

Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon

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

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Correlations between breeding date and the life history or energy stores of individuals might stem from a combination of two different mechanisms. The conventional view is that individual size and condition influence breeding date (i.e., condition dependence). A different view is that heritable maturation schedules allow temporally separated population components to adapt to selective regimes associated with particular breeding times (i.e., adaptation-by-time). Considering each of these hypotheses, we examined a population of sockeye salmon (*Oncorhynchus nerka*) for evidence of correlations among life history traits (age, body size, egg size, and reproductive life span), patterns of energy allocation (somatic energy stores and gonadal investment), and breeding date. Life history traits were measured for 705 individually tagged adult salmon monitored from the onset of breeding until death. Energy stores were quantified for 60 fish collected when they entered the stream and 46 fish collected at death.

Multiple regression models revealed that most of the variation could be explained by simple linear relationships among traits; older fish were larger, and larger fish had larger gonads, larger eggs, and more available energy when they started breeding. Condition dependence did not appear relevant to breeding date because fish that started breeding early were similar in size and did not have more stored energy than fish that would breed later. Similarly, adaptation-by-time had little influence on variation in body size or egg size (predicted relationships were significant but very weak). In contrast, adaptation-by-time appeared very important to variation in reproductive life span and patterns of energy allocation. Early-breeding fish lived considerably longer than late-breeding fish (females, $R^2 = 0.525$; males, $R^2 = 0.533$). This pattern arose because late-breeding fish expended more energy before breeding, and because late-breeding females invested more energy into egg production and retained less for metabolism during breeding. Adaptation-by-time may play an important role in life history evolution within some species, particularly those with breeding systems characterised by semelparity, capital breeding, and heritable breeding times.

A. P. Hendry and T. P. Quinn, School of Fisheries, Univ. of Washington, Box 357980, Seattle, WA 98195-7980, USA (present address of APH: Dept of Zoology, Univ. of British Columbia, 6270 University Blvd, Vancouver, BC, Canada V6T 1Z4 [ahendry@zoology.ubc.ca]). – O. K. Berg, Dept of Zoology, Norwegian Univ. of Science and Technology, NTNU, N-7034 Trondheim, Norway.

Correlations between breeding date and the life history or energy status of individuals have received much attention in the ecological literature (e.g., Price et al. 1988, Meijer et al. 1990, Ridgway et al. 1991, Schultz et al. 1991). Traditional investigations of these patterns

have focused on condition-dependent tactics in species characterized by iteroparity (individuals can reproduce more than once, Stearns 1992) and income breeding (continued feeding during reproduction, Jönsson 1997). In general, such studies have found that larger individu-

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als or those with greater energy stores tend to breed earlier in the season (e.g., Meijer et al. 1990, Ridgway et al. 1991, Schultz et al. 1991, Svensson and Nilsson 1995). Various explanations have been proposed for why condition-dependent breeding occurs, most of which relate to opportunities for energy acquisition by adults either before or after breeding.

A different hypothesis can be advanced for why particular traits may vary among individuals that breed at different times. Specifically, selective regimes that vary through the breeding season may lead to adaptive differences among temporally separated population components. Such "adaptation-by-time" would occur, for example, when early and late breeders experienced different selective regimes and were at least partially reproductively isolated. Thus, the fundamental difference between the two hypotheses is that condition dependence assumes breeding date within a season is an effect of variation in life history traits or energy stores, whereas adaptation-by-time assumes breeding date is a cause of such variation. These two mechanisms are not mutually exclusive, and they should not be viewed as strict alternatives. Rather, the dichotomy outlined above depicts extremes along a continuum where both mechanisms may make varying contributions to population structure.

In the present study, we illustrate how the condition-dependence and adaptation-by-time hypotheses might be invoked to examine variation in breeding date, life history, and energy allocation in a population of sockeye salmon (*Oncorhynchus nerka*). We first develop predictions that would logically derive from each hypothesis, and then set about testing them as might a researcher initially subscribing to one view or the other. By considering agreement between predicted and observed correlations, within the context of conditions favouring each mechanism, we evaluate the potential influence of condition-dependence and adaptation-by-time on population structure.

Sockeye salmon life history

Sockeye salmon embryos incubate in the gravel of streams over the winter, emerge in the spring, and then move rapidly to nearby lakes (Burgner 1991). After one or two years in a lake, juveniles migrate to the ocean, where they spend another two or three years before returning as adults to their natal lake. Returning adults cease to feed when they enter freshwater (often more than a month before breeding) and subsequent reproductive development and breeding takes place at the expense of stored energy (Gilhousen 1980, Brett 1995, Hendry 1998). All of the fish that enter fresh water go on to breed in that year (unless they die first), and no instances of reversion to the salt water form are known either before or after breeding (Burgner 1991).

During breeding, the female prepares a nest site for egg deposition, and then defends that site against encroachment by other females (Foote 1990). Owing to intense competition for nest sites in salmonids, the nests of early-breeding females are often disturbed by late-breeding females, causing very high mortality in the displaced eggs (Hayes 1987). Males compete for access to nesting females but do not provide parental care (Foote 1990, Quinn et al. 1996). Migration and breeding are energetically demanding, resulting in the depletion of energy stores by up to 70% (Gilhousen 1980, Brett 1995, Hendry 1998). Owing primarily to this energy depletion (as well as other factors, Dickhoff 1989), all sockeye salmon die a few weeks after they commence breeding (Burgner 1991). Strict semelparity negates investment into future reproduction, while exerting intense natural and sexual selection to maximize reproductive success during a single breeding season (Fleming and Gross 1994, Quinn and Foote 1994).

Like many other animals (Ims 1990), most salmon populations have a characteristic peak breeding period that is assumed to be a result of selection for the optimal timing of life history events (Cushing 1969, Brannon 1987). In many sockeye salmon populations, breeding begins explosively at about the same time each year, peaks within a week, and then diminishes in intensity for 3–5 weeks thereafter (e.g., Hendry et al. 1995, Quinn et al. 1996). Females typically deposit all of their eggs within a week of entering the stream and defend them until death, whereas males continue to seek matings until death (Quinn and Foote 1994, Hendry et al. 1995).

Condition dependence: predictions

In some species, the largest individuals or those with the most energy breed first, perhaps because they reach a threshold for successful reproduction earlier in the year (Meijer et al. 1990, Schultz et al. 1991, Svensson and Nilsson 1995). The salmon breeding system differs from these well-studied species in several important ways. First, salmon are capital breeders (*sensu* Jönsson 1997) and cannot accumulate additional energy by postponing reproduction (feeding ceases 1–2 months before breeding begins). Furthermore, the timing of freshwater entry (cessation of feeding) is heritable and quite synchronous within a given population (Burgner 1991), indicating that individuals do not delay freshwater entry in an effort to accumulate more energy. Second, because Pacific salmon are semelparous, post-breeding reconditioning and survival are irrelevant to an adult's choice of breeding date. Thus, salmon lack two of the often-cited incentives for "high quality" individuals to breed early in the year.

Competition for nest sites or mates could conceivably result in selection for condition-dependent tactics during breeding. For some sockeye salmon populations, intra-sexual competition can be very high during preferred periods, when not all females obtain sites nor do all males obtain mates (Quinn and Foote 1994, Hendry et al. 1995, Quinn et al. 1996). Large salmon often dominate small salmon in head-to-head conflicts and prior residency provides a competitive advantage (Foote 1990, Quinn and Foote 1994). Large fish might thus be able to monopolize limited resources at optimal times, forcing smaller individuals to delay breeding (the alternative mating tactic "sneaking" was not observed in our study system because "jack" males were absent). Moreover, early breeding by small individuals would not be favoured because (1) a small, early-breeding female would have her nest destroyed by large females that bred later (see below), and (2) early breeding would be more advantageous for large males, which can remain dominant for a longer period of time (Quinn and Foote 1994). We therefore predicted that if condition dependence was relevant in sockeye salmon populations, small individuals or those with less energy would delay breeding.

Adaptation-by-time: predictions

For adaptation-by-time to contribute to patterns of life history or energy allocation, several conditions must be satisfied; (1) gene flow must be restricted among fish that breed at different times ("isolation-by-time"), (2) the traits in question must be heritable, and (3) selection must be relatively consistent at a particular breeding time but differ among times. Several complementary lines of evidence indicate that isolation-by-time is prevalent in salmon. First, adjacent breeding aggregations that start breeding at slightly different times can show very little mixing within a season (Hendry et al. 1995). Second, breeding date has a high heritability ($h^2 = 0.55$, Siitonen and Gall 1989; $h^2 = 0.57$; Silverstein 1993; $h^2 = 0.65$, Su et al. 1997; $h^2 = 0.40$, Gharrett and Smoker 1993). Third, temporal components of populations typically differ in allelic frequencies at presumed-neutral genetic loci (Leary et al. 1989, Gharrett and Smoker 1993, Adams et al. 1994, Tallman and Healey 1994, McGregor et al. 1998). If neutral genetic markers differ among fish that breed at different times, heritable traits that are exposed to differential selection should demonstrate even greater divergence. Such traits could include age at maturity ($h^2 = 0.39-0.57$, Hankin et al. 1993), body size ($h^2 = 0.3-0.8$, Smoker et al. 1994); egg size ($h^2 = 0.60$, Su et al. 1997), and the fat content of muscle tissue ($h^2 = 0.47$, Gjerde and Schaefer 1989).

If salmon that breed at different times can adapt to selective regimes that vary predictably with time, we

predict that several patterns might evolve. First, early-breeding females should be larger than late-breeding females. Relative to small females, large fish can (1) bury their eggs deeper so that they are less likely to be disturbed by later females (van den Berghe and Gross 1984), (2) defend their nests from most intruders (Foote 1990, Fleming and Gross 1994), and (3) perhaps have longer reproductive life spans (van den Berghe and Gross 1986). Therefore, selection for traits that minimize the probability of nest disturbance (dig-up) should favour large size in females that breed early but not in females that breed late. Although large body size confers other benefits (e.g., more eggs), those advantages should remain relatively consistent among different breeding times.

A second prediction is that late-breeding females should have larger eggs. Although many factors influence egg size evolution in sockeye salmon (see Quinn et al. 1995), different lengths of the growing season provide the clearest prediction for adaptive variation through a season. Juvenile salmon (fry) that emerge late in the spring have reduced growing opportunities, and so will be smaller on a given day than those which emerged earlier. Because small fry grow slower and are more susceptible to predation (West and Larkin 1987), the offspring of late breeders would be at a selective disadvantage (within a population, late-breeding females give rise to late-emerging fry, Gharrett and Smoker 1993). Larger eggs in late-breeding females might be one way to compensate for this disadvantage because egg size is positively correlated with size of fry at emergence but does not influence time to emergence (Beacham et al. 1985, Hendry et al. 1998).

Third, early-breeding fish should have longer reproductive life spans (e.g., McPhee and Quinn 1998). For females, early breeders must live long enough to protect their eggs from disturbance by late breeders (the probability of having a nest disturbed is much higher for early than for late breeders, Hayes 1987). For males, long life in fish that begin breeding early in the season will allow them the potential to mate with later females, whereas males that begin breeding late cannot greatly increase their reproductive success by living for a long time (as the season progresses competition among males for the few remaining females increases dramatically; Hendry et al. 1995, Quinn et al. 1996).

A fourth prediction stems from conflicting demands placed on the limited energy stores of female salmon, such that increased retention of somatic energy stores for active metabolism will detract from the energy available for egg production. Early breeding females must retain more energy for active metabolism used during nest defence. In contrast, selection to retain metabolic reserves for nest defence should be relaxed in late-breeding females because they do not need to defend their nest sites for as long or as vigorously. Therefore, late females can allocate a greater propor-

tion of their energy to gonad production, perhaps offsetting some of the difficulties that their offspring incur owing to late emergence. We therefore predicted that early-breeding females would reserve more energy for active metabolism and late-breeding females would invest more into egg production.

Analytical approach

Life history traits and energy stores often vary as a result of physiological constraints and genetic covariance (Stearns 1992). These associations need to be considered in any test for relationships between such traits and breeding date. We developed conceptual models that incorporated trait correlations, and allowed the testing of predictions that derived from the condition-dependent and adaptation-by-time hypotheses (life history traits, Fig. 1; energy allocation, Fig. 2). We then quantified variation in breeding date, life history (age-at-maturity, body length, body weight, egg weight, and

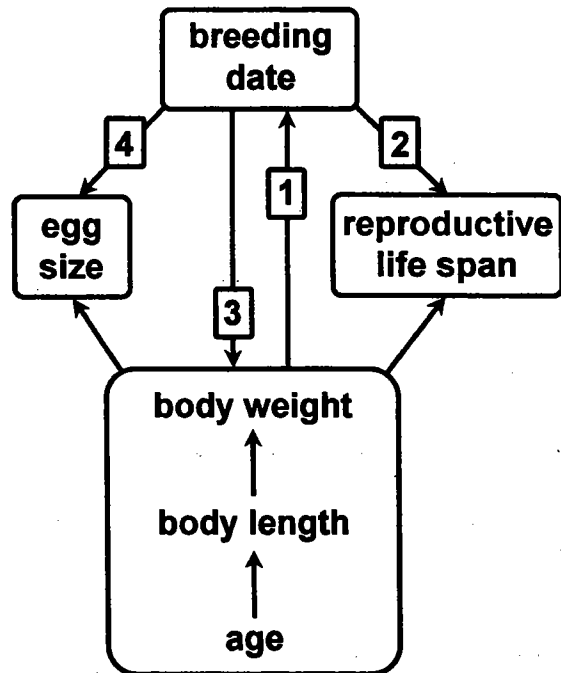


Fig. 1. A conceptual model depicting possible causal relationships among life history traits and breeding date. Each trait was considered in turn as a dependent variable in stepwise multiple regressions, potentially influenced by the variables with arrows leading to it (using fish tagged in 1995 and 1996). Age can affect body length, which in turn influences body weight (lower box). In some combination, these body size traits may then have proximate effects on egg size, breeding date, and reproductive life span. The condition-dependent prediction tested in the framework of this model was that large fish will breed earlier than small fish (1). Adaptation-by-time predictions were that early-breeding fish should live longer than late-breeding fish (2), early-breeding females should be larger than late-breeding females (3), and late-breeding females should have larger eggs (4).

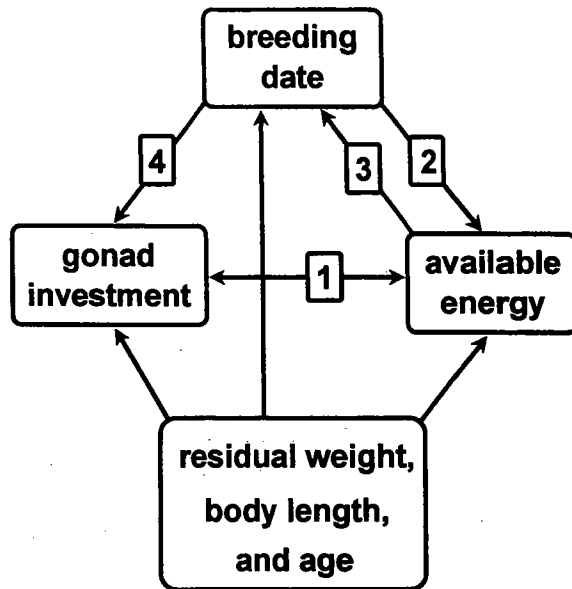


Fig. 2. A conceptual model depicting possible causal relationships between energy allocation and breeding date. These relationships were tested using data from fish sacrificed at stream entry (1996) in stepwise multiple regressions. Some combination of age, body length, and residual weight (lower box) can potentially influence breeding date, available energy (somatic energy available for metabolism at the onset of breeding, total kJ or kJ g^{-1}), and gonad investment (gonad size or gonad energy, total kJ or kJ g^{-1}). Available energy and gonad investment are expected to be constrained to some degree by an allocation trade-off (1) and breeding date may have a proximate influence on reproductive life span because late-breeding fish typically have greater pre-breeding energy costs (2). The condition-dependent prediction tested within this framework was that individuals with more energy will breed earlier than those with less energy (3). The adaptation-by-time prediction was that late-breeding females should reserve less energy for active metabolism (2) but invest more energy into their gonads (4).

reproductive life span), and energy allocation (energy contained in gonads and soma) within a population of sockeye salmon. The condition dependence and adaptation-by-time predictions were evaluated by considering breeding date as either a dependent or an independent variable in a series of multiple regression models. Specifically, we tested whether small individuals or those with less energy delayed breeding (as predicted under condition-dependence); and whether early-breeding fish had (1) larger body sizes, (2) smaller eggs, (3) longer reproductive life spans, and (4) more somatic energy but less gonad energy (all as predicted under adaptation-by-time).

Methods

Study site and fish tagging

Pick Creek ($59^{\circ} 33' 00''\text{N}$, $159^{\circ}04'18''\text{W}$) is a second-order stream flowing into Lake Nerka in the Wood

River lake system, Alaska (for a map see Quinn et al. 1995). Sockeye salmon breed in the lower 2 km of Pick Creek, which averages 33.1 cm deep (at the channel centre) and 7.8 m wide (Hendry 1998). Because the creek is short and spring-fed, water level, temperature, and discharge are nearly constant during the breeding season (Hendry 1998). The average number of sockeye salmon breeding in the creek over the past 10 years has been 9344 (inter-annual range = 6512–14073; Fisheries Research Inst., Univ. of Washington, unpubl.).

Large numbers of sockeye salmon begin to gather at the mouth of Pick Creek about a month before breeding begins. These fish remain in shoals along the shore and only enter the creek when maturation is imminent. At this time, the salmon enter a lagoon that is separated from the main part of Pick Creek by a shallow riffle. Capturing the fish in this lagoon (where very little breeding took place), and screening them for evidence of breeding activity (breeding fish show skin wounds associated with breeding aggression), ensured that none of the fish chosen for our study had begun breeding. Fish were captured using a seine net, anaesthetized using tricaine (MS-222), tagged using 3-cm Peterson discs encoded with individual alphabetic codes, and released. This is a well-established procedure that does not accelerate mortality or have lasting effects on fish behaviour (e.g., Quinn and Foote 1994, McPhee and Quinn 1998). In 1995, 226 fish were tagged 19–24 July, and an additional 40 were tagged on 1 August. In 1996, 200 fish were tagged 18–22 July, 119 were tagged 31 July–1 August, and 120 were tagged on 8 August.

At tagging, all fish were measured from the middle of their eye to the end of their hypural plate (body length, mm) and weighed (body weight, g). We used length as our standard measure of body size because, unlike weight, it would not be influenced by variation in gonad size. However, we also calculated the residual weight of each fish as a measure of its condition (e.g., Quinn and Foote 1994). Residual weight was the deviation of each fish's weight from the overall length-weight regression for each sex (ANCOVA revealed that slopes and intercepts of these relationships did not differ between years or between fish of different ages).

Daily surveys

Before any sockeye salmon entered Pick Creek, the entire stream was marked off into 97 sequential sections (each about 20 m in length), which facilitated our monitoring of the position and movement of tagged fish. On each day of the breeding season (with no exceptions), the location of each tagged fish (i.e., stream section) and its behavioural status (holding, moving, or breeding; alone, paired, or in a group) were recorded. These data were obtained by observation through binoculars from positions on the stream bank, a proce-

dure that did not disturb the fish until after their position and status had been recorded. Observations were usually very easy owing to clear and shallow water, and only a very small fraction of the tags could not be identified on a particular day. For example, of the 3022 total records of tagged fish in 1995, only 24 (<1%) could not be individually identified. On most days, the number of untagged males and females in each section was also counted. Exceptions included a few days when poor water conditions (e.g., heavy rain) or time limitations precluded an accurate census (2 d in 1995, 6 d in 1996). The daily counts were summed over all of the stream sections to estimate the size of the total breeding population in the creek on each day. Although total spawner counts were not exact, their purpose was simply to show trends with time.

The first day that each tagged fish was observed in Pick Creek (upstream of the lagoon) was used to indicate the onset of breeding by that individual (once fish entered the stream they stayed there until death). Stream entry date provided a reliable measure of the date of first breeding because (1) fish did not breed before they entered the stream, (2) both males and females were exposed to breeding competition as soon as they entered, and (3) individual fish usually engaged in typical breeding behaviour within a day of their entry (inferred from observations of tagged fish).

Tagged fish that died of senescence (no obvious wounds) or were killed by predators (very obvious wounds) were collected from the stream banks each day. Some tagged fish entered the stream but were not found dead (32.8% of the females and 63.4% of the males in 1995; 16.8% of the females and 37.8% of the males in 1996). These missing fish were either killed and eaten by bears, or their carcasses were washed into the lake or trapped at the bottom of the only large pool in the stream. Fish whose carcasses were recovered at death did not differ from those that disappeared; with respect to body length or body weight at tagging, or egg weight at recapture ($P > 0.10$ for each sex and trait, one-way ANOVA). Thus, to the best of our knowledge, the fish collected at death were an unbiased subsample of the tagged fish that entered the stream.

Reproductive life span was calculated for tagged fish that died of senescence as the difference between the date that the fish entered the stream and the last date that it was observed alive (life span was not calculated for those fish whose carcasses were not recovered at death). At the end of the study, one tagged fish remained alive in 1995 (24 August) but 15 were still alive in 1996 (27 August). Therefore, only females that entered before 16 August, 1996, and males that entered before 17 August, 1996, were included in the life span analysis. Only 1 female and 2 males that had entered earlier than these dates were still alive at the end of the study, and these fish were assumed to have died on the next day (each of the remaining fish was decrepit and

appeared near death when the last survey took place). The above cut-off dates eliminated any potential bias in reproductive life span arising from the termination of the study when a few fish were still alive.

Otoliths (ear bones with banding patterns that reflect fish age, Burgner 1991) were removed from all tagged fish whose carcasses were recovered at death and from all fish killed for energy determination (combined $N = 431$). Length-at-age relationships were established for females and males in each year using these fish. These length/age distributions were then used to assign ages to those fish that were tagged but not recovered at death ($N = 375$). This procedure for determining age was robust because only 5 of the 375 fish were in the area of size overlap between ages. These 5 intermediate fish were randomly divided between the two possible age classes.

Stream recaptures

After their entry into Pick Creek, each tagged fish was recaptured using salmon landing nets every 2–4 d. These fish were anaesthetized using MS-222, measured, weighed, and checked for reproductive condition. Reproductive condition was estimated based on our ability to express gametes by gently squeezing each fish's abdomen, on the relative amount of abdomen distension, and on the prevalence of wounds associated with breeding (see Hendry 1998 for details). All of the captured fish returned to their respective nest sites and engaged in typical breeding behaviour within 15 min of release. Repeated capture did not appear to influence life span because (1) tagged fish behaved normally after release, (2) tagged fish in the present study lived longer than those in studies where sockeye salmon were tagged but not repeatedly recaptured (Quinn and Foote 1994, Hendry et al. 1995, McPhee and Quinn 1998), and (3) tagged fish in Pick Creek did not seem to die earlier than un-tagged fish. For example, 14% of the fish that entered on the first day in 1995 had been tagged, and 14% of the fish that had died of senescence before 10 August had been tagged (based on a survey of all dead fish in the stream).

At the time of capture, a sample of 50–100 eggs was squeezed from each tagged female that had ovulated (73 in 1995, 180 in 1996). Within a day, the eggs of each female were placed on drying tissues to remove surplus fluids, and then about 40 eggs from each were transferred to a Petri-dish, weighed (nearest mg), and counted. Average egg size (fresh egg weight, mg) was determined as the weight of each egg sample divided by its number of eggs. For females with more than one egg sample, average egg weight was determined by averaging across the different samples (average standard deviation among fresh egg samples for a given female was only 2.7 mg).

Energy content

Energy stores were determined for 10 males and 10 females entering Pick Creek on each of three different dates in 1996 (21 July, 1 August, and 12 August). Energy stores were also determined for 23 fish of each sex collected at death (3–15 August). Using the procedures described in previous sections, length, weight, and age were determined for each of these 106 fish. Gonad size was then determined by removing and weighing the ovaries or testes. Each fish was thus divided into somatic tissue (all body parts excluding the gonads) and gonad tissue, which were then homogenized separately by first chopping with a knife and then grinding in a drill-powered meat grinder. Samples of soma and gonad homogenate (about 20 g each) were placed in sealed vials and stored at -20°C .

The somatic tissue of salmonid fishes contains only a negligible amount of carbohydrate ($< 1.0\%$; Jonsson et al. 1997). Therefore, body composition is commonly determined by measuring water, fat, protein, and ash content ("proximate" analysis; Brett 1995). In the present study, the water content of each sample of gonad and soma was determined by drying about 10 g of the homogenate at 55°C for two weeks. Fat content was then measured gravimetrically on the dried samples after extraction in a solvent composed of five parts petroleum ether and one part chloroform. This type of solvent extracted only neutral (storage) lipids, which compose $> 99\%$ by wet weight of the total muscle lipids of sockeye salmon (Hatano et al. 1995). Fat extraction was executed in two steps (3 + 3 d) using fresh solvents for each step. Ash content was determined by combustion of the fat-free samples at 550°C for 12 h. Protein was calculated as the difference between the weight of each fat-free sample and the weight of ash after its combustion (e.g., Berg et al. 1998).

The amount of fat and protein energy (as well as the combined total) was calculated for each sample on a wet weight basis ("specific energy", kJ g^{-1}), using energy equivalents of 36.4 kJ g^{-1} for fat and 20.1 kJ g^{-1} for protein (Brett 1995). Total energy for each fish was calculated for somatic tissue (specific energy in somatic homogenate \times somatic weight) and gonadal tissue (specific energy in gonadal homogenate \times gonad weight). Henceforth, we refer only to specific and total energy from fat and protein combined (for fat- and protein-specific values see Hendry 1998). Estimates of energy content using proximate analysis and energy equivalents (as above) are nearly identical to those obtained using bomb calorimetry (Craig et al. 1978).

Available energy and metabolic rates

Not all of the energy contained in the somatic tissue of a fish can be mobilized to fuel metabolism. One way to

estimate the fraction of energy that is not available is to measure the energy remaining in freshly-dead fish. In the present study, specific somatic energy at death averaged 2.96 kJ g^{-1} for males and 2.93 kJ g^{-1} for females (Table 3). Thus, mass-specific "available energy" could be estimated for individual fish (those described in the previous section) as their specific energy at stream entry minus 2.96 kJ g^{-1} for males and 2.93 kJ g^{-1} for females. Estimates of specific available energy were then multiplied by the somatic weight of each fish at stream entry to determine total available energy (kJ). This procedure estimated the relative amount of energy available to each fish (when it entered the stream) for future metabolic expenditures associated with breeding. These expenditures would be limited to metabolism because gonadal and secondary sexual development are complete at stream entry (A.P. Hendry unpubl.).

The later in the year a fish begins breeding, the more time it will have spent shoaling within the lake before breeding (fresh-water entry date and breeding date are not correlated within populations of Bristol Bay sockeye salmon, Rowse 1985, Jensen and Mathisen 1987). Therefore, it was important to consider pre-breeding metabolic costs when interpreting patterns of energy allocation relating to breeding date. We estimated the amount of energy that would be consumed in metabolism by fish shoaling at the mouth of Pick Creek. Water temperatures at this location were recorded from 19 July through 24 August in 1995 (and 1996) using HOBO temperature loggers (Onset Computer Corp., Pocasset, MA). Using the average temperature during this period (11°C), we estimated the amount of energy that would be consumed in standard metabolism by an average female as follows: $42 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (estimated from Fig. 4 in Brett and Glass 1973) $\times 0.00325 \text{ kcal per mg O}_2$ (conversion in Brett 1995) $\times 4.184 \text{ kJ kcal}^{-1} \times 24 \text{ h} \times 1.9 \text{ kg}$ (the mean weight of females that entered in the late part of the run was 1.893 kg). This calculation yielded an estimated cost owing to standard metabolism while shoaling at the mouth of Pick Creek of 27.2 kJ d^{-1} for females. The corresponding value for males was 34.7 kJ d^{-1} ($38 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, 2.8 kg). Multiplying these estimates by the number of days separating our collections indicated that cumulative metabolic costs before breeding were about 598 kJ (females) and 763 kJ (males) higher for fish in our last collection (12 August) than for fish in our first collection (21 July).

Multiple regression models

Associations among life history traits, energy allocation, and breeding date were analysed using a series of forward stepwise multiple regression models that treated each sex independently. Variables used in par-

ticular models included: year (1995 or 1996), age (2 or 3 years in the ocean), body length (mm), body weight (g), residual weight (g), gonad weight (g), egg weight (mg), reproductive life span (days from creek entry to death), total available energy (kJ), specific available energy (kJ g^{-1}), total gonad energy (kJ), specific gonad energy (kJ g^{-1}), and breeding date (date that a fish entered the stream). Body length, body weight, egg weight, and gonad weight were \log_{10} transformed for all analyses.

In stepwise model building, the probability of F for a factor to enter was $P < 0.05$ and to be removed was $P < 0.10$ (SPSS, v. 7.5). The first independent variable to enter each model was that which explained the most variation in the chosen dependent variable. Coefficients of determination (R^2) were used to express the proportion of variation in each dependent variable that was explained by a particular independent variable. Sequential improvements to the overall R^2 with the addition of other variables were interpreted as the additional amount of variation explained. For example, if adding a second factor improved the R^2 from 0.5 to 0.6, this second independent variable explained an additional 10% of the total variation (i.e., +10%). Because these models were stepwise, it is important to remember that sequential R^2 improvements do not necessarily reflect simple correlations between later entering variables and the dependent variable. For instance, body length often explained slightly more of the variation in a particular trait than did age. As a result, age provided only a slight improvement when it entered a model at a later step. If, however, age was forced into a model before length, it had a strong effect and length made only a slight improvement. Therefore, it is important to remember that length and age are highly correlated and their effects cannot easily be disentangled.

Two different categories of multiple regression models were used to test our predictions. One category of models evaluated the condition-dependent predictions by considering breeding date as a dependent variable that might be affected by life history traits (Fig. 1) or patterns of energy allocation (Fig. 2). The second category of models evaluated the adaptation-by-time predictions by considering breeding date as an independent variable that might influence variation in life history traits (Fig. 1) or energy allocation (Fig. 2).

Results

The first sockeye salmon to enter Pick Creek did so 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. 3). Peak counts were recorded on 9 August in 1995 (3749), and on 11 August in 1996 (5215). The exact date of peak breeding (i.e., egg deposition) was

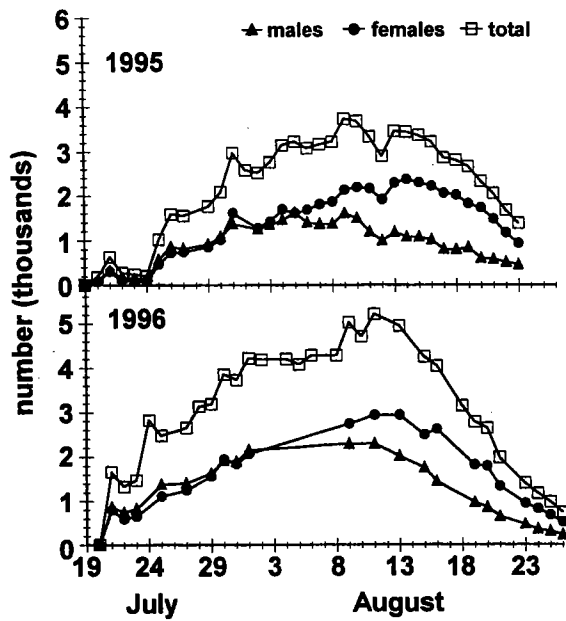


Fig. 3. Daily counts of sockeye salmon in Pick Creek during the breeding season. Females reproduced for about 1–5 d after stream entry and then guarded their eggs for the remainder of their lives. Males were sexually active at stream entry and remained so for the remainder of their lives, although with diminishing reproductive success.

not known but would have occurred in the first few days of August each year (inferred from fish densities coupled with observations and recaptures of tagged fish). The sex ratio was approximately equal for the first 16 d of the breeding period, after which time it became skewed towards females (Fig. 3). However, because males continue to seek matings for much longer than females, the operational sex ratio (based on sexually

active individuals) was probably biased toward males for almost the entire breeding season (e.g., Hendry et al. 1995, Quinn et al. 1996). In both years, the study was terminated when some fish remained alive in the stream (counts on the final day were 1429 in 1995 and 741 in 1996). Most of these remaining fish had started breeding much earlier but a few were still entering and would breed later (at least into September). Thus, the breeding period in Pick Creek lasted more than 35 d and some fish spawned more than 20 d after the peak.

All of the fish aged directly from otoliths ($N = 431$) had spent one full year as juveniles in fresh water, and then either two or three years in the ocean (2-ocean vs 3-ocean). Inclusion of the fish for which age was estimated from length (see Methods) revealed that most of the salmon in 1995 were 3-ocean (85.6% of the females and 67.4% of the males), whereas most in 1996 were 2-ocean (76.2% of the females and 82.1% of the males). Shifts in age composition between years are common in salmon populations, and arise owing to differential year-class strengths (Burgner 1991). In the present study, the dramatic difference in age composition between years resulted in inter-annual variation in life history traits (Table 1), as well as complex interactions between year, sex, and age effects (not shown). To better interpret the influence of sex and age on life history and energy stores, we used year-specific ANOVAs with fixed effects. Main effects were considered significant at $P < 0.05$, but interactions were considered significant at $P < 0.10$ (a conservative approach to the interpretation of main effects).

Based on tagged fish that entered Pick Creek (Table 1), males were longer and heavier than females ($P < 0.001$, both years) and 3-ocean fish were longer and heavier than 2-ocean fish ($P < 0.001$, both years), with no interaction between sex and age effects ($P > 0.400$, both years). The eggs of 3-ocean females were larger

Table 1. Variation in body length (mm), body weight (g), egg weight (mg), and reproductive life span (d) of tagged sockeye salmon that entered Pick Creek.

Sex and trait	Year	<i>N</i>	Average	Standard deviation	Coefficient of variation (%)
A) Females					
Body length	1995	119	494	24	4.9
	1996	197	451	33	7.3
Body weight	1995	118	2630	376	14.3
	1996	197	2040	534	26.2
Egg weight	1995	73	108	10	9.3
	1996	165	98	13	13.3
Life span	1995	69	20	6	30.0
	1996	113	17	5	29.4
B) Males					
Body length	1995	134	505	33	6.5
	1996	188	477	34	7.1
Body weight	1995	134	3166	660	20.8
	1996	188	2701	658	24.4
Life span	1995	11	17	2	11.8
	1996	75	17	4	23.5

Table 2. Variation in life history traits of sockeye salmon sampled for energy content at stream entry (Entry) or at death (Death) in Pick Creek, 1996.

Sex and trait	Collection period	N	Average	Standard deviation	Coefficient of variation (%)
A) Females					
Body length	Entry	30	449	29	6.5
	Death	23	447	31	6.9
Somatic weight	Entry	30	1566	357	22.8
	Death	23	1459	321	22.0
Gonad weight	Entry	30	388	97.7	25.2
	Death	-	-	-	-
B) Males					
Body length	Entry	30	473	37	7.8
	Death	23	464	40	8.6
Somatic weight	Entry	30	2550	688	27.0
	Death	23	2094	551	26.3
Gonad weight	Entry	30	60.4	11.7	19.4
	Death	23	14.9	6.8	45.6

than those of 2-ocean females ($P < 0.001$, both years). Reproductive life span did not differ between the sexes ($P > 0.150$, both years) or age classes ($P > 0.090$, both years), with an interaction between sex and age effects in one year (1995, $P = 0.337$; 1996, $P = 0.063$). The smaller sample sizes for the life span of tagged fish in 1995 than in 1996, particularly for males (Table 1), were due to much higher rates of predation by bears in 1995 (A.P. Hendry unpubl.).

Based on the fish sampled for energy content at stream entry (Table 2), males had greater somatic weights than females ($P < 0.001$) and 3-ocean fish had greater somatic weights than 2-ocean fish ($P < 0.001$), with an interaction between sex and age effects ($P = 0.008$). The interaction arose because the difference in somatic weight between 2-ocean and 3-ocean fish was greater for males than for females. Females had much heavier gonads than males ($P < 0.001$) and 3-ocean fish had heavier gonads than 2-ocean fish ($P < 0.001$), with no interaction between sex and age effects ($P = 0.246$). Gonad weights were more variable for females than for males at stream entry, but were more variable for males than for females at death (Table 2). This latter effect arose because males typically died with some milt remaining in their body cavity, whereas females invariably deposited all but a few of their eggs.

When they entered the stream, females had more mass-specific energy in their soma than did males ($P < 0.001$; Table 3) and fish of different ages did not differ in specific energy ($P = 0.293$), with no interaction between sex and age effects ($P = 0.574$). Owing to sex- and age-specific differences in body size, however, males had more total somatic energy than females ($P < 0.001$), 3-ocean fish had more total somatic energy than 2-ocean fish ($P < 0.001$), and the difference in somatic energy between fish of different ages was greater for males than for females (interaction, $P = 0.011$). At death, mass-specific somatic energy did not differ between males and females ($P = 0.181$; Table 3)

or between fish of different ages ($P = 0.418$), with no interaction between sex and age effects ($P = 0.186$). Once again owing to sex- and age-specific body size differences, however, total somatic energy at death was greater for males than for females ($P < 0.001$) and greater for 3-ocean than for 2-ocean fish ($P = 0.001$), with no interaction between sex and age effects ($P = 0.221$). Specific energy loss between stream entry and death was greater for females (2.00 kJ g^{-1}) than for males (1.21 kJ g^{-1}) but total energy loss was almost twice as much for males (4483 kJ) as for females (2364 kJ).

Females had much more energy in their gonads on a mass-specific basis than did males ($P < 0.001$) and 3-ocean fish had slightly higher specific gonad energy than 2-ocean fish ($P = 0.027$), with no interaction between sex and age effects ($P = 0.715$). Females also had much more total gonad energy than males ($P < 0.001$), 3-ocean fish had more total gonad energy than 2-ocean fish ($P = 0.003$), and the difference in total gonad energy with respect to age was much greater for females than for males (interaction, $P = 0.006$).

Multiple regressions

For the forward stepwise multiple regression models used in the present study, error terms were normally distributed and multicollinearity was low (except between age and length, when both were in a model). Life history traits were not very successful in explaining variation in breeding date (condition-dependent models). For males, year effects made a small but significant contribution to variation in breeding date ($R^2 = 0.075$), and residual weight had an even smaller effect ($R^2 = +0.036$; Table 4). For females, early breeders were longer ($R^2 = 0.120$), and heavier for their length ($R^2 = +0.067$), than late breeders (Table 4). In contrast to the low explanatory power of life history traits in condi-

tion-dependent models, energy allocation explained a substantial amount of the variation in female breeding date (Table 4). Females with more available specific energy (kJ g^{-1}) tended to breed earlier than those with less available energy ($R^2 = 0.376$). As we will later show, however, this difference was simply an artefact of higher cumulative pre-breeding energy expenditures in late-breeding fish (see Discussion). For males, breeding date was not correlated with available energy (residual weight and age were the only variables that entered the model; Table 4).

The adaptation-by-time multiple regression models (i.e., breeding date as an independent variable) explained most of the variation in life history traits (Table 5) and energy allocation (Table 6), and revealed a few strong and a few weak correlations with breeding date. Most of the variation in body length was explained through positive correlations with age (females, $R^2 = 0.807$; males, $R^2 = 0.714$), and the strength of this relationship was not an artefact of the age estimation method (for fish whose ages were read directly from otoliths, $R^2 = 0.819$ for females and $R^2 = 0.703$ for males). An additional, negative correlation with breeding date made a very slight but statistically significant improvement to the female length model (Table 5). Body weight was highly correlated with length (females, $R^2 = 0.938$; males, $R^2 = 0.928$), and then only slightly influenced by age, year, or breeding date (Table 5). Egg weight was positively correlated with body length ($R^2 = 0.523$), and then showed an increasing trend with residual weight ($R^2 = +0.039$), breeding date ($R^2 = +0.017$), and finally year ($R^2 = +0.009$; Table 5). A negative correlation with breeding date explained most of the variation in reproductive life span (females, $R^2 = 0.525$; males, $R^2 = 0.533$; Fig. 4). No other factors helped explain variation in male life span but the stepwise addition of other variables made sequentially small improvements for females (Table 5).

Total available energy at stream entry (fat + protein, kJ) was positively correlated with body length (females, $R^2 = 0.580$; males, $R^2 = 0.506$); and then negatively correlated with breeding date for females ($R^2 = +0.162$; Table 6), and positively correlated with residual weight for males ($R^2 = +0.091$; Table 6). In contrast, mass-specific available energy in females (kJ g^{-1}) was first negatively correlated with breeding date ($R^2 = 0.376$) and then positively correlated with length ($R^2 = +0.098$). None of these factors contributed to the corresponding male model (Table 6). Variation in gonad weight was explained primarily by length (females, $R^2 = 0.680$; males, $R^2 = 0.238$) and, in females, by a positive association with breeding date ($R^2 = +0.088$). Variation in total gonad energy of females was primarily explained by body length ($R^2 = 0.704$) but also by a positive correlation with breeding date ($R^2 = +0.083$), and residual weight ($R^2 = +0.024$). For males, only total available somatic energy explained a significant amount of the variation in total gonad energy ($R^2 = 0.335$). Length and then residual weight helped explain variation in specific gonad energy of females ($R^2 = 0.269$ and $R^2 = +0.108$). In the corresponding male model, specific gonad energy was positively correlated with breeding date ($R^2 = 0.181$; Table 6).

Discussion

Simple linear relationships among various life history and energy traits explained much of the variation in our regression models. In particular, older fish were longer, and older/longer fish were heavier and had more available energy, larger gonads, more gonad energy, and larger eggs (Tables 5 and 6). After accounting for these correlations, we found that some life history traits and energy allocation patterns were correlated with breeding date. The strongest of these correlations was that

Table 3. Variation in energy stores (by wet weight) for Pick Creek sockeye salmon collected at stream entry (Entry) or at death (Death) in Pick Creek, 1996.

Collection period		Specific somatic energy (kJ g^{-1})			Total somatic energy (kJ)	
		Average	Standard deviation	Coefficient of variation (%)	Average	Coefficient of variation (%)
A) Females						
Somatic energy	Entry	4.93	0.27	5.5	6641	27.0
	Death	2.93	0.22	7.5	4277	23.6
Gonad energy	Entry	7.79	0.52	6.7	3050	30.2
	Death	-	-	-	-	-
B) Males						
Somatic energy	Entry	4.17	0.32	7.7	10704	30.8
	Death	2.96	0.15	5.1	6221	28.9
Gonad energy	Entry	3.89	0.35	9.0	235	20.9
	Death	2.96	0.86	29.1	44	56.8

Table 4. Multiple regression statistics for forward stepwise models where breeding date was the dependent variable (i.e., condition-dependent models).

Independent	Females			Males		
	Order	R ²	t	Order	R ²	t
Life history models						
Body length	1	0.120	-6.5***	x	-	+1.6
Residual weight	2	0.187	-5.1***	2	0.111	-3.6***
Ocean age	x	-	+1.5	x	-	+1.1
Year	x	-	+1.4	1	0.075	+5.0***
Energy models						
Av. energy (kJ)	1	0.376	-4.1***	x	-	-1.4
Body length	x	-	+1.2	x	-	-0.7
Residual weight	x	-	-1.1	1	0.339	-3.8**
Av. energy (kJ g ⁻¹)	x	-	+0.9	x	-	-1.2
Ocean age	x	-	+0.1	2	0.467	+2.5*

Notes: "Order" indicates the order of entry for independent variables into each model. R² values are for the entire model at each step that a new variable entered. The t statistic is for the partial significance of each independent variable at the step that it entered the model. Variables that did not enter the model at any step are indicated with an x in the "order" column, and their partial t values are indicated (after all significant variables were added). The direction of the correlation for each factor can be inferred from the sign of the t value (+ or -). Sample sizes were 315 for the female life history models, 318 for the male life history models, 30 for the female energy models, and 30 for the male energy models. Available energy (Av. energy) is the estimated total energy (kJ) and mass-specific energy (kJ g⁻¹) available for metabolism to each fish as it entered the stream. Significance levels are P < 0.05 (*), P < 0.01 (**), and P < 0.001 (***).

late-breeding fish did not live nearly as long in the stream as did early-breeding fish (i.e., a negative correlation between reproductive life span and breeding date; Fig. 4). Furthermore, late-breeding females (but not males) had less energy available for metabolism and invested more energy into their gonads than did early-breeding females (Fig. 5). Several other trends were also evident but were not nearly as strong. For instance, early-breeding females (but not males) were slightly larger than late-breeding females, and late-breeding females had slightly larger eggs than did early-breeding females (Table 5). Concordance between these patterns and our initial predictions bear on the condition-dependence and adaptation-by-time hypotheses.

Do smaller fish, or fish with less energy, delay breeding?

In sockeye salmon, intra-sexual competition could conceivably favour condition-dependent breeding date because large or energy-rich individuals might be able to monopolize resources at optimal times, forcing small or energy-poor individuals to breed later. Contrary to this prediction, late males began breeding with only 314 kJ less energy than early males, despite the fact that late males would have expended at least 763 kJ more energy while holding in the lake. Early-breeding females had 909 kJ more energy than late-breeding females but this discrepancy could also be attributed to higher pre-breeding metabolic costs (598 kJ), and to greater gonad investment by late-breeding females (+ 594 kJ). Thus, at the time the first fish began breeding, those that

would breed later had at least as much available energy. We conclude that somatic energy stores did not influence the date that fish began breeding within Pick Creek.

We also found little evidence that breeding date was influenced by body size. Small males did not breed later than large males; and although small females tended to breed slightly later than large females, the relationship was relatively weak (length, R² = 0.120). Some females can apparently delay breeding for a short period of time under very high densities (Foote 1990) but most fish begin breeding within a few days of maturation, regardless of their size. If they did not do so, the quality of their eggs and their ability to release them would decrease rapidly (e.g., de Gaudemar and Beall 1998). In Pick Creek, females that entered the stream during the first 4 d of the breeding season in 1996 ranged in length from about 400 to 550 mm (mean = 470 mm). Daily surveys and stream recaptures indicated that the smaller individuals in this early group did not subsequently leave the stream or delay breeding. Thus, even if selection favours a delay in breeding by small females, other factors must be opposing the evolution of such a tactic.

We argue that the breeding date of salmon within a season is most likely the result of a genetic predisposition for individuals to mature and breed at a particular time of the year. This tendency is largely independent of individual size or energy stores because maturation date is heritable in salmon and closely linked to the onset of breeding (Leary et al. 1989, Siitonen and Gall 1989, Gharrett and Smoker 1993, Silverstein 1993, Su et al. 1997). Thus, condition-dependence is unlikely to

substantially influence variation in salmon breeding date. Instead, genetic variation in breeding date may be maintained by inter-annual shifts in optimal breeding times (e.g., van Noordwijk et al. 1981), and by a trade-off between the benefits of breeding at optimal times and the costs of competition for resources during those times.

Are early-breeding females larger, and do they have smaller eggs?

As predicted by the adaptation-by-time hypothesis (see Introduction), early-breeding females were larger than late-breeding females, and late-breeding females had larger eggs than early-breeding females (for a given body size). However, these trends were not very important within the context of overall life history variation (they explained little of the total variation). Thus, gene flow or a lack of strong selection may restrict the role of adaptation-by-time in structuring body size and egg size variation within the Pick Creek population. An additional constraint on adaptation may be the strong positive correlation between body size and egg size (present study; Quinn et al. 1995), which would hinder independent evolution of the two traits. In fact, absolute egg weight declined through the season because late-breeding females were smaller, whereas egg weight relative to body size increased through the season. Thus, early breeding may impose direct selection for larger body size (see Introduction) but late breeding might indirectly select for larger body size through selection for large eggs. Notwithstanding this constraint, we must conclude that adaptation-by-time did

contribution substantially to trends in body size or egg size.

Do early-breeding fish have longer reproductive life spans?

The adaptation-by-time hypothesis predicts that early-breeding fish will have longer reproductive life spans than late-breeding fish (because early fish must defend their nest against disturbance by late fish). We found this correlation to be very strong within the Pick Creek population (Fig. 4), in accordance with similar relationships documented in other salmon populations (Perrin and Irvine 1990, McPhee and Quinn 1998). Within Pick Creek, the trend toward longer life spans in early-breeding fish was not an artefact of changes in standard metabolism because average daily water temperatures did not change over the breeding season (Hendry 1998). Furthermore, the correlation between life span and breeding date was not the result of variation in the intensity of competition because breeding densities declined late in the season (Fig. 3). Thus, early-breeding fish experienced more competition over the course of their life and yet lived longer than late breeding fish. For Pick Creek sockeye salmon, the decline in life span through the breeding season probably occurs because late-breeding fish have less energy available for metabolic costs associated with breeding (see below), and therefore succumb more rapidly to rigours of reproduction.

Reproductive life span was not strongly correlated with body size, age, or residual weight for either males

Table 5. Multiple regression statistics for forward stepwise models seeking to explain variation in life history traits (see Fig. 1), using breeding date as an independent variable (i.e., adaptation-by-time models). Table 4 provides details on the presentation.

Dependent	Independent	Females			Males		
		Order	R ²	t	Order	R ²	t
Body length	Ocean age	1	0.807	+36.2***	1	0.714	+28.1***
	Breeding date	2	0.812	-2.8**	x	-	+1.8
	Year	x	-	-1.6	x	-	+1.2
Body weight	Body length	1	0.938	+68.6***	1	0.928	+63.8***
	Breeding date	2	0.942	-4.7***	2	0.930	-2.9**
	Ocean age	3	0.946	+4.7***	x	-	+1.6
	Year	4	0.948	+3.6***	3	0.931	+2.6**
Egg weight	Body length	1	0.523	+16.1***	-	-	-
	Residual weight	2	0.562	+4.6***	-	-	-
	Breeding date	3	0.579	+3.1**	-	-	-
	Year	4	0.588	+2.3*	-	-	-
	Ocean age	x	-	+1.3	-	-	-
Life span	Breeding date	1	0.525	-14.1***	1	0.533	-9.9***
	Year	2	0.567	-4.1***	x	-	-0.5
	Body length	3	0.579	2.3*	x	-	+0.5
	Ocean age	4	0.588	-2.0*	x	-	+0.9
	Residual weight	5	-	+1.2	x	-	-0.3

Notes: Sample sizes for the female models were 316 (body length), 315 (body weight), 238 (egg weight), and 181 (life span). Sample sizes for the male models were 318 (body length), 318 (body weight), and 86 (life span).

Table 6. Multiple regression statistics for forward stepwise models seeking to explain variation in energy allocation (see Fig. 2), using breeding date as an independent variable (i.e., adaptation-by-time). Table 4 provides details on the presentation ($N = 30$).

Dependent	Independent	Females			Males		
		Order	R^2	t	Order	R^2	t
Av. Energy (kJ)	Body length	1	0.580	+6.2***	1	0.506	+5.4***
	Breeding date	2	0.742	-4.1***	x	-	-0.6
	Residual weight	x	-	+1.1	2	0.597	+2.5**
	Ocean age	x	-	-0.9	x	-	+0.6
	Gonad energy (kJ)	x	-	+0.8	x	-	+1.6
Av. energy (kJ g ⁻¹)	Breeding date	1	0.376	-4.1***	x	-	-1.2
	Body length	2	0.474	+2.3*	x	-	+1.1
	Ocean age	x	-	-1.5	x	-	+1.1
	Gonad energy (kJ g ⁻¹)	x	-	+0.4	x	-	+1.1
	Residual weight	x	-	-0.2	x	-	+0.9
Gonad weight	Body length	1	0.680	+7.7***	1	0.238	+3.0**
	Breeding date	2	0.768	+3.2**	x	-	-1.4
	Residual weight	x	-	+1.8	x	-	+1.1
	Av. energy (kJ)	x	-	-0.9	x	-	+1.1
	Ocean age	x	-	-0.8	x	-	-0.5
Gonad energy (kJ)	Body length	1	0.704	+8.2***	x	-	+1.4
	Breeding date	2	0.787	+3.2**	x	-	+0.8
	Residual weight	3	0.811	+2.6*	x	-	-0.6
	Ocean age	x	-	-0.8	x	-	+0.4
	Av. energy (kJ)	x	-	+0.3	1	0.335	+3.8**
Gonad energy (kJ g ⁻¹)	Body length	1	0.269	+3.2**	x	-	+0.7
	Residual weight	2	0.377	+2.2*	x	-	+0.8
	Breeding date	x	-	+1.9	1	0.181	+2.5*
	Av. energy (kJ g ⁻¹)	x	-	-0.7	x	-	+1.9
	Ocean age	x	-	-0.5	x	-	+1.5

or females (Table 5). The lack of a robust relationship between body size and life span in Pick Creek contrasts with the conventional wisdom that larger salmon live longer during the reproductive period. In the most widely cited study, body size and life span were positively correlated for coho salmon (*O. kisutch*) in Deer Creek, WA (van den Berghe and Gross 1986). Unfortunately, the Deer Creek life span models did not consider breeding date, and length had only a modest ability to predict life span (males, $R^2 = 0.10$; females, $R^2 = 0.36$; van den Berghe and Gross 1986). We suspect that if breeding date had been included in the Deer Creek models, the effect of body size would have been considerably reduced, as was evident in the present study and that of McPhee and Quinn (1998). At present, convincing evidence that larger salmon live appreciably longer during breeding is lacking (see also Quinn and Foote 1994).

Do early-breeding females allocate energy differently than late-breeding females?

Owing to limited energy reserves, and conflicting demands on those reserves, salmon face a trade-off between the amount of energy they can invest into their gonads and the amount that they can retain for metabolism. Adaptation-by-time predicts that early breeding females will place a greater emphasis on the

retention of somatic energy stores for subsequent use during breeding competition (to facilitate the defence of their nest from potential intruders). For late-breeding females, selection will not favour so strong an apportionment of energy resources into stored energy, and should therefore allow increased investment into gonad production. We found strong evidence for the predicted influence of adaptation-by-time on energy allocation strategies within Pick Creek; early-breeding females had more stored energy at the onset of breeding, whereas late-breeding females invested more energy into egg production (Fig. 5).

The decline in available somatic energy through the breeding season arose in part because late-breeding fish consume more of their stored energy before they commence breeding. Assuming that the date of fresh-water entry is not correlated with breeding date, which appears to be the case within populations of Bristol Bay sockeye salmon (Rowse 1985, Jensen and Mathisen 1987), late breeders spend more time in the lake without feeding than do early breeders. We estimated that energy stores would be consumed while shoaling off the mouth of Pick Creek, owing standard metabolism alone, at average rates of approximately 34.7 kJ d⁻¹ (males) and 27.2 kJ d⁻¹ (females). Actual rates of energy consumption owing to metabolism during this period would be higher because the fish consume some additional energy in active metabolism. Thus, higher cumulative pre-breeding metabolic expenditure in late-

breeding fish probably contributed to their lower energy stores at the start of breeding. Nonetheless, late-breeding females clearly have a different allocation strategy as they invested considerably more energy into egg production than did earlier breeding females (Fig. 5).

Isolation-by-time

For adaptation-by-time to work, gene flow must be limited among fish that breed at different times (isolation-by-time). Isolation-by-time appears prevalent within salmon populations (see Introduction) but direct estimates of gene flow within the Pick Creek population are not currently available. Within the population, female-mediated gene flow within a breeding season would be low because an individual's eggs are deposited over a period of only 2–5 d. In contrast, male mediated gene flow would occur because some fish can remain sexually active for more than 20 d. However, the breeding period in Pick Creek lasted more than 35 d and the mating success of male sockeye salmon diminishes rapidly with the length of time they have been breeding (Quinn and Foote 1994, Quinn et al. 1996). Gene flow

between early- and late-breeding fish would also be limited across years (although not completely) because of the high heritability of breeding date in salmon (Siitonen and Gall 1989, Gharrett and Smoker 1993, Silverstein 1993, Su et al. 1997). Although early and late breeders in the Pick Creek population are certainly not completely reproductively isolated, gene flow seems to be sufficiently limited for strong selection to have resulted in adaptive clines in life history traits and energy allocation patterns through the breeding season.

Synopsis

Condition-dependence did not appear relevant to variation in breeding date for the population of sockeye salmon that we studied. Similarly, adaptation-by-time was not particularly important to variation in body size or egg size. Conversely, adaptation-by-time probably contributed to variation in reproductive life span and patterns of energy allocation with respect to breeding date. The Pick Creek population had a breeding season that was only about 35 d long, whereas many other salmon populations have much longer seasons. In populations with more protracted breeding seasons, adap-

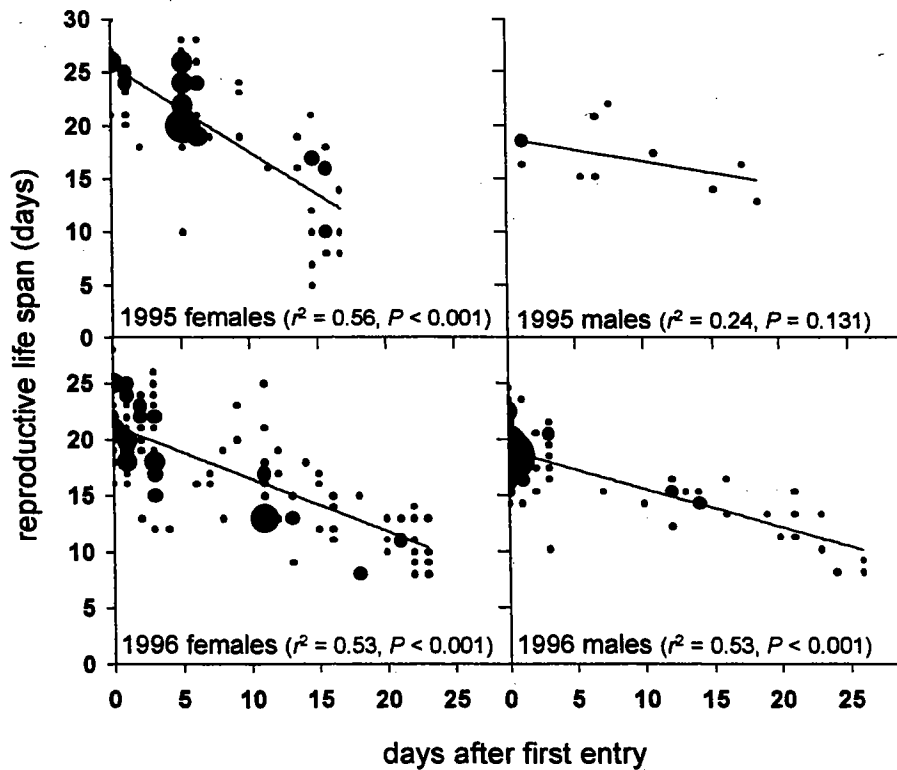


Fig. 4. The reproductive life span (days in the creek) of sockeye salmon that ultimately died of senescence. The X axis depicts the number of days after the run began that a particular tagged fish entered. Results of simple linear regressions for each sex and year are indicated. The width of each point is proportional to the number of fish showing that combination of life span and breeding date.

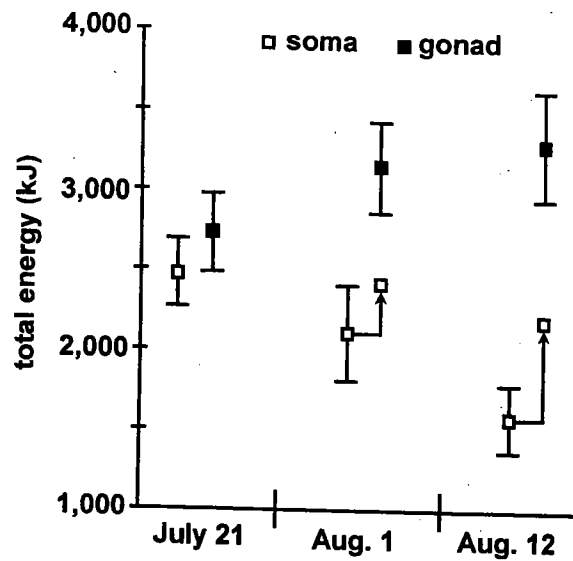


Fig. 5. Variation in energy allocation strategies with breeding date in female sockeye salmon. Depicted values are the total gonad energy (closed boxes) and total available somatic energy at stream entry (open boxes), with associated standard errors (bars). Arrows show the position of the mean value after it was corrected by subtracting cumulative metabolic expenditure during the longer period of pre-breeding lake residence by late-breeding females (27.2 kJ d^{-1}).

tation-by-time would be expected to have stronger effects, and the potential for condition dependence would be less (salmon have limited ability to delay breeding). Sockeye salmon of the Cedar River in Lake Washington, Washington, are an example of one such population, having a breeding season extending over more than three months. Hendry et al. (1998) found evidence of adaptation-by-time within the Cedar River population in temperature-specific development rates expressed by the embryos of fish that started breeding at different times.

Condition-dependence and adaptation-by-time are very different mechanisms but their effects are not mutually exclusive. In fact, some of the predictions that derive from one hypothesis are similar to those deriving from the other (e.g., a negative correlation between body size and breeding date). We have shown that the some of same trends traditionally considered to derive from condition-dependence can be interpreted plausibly in the context of adaptation-by-time. We thus caution that for an observed correlation between breeding date and a given trait, for salmon and probably other species, condition dependence cannot automatically be assumed. A purely correlative study, however detailed, cannot unequivocally reject one mechanism in favour of the other, nor can it precisely determine the relative contributions of each. We encourage researchers investigating life history, energy allocation, and breeding date to consider adaptation-by-time as a viable alternative (or complement) to condition dependence.

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