

Length of breeding life of coho salmon (*Oncorhynchus kisutch*)

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Since Pacific salmon (*Oncorhynchus* spp.) die on the breeding grounds after spawning, duration of individual life may affect survival of deposited eggs. In addition, breeding life of both sexes has implications for estimates of size of spawning populations. We therefore examined the contributions of body size, population density, water level, season, and year to length of breeding life in individual coho salmon (*O. kisutch*). Age 3 breeding males and females lived an average of 9 days (range, 2–30 days), and 2-year-old "jack" males averaged 8 days (range, 2–21 days). Sixteen percent of the variance among age 3 males and 44% of the variance among females could be explained by the variables examined. Density of adults made a significant negative contribution to life-span, while water level, season, and year were insignificant. Body size was the most important variable in explaining breeding life-span, being positively related and accounting for 10% and 36% of the variance in 3-year-old males and females, respectively. In contrast, none of these variables explained the observed variation in jack male breeding life. The differences between the sexes and between 2- and 3-year-old males are consistent with levels of competition on the breeding grounds. We show that the results on individual body size and breeding life span can be used to offset biases in population estimates.

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Puisque les saumons du Pacifique (*Oncorhynchus* spp.) meurent dans les frayères après la reproduction, la durée de vie d'un individu peut affecter la survie des oeufs pondus. En outre, la durée de la période de reproduction chez les deux sexes influence l'estimation de la densité des populations dans les frayères. Ces constatations nous ont amenés à examiner les contributions respectives de la taille des poissons, de la densité des populations, du niveau d'eau, de la saison et de l'année sur la durée de la vie après la reproduction chez quelques saumons coho (*Oncorhynchus kisutch*). Les mâles reproducteurs et les femelles de 3 ans vivent en moyenne 9 jours (étendue 2–30 jours), alors que les tacons génésiques de 2 ans vivent en moyenne 8 jours (étendue 2–21 jours). Seize pourcent de la variance enregistrée chez les mâles de 3 ans et 44% de la variance enregistrée chez les femelles s'expliquent par les variables étudiées. La densité des adultes apporte une contribution négative significative à la longévité, alors que le niveau d'eau, la saison ou l'année n'ont pas d'effet significatif sur ce paramètre. La taille du corps est la principale variable responsable de la longévité puisqu'elle apporte une contribution significative positive et qu'elle explique 10% de la variance enregistrée chez les mâles de 3 ans et 36% de la variance enregistrée chez les femelles de 3 ans. En revanche, aucune de ces variables ne réussit à expliquer la variation de la durée de la vie après la reproduction chez les tacons génésiques. Les différences entre les sexes et entre les mâles de 2 et de 3 ans sont reliées aux degrés de compétition enregistrés dans les frayères. Nous démontrons que les données sur la taille des individus et leur longévité après la reproduction peuvent servir à réajuster les estimations de densité des populations.

[Traduit par la revue]

Introduction

The length of life on the breeding grounds is poorly understood for adult Pacific salmon (*Oncorhynchus*). Published data on duration of spawning give only population means (e.g., Willis 1954; Killick 1955; Allen 1956; Schroder 1973; Crone and Bond 1976). However, larger individuals may have greater energy reserves (Schmidt-Neilsen 1984) and thus survive longer than smaller ones. Since females defend their nest sites to prevent subsequent reuse, such variation in female survivorship has possible implications for the survival of deposited eggs. Furthermore, variation in breeding life could greatly influence current methods of estimating the size of spawning populations (e.g., Neilson and Geen 1981).

To address the question of individual life-span, we studied the breeding life of a wild population of individually marked male and female coho salmon (*O. kisutch*). Coho salmon are one of five native North American Pacific salmon species that are born in freshwater, mature in the ocean, and return to their home streams as adults to breed (McPhail and Lindsey 1970). After breeding, all the adults die in the stream.

We examined several variables that might influence the

life-span of adults in the stream: body size, density, water depth, season, and year. Water level may be important because of its relationship to current speed (e.g., Foerster 1968, pp. 74–80). Density may be inversely related to resources for breeding (e.g., territories for females and mates for males) and thus contribute to fighting and reduced survivorship on the spawning grounds. Season could influence life-span through a change in temperature, or because later arriving fish on the spawning grounds are of different body condition than those arriving earlier (Williams et al. 1977). A significant year effect would suggest life-span was influenced by intergenerational differences in genetics or environmental experience. Understanding how these variables contribute to length of life on the spawning grounds will add to our knowledge of the evolutionary ecology of coho salmon and possibly improve our means of estimating population number at spawning.

Methods

The study population occupied a tributary to Deer Creek, itself a tributary to the Skykomish River, locally known as Deer Creek Junior, 1.8 km west of Index, Snohomish County, WA, U.S.A. The stream ranges from 2 to 4 m wide and has a midchannel depth of 10 to 40 cm. Adults were caught at a weir, approximately 10 m from the stream mouth, during November through January of 1981–1982 and 1982–1983; they were measured (fork length), sexed, and tagged using

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color-coded Petersen disk tags (Floy Tag Co., Seattle, WA). We determined age from scales and analyzed age 3 (one freshwater summer and two ocean summers) and age 2 (one freshwater and one ocean summer) individuals separately. All age 2 individuals were precocious males ("jacks"). We inspected the weir at 0800, 1600, and 2300 daily and released all fish above it, where 95% of spawning areas were located. We also inspected the condition of the fish in the stream, from the weir to 200 m upstream (beyond which fish movement was prevented by cascades). More frequent surveys of fish in the stream were made when fish activity was high. Dying individuals (those too weak to maintain an upright position or to stay in their territories) were checked frequently to determine the time of death to within 1 h. We defined death to occur when the fish ceased to respire. Spawning and mortality data were not collected between 2300 and 0800.

In addition to total time alive, the time to establishing a territory and time of territory abandonment were recorded for females. For analysis of the intervals between entry into the stream and initial nest construction, and termination of guarding to death, we use only those fish for which the intervals are known to within 1 h. Analysis of total breeding life is based on the interval between entry and death, measured to the nearest half day. Detailed subintervals were not measured for males because males moved extensively among female territories and did not help in either nest construction or guarding after spawning.

Water level (the height of the water column above the gravel substrate) was measured at 0800 daily on a fixed post near the weir. The average water level over the period each fish was alive on the spawning grounds was used in the analysis. "Seasonal" regression analyses were based on individual entry dates onto the spawning ground, relative to the date when the first fish entered the stream for that year. The "density" that was experienced by individuals of known breeding life was determined from the total number of fish (either males, females or jacks) that were in the stream while these individuals were alive. Those individuals whose total breeding life-span was unknown were assigned the mean breeding life in order to include them in the density of fish in the stream.

The statistics in the Results include means with standard errors; stepwise multiple regressions were calculated with the Statistical Package for the Social Sciences (version SPSSx 1983, McGraw-Hill Publications, New York). The probability level for statistical significance was 0.05.

Results

The total time alive on the spawning grounds was measured for 83 (52%) of 160 females that entered the stream in the two seasons. Of these, 4 died of predation (5%; mean life, 6.5 ± 2.1 days), and 15 (18%; 5.0 ± 0.8 days) had signs of previous spawning below the weir (i.e., frayed caudal fin from digging and thin abdomen indicating that most eggs were missing). These 19 fish were omitted from our analyses. The mean body size of omitted fish was not significantly different from the population mean (1981–1982: population mean, 54.98 ± 0.87 cm ($n = 36$), $t = 0.61$, 46 df, $p > 0.10$; 1982–1983: 63.06 ± 0.74 cm ($n = 88$), $t = 0.42$, 33 df, $p > 0.10$), suggesting that they were a random subsample of the population.

Life on the spawning ground was measured for 96 (46%) of 212 age 3 males and for 17 (47%) of 36 age 2 jack males that entered the stream (1981–1982: age 3, 49.7 ± 0.61 cm ($n = 129$); age 2, 33.4 ± 1.18 cm ($n = 18$); 1982–1983: age 3, 56.8 ± 1.03 cm ($n = 82$); age 2, 34.3 ± 0.90 cm ($n = 16$)). We have no record of predation on males in either year. Our sample includes some males that may have participated in spawning prior to their arrival at the weir because previous spawning could not be determined accurately for males.

The average time between capture at the weir and death was 9.0 ± 0.52 days for females (range, 3–17 days, $n = 64$), 9.4 ± 0.61 for age 3 males (2–30 days, $n = 96$), and 7.8 ± 1.16 for

jacks (2–21 days, $n = 17$). The difference among these average life-spans is not statistically significant (age 3 males vs. females, $t = 0.51$, 158 df, $p > 0.50$; age 3 males vs. jacks, $t = 1.28$, 111 df, $p > 0.20$; females vs. jacks, $t = 1.42$, 79 df, $p > 0.10$). However, as explained below, the life-span of the groups is influenced by different variables.

Figure 1 shows the relationship between body size and life-span for age 3 coho. Within-year correlations are statistically significant for females in both years (1981–1982: $n = 36$, $r = 0.51$, $p < 0.001$; 1982–1983: $n = 28$, $r = 0.46$, $p < 0.03$), but only for the 2nd year in males (1981–1982: $n = 67$, $r = 0.10$, $p = 0.40$; 1982–1983: $n = 29$, $r = 0.41$, $p < 0.02$). The slopes and intercepts are not significantly different between years for either sex (females: $t = 0.24$, 62 df, $p > 0.50$; males: $t = 1.45$, 94 df, $p > 0.10$). Overall regression equations for females and males respectively are: y (days alive) = $-9.0 + 0.314x$ (length) ($n = 64$, $r = 0.65$, $p < 0.001$, Fig. 1A), and $y = -1.4 + 0.203x$ ($n = 96$, $r = 0.33$, $p < 0.001$, Fig. 1B). A significant difference in the variances in lifespans of males and females prevents pooling of the data ($F = 20.6$; 2, 156 df, $p < 0.001$).

Jacks, like 3-year-old males, died after completing spawning. However, a simple regression of body size and life-span was not statistically significant in either year for jacks (Fig. 2; 1981–1982: $n = 11$, $r = 0.14$, $p > 0.50$; 1982–1983: $n = 6$, $r = 0.38$, $p > 0.20$). Furthermore, it was not statistically significant when the data were pooled (1981–1983: $y = 3.17 \pm 0.153x$, $n = 17$, $r = 0.14$, $p = 0.50$).

The relative contribution of body size, population density, water level, season, and year to number of days alive on the spawning ground was determined by a stepwise multiple regression. Together, these variables accounted for 44% of the variance in female stream life (Table 1; $r = 0.71$, $p < 0.001$). Body size was positively correlated with female life-span, while female density was negatively correlated. Water level, season, and year did not make individually significant contributions to female life span.

For age 3 males, 16% of variance in stream life was accounted for (Table 1; $r = 0.36$, $p < 0.001$). Body size was positively correlated, while density of both males and females was negatively correlated. The remaining variables were not significant. In contrast to 3-year-olds, the life-span of jack males could not be significantly explained.

(We have not presented the simple regression results for water level, season, or year. Although these variables were individually significantly correlated with the life-span of age 3 males and females, the apparent contributions were not realized in the multiple regression analysis. Therefore, the simple regression results for these variables are probably spurious, and their presentation is not warranted.)

Females began digging the first nest an average of 10.8 ± 1.9 h after passing the weir (range, 4–24 h, $n = 25$). Capture and tagging may have prolonged this time slightly. After nest construction, females rarely left their territory site until approaching death. The mean time between leaving their territory and death was 8.7 ± 1.6 h (range, 2–24 h, $n = 19$). Large and small females did not differ significantly in their time to starting a nest or between leaving their territory and death (comparing females larger and smaller than the mean size: time to starting the first nest, $t = 0.072$, 23 df, $p > 0.50$; absence from the territory until death, $t = 0.147$, 17 df, $p > 0.50$). Thus, few females were absent from their territory for more than 24 h, and large females spent more time guarding their nest site.

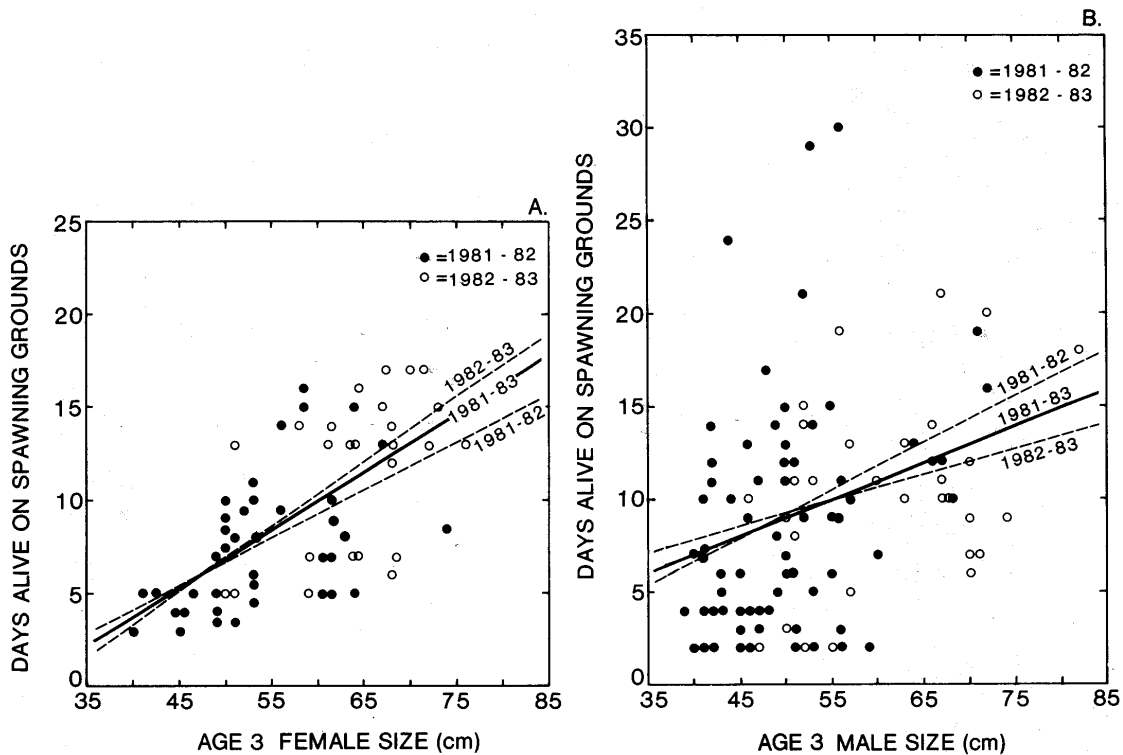


Fig. 1. Body size and the number of days alive on the spawning ground for age 3 coho salmon. (A) Females. (B) Males.

Discussion

We have shown that body size is one of the major determinants of adult life-span on the spawning grounds. Salmon cease feeding upon entry into freshwater (Foerster 1968, p. 71); they maintain their bodily functions and develop their gonads from stored energy reserves. These reserves, however, will be depleted faster in smaller individuals, since basal metabolic rates are inversely related to fish size (Schmidt-Neilsen 1984). Furthermore, swimming costs in energy per unit fish weight decrease with fish size (Schmidt-Neilsen 1984, pp. 185-186). Thus, physiological conditions probably predispose larger individuals to longer life-spans on the spawning grounds.

However, there were considerable sex and age differences in the relationship between life-span and body size. In particular, the variance in life-span of males was significantly greater than that for females. This may have arisen because some males probably spawned prior to their arrival at the weir. Unfortunately, we could not exclude such males from our analysis. Also, fighting behaviour probably contributed to variance in males. Although females fight (Schroder 1981), adult males are much more aggressive, sustaining wounds that probably decrease their life-span. Such injuries would contribute to the variance that went unexplained in our statistical analysis.

The significant contribution made by male and female density highlights the importance of fighting behaviour to the life-span of both sexes. Male life-span decreased as the number of males and females increased, while female life-span decreased only with increasing female number. This difference between the

sexes was due to increased male fighting as the number of females in the stream increased. With few females in the stream, or most females already spawned, males were quiescent and stayed in refuges along the stream banks. However, as new females entered, these males emerged to compete among themselves for access to the females. Thus, the presence of females influences male activity, and male density determines the amount of fighting that occurs for these females (see also Sargent et al. 1986). By contrast, females were concerned only with accessing or defending territories in competition with females.

Some males in the stream employed alternative reproductive tactics (Gross 1984), such as sneaking spawnings, and thereby avoided costs of fighting. This was especially true for jacks and smaller age 3 males (Gross 1985). The lack of a significant body size relationship for life-span in jacks is probably in part due to their sneaking behaviour. Sneaking will increase variability in life-span because individuals that are caught by large males can suffer severe wounding (see also Bohlin 1975) while successful individuals conserve energy. That jack males did not live longer on average than 3-year-old males, even though the former were primarily sneakers, suggests that jack life-span is ultimately restricted by energy limits as well. It is interesting that in the multiple regression the largest contribution to jack life-span was made by jack density. Since jacks will fight among themselves for hiding places (Gross 1984), the importance of aggression to life-span probably applies to jacks as well.

The life-span of salmon on the spawning grounds has several

TABLE 1. The relative contributions of body size, density, water level, season, and year to days alive on the spawning ground for coho salmon

Group	N	Statistic	Body size	Density			Water level	Season	Year	Total
				Age 3 males	Age 3 females	Age 2 males				
Female (age 3)	64	%	36	4	7	<1	2	<1	<1	44
		p	<0.001	0.07	<0.05	0.76	0.27	0.35	0.72	<0.001
Male (age 3)	96	%	10	4	3	<1	<1	<1	<1	44
		p	0.002	0.01	<0.05	0.89	0.35	0.28	0.80	<0.001
Jack (age 2)	17	%	<1	<1	<1	5	<1	<1	<1	—
		p	0.84	0.93	0.91	0.35	0.70	0.67	0.88	—

NOTE: The percentages are the proportion of explained variance and *P* is the two-tailed statistical probability level for significance of the correlation.

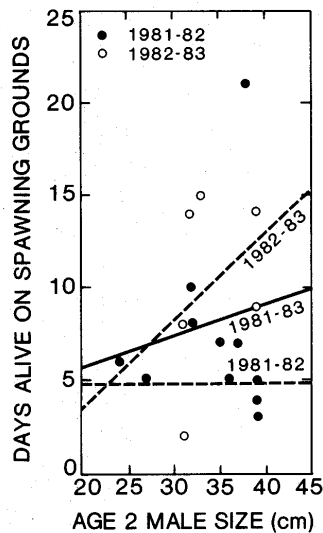


FIG. 2. Body size and the number of days alive on the spawning ground for 2-year-old male coho salmon ("jacks").

theoretical and practical implications. First, the longer period of parental care of larger females will, on average, improve egg survival because guarding reduces the likelihood of nest site reuse, a major source of brood mortality in some streams (Ginetz 1977; McNeil 1966; Neilson and Banford 1983). The effect of larger body size complements a previous finding that larger females make deeper nests, which also increases egg survivorship (van den Berghe and Gross 1984).

A second implication is that estimates of population numbers from spawner counts could probably be improved by incorporating fish size. One of the more common techniques for spawner enumeration is to make periodic counts of fish on the spawning grounds and to adjust these to an average life-span (Neilson and Geen 1981; Cousens et al. 1982). However, our results show that larger fish will be overrepresented and the converse is true for smaller fish. As shown in Fig. 3A, the enumeration of spawners from residence time should include an estimate or subsample of the size-frequency distribution. Total

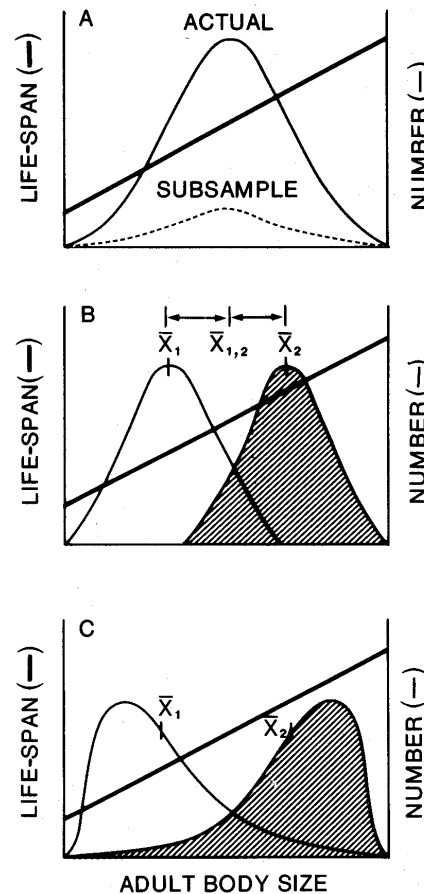


FIG. 3. Schematic illustration of the significance of incorporating body size variation into spawner enumeration based on life-span. (A) An estimate of body size variation (broken line) multiplied by a regression relationship between body size and life-span (straight line) can be used to calculate the total number of spawners in a population (see text). (B) Differences in mean body size among years can greatly influence annual calculations of spawner number. (C) Skewness in body size distribution can greatly influence calculations of spawner number made from average life-span alone.

population size could be calculated from:

$$N \left[\frac{\text{total fish days in stream}}{\sum (\text{no. of fish of each size in subsample}) \times (\text{expected size specific life-spans})} \right]$$

where N is the number of fish in the subsample. Note that the accuracy of the population estimate will depend on having a representative subsample and reasonable knowledge of total fish days on the spawning grounds.

Since body size often differs among years, the use of an average life-span to estimate spawner number may also give highly misleading results (Fig. 3B). In Deer Creek Junior, for example, the mean body size of 3-year-olds was significantly different in 1981–1982 from 1982–1983. If the combined average survivorship for the 2 years is used to estimate the female population size in 1982–1983, the estimate is 48% too high! For comparison, a random subsample of 20 females was used to calculate from our formula the number of females in Deer Creek Junior for 1982–1983. This resulted in an estimate that is only 3% higher than from the actual value for that year.

A further factor that complicates an average life-span index for enumerating spawners is skewness in adult size distributions (Fig. 3C). Skewed distributions to the left would result in underestimates of adult spawners, and skews to the right, overestimates. Since selective fishing pressure is known to impact strongly on body size distribution (Peterson 1954), miscalculation of spawner number from use of an average life-span could be common. Subsampling populations for body size and incorporating size-specific survivorships from regression formulae may therefore be a useful method for reducing spawner enumeration error.

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