Reproductive life-span and sources of mortality for alternative male life-history strategies in sockeye salmon, *Oncorhynchus nerka*

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Abstract: In anadromous salmonid fishes, a fraction of the males ("jacks") spend fewer years at sea than females and most males in the population. It has been hypothesized that the higher survival rates of jacks at sea are balanced by their reduced reproductive success. One component of reproductive success is in-stream longevity, and jacks were reported to have a shorter reproductive life-span than older males. To test this hypothesis, we examined the interactions between arrival date, mode of death (senescent, bear-killed, gull-killed, stranded), and reproductive life-span of male sockeye salmon, *Oncorhynchus nerka* (Walbaum in Artedi, 1792), in a small Alaskan creek. Of the senescent males, early-arriving fish lived longer than later arrivals, and jacks and older males had similar reproductive life-spans (p = 0.932). Jacks were less susceptible to premature mortality (mostly from bears and gulls) than older males. The life-span of fish that died prematurely was greater for jacks than non-jacks ($p < 0.001$). Considering all sources of mortality (both premature and senescent), jacks had a greater mean life-span than older males (5.84 vs. 3.12 days; $p < 0.001$). Despite this fact, jacks are scarce (1.7% in this population), suggesting that they suffer in other components of fitness such as proportion of eggs fertilized.

Résumé : Chez les poissons salmonidés anadromes, une fraction des mâles (les madeleinaux) passent moins d'années en mer que les femelles et la plupart des autres mâles de la population. On a avancé l'hypothèse selon laquelle la survie accrue des madeleinaux en mer est contrebalancée par leur succès reproductif plus faible. Une des composantes du succès reproductif est la longévité dans le cours d'eau et les madeleinaux sont réputés avoir une durée de vie reproductive inférieure à celle des mâles plus âgés. Afin de vérifier cette hypothèse, nous avons étudié les interactions entre la date d'arrivée, les causes de mortalité (sénescence, prédation par les ours, prédation par les goélands, échouage) et la durée de la vie reproductive de saumons rouges, *Oncorhynchus nerka* (Walbaum in Artedi, 1792), dans un petit cours d'eau de l'Alaska. Parmi les mâles sénescents, les poissons qui arrivent tôt vivent plus longtemps que ceux qui arrivent tard; les madeleinaux et les mâles plus âgés ont des durées de vie reproductive semblables (p = 0,932). Les madeleinaux sont moins susceptibles de mourir prématurément (principalement de la prédation par les ours et les goélands) que les mâles plus âgés. La durée de vie des poissons morts prématurément est plus grande chez les madeleinaux que chez les poissons plus âgés (p < 0,001). Compte tenu de toutes les causes de mortalité (tant la mortalité prématurée que celle par sénescente), les madeleinaux ont une durée de vie reproductive moyenne supérieure à celles des mâles plus âgés (5,84 contre 3,12 jours; p < 0,001). Malgré tout, les madeleinaux sont rares (1,7 % de la population étudiée), ce qui laisse croire qu'ils sont désavantagés dans d'autres composantes de leur fitness, par exemple le pourcentage d'oeufs fécondés.

[Traduit par la Rédaction]

Introduction

In a number of animal species, males display alternative life-history strategies that are manifested as dramatic differences in age and size at maturity, courtship and parental behavior, color and morphology, and other traits (Taborsky 1994; Gross 1996). Such alternatives have been closely studied in fishes, including centrarchid sunfishes and salmonids. In sunfishes (e.g., the bluegill, *Lepomis macrochirus* Rafinesque, 1819), the "normal" males delay maturation for several years and then construct nests, court females, and guard young. The "alternative" life-history pathway involves earlier maturity, female mimicry, sneak fertilizations, and abandonment of young to the care of cuckolded parental males (Dominey 1980; Gross 1982). In salmonid fishes, the male life-history patterns do not involve parental care, as only females construct and defend nests. However, in many species, a fraction of the males ("jacks") spend fewer years at sea than females in the population and "normal" males, and some males mature without having migrated to sea at all ("mature" or "precocious parr"; see review by Fleming and Reynolds 2004).

The tendency to mature early is a phenotypically plastic trait, influenced by large size prior to seaward migration (Vøllestad et al. 2004 and references therein). However, there is also a genetic component to the alternative male life-history strategies, as indicated by variation in the prevalence

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of jacks among populations (Young 1999; Healey et al. 2000; Quinn et al. 2001), and the results of controlled breeding studies (Iwamoto et al. 1984; Hard et al. 1985; Heath et al. 1994). The existence of these alternative life-history patterns is of considerable interest to evolutionary biologists, and Gross (1985) hypothesized that they constitute evolutionarily stable strategies. In support of this hypothesis, he reported that the average reproductive opportunity of coho salmon, *Oncorhynchus kisutch* (Walbaum, 1792), jacks was similar to that of much larger, older males (Gross 1985). Reproductive opportunity for the two forms was estimated from the probability of survival at sea, the mean number of days alive on the breeding grounds, and physical proximity to females at the moment when eggs were released (a proxy for fertilization success). Males remain sexually active throughout their lives on the breeding grounds, so longevity is an important component of reproductive opportunity. In the stream that Gross (1985) studied, jacks did not live as long as older males (8.4 vs. 12.7 days) and were not as close when eggs were released, but their higher marine survival resulted in similar overall estimates of fitness between forms. However, more recent theoretical papers (e.g., Repka and Gross 1995; Gross and Repka 1998) showed that this polymorphism can be maintained even if fitnesses are not equal.

van den Berghe and Gross (1986) reported that larger female salmon lived longer than smaller ones, but other studies did not find an effect of body size on reproductive life-span among salmon of comparable ages (Quinn and Foote 1994; Hendry et al. 1999). However, early-arriving salmon tend to live longer than later arrivals (Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; Dickerson et al. 2002), so any analysis of reproductive life-span needs to explicitly consider arrival date. Accordingly, the purpose of this study was to quantify the reproductive life-span of jacks and older salmon in a natural population, testing the generality of Gross's finding that jacks do not live as long as older males after removing the covariation, which was due to arrival timing. Specifically, we wanted to test whether the jacks and non-jack males differed significantly in the number of days between entry onto the spawning grounds and their death of senescence. The study was conducted in Hansen Creek, Alaska, where sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) are subject to predation from brown bears (*Ursus arctos* L., 1758; henceforth bears) and glaucous-winged gulls (*Larus glaucescens* Naumann, 1840; henceforth gulls; Quinn and Buck 2001). These sources of "premature" mortality were apparently absent in the stream studied by Gross (1985). Thus, our second objective was to determine whether the predation pressures exerted by bears and gulls were similar or dissimilar for jacks and non-jack males, and whether the average reproductive life-span (considering all sources of mortality) differed between these male life-history patterns.

Materials and methods

Study area

Hansen Creek drains a series of spring-fed ponds and a large beaver pond, and flows into Lake Aleknagik, in the Wood River lakes system, Bristol Bay, Alaska (Fig. 1). Hansen Creek is approximately 2 km long and it averages 3.9 m wide and 10 cm deep (Marriott 1964). The water is clear, maintains a steady flow throughout the spawning season, and is sufficiently small to make daily surveys of the entire creek throughout the spawning season practical. These characteristics make Hansen Creek an ideal stream in which to observe the behavior and activity of spawning salmon. Moreover, its small size mitigates against the tendency to miss small salmon in carcass surveys of larger rivers (Zhou 2002).

Tagging

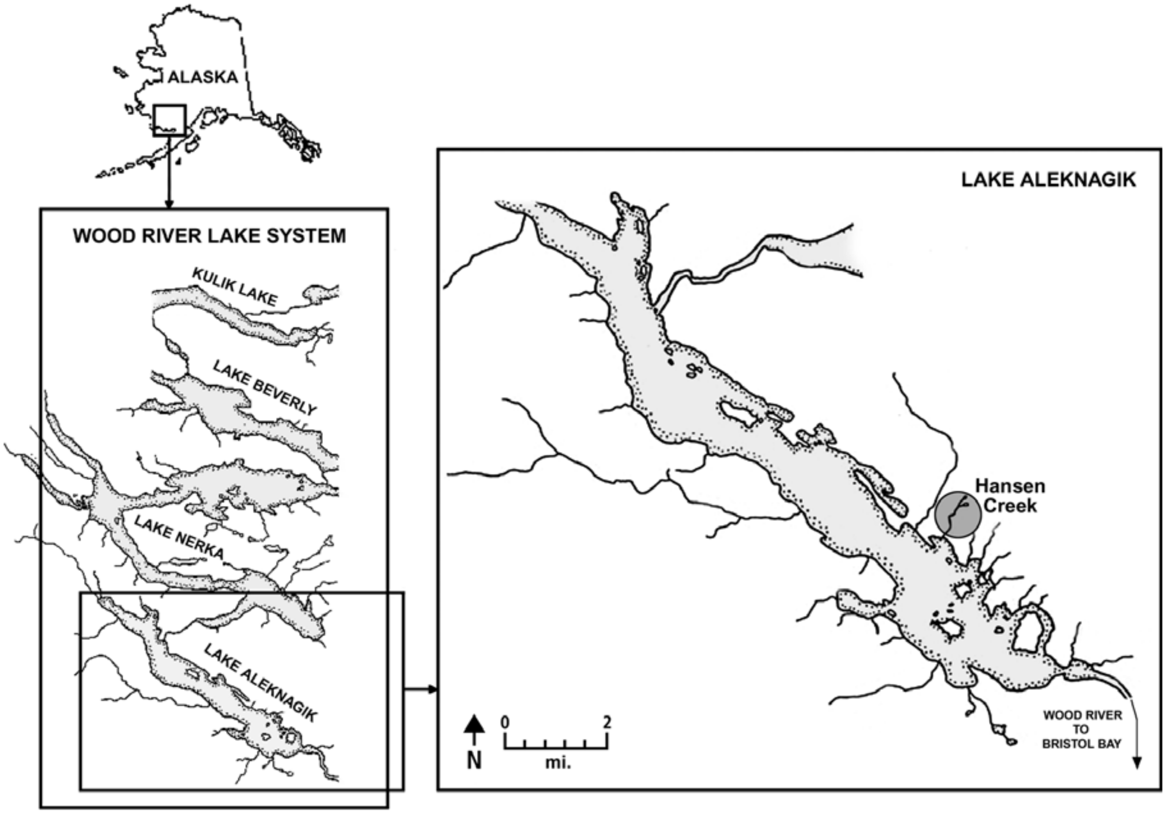
Adult sockeye salmon were captured using a beach seine (100 m of 3.5-cm cotton mesh) as they schooled in the lake at the mouth of Hansen Creek prior to migrating upstream to spawn in 1999–2004. Fish were removed from the net and marked with external, individually coded plastic disk tags (3 cm diameter). The sex of the fish was recorded, body length was measured (mid-eye to hypural plate), and it was placed back into the lake to recover. The random samples of sockeye captured and tagged at the mouth of the creek yielded no jacks (as inferred from length frequency distributions). This was not surprising, as they only constitute 1.7% of the males at this stream based on annual carcass surveys since 1947 (Quinn et al. 2001; Fisheries Research Institute, unpublished data). Therefore, to obtain jacks for comparison with the older males, jacks were captured in the stream from 2002 to 2004, measured, and marked with smaller, 2-cm disk tags. Length measurements from known-aged Hansen Creek fish collected from 1999 to 2004 (Fig. 2A) were used to corroborate the status (jack or non-jack male) assigned to each fish in this study (Fig. 2B).

Data collection and analysis

Daily surveys for tagged fish were conducted on Hansen Creek throughout the run since 1999. Surveys began on the first day salmon were observed entering the stream and continued until nearly all the fish were dead. When tagged fish were observed, their identity was recorded. At death, tagged fish were categorized as senescent, stranded, bear-killed, or gull-killed. Hansen Creek has a shallow, wide delta that salmon must navigate as they attempt to enter the stream, and many salmon strand there or are attacked by gulls in years when the lake level is low (Quinn and Buck 2001). The delta is too shallow for spawning and ends in a discrete bend, above which the water level in the stream is deep enough for spawning to occur and is independent of lake level. Prespawning mortality at the delta is highly size selective (Quinn and Buck 2001) and jacks are much less sensitive to stranding than older, larger males. The mortality at the delta is largely a function of lake level (lower lake level results in higher mortality rates; T.P. Quinn, unpublished data). As we were primarily concerned with reproductive life-span on the spawning ground, fish that died at the delta were excluded from this study.

Tagged fish were assigned to one of four modes of death based on the following classification scheme: (*i*) senescent fish were easily identified by their drab coloration, frayed tail and fins, body scars, fungus, rough skin, and lack of penetrating wound marks; (*ii*) in-stream stranded fish were also characterized by a lack of penetrating wounds but

Fig. 1. Map (1 mi. = 1.609 344 km) of Lake Aleknagik and Hansen Creek relative to the Wood River Lakes, southwest Alaska.



tended to be brightly colored, in fresh condition, and were found in shallow areas such as sand or gravel bars; (*iii*) bear-killed fish were distinguished by any of a variety of penetrating wounds caused by canine teeth and were characterized by large pieces of flesh and (or) body parts missing; and (*iv*) gull-pecked fish had distinctive radial chiseling wounds that penetrated into the body cavity. Most often, these wounds were observed around the gill plates, vent, and below the pectoral fins. In-stream stranding occurs almost exclusively when large salmon enter shallow areas of the stream and cannot extricate themselves. Jacks are substantially smaller than their older counterparts, and seldom suffer this form of premature mortality.

The first day that an individual was seen in the stream was recorded as the date of entry, and subsequent daily stream surveys allowed us to follow the fates of individual fish throughout the duration of the breeding period. Reproductive life-span was then calculated as the date when it was observed dead minus the date of entry. Thus, a fish that was observed alive for 3 consecutive days and then found dead would have a reproductive life-span of 4 days, and one found dead on the first day in the stream would have a reproductive life-span of 1 day. Most fish were observed daily until they were recovered dead, but some were seen daily and then disappeared. Given the high rates of bear predation, the tendency of bears to remove carcasses from the riparian zone of streams (Reimchen 2000; Gende and Quinn 2004), and the identical size frequency distributions and longevities of bear-killed and "missing" salmon (Quinn and Buck 2001; T.P. Quinn, unpublished data), we concluded that the missing fish had been killed by bears, and we analyzed the data accordingly.

We standardized arrival date as the arrival date for each fish minus the arrival date of the earliest individuals in that year, which allowed us to compare reproductive life-span among years that differed slightly in run timing. We removed the confounding effect of arrival date on reproductive life-span by analysis of covariance (ANCOVA), with reproductive life-span as the dependent variable, arrival date as the independent variable, and status (jack or non-jack male) as the fixed grouping factor. Differences in elevations of these lines reflect differences in reproductive life-span for a common arrival date, whereas differences in slope indicate that the relationship between arrival date and reproductive life-span differed between the two groups. We first tested for differences in the slopes of the lines relating reproductive life-span to arrival date (i.e., the interaction term from the ANCOVA). If this term was not significant, it was removed and the model was run again, revealing the effect of the grouping factor (status) and allowing comparisons of life-span at a common arrival date (adjusted means). These are standard procedures for removing the effects of a covariate (Huitema 1980).

Results

A total of 500 non-jack males and 79 jacks were tagged, released, and categorized by mode of death during the course of this study. The percentages of fish that senesced or suffered premature mortality varied considerably among

Fig. 2. Length frequency histograms from Hansen Creek from 1999 to 2004. (A) Known-age male sockeye salmon determined from otolith sampling for ocean-age-1 jacks (solid bars), ocean-age-2 males (open bars), and ocean-age-3 (shaded bars) males. (B) Inferred age of study fish based on length frequency distributions (solid bars, jacks; open bars, non-jack males).

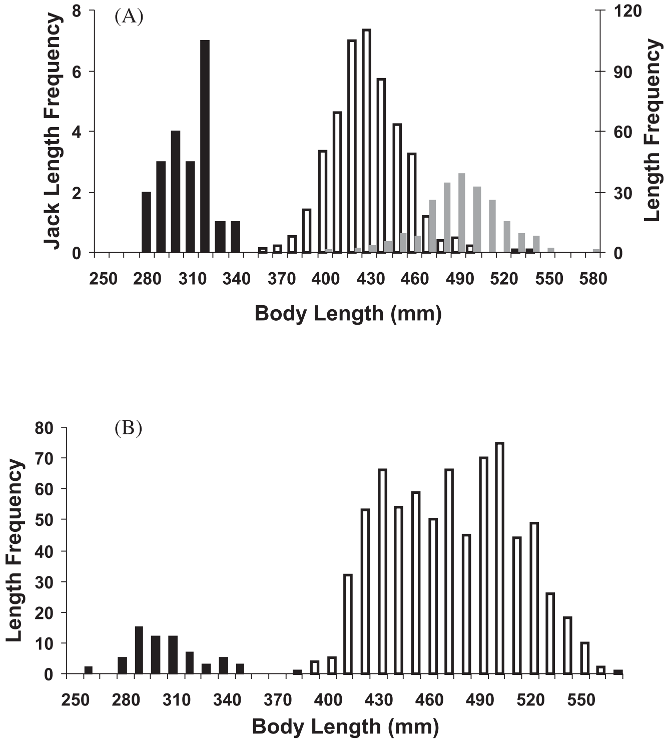


Table 1. Numbers of tagged male sockeye salmon (*Oncorhynchus nerka*) recovered at death, categorized by mode of death in Hansen Creek from 1999 to 2004.

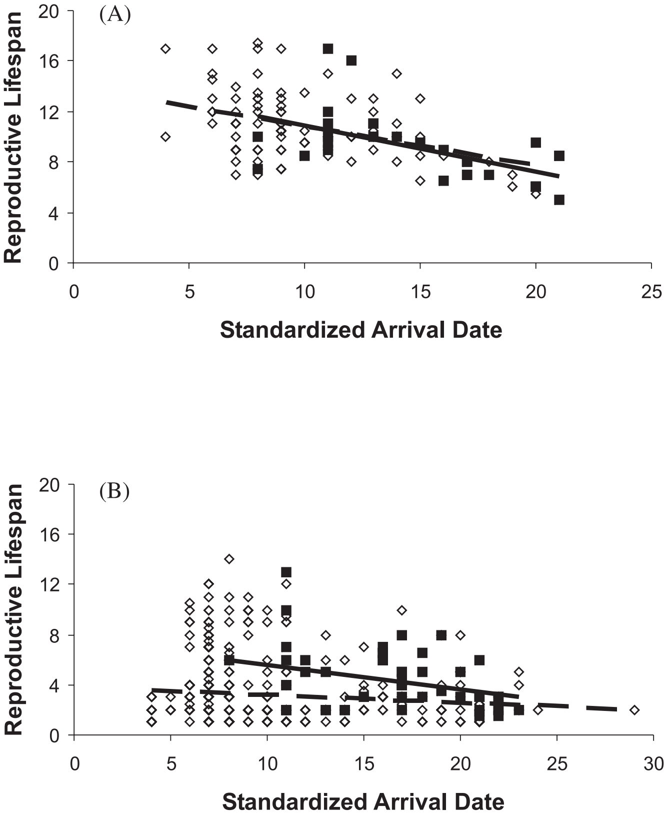
Status and mode of death	1999	2000	2001	2002	2003	2004
Non-jack males						
N	74	104	103	76	67	76
Senescent (%)	50.0	3.8	1.0	23.7	34.3	7.9
Bear (%)	44.6	86.5	88.3	63.2	47.8	76.3
Gull (%)	4.1	0.0	0.0	2.6	10.4	6.6
Stranded (%)	1.4	9.6	10.7	10.5	7.5	9.2
Jack males						
N	0	0	0	55	10	14
Senescent (%)	0.0	0.0	0.0	29.1	40.0	71.4
Bear (%)	0.0	0.0	0.0	1.8	40.0	14.3
Gull (%)	0.0	0.0	0.0	69.1	20.0	14.3

years (Table 1). However, a few general patterns were evident. Although predation by gulls was not a significant source of mortality for non-jack males, gulls killed up to 69.1% of the jacks. Predation by brown bears was the primary source of premature mortality for non-jack males (up to 88.3%) and a lesser but still significant source for jacks (up to 40.0%).

First, we were interested in whether the reproductive life-span to a senescent death differed between jacks ($n = 30$) and non-jack males ($n = 89$). There was no interaction between arrival date and status ($p = 0.659$), allowing a direct comparison of reproductive life-span at a common arrival date (Fig. 3A). This revealed no difference in reproductive life-span between jacks and non-jack males ($p = 0.932$; adjusted mean life-span and 95% (hereafter presented as lower bound ≤ adjusted mean life-span ≤ upper bound): $9.37 \le 10.36 \le 11.35$ and $9.89 \le 10.41 \le 10.94$ for jacks and non-jack males, respectively). Although they were not the focus of this particular study, we also tagged female sockeye salmon in Hansen Creek and found that their senescent life-span ($n = 61$) did not differ significantly from that of the male salmon (when females are included in the analysis, $p = 0.982$; adjusted mean female life-span and 95% CI: $9.97 \le 10.59 \le 11.22$; unpublished data).

Second, to test whether the life-span of individuals killed prematurely (i.e., owing to bear predation, gull predation, stranding) differed, we again employed an ANCOVA. A plot of life-span versus arrival date for this subset of individuals indicated that the variance in life-span decreased as a function of arrival date (Fig. 3B). This pattern is not unexpected

Fig. 3. Relationship between reproductive life-span and standardized arrival date for the subset of tagged sockeye salmon jacks (■, solid line) and non-jack males (◇, dashed lines) that were recovered as senescent dead (A) or premature mortalities (B) in Hansen Creek. For the subset of senescent jacks, reproductive life-span = –0.3729(arrival date) + 14.66; $n = 30$; $r^2 = 0.32$. For senescent non-jack males, reproductive life-span = –0.3141(arrival date) + 13.93; $n = 89$; $r^2 = 0.16$. In B, tagged jacks ($n = 49$) and non-jack males ($n = 411$) that died prematurely on the spawning grounds (bear killed, gull killed, or stranded) were included.



because, regardless of arrival date, the minimum possible life-span is 1 day (for individuals killed their first day in the stream) but the maximum life-span (i.e., life-span for senescent individuals) decreases with time (Fig. 3A). To account for the nonconstant variance, we first $\log_e$ transformed the life-span data and then ran the ANCOVA with the transformed data. The interaction term (arrival date × status) was not significant ($p = 0.316$), allowing a direct comparison of $\log_e$-transformed life-span at a common arrival date. This approach revealed that for the subset of fish which died prematurely the reproductive life-span of jacks ($n = 49$) exceeded that of non-jack males ($n = 411$, $p < 0.001$). After retransforming the adjusted mean and 95% CI to the original units (i.e., $e^{\log_e(\text{days})}$ = days), this difference translated to an adjusted mean life-span and 95% CI of $3.42 \le 4.21 \le 5.18$ and $2.27 \le 2.42 \le 2.59$ for jacks and non-jack males, respectively.

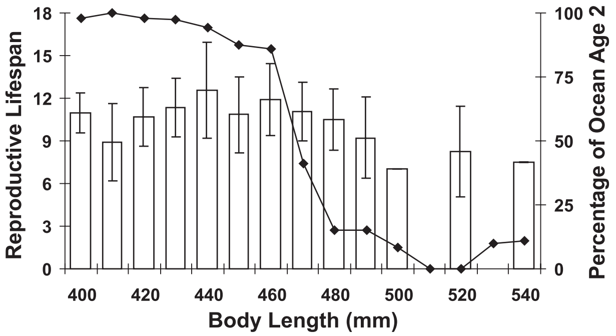
Finally, we employed ANCOVA to test whether the realized life-span, combining sources of mortality, differed between jacks ($n = 79$) and non-jack males ($n = 500$). Again, we first $\log_e$ transformed the life-span data to account for the decreasing variance in life-span with arrival date. Again, the interaction term (arrival date × status) was not significant ($p = 0.112$), permitting a direct comparison of life-span at a common arrival date. Thus, after considering all sources of mortality (senescent, bear-killed, gull-killed, stranded), jacks had a greater reproductive life-span than non-jack males ($p < 0.001$). We then transformed the adjusted mean life-span and associated 95% CI data back into the original units (i.e., days alive on the spawning ground as compared with $\log_e$(days)), resulting in the following adjusted mean life-span and corresponding 95% CI of $4.79 \le 5.84 \le 7.12$ and $2.90 \le 3.12 \le 3.36$ for jacks and non-jack males, respectively.

Discussion

Our analysis of the reproductive life-span and various sources of mortality for alternative male life-history strategies in sockeye salmon yielded several general conclusions. First, premature mortality owing to predation by bears and gulls could be substantial. Second, after we removed the covariation owing to arrival date, senescent jacks lived as long on the spawning grounds as senescent non-jack males. Jacks were susceptible to both mortality sources, whereas premature mortality on non-jack males was primarily due to bear predation. Third, after removing the covariation owing to arrival date, we found that the reproductive life-span of jacks exceeded that of non-jack males that died prematurely. Fourth, after considering all sources of mortality (senescent or premature mortality), we again found that jacks lived longer than older males. Taken together, these results indicate that at the very least the reproductive life-span of jacks cannot be assumed to be significantly shorter than non-jack males.

Gross (1985) found that jacks did not live as long as non-jack males on the spawning grounds. However, van den Berghe and Gross (1986) found no difference in reproductive life-span between jacks and non-jack males ($p = 0.20$) from the same study site. The lack of difference in reproductive life-span which we observed only strengthens Gross's original finding that disruptive selection has led to the evolution of alternative male life-history strategies in salmon. That is, if there had been no difference in reproductive life-span in his original study, the estimated fitness of jacks would actually have exceeded that of non-jack males based on the calculations by Gross (1985). Although it has subsequently been shown that equal fitness is not a necessary precursor for the maintenance of alternative polymorphs within a population (e.g., Repka and Gross 1995; Gross and Repka 1998), estimates of fitness are still central to any theoretical investigation of the appearance and maintenance of alternative life-history strategies.

Fig. 4. Relationship between reproductive life-span (mean ± SD) and body length (in 10-mm bins) for the subset of senescent non-jack males (open bars). The second *y* axis displays the relationship between body length and the percentage of non-jack males in a given length bin that spent 2 years in the ocean (solid line; one minus this percentage represents the percentage of non-jack males that spent 3 years in the ocean).



van den Berghe and Gross (1986) found that "season" (i.e., arrival date) was a significant predictor of female and age-3 male life-span from simple regressions. However, in attempting to explain the observed longevity of females, age-3 males (i.e., non-jack males), and jacks, the authors employed a stepwise multiple regression analysis using numerous abiotic and biotic factors as predictor variables. From the multiple regression, arrival date ("season") did not contribute significantly to life-span. Consequently, they concluded that the result from the simple regression was most likely spurious. Rather, they found that body size was a significant predictor of life-span in females for both years and in non-jack males for 1 of 2 years. Interestingly, they found that the life-span of jacks could not be explained by any of their predictor variables.

We found a significant negative relationship between arrival timing on the spawning grounds and reproductive life-span of senescent individuals (Fig. 3A) that was consistent with many other studies of Pacific salmon (Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; Dickerson et al. 2002). Furthermore, the breeding life-span of senescent individuals did not increase with body length (Fig. 4). In particular, senescent jacks and non-jack males had similar breeding life-spans for a given arrival date (adjusted mean life-span and 95% CI of $9.37 \le 10.36 \le 11.35$ and $9.89 \le 10.41 \le 10.94$ for jacks and non-jack males, respectively). This suggests that older males cannot be assumed to live longer than jacks on the spawning grounds, even in the absence of size-selective mortality agents such as bears.

Although breeding life-span for a given arrival date did not differ between the two life-history forms, differences in arrival patterns between jacks and non-jack males could lead to differences in "realized" longevity. Our daily surveys indicated that jacks were not among the first males to arrive (Figs. 3A, 3B). This might result from the scarcity of jacks (i.e., less likely to be observed first) or from an actual difference in arrival timing. To disentangle the two explanations, we compared median arrival dates. All jacks arriving in 2002–2004 were tagged and the arrival pattern was therefore known. The arrival of tagged males did not fully represent the arrival pattern of non-jack males, so we estimated arrival from daily counts of live and dead salmon in the entire creek throughout the season. All carcasses were removed from the stream channel each day to avoid repeat counting, allowing us to estimate the number of fish arriving each day as $(\text{live}_t + \text{dead}_t) - \text{live}_{t-1}$, where t represents the day of the run. By these methods we estimated median arrival dates of 1 August for both jacks and older males. Thus, jacks are not observed as the first-arriving or the last-arriving males, but the distribution of arrival dates is centered around the same date as that of the much more numerous older males.

Given that a year when many fish were killed by bears (e.g., 2001) or gulls (e.g., 2002) might skew the results (e.g., few fish live out their senescent life-span in such years), we took caution to collect data over multiple years. Conditions ranged considerably over the six spawning seasons included in this analysis. For instance, spawner abundance ranged from a low of 1 976 in 2001 to a high of 19 970 in 1999. Predation intensities were also quite variable. Over the six spawning periods included in this analysis, bear predation ranged from 44% to 88% on tagged non-jack males, and gull predation on jacks ranged from 14% to 69%.

Premature mortality in the form of bear predation, gull predation, and in-stream stranding strongly affected in-stream longevity of jacks and non-jack males within Hansen Creek. For the subset of individuals that died prematurely, the reproductive life-span of jacks exceeded that of non-jack males ($p < 0.001$). Although two sources of predation substantially truncated the reproductive life-span of jacks (i.e., gulls and bears), only bears were a significant source of mortality on non-jack males (Table 1).

General observations of behavior of jacks and non-jack males provided some insight into differences in mortality. Males typically form size-structured dominance hierarchies around sexually active females, with larger males gaining closest proximity to the focal female (Foote et al. 1997; Healey and Prince 1998). Jacks employ a different strategy altogether, i.e., they gain access to females by sneaking fertilizations instead of fighting for position and access to females (Gross 1985). Jacks sneak in and occupy the area adjacent to the female during egg deposition (Foote et al. 1997). Hansen Creek is shallow and relatively devoid of woody debris and structure. Jacks made use of undercut banks and often situated themselves adjacent to redds to maintain proximity to ripe females. Larger individuals were more visible in the shallow water and had very few predation refuges within this particular creek. Jacks were often observed being chased by females. Movement data suggests that jacks stay in the same general vicinity and that their movement patterns do not differ from non-jack males (H.B. Rich, Jr., S.M. Carlson, and T.P. Quinn, unpublished data).

The rates of predation by bears on sockeye salmon in the streams of the Wood River lakes are primarily determined by stream size (higher percentages of the fish are killed in small streams such as Hansen Creek than in larger creeks; Quinn et al. 2001) and density (higher percentages of the fish are killed when densities are low; Quinn et al. 2003). The rates of predation observed in this study are thus consistent with what we observe in this region, given the size of the stream and densities of salmon. Bear predation is size selective (i.e., larger salmon are more vulnerable than smaller ones; Quinn and Kinnison 1999; Ruggerone et al. 2000; Quinn and Buck 2001), so the lower rate of predation on jacks was not unexpected.

Gulls are a less-common source of mortality. Quinn and Buck (2000) documented scavenging by bears and gulls on Hansen Creek sockeye salmon, and Mossman (1958) and Mathisen (1962) reported gull predation on adult sockeye salmon (primarily females) in Hansen Creek. The prevalence of gull predation may be restricted to Hansen Creek and other similarly shallow creeks, as we see few gull-killed fish in larger creeks. Thus, the attributes that make this stream ideal for observing salmon also may increase the susceptibility of jacks to predation by gulls, and larger salmon to bears. To the extent that gull predation is unique to Hansen Creek, predation pressure and premature mortality in general are probably much lower for jacks than non-jack males because bears tend to kill larger fish. In streams with size-selective bear predation and no predation by gulls on jacks, the overall reproductive life-span of jacks might routinely exceed that of older males.

Evolutionary implications

The model presented by Gross (1985) indicated similar mean fitness for jacks and older males in coho salmon, despite the shorter breeding life of jacks. Our finding (comparable reproductive life-span regardless of male life-history type) gives the jacks an advantage, assuming the other components of the equation are true. The first component was survival to maturity, and it was assumed that jacks have an advantage because they spend less time at sea. The chronology of mortality at sea is not known with certainty, but various lines of evidence (and intuition) indicate that mortality rates are highest on the salmon as they enter the ocean and diminish as they grow (Ricker 1976). In this case the survival advantage of jacks might not be high because they would still spend a full year at sea before returning. On the other hand, the largest smolts are most likely to become jacks, and large smolts are also most likely to survive at sea (e.g., Henderson and Cass 1991). Gross (1985) estimated the other component of the equation, fertilization success, from the proximity of males to the female at the moment of egg release. Parentage studies reveal that alternative male life-history types can fertilize a significant fraction of the eggs (reviewed by Fleming and Reynolds 2004), though distance from the female is probably not a very accurate estimator.

In summary, the alternative life-history pathways of male salmon are a fascinating aspect of the biology of these fishes. Our evidence that the reproductive life-span of jacks was comparable with that of much larger males (about 4–5 times their mass) contributes to the perspective that they may exist in frequency-dependent balance with older males. A deeper understanding of these alternative pathways will benefit from further studies of (*i*) the realized reproductive success of these small males (e.g., with parentage analysis) in natural situations; (*ii*) the interplay between genetic and environmental controls of growth rate, smolt size, and the "decision" to mature as jacks; and (*iii*) the factors responsible for variation in the proportion of jacks among different populations and species of salmon.

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