size was estimated by weighing and counting a ~15-g sample of eggs from ripe females. We established a length–fecundity relationship for the population by sacrificing 155 females prior to spawning. Body length, hump depth, snout length, and total egg mass were recorded. Length explained 66% of the variation in total egg mass ($F = 98.890$, df $= 1, 149$, $P < 0.001$; Appendix B). Fecundity can then be estimated as the estimated total egg mass divided by the mean individual egg mass.

For fish captured after their first day of entry into the spawning grounds we estimated freshwater age (days in freshwater) based on criteria validated by repeated observations of tagged fish. Fish were aged as 1 d if they had sea lice (a parasitic marine copepod, *Lepeophtheirus salmonis*) present on body and/or slime present, few or no scratches on flesh, and no visible decay of skin or fins; 2 d if they had no slime or sea lice, few or no scratches, and no decay of skin or fins; 3 d if scratches were present and the belly and fins were beginning to show decay; 4 d if decay was prominent on the belly and fins and color was fading; and ≥5 d if prominent decay was present.

Each day all pink salmon were counted, and tagged males were observed to determine dominance. In 1997 observations were made in two ~100-m-long sections of the creek due to the large numbers of fish present. In 1998 observations were made on the entire reach. We observed fish behavior in the afternoon by walking up the bank of the creek and observing the fish with binoculars to avoid disturbing spawning behavior. Males were categorized as "3" (dominant; closest to the female in proximity or the sole male courting a ripe female), "2" (subdominant; involved in courting but not closest to the female), or "1" (alone; not involved in courting). Two estimates of potential reproductive success were calculated from these observations. First, the dominance scores of each male were averaged over his life in the stream to yield "average dominance." Second, "days dominant" was the total number of days a given male was seen in the dominant or primary position with a ripe female. Tagged fish recovered dead were classified as having been killed by bears or died of senescence but only 20–31% of tags were recovered each year. Fish not recovered were probably washed out by high flows and tides or were removed by bears (Gende et al. 2004). We estimated the longevity of fish we did not find dead by adding one day to the last day the fish was observed alive but we made no assumptions about the mode of death.

Microsatellite loci were used to conduct the parentage analysis. They are particularly useful for kinship analysis because they are neutral markers that are Men-

delian inherited and highly variable (Wright and Bentzen 1994). Total genomic DNA was isolated from the fin tissues and the region of interest (six microsatellite loci) was amplified using polymerase chain reaction to increase the number of copies of each allele at each locus. Electrophoresis was then used to separate the alleles to allow for size determination. Differences in alleles are due to differences in the number of base pairs of the fragment in question. See Appendix A for details.

Tests for deviations from Hardy-Weinberg equilibrium were done using GENEPOP, version3.1 (Raymond and Rousset 1995). A simulation, run using pedigree version 3.0 (Craig Busack, [Washington Department of Fish and Wildlife Seattle, Washington, USA], unpublished software program) to test the ability to determine parentage using the loci chosen, indicated >99.9% chance of correctly determining parentage via exclusion. Tests for Hardy-Weinberg equilibrium showed an excess of homozygotes at most loci (Appendix A), probably due to scoring errors, null alleles, and large-allele drop out. To account for this, in the parentage analysis all homozygotes were treated as heterozygotes where one allele was known and the other allele was treated as missing data. PAPA is a likelihood-based parentage-allocation computer program that determines the likelihood that a parent pair produced the genotype found in the offspring (Duchesne et al. 2002), and was used to do the parentage analysis. Unlike similar programs, PAPA is designed for situations where the identity of neither parent is known, which is commonly the case with fishes. In the case of microsatellites, which are composed of 2–4 base-pair repeats, it is most likely that errors in scoring will result in an allele that appears to be one set of repeats larger or smaller than the actual size. PAPA allows for transmission errors due to errors in genotyping by creating a matrix of probabilities, with the allele of the same size being the most probable choice and those larger and smaller being less probable the further away they are. It also factors in the probability of mutations having occurred.

To assess the relative importance of morphology, life history, and behavior to reproductive success, general linear models were used. The number of offspring produced was used as the dependent variable, the sexes were analyzed separately and year was included in all models to account for interannual variation (SPSS 2001; see Appendix B for details of models used).

## RESULTS

There is a general tendency for heterozygosity deficiencies relative to expectations under Hardy-Weinberg (HW) equilibrium, with the departures from HW equilibrium statistically significant ($P < 0.05$) for all six loci in 1997 but only for one loci in 1998 (Appendix A).

Of the adult offspring sampled in 1999 and 2000, 723 (34%) were assigned to at least one parent (28% from 1999 and 36% from 2000), giving us 297 male
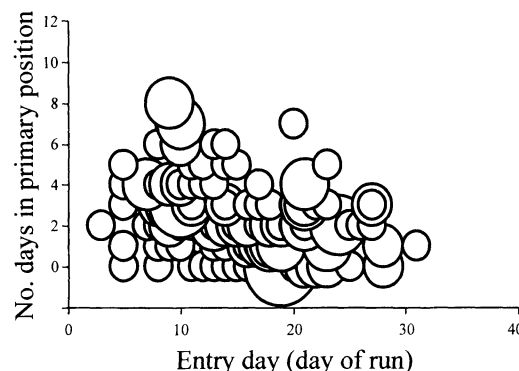


FIG. 1. Interactive effects of male pink salmon dominance (days in the primary courting position) and day of entry into the spawning grounds (relative to the first day of run) on offspring production. Each circle represents an individual male; circle size represents the number of offspring (smallest = 0 offspring, largest = 6 offspring).

parents, and 271 female parents with identified offspring. Unidentifiable offspring were the result of there being no possible identifiable parents. Variance in reproductive success was similar between females and males ($F = 1.77$, df $= 2, 2$, $P = 0.36$).

For males, no relationship was found between the number of offspring produced and body size, body shape (hump depth and snout length), or mode of death ($P > 0.05$; Appendix B). However, males with a longer instream life-span produced more offspring than shorter-lived males ($F = 7.473$, df $= 1, 390$, $P = 0.007$; Appendix B). Males with higher average dominance scores produced more offspring than did males with lower dominance scores ($F = 5.385$, df $= 1, 159$, $P = 0.022$) and early arriving males produced more offspring than did later arriving males ($F = 4.939$, df $= 1, 159, P = 0.028$), but there is an interaction between entry timing and dominance that is approaching significance ($F = 3.709$, df $= 1, 159$, $P = 0.056$; Appendix B). Early in the season, males with high dominance scores produced the most offspring, but as the season progressed the benefits of dominance diminished (Fig. 1).

For females, no relationship was detected between the number of offspring produced and estimated fecundity, egg size, body shape (hump depth, snout length), mode of death, or instream longevity ($P > 0.05$; Appendix B). There was also no difference in the mean body size or entry day of females that produced offspring and those that did not ($P > 0.05$; Appendix B). However, there was evidence of stabilizing selection on entry date and possibly on fish length. In 1998, variance in arrival timing was higher in females that did not have any identified offspring than in those that had at least one ($F$ test: $F = 1.711$, df $= 354, 26$, $P = 0.05$) because many of the earliest and latest females did not successfully reproduce, although this relationship was not apparent in 1997 ($F$ test: $F = 0.601$, df $= 176, 18$, $P = 0.31$; Fig. 2). Variance in length was
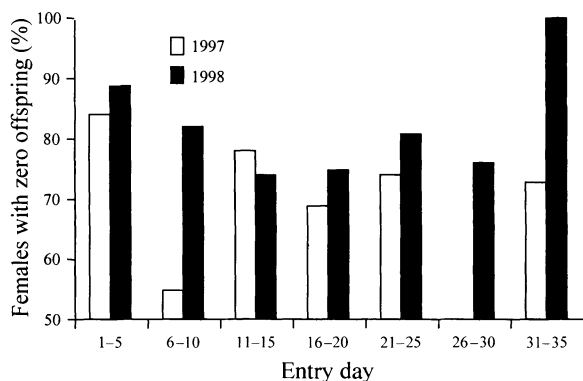
REPORTS

FIG. 2. Percentage of female pink salmon that produced no identified adult offspring as a function of entry day (day from the first day of the run) in 1997 and 1998.

significantly higher among females that had no offspring than among those with at least one offspring in 1998 (*F* test: *F* = 1.299, df = 377, 111, *P* = 0.04). Females of mid-size were most successful in 1998, although there was no pattern in 1997 (Fig. 3).

## DISCUSSION

All cases of deviations from Hardy-Weinberg equilibrium were the result of excessive homozygous individuals, probably due to a combination of null alleles, large-allele drop-out (larger alleles are harder to amplify, thus tend to have weaker signals), and scoring error. This would hinder analysis of population structure but it does not decrease confidence in our parentage assignments because the unidentifiable offspring had no known parents rather than too many possible parents (in only three cases, due to genotypic similarities between adults, was more than one adult of the same sex indicated as the most likely parent).

Our assignment rate of offspring to parents was low (34%) probably as a result of genotyping errors, mutations, and strays (fish sampled as offspring that were actually spawned elsewhere)—although the most important factor contributing to our low assignment rate was probably unsampled parents. There are four larger populations in streams nearby (each with >10 000 pink salmon) and even a small proportion of strays could result in nonnative fish in our population. Despite our best efforts it is likely that a number of salmon were killed and eaten by bears or died and were washed away without being sampled. Despite these problems, there was a sufficient sample size to yield insights in the factors that were associated with reproductive success.

Neither body size nor shape (hump depth and/or snout length) was a significant predictor of offspring production in males, although both have been correlated with dominance (e.g., Fleming and Gross 1994, Quinn and Foote 1994). Larger males in this population had higher dominance scores (Dickerson et al. 2002), and males with higher dominance scores produced more offspring, but the effects of arrival timing could

counterbalance these traits. As the season progresses and the operational sex ratio shifts to a large number of males per ripe female (Quinn et al. 1996), the influence of size on dominance decreases if larger males can no longer defend access to ripe females. This could reduce the influence of size on offspring production towards the end of the season and weaken an overall correlation between male size and reproductive success.

Longer-lived males were more successful, perhaps because they participated in more spawning events than shorter-lived fishes. However, males in this population that were killed by bears had a 25% reduction in average life-span (Dickerson et al. 2002), yet mode of death did not influence reproductive success but lifespan did. In habitat like this creek, where fast water and woody debris hinder predation, bears tend to kill salmon that are nearing death, so much of their reproduction would have already taken place (Gende et al. 2004).

Dickerson et al. (2002) showed that in this population larger females had larger and more numerous eggs than smaller females, and there was variation in these traits (ranges: length, 302–504 mm; fecundity, 625–4121; and mean egg mass, 0.10–0.24 g). The advantage of large size has been predicted by authors combining the individual components of fitness such as fecundity and egg burial depth (e.g., van den Berghe and Gross 1989), and is suggested by Helle's (1989) correlation between the average size of chum salmon, *Oncorhynchus keta* females in a population and the production of progeny, even beyond the effect of fecundity. However, extensive analysis of demographic data in another population (Holtby and Healey 1986) revealed no evidence that larger females were more productive than smaller ones. We also found no increase in production of progeny with female size. We do not suggest that fecundity and egg size do not affect reproductive success but rather that the influence of these factors was too weak to be detected in a study such as this that integrated all forms of mortality. Had we studied the
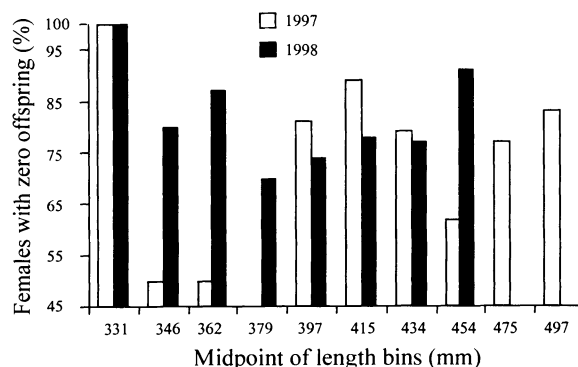


FIG. 3. Percentage of female pink salmon that produced no identified adult offspring as a function of body length in 1997 and 1998.

production of juveniles we might have detected a relationship.

After egg deposition, the primary activity of females on the spawning grounds is nest defense (Fleming 1998), thus, longer-lived females were predicted to have greater reproductive success, but we found no such relationship. The average life-span of a female was 8.5–9.9 d (depending on the year), and the spawning season spanned more than a month, especially during the years with high densities (1997 and 1999; Appendix A). No female could protect her eggs throughout the entire run and most only guarded for ~30% of the run. The duration of nest guarding may have only a small influence on reproductive success but selection will still favor it because there is no other profitable activity for the semelparous female to pursue.

Entry date (date of entry onto the spawning grounds) exhibited the strongest influence on female reproductive success. In 1998, stabilizing selection appeared to act on entry date (fish with intermediate dates produced the most offspring). This was not apparent in 1997, but we were unable to sample the end of the run that year and could have missed enough of the late fish to mask evidence for stabilizing selection. A mid-range entry could benefit a female both because of access to a greater choice of males than later arrivals and by reducing risk of nest disturbance by other females compared to earlier arriving females (van den Berghe and Gross 1989), although late arrivals should have the least risk of nest disturbance (Smoker et al. 1998). Time of egg deposition can determine when the fry emerge from their redds, and those emerging early, at low densities, may be more vulnerable to predators (Hunter 1959), although developmental compensation can occur resulting in a tighter emergence timing than timing of egg deposition alone would indicate (Holtby et al. 1989). Also important to emergence timing is prey availability—early and late fry may miss the optimal window of food availability, and the date of seaward migration strongly affects survival of pink salmon (Mortensen et al. 2000).

There was no way to analyze patterns of ocean mortality in this study but marine processes influenced the results because reproductive success was defined as number of adult offspring returning to spawn. For salmon, most mortality occurs in fresh water, and variability in mortality is also higher at this stage than at sea (geometric mean variance 0.54 vs. 0.33; Bradford 1995). Total mortality from egg to adult for pink salmon is ~99.73%, with ~91% of this mortality occurring during the egg to fry period and ~9% occurring during the fry to adult period (Bradford 1995).

In summary, the correlations (or lack thereof) between adult traits and lifetime reproductive success resulted from processes on the breeding grounds, some of which we were able to measure, and from complex physical processes during the incubation and marine periods that were not directly sampled, and probably

vary considerably among years. These processes will have acted on the population for countless generations, so the absence of strong linear trends is not surprising and may be a result of these effects being too weak to be detected by this study. Nevertheless, the failure to detect some of the very intuitive, predicted effects of size on reproductive success sends a cautionary note that it is not safe to assume these effects in models of salmon population dynamics and evolution.

## LITERATURE CITED

Beacham, T. D., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42:485–508.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327–1338.

Dickerson, B. R., T. P. Quinn, and M. F. Willson. 2002. Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. Ethology, Ecology, and Evolution 14:29–44.

Duchesne, P., M. H. Godbout, and L. Bernatchez. 2002. PAPA: a computer program for simulated and real parental allocation. Molecular Ecology Notes 2:191–194.

Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):59–76.

Fleming, I. A., and M. R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution 48:637–657.

Foote, C. J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. Behaviour 115:283–313.

Foote, C. J., G. S. Brown, and C. C. Wood. 1997. Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54:1785–1795.

Gende, S. M., T. P. Quinn, R. Hilborn, A. P. Hendry, and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos 104:518–528.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Helle, J. H. 1989. Relation between size-at-maturity and survival of progeny in chum salmon, *Oncorhynchus keta* (Walbaum). Journal of Fish Biology 35(Supplement A):99–107.

Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:1946–1959.

Holtby, L. B., T. E. McMahon, and J. C. Scrivener. 1989. Stream temperatures and interannual variability in the emigration timing of coho salmon, *Oncorhynchus kisutch*, smolts and fry and chum salmon, *O. keta*, fry from Car-

nation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **46**:1396–1405.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada **16**:835–885.

McPhee, M. V., and T. P. Quinn. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon. Environmental Biology of Fishes **51**:369–375.

Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham. 2000. The relationship between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fishery Bulletin **98**:319–335.

Quinn, T. P., M. D. Adkison, and M. B. Ward. 1996. Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratios. Ethology **102**:304–322.

Quinn, T. P., and G. B. Buck. 2001. Size and sex selective mortality on adult Pacific salmon: bears, gulls and fish out of water. Transactions of the American Fisheries Society **130**:995–1005.

Quinn, T. P., and C. J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. Animal Behaviour **48**:751–761.

Quinn, T. P., S. M. Gende, G. T. Ruggerone, and D. E. Rogers. 2003. Density-dependent predation by brown bears (*Ursus*

*arctos*) on sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences **60**:553–562.

Raymond, M., and F. Rousset. 1995. GENEPOP: population genetics software for exact tests and ecumenicism. Journal of Heredity **86**:248–249.

Smoker, W. W., A. J. Gharrett, and M. S. Stekoll. 1998. Genetic variation of return date in a population of pink salmon: a consequence of fluctuating environment and dispersive selection? Alaska Fishery Research Bulletin **5**:46–54.

Smoker, W. W., A. J. Gharrett, M. S. Stekoll, and S. G. Taylor. 2000. Genetic variation of fecundity and egg size in anadromous pink salmon, *Oncorhynchus gorbuscha*, Walbaum. Alaska Fishery Research Bulletin **7**:44–50.

SPSS. 2001. SPSS for windows. Release 11.0.1. SPSS, Chicago, Illinois, USA.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Steen, R. P., and T. P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Canadian Journal of Zoology **77**:836–841.

van den Berghe, E. P., and M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution **43**:125–140.

Wright, J. M., and P. Bentzen. 1994. Microsatellites: genetic markers for the future. Reviews in Fish Biology **4**:384–388.

## APPENDIX A

Details of methods used in the paper, including a figure showing the daily count of live pink salmon over the periods 1997–2000 and tables showing (Table A1) locus descriptions from the loci used in parentage analysis of pink salmon in 1997 and 1998 and (Table A2) sequences of the primers used to amplify the loci used in the parentage analysis, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-017-A1.

## APPENDIX B

Statistical tables for models used in the analysis, including (Table B1) linear regression demonstrating the variation in fecundity explained by fish length and individual egg mass, (Table B2) general linear models used to analyze male pink salmon reproductive success, and (Table B3) general linear models used to analyze female pink salmon reproductive success, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-017-A2.