Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores)

Andrew P. Hendry, Ole K. Berg and Thomas P. Quinn

Breeding location choice provides a mechanism by which individuals can directly influence their reproductive success. Location choice should therefore reflect individual condition, habitat features, and the intensity of competition; with these factors then influencing reproductive success. To test whether such patterns were detectable in the wild, we tagged 705 sockeye salmon (*Oncorhynchus nerka*) in a natural population, and monitored them from when they started breeding until they died. We evaluated the role of individual condition (size, secondary sexual traits, energy stores) in the acquisition of breeding locations that differed in the intensity of competition (female density, sex ratio) and habitat features (water depth, water velocity). We then evaluated the influence of breeding location on reproductive life span and energy stores. At a coarse level (20-m stream sections), females consistently settled in certain locations, and these locations sustained high densities and held larger females. At a fine scale (0.5-m breeding sites), (1) larger fish occupied deeper water (males, $r^2 = 0.072$; females, $r^2 = 0.199$), (2) higher levels of competition reduced reproductive life span for males ($r^2 = 0.139$) but not females, and (3) fish with shorter reproductive life spans died with more energy remaining in their muscle tissue (males, $r^2 = 0.414$; females, $r^2 = 0.440$). These patterns were nested within a tendency for late breeding fish to have shorter reproductive life spans. Energy stores and secondary sexual traits did not influence breeding location choice, and larger fish did not acquire locations of higher intrinsic quality (i.e., those sections settled first and sustaining higher competition). Our study provides evidence that some aspects of individual condition influence breeding location choice, which then influences components of reproductive success.

A. P. Hendry, O. K. Berg and T. P. Quinn, School of Aquatic and Fishery Sciences, Univ. of Washington, Box 355020, Seattle, WA 98195, USA (present addresses: APH: Organismic and Evolutionary Biology Program, Univ. of Massachusetts, Amherst, MA 01003-5810, USA [ahendry@bio.umass.edu]; OKB: Dept of Zoology, Norwegian Univ. of Science and Technology, NTNU, N-7491 Trondheim, Norway).

Animal breeding systems are often characterized by intense intra-sexual competition for breeding locations or mates (Emlen and Oring 1977, Kvarnemo and Ahnesjö 1996, Reynolds 1996). Within such systems, lifetime reproductive success can be influenced by the intrinsic quality of breeding sites, the intensity of competition, competitive ability, and reproductive life span (Clutton-Brock 1988). We studied the causes and consequences of breeding location choice in relation to these factors within a population of sockeye salmon (*Oncorhynchus nerka*). The sockeye salmon breeding system is characterized by competition among females for nest sites, and among males for access to females (Hanson and Smith 1967, Foote 1990, Quinn and Foote 1994, Quinn 1999). Breeding takes place without feeding (capital breeding) and all fish die within weeks of when they start breeding (semelparity).

Breeding location choice allows individual animals to directly influence their reproductive success (Clutton-Brock 1988). If location choice is adaptive, several patterns should be detectable in natural populations. First, individuals should select locations that balance intrinsic habitat quality against the cost of competition (Fretwell and Lucas 1970, Conradt et al. 1999) or the risk of predation (Sih 1994, Candolin and Voigt 1998). Second, breeding location choice should be influenced by individual condition because condition influences competitive ability, and because different phenotypes may be best suited for different habitats (Lugli et al. 1992, Kvarnemo 1995). Third, individual condition, habitat features, and competition should influence components of reproductive success (Côté and Hunte 1989, Huhta et al. 1998). We investigated the role of individual condition (size, secondary sexual traits, energy stores) in the choice of fish among breeding locations that differed in habitat features (water depth and velocity) and the intensity of competition (female density or sex ratio). We then investigated the consequences of breeding location for reproductive life span (from the start of breeding until death) and energy stores.

The ability to characterize breeding locations and understand factors influencing their choice depends on spatial scale (Orians and Wittenberger 1991, Huhta et al. 1998). Many animals breed in their natal area, select a general "patch" (macrohabitat) within that area, and a specific "site" (microhabitat) within that patch. This hierarchy of spatial scales is relevant for sockeye salmon because they return to their natal area for breeding (Quinn et al. 1999), form discrete breeding aggregations within the natal area (Hendry et al. 1995), and select specific nest sites and mates within the breeding aggregation (Foote 1990, Quinn and Foote 1994). Because the causes and consequences of location choice may vary among these levels, we conducted our investigation at two spatial scales (20-m stream sections and 0.5-m breeding sites).

Predictions

1. Body size should influence the choice of breeding locations that differ in water depth or velocity. First, shallow water may be inaccessible to large salmon and may increase susceptibility to predation (Quinn and Kinnison 1999). Second, large salmon are more powerful swimmers (Brett 1995), and are better able to dig nests in the larger gravel found in fast water (Kondolf and Wolman 1993). Third, large females dig deeper nests (Steen and Quinn 1999), which are less susceptible to gravel scour in fast water. We predicted that large males and females would occupy deeper or faster water.

2. Locations of high intrinsic quality (i.e., ignoring any cost of competition) should be chosen first and sustain higher levels of competition. For female salmon such locations provide better habitat for breeding or egg incubation (Hoopes 1972, Foote 1990). For male salmon they provide better breeding habitat, or access to more or larger females (Fleming and Gross 1994, Quinn and Foote 1994, Quinn et al. 1996). More competitive individuals should be better able to occupy high-quality sites. Competitive ability in salmon is determined by prior residence and body size (Schroder 1981, Foote 1990), secondary sexual traits (Quinn and Foote 1994), and perhaps vigor or energy stores. We predicted that salmon settling in sites of high intrinsic quality (i.e., those settled first and sustaining higher competition) would be larger, or would have larger secondary sexual traits or more energy.

3. The strongest determinant of reproductive life span for senescing sockeye salmon is breeding date: early breeding fish live longer than late breeding fish (McPhee and Quinn 1998, Hendry et al. 1999). In the present paper we were interested in how other factors influence life span, making it critical to control for breeding date. We also wanted to determine if the effects of breeding date on life span persist when the analysis is extended to include all fish in the population (e.g., including those that died of predation). We predicted that early-breeding fish would live longer even in this more inclusive analysis.

4. Higher levels of competition increase the number and intensity of aggressive encounters (Quinn et al. 1996, Quinn 1999; but see Quinn and McPhee 1998). Because increased aggression increases energy expenditure and the possibility of injury, higher levels of competition may decrease reproductive life span (e.g., van den Berghe and Gross 1986). Energy stores at the start of breeding might also influence life span. We predicted that higher levels of competition, or lower pre-breeding energy stores, would shorten the reproductive life span of sockeye salmon.

5. Salmon that do not perish from stranding or predation probably die because of insufficient energy (Brett 1995). Energy stores at death nevertheless vary among individuals (Hendry and Berg 1999), indicating some can live with less energy. One factor suggesting that energy at death may be aggressive encounters that cause injuries, and therefore accelerate senescence or increase susceptibility to disease. We predicted that greater somatic energy stores would be found in dead fish that had shorter life spans (because they died of something other than energy depletion) or those experiencing higher levels of competition (because this would increase energy use).

Methods

Over two summers (1995 and 1996), we captured 705 pre-breeding adult sockeye salmon from a lagoon at the

mouth of Pick Creek, Alaska (59° 33′ 00″ N, 159° 04′ 18″ W; Hendry et al. 1999; for a map see Hendry and Berg 1999). Each fish was anaesthetized (MS222), measured for length, weighed, photographed, and tagged with a highly visible, individually coded 3-cm disk tag. Capture and tagging procedures were standard for salmon and do not interfere with subsequent breeding (Hendry et al. 1999).

Breeding date, reproductive life span, and competition

The entire length of Pick Creek (about 2 km) was marked off into sequential sections. In 1995, we established 97 sections, each 20 m in length, reflecting the approximate length of habitat-specific breeding aggregations. In 1996, 94 sections were established based on distinct habitat types (pool, riffle, glide). These sections averaged 23.1 m in length (SD = 5.2 m). Once breeding began, the number of males and females in each section was counted daily until 23 August 1995 and 26 August 1996. Surveys were not conducted on two days in 1995 and six days in 1996 (Hendry et al. 1999). For these days, the number of fish in each section was estimated as the average of the immediately preceding and subsequent days. This was justified because of the consistent trends from one day to the next (Fig. 1). The density of fish was occasionally too high to accurately count males and females separately. When this occurred, both sexes were counted together and the total was multiplied by the average proportion of each sex in

that section on the preceding and subsequent days. Near the end of the season, the total breeding area within each stream section was measured. Daily densities for males and females were calculated for each section as the number of fish on that day divided by the total breeding area.

Each tagged fish's location (stream section) was determined daily by observation with binoculars (Hendry et al. 1999). The first day a fish was observed in Pick Creek was considered the onset of breeding by that individual ("breeding date", Hendry et al. 1999). Reproductive life span was calculated as the difference between the date each fish entered the stream and the last date it was observed alive. Hendry et al. (1999) analyzed reproductive life span for fish that died of senescence. Here we include all fish that entered the creek, were observed to participate in breeding, and for which the relevant variables were measured.

Daily surveys were used to determine the location and date each tagged fish settled (after which it remained for at least 4 d). Daily densities of fish in each section were then used to determine the intensity of competition where and when each fish settled ("initial competition"). Our measure of competition for tagged females was the density of other females in that section (e.g., McPhee and Quinn 1998), and for tagged males was the sex ratio in that section (male density divided by female density; e.g., Mathisen 1962). Daily levels of competition experienced by each fish were averaged over its entire life span to estimate "life-time competition".
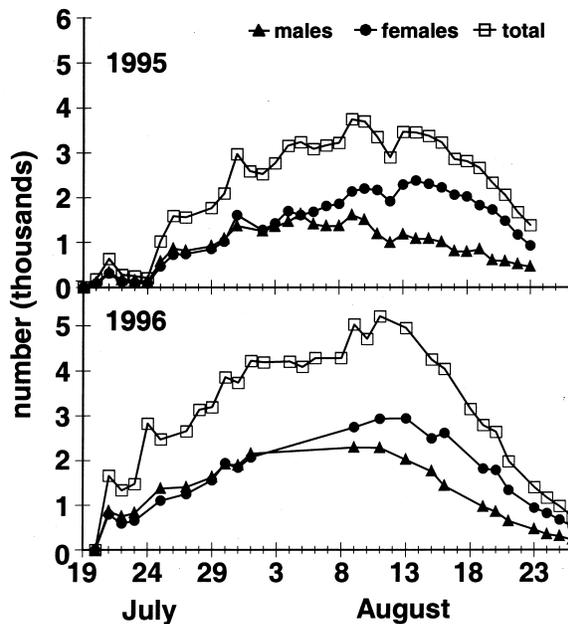
Habitat

Coarse-scale habitat variation was based on average values for stream sections. In 1995 and 1996, water temperature and dissolved oxygen were measured once in each section using an Oxyguard Handy Probe (Point Four Systems, Inc.), and water temperature was recorded every 36 min in three sections (1940 m, 1160 m, and 280 m upstream from the lake) using automatic temperature loggers (Hobo Logger, Onset Computer Corp.). In 1995, geometric mean gravel size was determined for 10 stream sections by measuring the median diameter of 100 randomly selected rocks ("pebble count", Kondolf and Li 1992). In 1998, we used detailed maps to locate the positions of all 1995 and 1996 sections, which was possible because the creek is stable between years owing to ground water inputs and a very small drainage area (11.7 km²). At the center of each section, we measured the width of the wetted channel, and water depth and velocity at five equidistant points across the channel. Water velocity was recorded at a height of 0.4 times the water depth using a current velocity meter (Model 2100, Swoffer Instruments, Inc.). The five measurements were averaged for each section.

Fig. 1. Daily counts of sockeye salmon in Pick Creek during the breeding season.

Fine-scale habitat variation was based on locations occupied by individual tagged fish (within 0.5 m). Each fish was located by observation from the stream bank, and water depth and velocity were measured at that location. These measurements were made on 22–25 July ($N = 34$), 28–30 July ($N = 80$), and 9 August ($N = 94$) in 1995; and on 25 July ($N = 114$), 2 August ($N = 163$), 12 August ($N = 111$), and 19 August ($N = 85$) in 1996. Depths and velocities were averaged across days when individual fish had measurements on multiple days. Further details are provided in Hendry (1998: 135).

Body size and shape

At tagging, all fish were measured for length using calipers (middle of eye to end of hypural plate, mm), weighed (g), and photographed (color positive film, 35-mm lens). The camera was mounted on a tripod 120 cm directly above each fish, and a standard ruler was placed in each photography. The slides were projected using a 35-mm lens to a size of 30×40 cm and an Ikegami CCD camera (Model ICD-200) was used to transfer the image to a Matrox PIP512 frame-grabber. Optimas (V. 3.01) was used to digitize landmarks delineating body depth (anterior insertion of dorsal fin to bottom of abdomen, perpendicular to lateral line), snout length (tip of upper jaw to middle of eye), adipose fin length (anterior insertion to posterior margin), and caudal peduncle depth (at its shallowest point). Computed distances between landmarks were adjusted to actual trait sizes (mm) using the standard ruler in each photograph. Variation owing to state of maturity was minimized by only analyzing fish photographed within 6 d of when they started breeding (i.e., first observed in creek). These methods produce measurements highly correlated with those obtained using calipers (Hendry 1998: 65).

Analysis of covariance (ANCOVA) and linear regressions were used to remove effects of body size from morphological measurements. ANCOVA confirmed homogeneity of slopes between years, within each sex, for relationships between each trait and body length ($\log_{10}$ throughout). Linear regressions of each trait on length (by sex and year) were used to calculate residual trait sizes ("first-order residuals"). ANCOVA then confirmed homogeneity of slopes between years, within each sex, for relationships between first-order residuals (i.e., "trait-at-length") and first-order residuals from the body length/mass regression (i.e., "mass-at-length"). Linear regressions of each trait-at-length on mass-at-length (by sex and year) were then used to again calculate residual trait sizes ("second-order residuals"). For more details and complete ANCOVA and regression statistics see Hendry (1998: 83–84).

Second-order residuals were analyzed using principal components (years pooled) in order to develop a few variables that best summarized the morphological variation. Factors were extracted using the correlation matrix and were not rotated. Factor scores were determined for each fish using the regression method (SPSS, V. 7.5). The first factor extracted for females had positive loadings for body depth (0.705) and caudal peduncle depth (0.394), but negative loadings for snout length (-0.643) and adipose fin length (-0.420). To combine only positively covarying traits, the first two traits were analyzed separately from the second two traits, extracting a "secondary sexual" factor (loadings of 0.743 for each trait, 55.2% of the variation) and a "depth/caudal" factor (loadings of 0.749 for each trait, 56.2% of the variation). For males, a single "secondary sexual" factor was extracted. Factor loadings were 0.454 (body depth), 0.619 (snout length), 0.651 (caudal peduncle depth), and 0.553 (adipose fin length), accounting for 33.0% of the variation. Although principal components explained only a moderate amount of the variation, it is important to remember that all effects of size were first removed from the traits.

Energy

We estimated energy stores at the start of breeding using a small piece of muscle tissue removed from the dorsal hump (just anterior to the dorsal fin insertion) of a subset of the fish at tagging (79 males and 71 females in 1995; 98 males and 124 females in 1996). These "muscle cores" (average wet mass = 0.47 g, SD = 0.22) were extracted with an 8-mm-diameter coring instrument (Miltex 33-28) used for non-lethal sampling of muscle tissue from large salmonids (Crawford et al. 1977). This procedure did not affect reproductive life span in our study (A. Hendry unpubl.). We then estimated energy stores at death by collecting freshly-dead tagged fish from the stream and dissecting a piece of skeletal muscle (excluding the skin), from the left side of the hump just anterior to the dorsal fin ("muscle sample"; e.g., Hendry and Berg 1999).

To determine % dry mass ($100 \cdot$ dry mass/wet mass), all muscle cores and samples were dried for 24 h at 105°C. To determine mass-specific energy (kJ g^{-1} wet mass) a subset of the 1995 muscle samples ($N = 68$) and muscle cores ($N = 21$) were then burned at 30 atmospheres of oxygen in a bomb calorimeter (Model 1341, Parr Instruments). The % dry mass of muscle cores was a good predictor of mass-specific energy determined using calorimetry (linear regression: females, $r^2 = 0.485$, $F_{1,11} = 9.43$, $P = 0.012$; males, $r^2 = 0.823$, $F_{1,6} = 27.99$, $P = 0.002$). The % dry mass of muscle samples was an excellent predictor of (1) mass-specific energy determined using calorimetry (linear regression: females, $r^2 = 0.942$, $F_{1,59} = 937.2$, $P < 0.001$; males, $r^2 = 0.913$,

$F_{1,8} = 73.40$, $P < 0.001$), and (2) mass-specific energy in the entire somatic tissue as previously determined using proximate analysis by Hendry and Berg (1999) (linear regression: females, $r^2 = 0.956$, $F_{1,27} = 9.43$, $P < 0.001$; males, $r^2 = 0.948$, $F_{1,24} = 9.43$, $P < 0.001$).

Analytical approach and statistics

We first examined coarse-scale variation (i.e., among stream sections). We determined (1) the date when females first settled within a section (the first day after which female density remained higher than one per 20 m²), and (2) the average density of females in each section during peak breeding ("peak density", 5–8 Aug.). This time interval was chosen because it was when the most females would be actively and effectively defending their nests (although absolute densities were higher later, early arrivals were becoming senescent). Seventeen stream sections were occupied on the first day of settling in 1996, and on the first three days of settling in 1995. We considered these sections to be those "settled first". All other sections were considered "not settled first", and included sections "settled later" and sections "never settled". We compared peak density, stream width, water depth and velocity, and the mean length of males and females (based on tagged fish in these sections) among these categories. We also used linear regressions to test whether female density in settled sections during peak breeding was related to mean gravel size, water depth or velocity, or distance from the creek mouth.

We next examined fine-scale variation (i.e., individual tagged fish). Step-wise multiple regressions (years pooled; $P < 0.05$ for entry, $P < 0.10$ for removal; SPSS, V. 7.5) were used to investigate the relative importance of predicted relationships within the context of other potential causal factors. Energy data were available for only a subset of the fish, and so two sets of regressions were performed, one for predictions not relating to energy content and another for predictions relating to energy content. Only fish that died of senescence were used when analyzing energy at death. Path diagrams (Kingsolver and Schemske 1991, Sokal and Rohlf 1995) were used to illustrate the relative importance of various factors influencing reproductive life span. Note that path coefficients do not exactly match partial regression coefficients from regression analyses because the path models were built using a consistent set of individuals, whereas the different regressions used different subsets of fish. For the presentation of fine scale analyses, and in the Discussion, r^2 values and levels of significance are for partial coefficients of determination in multiple regression models (i.e., all other significant variables included in the model). Other statistics appear in the tables.

Results

Breeding distribution and habitat variation

The first sockeye salmon entered Pick Creek on 20 July in 1995, and on 21 July in 1996. The number of live fish in the creek then increased over the next 20–21 d (Fig. 1). The sex ratio was approximately 1:1 for the first 16 d, after which it was skewed toward females (Fig. 1). The distribution and density of breeding salmon was roughly similar between years but varied both spatially and temporally within years (Fig. 2). Stream sections settled first in 1995 and 1996 (and 1997, pers. obs.) showed strong correspondence. These sections attained higher densities of females early in the season (Fig. 3), and sustained higher densities during peak breeding (Table 1).

Water depth, velocity, temperature, gravel size, and dissolved oxygen showed only minor spatial and temporal variation among sections (Table 1; below). No areas within the stream showed temperature anomalies and dissolved oxygen was high throughout (> 95% saturation). Water temperature fluctuated daily by up to 7.7°C (average fluctuation = 3.7°C) but average temperature was consistent across days (SD = 0.6°C), and showed no temporal trend (e.g., average temperature 20 m upstream of the lake vs. date in 1995, linear regression: $r^2 = 0.01$, $F_{1,35} = 0.22$, $P = 0.64$). The arithmetic mean across sections of geometric mean gravel size was 11.78 mm (SD = 2.24 mm).

Coarse scale analysis: among stream sections

The stream sections settled first by females were not distinct with respect to width, depth, velocity, or gravel size (Table 1). Although females seemed to avoid shallow and slow water, particularly in 1995 (Fig. 4), this pattern was not statistically significant (Table 1). Our sample sizes may have been too small (17 sections settled first) to detect a weak tendency for females to avoid shallow water (i.e., moderate effect size but low power, Table 1). Females in sections settled first were larger than females in sections settled later but male length did not differ between these categories (although observed power was low, Table 2). Female density during peak breeding was higher in sections settled first than in sections settled later (Table 1, Fig. 3).

Female density in stream sections during peak breeding (5–8 Aug.) was not correlated with geometric mean gravel size (1995, $r^2 = 0.089$, $F_{1,9} = 0.78$, $P = 0.403$), water depth (1995, $r^2 = 0.012$, $F_{1,85} = 1.07$, $P = 0.304$; 1996, $r^2 = 0.005$, $F_{1,82} = 0.42$, $P = 0.517$), or water velocity (1995, $r^2 = 0.033$, $F_{1,85} = 2.89$, $P = 0.093$; 1996, $r^2 = 0.033$, $F_{1,82} = 2.79$, $P = 0.099$). Although peak densities were higher in sections closer to the lake (1995, $r^2 = 0.047$, $F_{1,85} = 4.19$, $P = 0.044$; 1996, $r^2 = 0.213$,
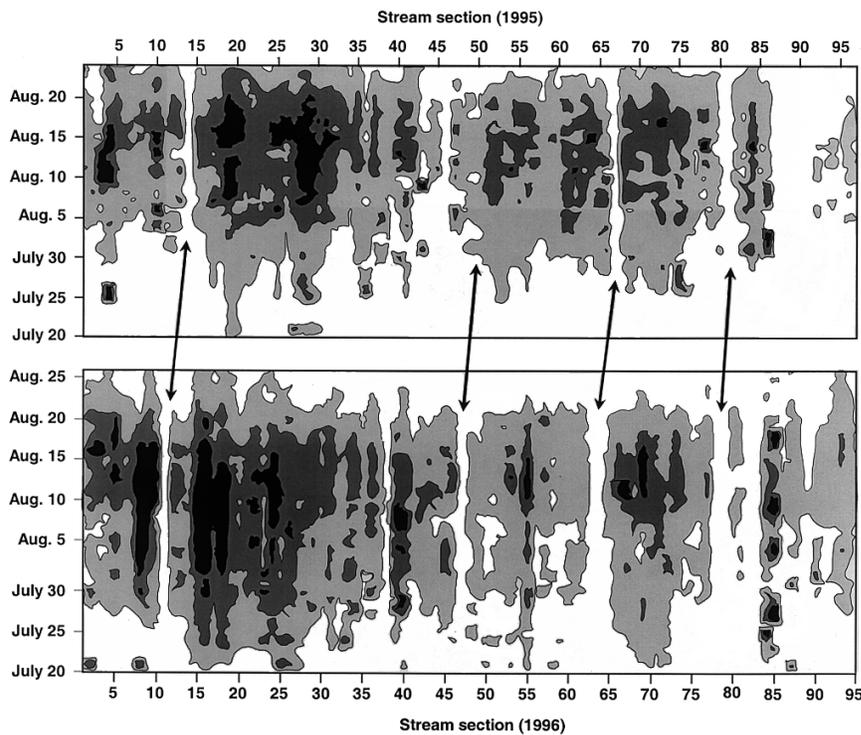
Fig. 2. Temporal and spatial distribution of females breeding in Pick Creek. Light shading indicates the presence of 1–2 females per 10 m², medium shading indicates 2–3 females per 10 m², and dark shading indicates > 3 females per 10 m². Stream sections were not established at identical locations in the two years. Arrows indicate how four of the sections corresponded between years.

$F_{1,82} = 22.17$, $P < 0.001$), settlement did not proceed sequentially upstream (e.g., the 17 sections settled on the first day in 1995, numbered upstream from the lake, were 17, 19–25, 28–29, 36, 41, 52–54, 58, and 73).

Fine scale analysis: breeding sites of tagged fish

Regression models explained 23% of the variation in the water depth occupied by breeding females, and 12.1% of the variation for males (Table 3). Our prediction that larger fish would occupy deeper water was supported (females, $r^2 = 0.149$, $P < 0.001$; males, $r^2 = 0.086$, $P < 0.001$). Breeding date was the next most important predictive variable for both sexes: late breeding fish occupied shallower water (Table 3). Our prediction that larger fish would occupy faster water was not supported (Table 3): no effect for females ($r^2 < 0.001$, $P = 0.980$) and a slight negative effect for males ($r^2 = 0.024$, $P = 0.049$). (Water depth and velocity measurements for tagged fish were not correlated: Pearson's; females, $r = 0.034$, $P = 0.606$; males, $r = -0.088$, $P = 0.242$.) Based on tagged fish whose habitat was measured on more than one day, individual males experienced more temporal variation than did females for water depth (SD = 11.4 vs 8.3 cm, two-tailed t test: $t_{141} = 2.51$, $P = 0.021$) but not water velocity (SD = 9.4 vs 7.5 cm s^{-1}, two-tailed t test: $t_{139} = 1.62$, $P = 0.107$). Water depth averaged 11.4 cm shallower on the second

of subsequent samples for males, indicating that individuals moved into shallower water later in life (the creek did not appear to decrease in average depth through the breeding season).

Regression models had varying degrees of success in explaining variation in breeding site choice with respect to initial competition (female density for females, sex ratio for males). More of the variation could be explained for females than for males (25.0% vs 6.2%; Table 3), and breeding date had the strongest effect for both sexes: late-breeding females settled in sections of higher density and late-breeding males settled in sections of lower sex ratio. Our prediction that larger fish would settle in sections of higher competition was not supported: no effect for males ($r^2 < 0.001$, $P = 0.924$) and a negative effect for females ($r^2 = 0.020$, $P = 0.028$). The level of competition where fish settled was also independent of secondary sexual traits and energy stores (Tables 3, 4).

Fine scale analysis: reproductive life span of tagged fish

Regression models explained 49.5% of the variation in reproductive life span for females and 29.1% for males (Table 3). The previously demonstrated tendency for early-breeding fish to live longer than late-breeding fish (Hendry et al. 1999) held true for the more inclusive data set used here (females, $r^2 = 0.328$, $P < 0.001$;
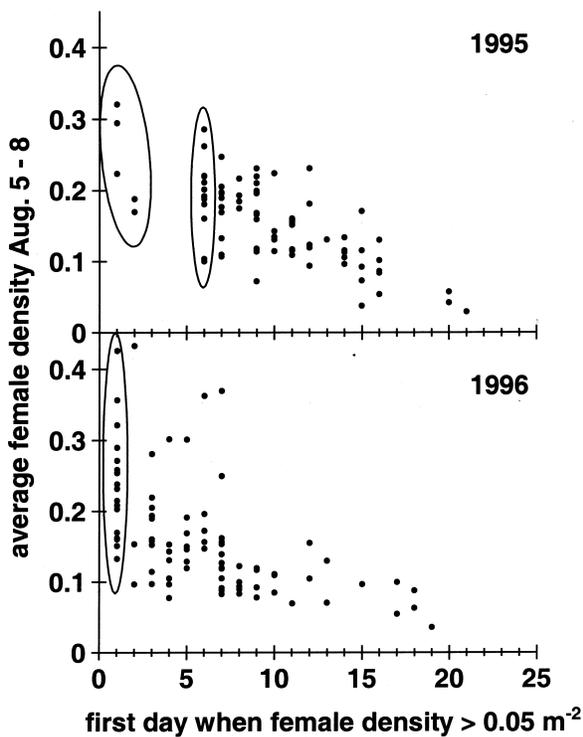
412

Fig. 3. Relationship between the date that females first settled in a stream section (a density of 1.0 females per 20 m² maintained thereafter), and the average density of females in that section during the peak of breeding (5–8 Aug.). Ellipses indicate the first 17 sections settled by females in each year.

males, $r^2 = 0.410$, $P < 0.001$). (The partial r^2 for males is higher than the overall R^2 in Table 3 because of negative covariance between breeding date and sex ratio when both are in the model.) Our prediction that fish experiencing higher levels of competition would have shorter life spans was supported for males ($r^2 = 0.210$, $P < 0.001$) but not females ($r^2 = 0.002$, $P = 0.535$).

Path models and standardized path coefficients (p) illustrated how reproductive life span may be influenced by breeding date directly, and indirectly through other factors. For females, the total negative effect of breeding date on life span ($p = -0.640$) was mostly attributable to direct effects ($p = -0.573$) but also to a slight negative indirect effect ($p = -0.067$): late-breeding females were smaller than early-breeding females, and smaller females did not live as long as larger females (Fig. 5). For males, the total negative effect of breeding date on life span ($p = -0.369$) was attributable to a strong direct negative effect ($p = -0.701$), a moderate indirect positive effect acting through competition ($p = 0.295$, but see Discussion), and a weak indirect positive effect acting through water depth ($p = 0.042$).

Fine scale analysis: energy stores of tagged fish

Our prediction that individuals with greater energy stores would settle in areas of higher competition was not supported: % dry mass of muscle cores was not correlated with initial female density for females ($r^2 = 0.003$, $P = 0.660$), or with initial sex ratio for males ($r^2 = 0.010$, $P = 0.349$). Our prediction that individuals with greater energy stores at the start of breeding would live longer was also not supported: no effect for females

Table 1. Comparison of stream sections (mean $\pm$ SD) settled first by females, settled later, and never settled, with their combined total (i.e., available habitat).

	N[5]	Density of females[1]	Stream width (m)	Water depth (cm)	Velocity (cm s^{-1})
1995					
Total	96	–	7.8 ± 2.6	32.7 ± 16.8	0.226 ± 0.137
Settled first	17	2.07 ± 0.60	7.6 ± 2.6	33.8 ± 14.7	0.248 ± 0.124
Settled later	70	1.43 ± 0.52	7.8 ± 2.6	33.6 ± 17.6	0.219 ± 0.141
Never settled	9	–	7.6 ± 3.1	23.1 ± 12.1	0.231 ± 0.140
Levene's[2]: F (P)		0.02 (0.895)	1.42 (0.237)	1.95 (0.166)	1.78 (0.186)
ANOVA[3]: F (P)		19.6 (<0.001)	0.07 (0.94)	1.62 (0.20)	0.32 (0.73)
ANOVA: Power		–	0.06	0.34	0.10
K-S[4]: Z (P)		1.83 (0.002)	0.70 (0.709)	1.04 (0.228)	0.098 (0.292)
1996					
Total	93	–	7.7 ± 2.7	33.8 ± 17.6	0.212 ± 0.130
Settled first	17	2.39 ± 0.79	8.0 ± 3.2	37.9 ± 18.8	0.225 ± 0.110
Settled later	69	1.44 ± 0.76	7.7 ± 2.6	33.4 ± 18.5	0.211 ± 0.132
Never settled	7	–	7.2 ± 3.4	26.9 ± 16.3	0.200 ± 0.178
Levene's[2]: F (P)		0.25 (0.618)	0.05 (0.831)	0.01 (0.985)	0.37 (0.546)
ANOVA[3]: F (P)		21.1 (<0.001)	0.27 (0.77)	0.93 (0.40)	0.11 (0.89)
ANOVA: Power		–	0.091	0.207	0.067
K-S[4]: Z (P)		2.40 (<0.001)	0.70 (0.705)	0.77 (0.596)	0.80 (0.547)

[1] Number of females per 10 m² (mean $\pm$ SD) during peak breeding (5–8 Aug.).
[2] Comparison of variance using Levene's test (P values in parentheses).
[3] Comparison of means using single factor ANOVA with fixed effects (P values in parentheses).
[4] Comparison of cumulative distributions using Kolmogorov-Smirnov tests (P values in parentheses).
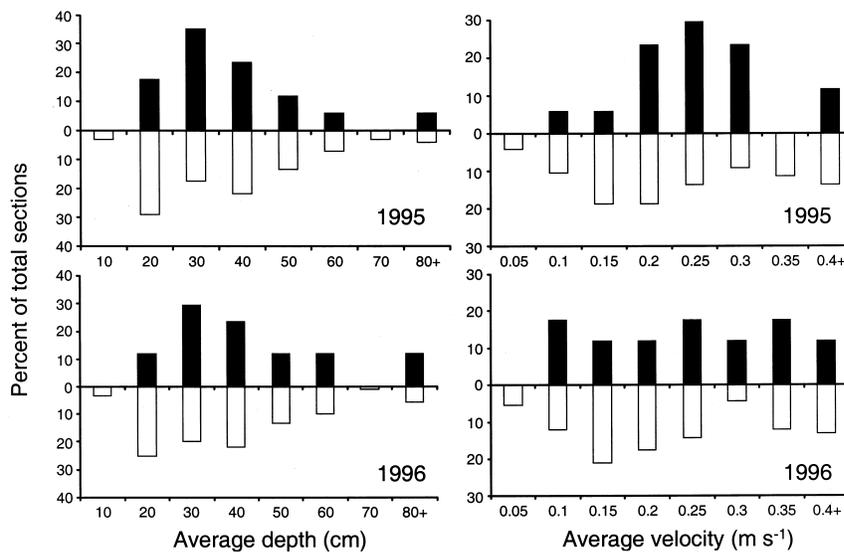[5] One section was excluded each year because it was too deep for accurate observations.

Fig. 4. Comparison of water depth and velocity in Pick Creek stream sections available for breeding (light bars) and the first 17 sections settled by females (dark bars).

Table 2. Comparison of the body length of tagged males and females (presented as anti-logged means) in the first 17 sections to be settled by females vs those settled later.

	Females		Males	
	N	Length (mm)	N	Length (mm)
1995				
Settled first	42	498.9	36	508.2
Settled later	52	490.9	49	503.5
1996				
Settled first	44	457.1	45	487.5
Settled later	110	449.8	96	475.3
ANOVA results[1]				
Year: F (P)	167954.0 (0.002)		31.5 (0.112)	
Settling category: F (P)	5939.8 (0.008)		3.9 (0.298)	
Interaction: F (P)	0.001 (0.981)		0.75 (0.388)	
Power[2]	–		0.124	

[1] Comparison of mean body length between the settling categories using two-factor ANOVA (settling category fixed, year random), with P values in parentheses.
[2] Observed power of the test for differences between settling categories in ANOVA.

$(r^2 = 0.034,\ P = 0.167)$ and a negative effect for males $(r^2 = 0.130,\ P = 0.011)$. In contrast, regression models predicting muscle energy stores at death explained as much as 66.9% of the variation for females and 41.4% for males (Table 4). Our prediction that longer-lived fish would die with less energy in their muscle tissue was strongly supported (males, $r^2 = 0.414$, $P < 0.001$; females, $r^2 = 0.447$; $P < 0.001$). Energy stores at the start of breeding did not influence energy stores at death (males, $r^2 = 0.110$, $P = 0.105$; females, $r^2 = 0.005$, $P = 0.660$).

Discussion

1. Larger fish occupy deeper water

Our ability to detect associations between habitat features and the physical traits of fish, or their choice of breeding locations, depended on spatial scale. At a coarse scale (20-m stream sections), the size of fish did not seem to correlate with their choice of particular habitat features. Although specific sections were consistently settled first and attained higher densities (two measures of preference), and were occupied by larger females, these sections were not deeper or faster than the other sections. At this spatial scale, limited habitat variation and high breeding densities may have compelled females to use most of the available habitat, thereby obscuring relationships between habitat features, body size, and female preference. Similarly, Hoopes (1972) found little influence of water depth or velocity on breeding density in another sockeye salmon population. Systems where female distribution is related to depth or velocity typically have heterogeneous habitat and few spawners (e.g., Knapp and Preisler 1999).

414

Table 3. Stepwise multiple regression results for tests of specific hypotheses not relating to energy stores (coefficients of determination for the full model at each step are outside the brackets, partial t-statistics for each entering variable are inside the brackets). NS: independent variables that were not significant. NT: independent variables not tested in a given model.

Model		Independent variables[1]			
Females	N[5]	Breeding date	Body length	BD/CPD[4]	Velocity
Water depth	191	0.230 (−2.7[b])	0.199 (6.9[c])	NS	NT
Water velocity	191	NS	NS	NS	NT
Initial competition[2]	203	0.232 (7.8[c])	0.250 (−2.2[a])	NS	NT
Life span	187	0.404 (−11.2[c])	0.441 (3.5[b])	0.473 (−3.3[b])	0.495 (−2.8[b])
Males	N	Breeding date	Body length	Lifetime competition[3]	Water depth
Water depth	167	0.121 (−3.0[b])	0.072 (3.6[c])	NT	NT
Water velocity	165	NS	0.024 (−2.0[a])	NT	NT
Initial competition[2]	196	0.062 (−3.6[c])	NS	NT	NT
Life span	163	0.124 (−4.8[c])	NS	0.263 (−5.5[c])	0.291 (−2.5[a])

[1] Order of entry of independent variables into a model can be inferred from the order of increasing R^2 values. Additional non-significant independent variables tested in all models were mass-at-length and secondary sexual trait size. Additional non-significant variables in the life span models were water depth (both sexes), water velocity (males), and life time competition (females).
[2] Competition where and when a fish initially settled: female density for females, sex ratio for males.
[3] Competition averaged over the fish's entire life: female density for females, sex ratio for males.
[4] Factor scores from principal components analysis summarizing variation in body depth and caudal peduncle depth.
[5] Samples sizes vary because not all variables were measured for all fish.
[a] $P<0.05$, [b] $P<0.01$, [c] $P<0.001$.

At a fine scale (0.5-m breeding sites), larger fish occupied deeper water (males, $r^2 = 0.086$; females, $r^2 = 0.149$) but not faster water (males, $r^2 = 0.024$; females, $r^2 < 0.001$). The large amount of unexplained variation in these models (Table 3) may stem from unmeasured factors that influence breeding site choice. Females may respond to site-specific cues that indicate a high-quality incubation environment for embryos but which may not correlate with water depth or velocity. Females may also balance the intrinsic quality of a site against the cost of competition for that site. For males, a balance between the abundance of ripe females and male competition may be more important than specific habitat features (Quinn et al. 1996). The lower predictive ability of habitat models for male size than female size may stem from greater independence of males from habitat features, and their tendency to move among females and locations during the breeding season (Hanson and Smith 1967, Quinn et al. 1996).

2. Competitively superior fish do not settle where competition is higher

Sockeye salmon entering Pick Creek encounter an array of stream sections differing in the level of competition

Table 4. Stepwise multiple regression results for tests of specific hypotheses relating to energy stores (coefficients of determination for the full model at each step are outside the brackets, partial t-statistics for each entering variable are inside the brackets). NS and NT as for Table 3.

Model		Independent variables[1]			
Females	N[5]	Breeding date	Body length	Velocity	BD/CPD[4]
Initial competition[2]	77	0.235 (4.8[c])	NS	NT	NS
Life span	62	0.483 (−7.5[c])	0.557 (3.1[b])	0.625 (−3.3[b])	0.659 (−2.4[a])
Males		Breeding date	Lifetime completion[3]	Energy entry	Body length
Initial competition[2]	84	NS	NT	NS	NS
Life span	37	0.225 (−3.2[b])	0.356 (−2.6[a])	0.471 (−2.7[a])	NS
Energy at death		Life span	Mass/length[7]	SSC[8]	BD/CPD[4]
Females[6]	46	0.440 (−5.9[c])	0.536 (3.0[b])	0.587 (−2.3[a])	0.630 (−2.2[a])
Males	26	0.414 (−4.2[c])	NS	NS	NS

[1] Order of entry of independent variables into a model can be inferred from the order of increasing R^2 values. These results should not be used to infer significance of hypotheses tested in Table 3 because the results reported here are only for the subset of fish for which energy data were available. Additional non-significant independent variables were mass-at-length and secondary sexual trait size (Initial competition and Life span models; both sexes), energy at entry (Initial competition and Life span models; females), water depth (Life span models; both sexes), and water velocity (Life span model; males), and Lifetime competition (Energy at death models; both sexes).
[2–5] as for Table 3.
[6] A fifth variable entering the model for female energy at death was the intensity of competition ($R^2 = 0.669$, $t = −2.2$[a]).
[7] Residuals from log10 body length vs log 10 mass relationships (i.e., mass-at-length).
[8] Factor scores from principal components analysis summarizing variation in secondary sexual traits (see Methods).
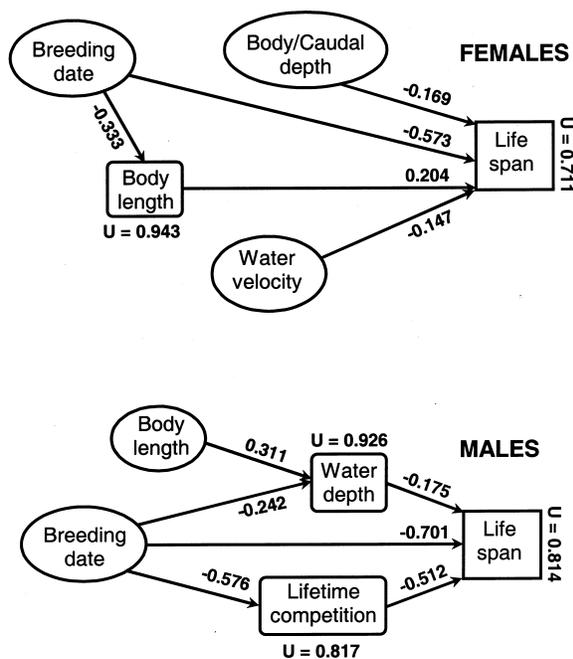[a] $P<0.05$, [b] $P<0.01$, [c] $P<0.001$.

Fig. 5. Path models illustrating how breeding date and other factors directly and indirectly influence reproductive life span. Models were built using variables found significant in stepwise regressions (Table 3). In path models, dependent variables are called "criterion" variables and independent variables are called "predictor" variables. Ellipses signify predictor variables, rounded rectangles signify variables acting as both predictor and criterion, and sharp rectangles signify criterion variables (life span). Arrows signify cause and effect relationships and are accompanied by path coefficients indicating the strength and direction of the association (standardized partial regression coefficients). Variation attributable to unmeasured parameters is signified for each criterion variable with a "U". The general rule for interpreting path models is: "The correlation between two variables is the sum of the products of the chains of path coefficients or correlations along all of the paths by which they are connected" (Sokal and Rohlf 1995: 637).

(Fig. 2). Sections that were settled first and attained higher levels of competition (Fig. 3) are expected to be those of higher intrinsic quality. We therefore predicted that more competitive fish would be found in these areas. At a coarse scale, this prediction seemed substantiated because the sections settled first and supporting higher densities had larger females (Table 2). This effect may, however, be an artifact of correlations with breeding date because early females settled in the first sites, these sites attained higher densities, and early females were larger. When we controlled for effects of breeding date by analyzing tagged fish, the only remaining correlation was that smaller females settled in sites of higher density (Table 3).

Why do smaller females (with presumably lower competitive ability) settle in sections with higher densities? One possibility is that these females may obtain breeding sites of low quality within those sections. This

would occur if the best sites were occupied first, and late-arriving females could not displace females already present (Foote 1990). Several lines of evidence suggest this may be important within Pick Creek. First, females occupying the sections settled first were larger and would be difficult to displace. Second, late-arriving females were smaller and tended to settle in shallower water (which would perhaps be of lower quality). Relationships among competitive ability, site quality, and intensity of competition thus depend on spatial scale and time of breeding. Disentangling these relationships will be difficult in observational field studies.

Why do males with traits conferring greater competitive ability not settle in sections with higher levels of competition (and presumably higher intrinsic quality)? For salmon, the strongest determinant of mate choice by males is female proximity to oviposition (Schroder 1981, Hamon et al. 1999), and a very important aspect of competitive ability is prior residence (intruders displace residents only when they are larger, Foote 1990). Less competitive males may settle and remain in high-quality sections, whereas more competitive males may distribute themselves across a broader area according to the proximity of individual females to oviposition. We suggest that smaller males maximize the benefits of prior residence, whereas larger males take advantage of their superior competitive ability.

3. Late-breeding fish have shorter life spans

Our previous work demonstrated that breeding date is the strongest determinant of reproductive life span for Pick Creek sockeye salmon that die of senescence: early breeders live longer than late breeders (Hendry et al. 1999). Here we tested again for this effect, after including fish that died of all causes and considering possible effects of habitat, competition, secondary sexual traits, and energy stores. The negative effect of breeding date on reproductive life span remained strong (females, $r^2 = 0.410$; males $r^2 = 0.328$), but was weaker than for senescent fish only (Hendry et al. 1999). The weaker correlation for fish that died of all causes was probably because predation has a stronger effect on truncating the life span of early fish than that of late fish (because late fish die sooner anyway), particularly for males because they experience higher predation (Quinn and Kinnison 1999).

Path models generated additional insights into possible causal effects of breeding date on reproductive life span (Fig. 5). For females, most of the negative influence of late breeding could be attributed to strong direct effects ($p = -0.573$) but also to some weak indirect effects ($p = -0.068$): late-breeding females were smaller and smaller females had shorter life spans. The additional weak negative direct effect of water velocity on life span ($p = -0.147$) may arise because

increased swimming activity increases metabolic costs (Brett 1995). For males, the direct negative effect of breeding date appeared much stronger ($p = -0.701$) than its total effect ($p = -0.364$). This occurred because breeding date seemed to have a *positive indirect* influence on life span: late breeding males experienced lower life-time sex ratios, which increased life span. This indirect effect may be spurious. Although sex ratio decreases through the breeding season (Fig. 1), the operational sex ratio (OSR) likely increases (Hendry et al. 1995, Quinn et al. 1996). OSR is probably a better surrogate than sex ratio for male-male competition, and hence late breeding fish may actually experience higher competition. If so, the actual indirect effects of breeding date on life span (through competition) will be negative rather than positive.

4. Higher levels of competition reduce life span for males but not females

After controlling for effects of breeding date, males that experienced higher levels of competition (sex ratio) did not live as long ($r^2 = 0.210$). This relationship was also evident if the analysis was restricted to fish that died of senescence ($r^2 = 0.280$). The only other study testing for an effect of competition on male life span within a natural population was for coho salmon (*O. kisutch*) in Deer Creek, WA (van den Berghe and Gross 1986). The Deer Creek study found that higher competition reduced male life span but the effect was weak ($r^2 = 0.04$) and breeding date was not considered. Increased male–male competition may reduce reproductive life span because increasing competition increases aggressive interactions (below a threshold level; Quinn et al. 1996, Quinn 1999), which should increase energy expenditure and the possibility of injury.

The level of competition experienced by females (local density) did not influence their life span. The failure to detect such a relationship in three sockeye salmon populations (Adkison 1994, McPhee and Quinn 1998; our results) contrasts with the reported decline in life span with increasing density for female coho salmon in Deer Creek (van den Berghe and Gross 1986). However, the effect for females in Deer Creek was weak ($r^2 = 0.07$) and breeding date was not considered. We could generate a similar result by ignoring breeding date and only considering fish that died of senescence: female life span becomes positively correlated with body size ($r^2 = 0.168$) and negatively correlated with density ($r^2 = 0.035$). Negative correlations between density and life span may thus arise simply because both are correlated with breeding date.

Differential effects of competition on longevity for males (negative correlation) vs. females (no correlation) may be the result of sex-specific behavior. Females establish a nest site soon after they start breeding and

remain there for the duration of their life (Foote 1990, Quinn and Foote 1994), whereas males often leave females immediately after oviposition and attempt to breed with other females (Mathisen 1962, Hanson and Smith 1967, Foote 1990). During competitive interactions, females thus have the advantage of prior residence for almost their entire reproductive life, whereas males are prior-residents only if they remain within a restricted area. This difference in territorial behavior leads to a longer period of intense competition among males than females, which might exacerbate negative effects of competition on male life span.

5. Longer life leads to lower energy stores at death

Our prediction that long-lived fish would have less energy in their muscle tissue at death was strongly supported for females ($r^2 = 0.447$) and males ($r^2 = 0.414$). The short-lived senescent fish may thus (1) be more likely to die of factors other than energy depletion, or (2) have a higher energy threshold below which death occurs. The short-lived fish within Pick Creek, and hence those with more energy at death, began breeding late in the season. Why might late-breeding fish have a higher energy threshold below which death occurs, or an increased probability of mortality owing to other causes? One possibility is that disease prevalence may increase through the breeding season, owing to increasing numbers of dead and dying salmon.

Another possibility is that because early-breeding fish experience stronger selection for longer life span, they may have evolved greater resistance to low energy stores. Restrictions on gene flow between early and late breeders (isolation-by-time), coupled with variation in selection through the breeding season, may generate adaptive temporal clines in life history traits (adaptation-by-time; Hendry et al. 1999). The strongest of these clines is the longer life span of early-breeding fish, which can be attributed in part to their greater somatic energy stores at the start of breeding (Hendry et al. 1999). Evolution of greater resilience by early-breeding fish in the face of low energy might be another adaptive mechanism by which their life span can be increased.

References

Adkison, M. D. 1994. Application of mathematical modeling to problems in salmon biology and management. – Ph.D. thesis, Univ. of Washington, Seattle, WA.

Brett, J. R. 1995. Energetics. – In: Groot, C., Margolis, L. and Clarke, W. C. (eds), Physiological ecology of Pacific salmon. UBC Press, pp. 3–68.

Candolin, U. and Voigt, H.-R. 1998. Predator-induced nest site preference: safe nests allow courtship in sticklebacks. – Anim. Behav. 56: 1205–1211.

Clutton-Brock, T. H. (ed.) 1988. Reproductive success: studies of individual variation in contrasting breeding systems. – Univ. of Chicago Press.

Conradt, L., Clutton-Brock, T. H. and Guinness, F. E. 1999. The relationship between habitat choice and lifetime reproductive success in female red deer. – Oecologia 120: 218–224.

Côté, I. M. and Hunte, W. 1989. Self-monitoring of reproductive success: nest switching in the redlip blenny (Pisces: Blenniidae). – Behav. Ecol. Sociobiol. 24: 403–408.

Crawford, B. A., Leider, S. A. and Tipping, J. M. 1977. Technique for rapidly taking samples of skeletal muscle from live adult steelhead trout. – Prog. Fish-Cult. 39: 125.

Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. – Science 197: 215–223.

Fleming, I. A. and Gross, M. R. 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: 283–314.

Fretwell, S. D. and Lucas, H. L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

Hamon, T. R., Foote, C. J. and Brown, G. S. 1999. Use of female nest characteristics in the sexual behaviour of male sockeye salmon. – J. Fish Biol. 55: 459–471.

Hanson, A. J. and Smith, H. D. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age-groups. – J. Fish. Res. Bd. Can. 24: 1955–1977.

Hendry, A. P. 1998. Reproductive energetics of Pacific salmon: strategies, tactics, and trade-offs. – Ph.D. thesis, Univ. of Washington, Seattle, WA.

Hendry, A. P. and Berg, O. K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. – Can. J. Zool. 77: 1663–1675.

Hendry, A. P., Leonetti, F. E. and Quinn, T. P. 1995. Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*). – Can. J. Zool. 73: 339–352.

Hendry, A. P., Berg, O. K. and Quinn, T. P. 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. – Oikos 85: 499–514.

Hoopes, D. T. 1972. Selection of spawning sites by sockeye salmon in small streams. – Fishery Bull. 70: 447–458.

Huhta, E., Jokimäki, J. and Rahko, P. 1998. Distribution and reproductive success of the pied flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics; the effect of scale. – Ibis 140: 214–222.

Kingsolver, J. G. and Schemske, D. W. 1991. Path analyses of selection. – Trends Ecol. Evol. 6: 276–280.

Knapp, R. A. and Preisler, H. K. 1999. Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). – Can. J. Fish. Aquat. Sci. 56: 1576–1584.

Kondolf, G. M. and Li, S. 1992. The pebble count technique for quantifying surface bed material size in instream flow studies. – Rivers 3: 80–87.

Kondolf, G. M. and Wolman, M. G. 1993. The sizes of salmonid spawning gravels. – Water Resources Res. 29: 2275–2285.

Kvarnemo, C. 1995. Size-assortative nest choice in the absence of competition in males of the sand goby, *Pomatoschistus minutus*. – Environ. Biol. Fishes 43: 233–239.

Kvarnemo, C. and Ahnesjö, I. 1996. The dynamics of operational sex ratios and competition for mates. – Trends Ecol. Evol. 11: 403–408.

Lugli, M., Bobbio, L., Torricelli, P. and Gandolfi, G. 1992. Breeding ecology and male spawning success in two hill-stream populations of the freshwater goby, *Padogobius martensi*. – Environ. Biol. Fishes 35: 37–48.

Mathisen, O. A. 1962. The effect of altered sex ratios on the spawning of red salmon. – In: Koo, T. S. Y. (ed.), Studies of Alaska red salmon. Univ. of Washington Press, pp. 141–222.

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

Orians, G. H. and Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. – Am. Nat. 137(Suppl.): 29–49.

Quinn, T. P. 1999. Variation in Pacific salmon reproductive behaviour associated with species, sex and levels of competition. – Behaviour 136: 179–204.

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

Quinn, T. P. and McPhee, M. V. 1998. Effects of senescence and density on the aggression of adult female sockeye salmon. – J. Fish. Biol. 52: 1295–1300.

Quinn, T. P. and Kinnison, M. T. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. – Oecologia 121: 273–282.

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

Quinn, T. P., Volk, E. C. and Hendry, A. P. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). – Can. J. Zool. 77: 766–775.

Reynolds, J. D. 1996. Animal breeding systems. – Trends Ecol. Evol. 11: 68–72.

Schroder, S. L. 1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. – Ph.D. thesis, Univ. of Washington, Seattle, WA.

Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behaviour. – J. Fish Biol. 45(Suppl. A): 111–130.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd ed. – W. H. Freeman & Co.

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

van den Berghe, E. P. and Gross, M. R. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). – Can. J. Zool. 64: 1482–1486.