The evolutionary effects of bear predation on salmon life history and morphology

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This is to certify that I have examined this copy of a doctoral dissertation by

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Abstract

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The power of selection to drive evolution has captivated evolutionary biologists since Darwin. It is often noted that conspecific populations differ in phenotypic traits, and divergent selection appears to be a critical force generating this biological diversity. Until recently, most research focused on the role of resource competition in driving divergence but other factors may also be important. The overarching goal of my dissertation research was to examine the role of natural selection in the form of predation in driving adaptive population divergence.

To achieve this goal, I investigated the effects of predation from bears on the evolution of salmon. My research was carried out on sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lakes system in southwestern Alaska. Previous research in this system has demonstrated that the percent of salmon killed by bears varies among populations, as does the tendency of bears to kill salmon early or late in their reproductive life. This previous research laid the foundation for my research because it allowed me to test whether trait divergence among populations was related to the local predation intensity.

I employed a comparative approach to quantify trait divergence among populations, and to then relate trait divergence to predation intensity. I focused on salmon life history traits (reproductive lifespan, rates of senescence) as well as morphological traits (body size and shape). My results demonstrate that among population variation in senescence rates, body size and shape is closely associated with the degree of predation experienced. In particular, variation in senescence was related to the extent to which bears killed salmon that exhibited little senescence; populations senesce at slower rates when they have been historically exposed to bear predation that selectively targets fish showing more advanced senescence. Variation in body size and shape was also related to the intensity of bear predation; populations are smaller and more shallow-bodied when they have been exposed to more intense bear predation. In general, my dissertation research contributed to a small but growing body of research demonstrating the importance of divergent selection due to predation in driving adaptive population divergence.

Introduction

The power of natural selection to drive biological diversity has fascinated biologists since the time of Darwin. While it is often noted that populations of the same species differ greatly in phenotypic traits it remains ultimately unclear what underpins these findings. Divergent selection (e.g., due to predation) is often invoked to explain phenotypic differentiation among conspecific populations (Schluter 2000; Vamosi 2005). A classic example is provided by Trinidadian guppies (*Poecilia reticulata*); male color patterns (Endler 1980, 1995), life history traits (Reznick and Endler 1982; Reznick et al. 1996; Reznick et al. 2004), and locomotor performance (O'Steen et al. 2002; Ghalambor et al. 2004) all vary among sites with different levels of predation. Threespine stickleback, *Gasterosteus aculeatus*, are another example; populations vary in life-history traits, armor, and size as a function of predation intensity (Reimchen 1991, 1994; Walker 1997; Vamosi and Schluter 2004). This and other research has greatly advanced our understanding of the importance of divergent selection due to predation in driving adaptive population divergence; however, several key questions remain unanswered. The overarching goal of my dissertation was to tackle some of these questions. Herein, I provide a brief overview of three outstanding questions in evolutionary biology, introduce the study system, present the predictions that I formulated and tested, and provide a summary of my results.

Three key questions

Does condition-dependent predation drive senescence variation among natural populations?

Senescence, the post-maturation physiological deterioration associated with aging, is revealed by age-specific declines in reproductive performance or survival. The evolutionary theory of senescence (ETS) suggests that senescence is caused by the decreasing strength of selection with advancing age (Medawar 1952; Williams 1957; Hamilton 1966). In populations experiencing high extrinsic rates of mortality, senescence rates are predicted to increase due to the accumulation of mutations that *a*) are deleterious but expressed only late in life (mutation accumulation) (Medawar 1952) or *b*) improve early-life fitness at the expense of late-life fitness (antagonistic pleiotropy) (Williams 1957). These mutations accumulate because their deleterious effects are not expressed until late in life, few individuals reach advanced ages in nature, and consequently selection has little substrate to act on and the mutations persist.

One of the primary predictions of the evolutionary theory of senescence is that populations experiencing high rates of extrinsic mortality should also evolve faster rates of senescence rates than populations experiencing relatively lower rates of extrinsic mortality (Williams 1957). This prediction has received broad support from a number of studies showing that rates of senescence tend to increase as rates of extrinisic mortality also increase (Austad 1993; Tatar et al. 1997; Dudycha and Tessier 1999; Dudycha 2001; Reznick et al. 2001; Bryant and Reznick 2004). Nevertheless, a number of recent studies have produced conflicting results (Williams and Day 2003; Reznick et al. 2004). Inherent in the above simple version of the ETS is that covariance between individual senescence and susceptibility to extrinsic mortality is negligible. And yet it follows that individuals that senesce rapidly might weaken and therefore become more susceptible to extrinsic mortality (i.e., condition-dependent mortality). Indeed, recent theoretical (Williams and

Day 2003) and empirical (Reznick et al. 2004) work suggests that the presence of such covariance can lead to deviations from the standard predictions of the ETS that senescence rates should increase with increasing rates of extrinsic mortality. To date, no work has formally evaluated the relative importance of condition-independent (classic ETS) versus condition-dependent mortality in driving among population senescence variation. I attempted to tackle this challenge in the first two chapters of my dissertation. by comparing reproductive life span and rates of senescence in salmon populations subject to bear predation. In chapter 1, I show that reproductive lifespan does not vary between ages or sexes within a population, which facilitated a test of among population variation. In chapter 2, I show that condition-dependent predation from bears drives senescence variation in natural populations of salmon.

Which mechanism, mutation accumulation or antagonistic pleiotropy, leads to senescence in natural populations of salmon?

Studies which document a trade-off between early and late life performance (i.e., increased senescence) are generally interpreted as evidence of antagonistic pleiotropy (Partridge and Gems 2002). Laboratory studies, particularly on the fruit fly, *Drosophila melanogaster,* tend to provide support for role of antagonistic pleiotropy (reviewed in (Partridge 2001; Partridge and Gems 2002)). However, few studies have tested the critical prediction of a trade-off between early-life and late-life performance in nature (but see ((Dudycha and Tessier 1999; Hendry et al. 2004). My third chapter demonstrates a trade-off between reproductive investment and future survival (senescence rates) in salmon populations and thereby provides support for the importance of antagonistic pleiotropy in natural populations.

Does variation in selection imposed by bears drive morphological divergence among salmon populations?

To reiterate, divergent selection appears to be a critical force driving adaptive divergence. In particular, phenotypic differentiation may arise due to divergent selection acting *a*) within a population due to resource limitation or *b*) among populations due to differences in environment (Schluter 2000). Regarding the former process, research on Darwin's ground finches (*Geospiza* spp. (Schluter and Grant 1984)), crossbills (*Loxia curvirostra* complex (Benkman 2003)), and threespine stickleback (Schluter 1995) have verified the importance of resource competition in driving adaptive radiation. Regarding the latter process, few studies have actually tested whether selection pressures are truly divergent in differing environments. The aforementioned research on guppies and stickleback, for instance, all demonstrated that qualitative differences in predation influence trait divergence among populations. Two notable exceptions exist – both published in recent months. Svennson et al. (2006) demonstrated the importance of divergent *sexual* selection in driving adaptive population divergence of damselflies (*Calopteryx splendens*) while Nosil and Crespi (2006) demonstrated that divergent *natural* selection in the form of predation could drive the adaptive divergence of walking sticks (*Timema cristinae*). In chapter 4, I show that divergent selection in the form of bear predation has driven phenotypic differentiation in the morphology (body size and shape) of salmon populations.

The system and study sites

Pacific salmon

Pacific salmon (*Oncorhynchus* spp.) have a complicated life history involving both anadromy (migration to the ocean) and semelparity (single breeding bout). Pacific salmon are a useful system for studying the factors that drive adaptive population divergence for a number of reasons. First, salmon are philopatric and, as such, they form discrete breeding populations that are then subject to differing conditions on the breeding grounds. Second, these populations are broadly distributed and, consequently, are found in a wide variety of breeding habitats (creeks, rivers, lake beaches) and rearing habitats (creeks, rivers, lakes, estuaries, ocean)(Quinn 2005) thus exposing them to disparate environments/selective regimes. Third, though gene flow (a process which can impede the adaptive process) occurs between populations, it appears to be limited between proximate salmon populations (e.g., (Gustafson et al. 1997)). Thus, their strong homing tendency provides an opportunity to study how divergent natural selection between environments can drive adaptation to local conditions. Indeed, considerable intraspecific variation exists in phenotypic traits that presumably reflect evolutionary adaptation to these local breeding and rearing environments (Taylor 1991; Quinn et al. 2001b).

Sockeye salmon

My dissertation research focused on sockeye salmon, *Oncorhynchus nerka*, because populations of this species are known to differ in many traits including age composition, size-at-age, and the extent of sexual dimorphism (Quinn et al. 2001b). In

North America, sockeye salmon range from the Columbia River in the south to Alaska in the north. They lay their eggs in the gravel of streams, rivers and lake beaches in late summer and fall. Embryos incubate for several months prior to hatching, after which they complete yolk-sac absorption and then migrate to a nursery lake where the feed for 1-2 years prior to migrating to the ocean. After 1-3 years in the North Pacific Ocean, individuals migrate back to their natal habitat, attempt to reproduce, and die. Like all Pacific salmon, sockeye salmon are capital breeders and so rely on stored energy to fuel future metabolism. In the absence of a premature death (i.e., due to predation, parasites, or stranding in areas of low water), they live approximately 1-3 weeks on the breeding grounds prior to senescent death (McPhee and Quinn 1998; Hendry et al. 1999; Carlson et al. 2004). My research focused exclusively on this period when the salmon were on the breeding grounds.

The Wood River system

The Wood River system in southwestern Alaska has over 50 discrete breeding populations of sockeye salmon. Many of the populations in this system breed in creeks where they are vulnerable to intense predation from brown bears (Quinn et al. 2001b). Previous research has demonstrated that the percent of salmon killed by bears in a given population is a function of both habitat attributes (the percent killed decreases as stream width increases)(Quinn et al. 2001b) and the density of breeding salmon (the percent killed decreases as the density of salmon increases)(Gende et al. 2004). Moreover, this predation is clearly a selective force because bear predation is size selective (Quinn and Kinnison 1999; Ruggerone et al. 2000) and sex selective (Quinn and Kinnison 1999). To study the evolutionary effects of bear predation on sockeye salmon, I studied six salmon populations within the Wood River system that differed in the percent of salmon killed but little else other than the physical habitat attribute of creek size that controls predation. Specifically, all populations breed in creeks, have similarly easy migrations from the ocean (Burgner 1991), and migrate from the ocean to freshwater during the same time of the year (late June – early July)(Hodgson and Quinn 2002). Moreover, in these creeks, sockeye salmon are either the only salmon species present, or they constitute > 99% (Fisheries Research Institute, unpublished data).

Predictions

Given the hypothesized role of bear predation in driving the adaptive population divergence of sockeye salmon populations, I formulated and tested the following predictions:

Prediction 1: Reproductive lifespan does not differ *within* a population between salmon of different marine ages or between males and females.

Prediction 2: Senescence rates vary *among* salmon populations.

Prediction 3: The percent of salmon killed by bears varies *among* populations.

Prediction 4: The tendency of bears to kill salmon that recently arrived on the spawning grounds (little senescence) versus those that arrived much earlier (advanced senescence) varies *among* salmon populations.

Prediction 5: Among population variation in rates of senescence reflects the tendency of bears to kill salmon exhibiting advanced senescence, and not simply the percent of bear-killed salmon in a given population.

Prediction 6: Among population variation in rates of senescence parallel among population variation in total and mass-specific somatic and gonadal energy; populations with the most rapid senescence are predicted to invest relatively more energy into gonadal stores than populations with reduced rates of senescence.

Prediction 7: The strength and form of natural selection acting on body size (length) and body shape (body depth and jaw length) varies *among* salmon populations.

Prediction 8: Among population variation in the strength of directional selection parallels the among population variation in the intensity of bear predation.

Prediction 9: Among population variation in the strength of directional selection parallels trait divergence among populations.

The first through sixth predictions allowed a test of the evolutionary effect of bear predation on salmon life history (rates of senescence). In particular, the first prediction (intra-population variation in reproductive lifespan) set the stage for testing the second prediction (inter-population variation). The third and fourth predictions facilitated a test of the fifth prediction (can we explain variation in senescence rates?). The sixth prediction allowed a test of the ultimate cause of inter-population variation in senescence rates. The final three predictions facilitated a test of the evolutionary effect of bear predation on salmon morphology (body size and shape). In particular, the seventh prediction enabled a formal test of whether selection is truly divergent among populations in different environments. The eighth prediction allowed a determination of whether the mechanism of divergent selection was correctly identified. The final prediction permitted a test of whether the populations have attained evolutionary equilibrium (stabilizing selection around each population’s mean trait value) or whether differentiation is still ongoing (directional selection acting in each population to push the mean trait value toward the population’s adaptive peak).

Summary of the results

In chapter 1, I examined within population variation in reproductive lifespan to test the prediction that reproductive lifespan does not vary between ages or sexes within a population (*Prediction 1*). Previous work on Pacific salmon has demonstrated that individuals that arrive on the breeding grounds relatively early live longer than their later arriving counterparts (Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; Dickerson et al. 2002). To account for this known source of variation, I followed the fates of individually tagged salmon that entered the stream to breed over a range of arrival dates. For the subset of senescent individuals (i.e., those not killed by bears), I found no difference in reproductive lifespan between males that had spent one year in the ocean versus those that had spent 2-3 years in the ocean (Figure 1.3), after controlling for arrival date. Moreover, I found no difference in the reproductive lifespan of males and females, after removing the known variation in reproductive lifespan due to arrival date.

In chapter 2, I quantified among population variation in senescence rates (*Prediction 2*), the percent of salmon killed by bears (*Prediction 3*), and the tendency of bears to remove fish exhibiting little senescence (i.e., fish that recently arrived on the breeding grounds; *Prediction 4*). All three of these parameters varied among populations, facilitating a test of the importance of condition-independent (percent killed) versus the condition-dependent (tendency of bears to kill salmon showing little/advanced senescence) mortality to driving senescence variation among natural populations (*Prediction 5*). Senescence was closely associated with the degree of condition-dependent mortality (bears killing salmon exhibiting advanced senescence; Figure 2.6A), and not by the rate of extrinsic mortality (percent of salmon killed by bears; Figure 2.6B).

In chapter 3, I explored the ultimate cause of senescence variation in natural populations of salmon: mutation accumulation or antagonistic pleiotropy. In general, a trade-off between early-life performance and late-life performance (i.e., senescence) is interpreted as evidence in favor of antagonistic pleiotropy but few studies have tested for this critical trade-off in natural populations. To test for evidence of this trade-off (*Prediction 6*), I sacrificed twenty early arriving males from four salmon populations and used bomb calorimetry to estimate the energy density (i.e., mass-specific energy, $kJ \cdot g^{-1}$) and total energy (mass × energy density) of the somatic and gonadal tissues. My results demonstrate that the population exhibiting the most rapid senescence also had elevated gonadal energy density (Table 3.4). This result contributes to a small but growing body of work suggesting that antagonistic pleiotropy leads to senescence in natural populations.

In chapter 4, I estimated selection due to bear predation in three salmon populations, which enabled a test of whether selection was divergent in different environments (*Prediction 7*). In particular, I estimated the strength and form of selection acting on salmon body size and shape in each population. My results show that the form of selection was consistent (directional) but that the direction and strength of selection differed among populations. The direction and magnitude of divergent selection was inversely related to the intensity of bear predation (*Prediction 8*); the salmon population subject to the most intense predation had the strongest selection favoring short and shallow-bodied individuals (Table 4.4, Figures 4.4-4.5) whereas the population subject to the least intense predation had the strongest selection favoring long and deep-bodied individuals (Table 4.4, Figures 4.4-4.5). Moreover, the former population is characterized by the smallest individuals overall whereas the latter population is characterized by the largest individuals overall (Figure 4.3; *Prediction 9*). I conclude that divergent selection due to bear predation can be an important force driving adaptive divergence of salmon populations.

Conclusion

The overarching goal of my dissertation research was to answer outstanding questions in evolutionary biology, focusing on the evolutionary effects of predators on their prey. I approached this goal by studying the effects of bear predation on salmon life history and morphology. Predation is notoriously difficult to study in wild populations and my work benefited immensely from previous research in the Wood River system quantifying various aspects of the intensity of bear predation on salmon (e.g., percent killed, selectivity of bears for newly arrived fish). I used a comparative approach to test for trait divergence among populations, and then asked whether trait divergence reflected the intensity of bear predation. My research showed that among population variation in rates of senescence, body size and shape paralleled among population variation in the intensity of bear predation; salmon from populations that received intense bear predation exhibited rapid senescence and were relatively short and shallow-bodied compared to populations receiving reduced predation pressure. Perhaps most importantly, my dissertation research contributed to the growing body of research suggesting that predation can be a critical force driving adaptive population divergence.

Papers derived from this research

I. Carlson, S. M., Rich, H. B., Jr., and T. P. Quinn. 2004. Reproductive life-span and sources of mortality for alternative male life-history strategies in sockeye salmon, *Oncorhynchus nerka*. Can. J. Zool. 82: 1878-1885.

II. Carlson, S. M., Hilborn, R., Hendry, A. P., and T. P. Quinn. In review. Condition-dependent predation by bears drives senescence in natural populations of salmon. Proc. R. Soc. Lond. B.

III. Carlson, S. M., Shearer, K., and T. P. Quinn. In preparation. Senescence variation in natural populations of salmon: the role of energy reserves and energy allocation. Intended for Evol. Ecol. Res.

IV. Carlson, S. M., Rich, H. B., Jr., and T. P. Quinn. In review. Does variation in selection imposed by bears drive divergence among populations in the size and shape of sockeye salmon? Evolution.

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Chapter 1: Reproductive lifespan and sources of mortality for alternative male life history strategies in sockeye salmon, *Oncorhynchus nerka*

Synopsis

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 lifespan 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 lifespan of male sockeye salmon (Oncorhynchus nerka Walbaum, 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 lifespans ($p = 0.932$). Jacks were less susceptible to premature mortality (mostly from bears and gulls) than older males. The lifespan 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 average lifespan 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.

Introduction

In a number of animal species, males display alternative life history strategies, 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., 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 (termed 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 (termed 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 of jacks among populations (Young 1999; Healey et al. 2000; Quinn et al. 2001b), 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 average 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 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 lifespan 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 lifespan needs to explicitly consider arrival date. Accordingly, the purpose of this study was to quantify the reproductive lifespan 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 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, 1792) are subject to predation from brown bears (*Ursus arctos* Linnaeus, 1758) and glaucous-winged gulls (*Larus glaucescens* Naumann, 1840; (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 lifespan (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 (Figure 1.1). Hansen Creek is approximately 2 km long and it averages 3.9 meters 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 (Zhous 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. 2001b), and 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 1999-2004 (Figure 1.2A) were used to corroborate the status (jack or non-jack) assigned to each fish in this study (Figure 1.2B).

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. Pre-spawning 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; Quinn unpublished data). As we were primarily concerned with reproductive lifespan 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: 1) senescent fish were easily identified by their drab coloration, frayed tail and fins, body scars, fungus, rough skin, and lack of penetrating wound marks; 2) in-stream stranded fish were also characterized by a lack of penetrating wounds but tended to be brightly colored, in fresh condition, and were found in shallow areas such as sand or gravel bars; 3) 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 4) gull pecked fish had distinctive radial chiseling wounds which 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 lifespan was then calculated as the date when it was observed dead minus the date of entry. Thus a fish that was observed alive for three consecutive days and then found dead would have a reproductive lifespan of four days, and one found dead on the first day in the stream would have a reproductive lifespan of one 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), 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, allowing us to compare reproductive lifespan among years that differed slightly in run timing. We removed the confounding effect of arrival date on reproductive lifespan by Analysis of Covariance (ANCOVA) with reproductive lifespan 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 lifespan for a common arrival date whereas differences in slope indicate that the relationship between arrival date and reproductive lifespan differed between the two groups. We first tested for differences in the slopes of the lines relating reproductive lifespan 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 lifespan 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 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 lifespan 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 lifespan at a common arrival date (Figure 1.3A). This revealed no difference in reproductive lifespan between jacks and non-jack males ($p = 0.932$; adjusted mean lifespan and 95% CI: $9.37 \leq 10.36 \leq 11.35$ and $9.89 \leq 10.41 \leq 10.94$ 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 lifespan ($n = 61$) did not differ significantly from that of the male salmon (when females are included in the analysis, $p = 0.982$; adjusted mean female lifespan and 95% CI: $9.97 \leq 10.59 \leq 11.22$ unpublished data).

Second, to test whether the lifespan of individuals killed prematurely (i.e., due to bear predation, gull predation, stranding) differed, we again employed an ANCOVA. A plot of lifespan versus arrival date for this subset of individuals indicated that the variance in lifespan decreased as a function of arrival date (Figure 1.3B). This pattern is not unexpected because, regardless of arrival date, the minimum possible lifespan is one day (for individuals killed their first day in the stream) but the maximum lifespan (i.e., lifespan for senescent individuals) decreases with time (Figure 1.3A). To account for the non-constant variance, we first log_e transformed the lifespan 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 lifespan at a common arrival date. This approach revealed that, for the subset of fish that died prematurely, the reproductive lifespan of jacks ($n = 49$) exceeded that of non-jack males ($n = 411$; $p < 0.001$). After re-transforming the adjusted mean and 95% confidence interval to the original units (i.e., e^(log_e (days) = days), this difference translated to an adjusted mean lifespan and 95% CI of: $3.42 \leq 4.21 \leq 5.18$ and $2.27 \leq 2.42 \leq 2.59$ for jacks and non-jack males, respectively.

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

Discussion

Our analysis of the reproductive lifespan and various sources of mortality for alternative male life history strategies in sockeye salmon yielded several general conclusions. First, premature mortality due to predation by bears and gulls could be substantial. Second, after we removed the covariation due 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 due to arrival date, we found that the reproductive lifespan 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 lifespan 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 lifespan between jacks and non-jack males ($p = 0.20$) from the same study site. The lack of difference in reproductive lifespan that 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 lifespan 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). While 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.

van den Berghe and Gross (1986) found that "season" (i.e., arrival date) was a significant predictor of female and age-3 male lifespan 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 step-wise multiple regression analysis using numerous abiotic and biotic factors as predictor variables. From the multiple regression, arrival date ("season") did not contribute significantly to lifespan. 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 lifespan in females for both years and in non-jack males for one of two years. Interestingly, they found that the lifespan 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 lifespan of senescent individuals (Figure 1.3A), 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 lifespan of senescent individuals did not increase with body length (Figure 1.4). In particular, senescent jacks and non-jack males had similar breeding lifespans for a given arrival date (adjusted mean lifespan and 95% CI of $9.37 \leq 10.36 \leq 11.35$ and $9.89 \leq 10.41 \leq 10.94$ 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 lifespan for a given arrival date did not differ between the two life history forms, differences in arrival patterns between jacks and non-jacks could lead to differences in “realized” longevity. Our daily surveys indicated that jacks were not among the first males to arrive (Figure 1.3A, 1.3B). 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 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 nor 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 lifespan 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% percent 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 male sockeye salmon within Hansen Creek. For the subset of individuals that died prematurely, the reproductive lifespan of jacks exceeded that of non-jack males ($p < 0.001$). While two sources of predation substantially truncated the reproductive lifespan of jacks (i.e., gulls and bears, Table 1), 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 - 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. Unpublished movement data suggests that jacks stay in the same general vicinity and that their movement patterns do not differ from non-jack males (Rich et al. 2006).

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. 2001b)) and density (higher percentages of the fish 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 (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 lifespan of jacks might routinely exceed that of older males.

Evolutionary Implications

The model presented by Gross (1985) indicated similar average fitness for jacks and older males in coho salmon, despite shorter breeding life of jacks. Our finding (comparable reproductive lifespan 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 lifespan of jacks was comparable to 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: 1) the realized reproductive success of these small males (e.g., with parentage analysis) in natural situations, 2) the interplay between genetic and environmental controls of growth rate, smolt size, and the “decision” to mature as jacks, and 3) the factors responsible for variation in the proportion of jacks among different populations and species of salmon.

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Table 1.1. Numbers of tagged male sockeye salmon recovered at death, categorized by mode of death in Hansen Creek, 1999 – 2004.

Year		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
	strand (%)	1.4	9.6	10.7	10.5	7.5	9.2
Jacks	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

Figure 1.1. Map of Lake Aleknagik and Hansen Creek relative to the Wood River Lakes, SW Alaska.

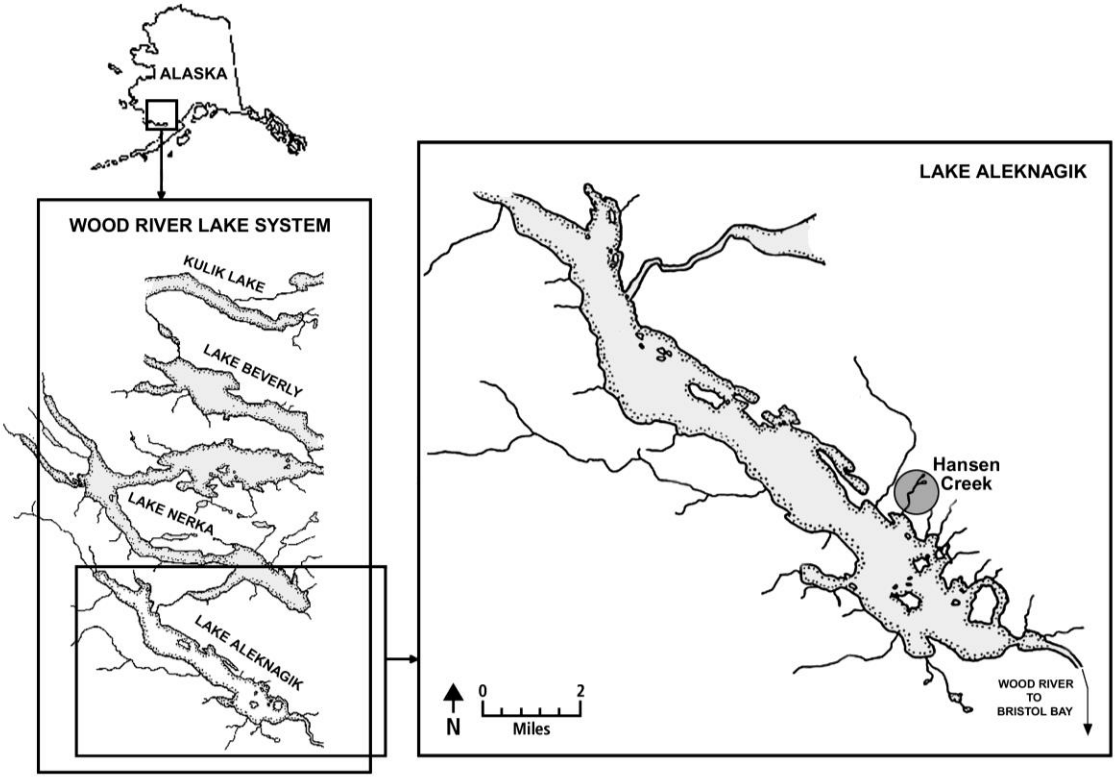
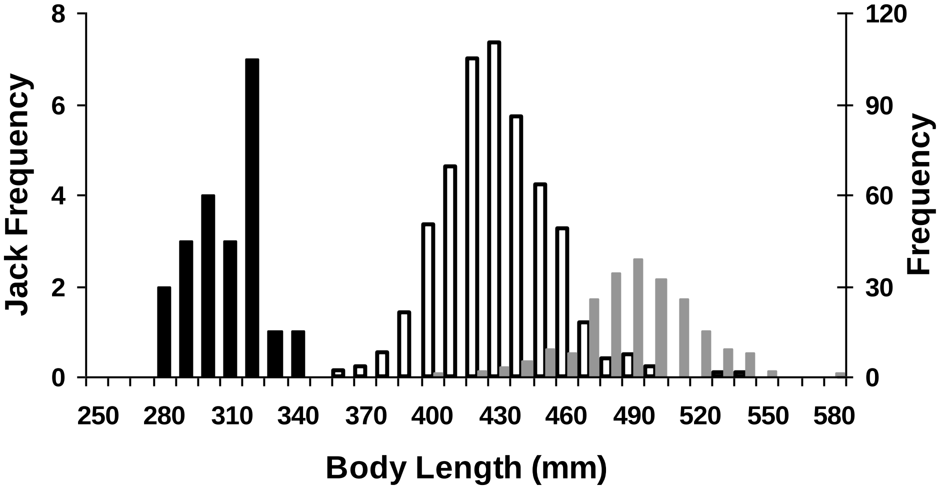


Figure 1.2. Length frequency histograms from Hansen Creek, 1999 – 2004. The top panel (2A) represents known-age male sockeye salmon determined from otolith sampling for ocean age 1 “jacks” (solid black bars), ocean age 2 (open bars), and ocean age 3 (solid gray bars) males. The bottom panel (2B) represents the inferred age of study fish based on length frequency distributions (jacks, solid bars; non-jack males, open bars).

A)



B)

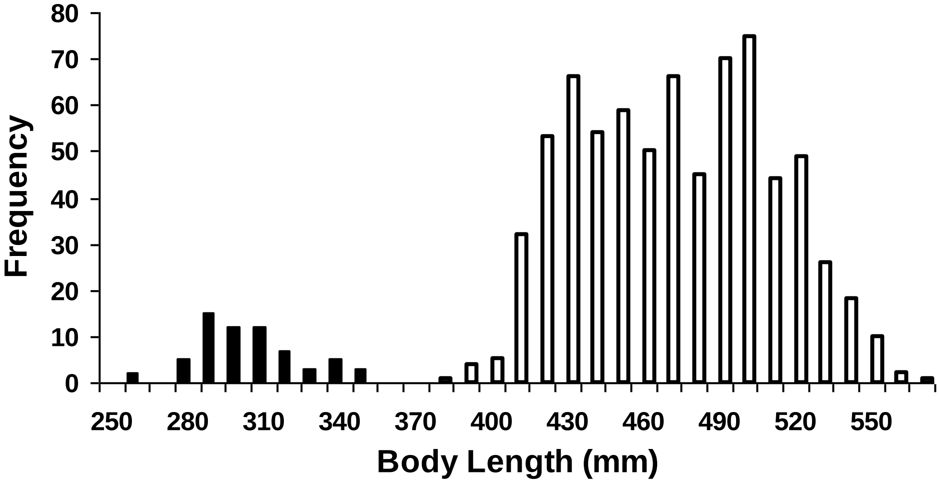


Figure 1.3. Relationship between reproductive lifespan and standardized arrival date for the subset of tagged sockeye salmon jacks (solid squares, solid line) and non-jack males (open diamonds, dashed lines) that were recovered as senescent dead (3A) or premature mortalities (3B) in Hansen Creek, AK. For the subset of senescent jacks, reproductive lifespan = -0.3729*arrival date + 14.66; n = 30; $r^2 = 0.32$. For senescent non-jack males: reproductive lifespan = -0.3141*arrival date + 13.93; n = 89; $r^2 = 0.16$. The bottom panel includes tagged jacks (n = 49) and non-jack males (n = 411) that died prematurely on the spawning grounds (bear killed, gull killed, or stranded).

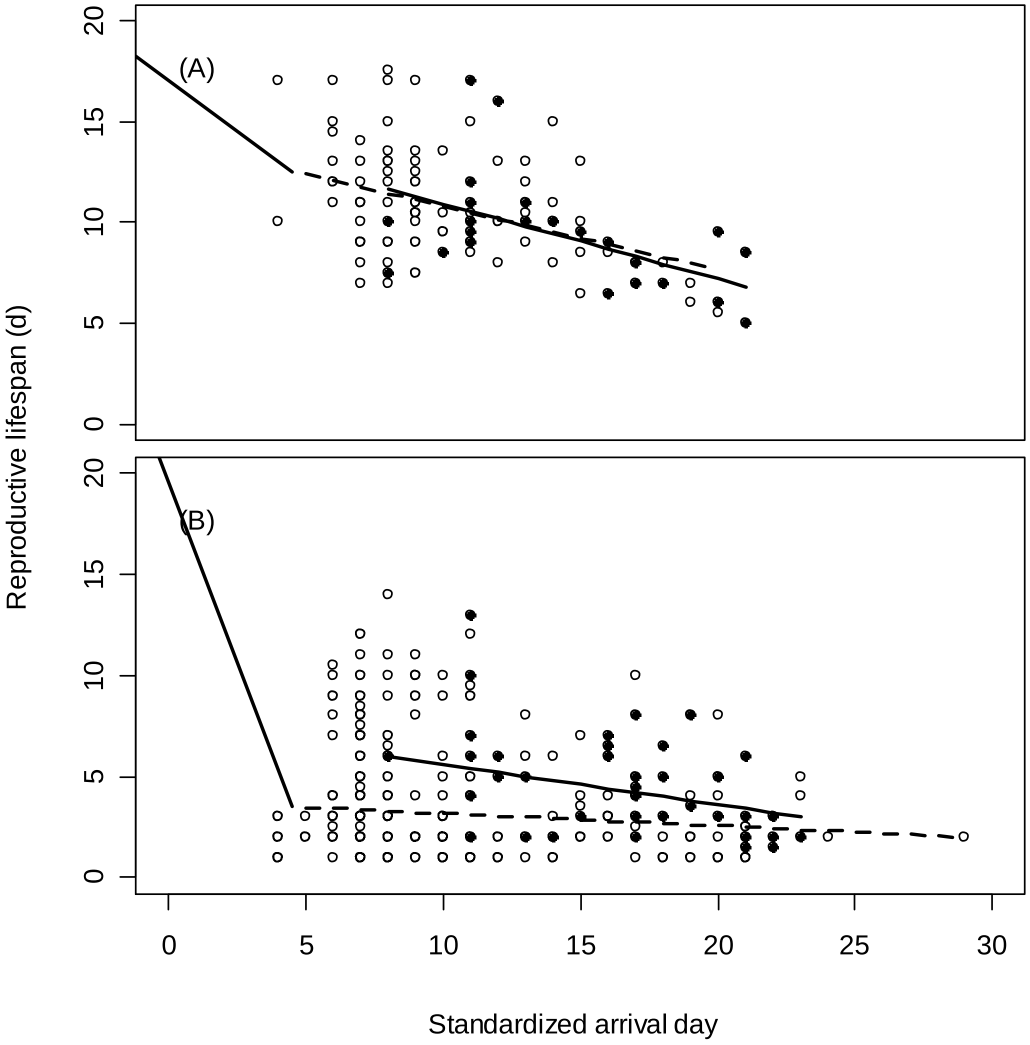
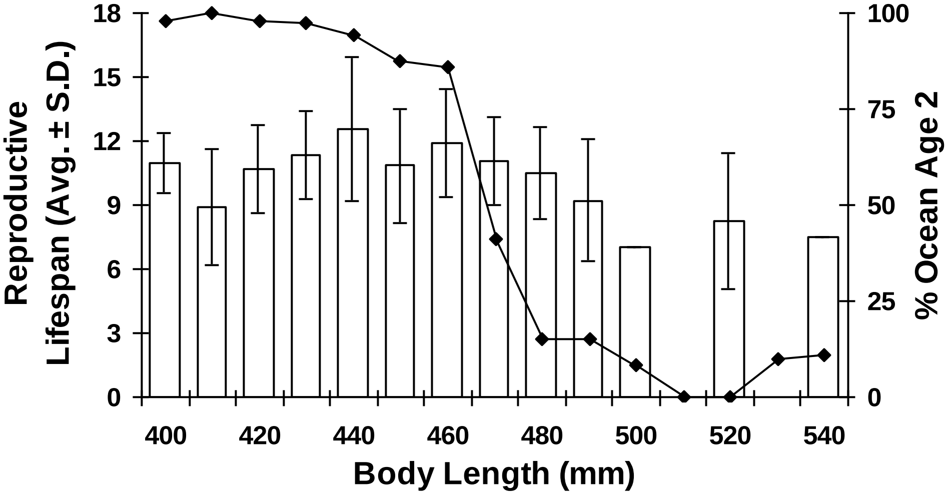


Figure 1.4. Relationship between reproductive lifespan and body length (in 10 mm bins) for the subset of senescent non-jack males (open bars). The second y-axis displays the relationship between body length and the percentage of non-jack males in a given length bin that spent two years in the ocean (solid line; one minus this % represents the % of non-jack males that spent three years in the ocean).



Chapter 2: Condition-dependent predation by bears drives senescence in natural populations of salmon

Synopsis

Evolutionary theory predicts that populations experiencing higher rates of environmentally caused ("extrinsic") mortality should senesce more rapidly, but this theory usually neglects the relationship between individual condition and extrinsic mortality. We here examine the causes of senescence rates in natural populations of sockeye salmon (*Oncorhynchus nerka*) subject to varying degrees of predation by brown bears (*Ursus arctos*). In particular, we relate senescence rates in six populations to their history of overall extrinsic mortality rates and degrees of condition-dependent mortality. Senescence rates are determined by modeling the mortality of individually-tagged breeding salmon at each site. The rate of extrinsic mortality is determined as the long-term average percentage of salmon killed by bears. The degree of condition-dependence in that mortality is determined as the extent to which bears kill salmon that exhibit little senescence. We show that variation in senescence is closely associated with the degree of condition-dependent mortality, and not by the rate of extrinsic mortality. Specifically, populations senesce at slower rates when they have been historically exposed to bear predation that selectively targets fish showing more advanced senescence. Our results show that condition-dependent susceptibility to extrinsic mortality may be a critical force driving senescence variation in natural populations.

Introduction

Senescence is the physiological deterioration associated with aging, and is manifest as declines in survival or reproductive performance with increasing age.

Senescence is thought to have its evolutionary origin in the action of environmentally caused mortality (hereafter "extrinsic mortality"), because this inevitably reduces the number of individuals reaching increasingly advanced ages. Older individuals should therefore be subject to weaker selection than should younger individuals, and so should contribute proportionally fewer genes to the next generation (Hamilton 1966; Baudisch 2005). Under these conditions, mutations should accumulate that (1) improve early-life performance even at the expense of late-life performance (antagonistic pleiotropy, (Williams 1957)) or (2) are deleterious only late in life (mutation accumulation, (Medawar 1952)). By extension, populations experiencing higher extrinsic mortality should be under weaker selection late in life, and might therefore evolve more rapid senescence (Medawar 1952; Williams 1957). This classic evolutionary theory of senescence (ETS) has received broad support from studies showing that populations or species subject to higher rates of extrinsic mortality typically show faster senescence (Austad 1993; Tatar et al. 1997; Dudycha and Tessier 1999; Dudycha 2001; Reznick et al. 2001; Bryant and Reznick 2004). And yet, opposing results in some recent work suggest that closer examination is necessary (Williams and Day 2003; Reznick et al. 2004; Bronikowski and Promisiow 2005; Williams et al. 2006).

The classic ETS assumes that the state of senescence for an individual at a given time does not influence its susceptibility to *extrinsic* mortality at that time (Williams 1957). And yet it seems likely that individuals at more advanced stages of senescence are in poorer condition, and are therefore more susceptible to extrinsic mortality, particularly that due to predation (i.e., condition-dependent mortality). Indeed, Abrams (1993) suggested that higher mortality should select for *decreased* senescence whenever traits sensitive to senescence increases susceptibility to extrinsic mortality. Recent theoretical (Williams and Day 2003) and empirical (Reznick *et al.* 2004) work further suggest that covariance between individual condition and extrinsic mortality can cause deviations from the classic ETS. To date, however, studies of senescence in nature have not evaluated the relative importance of extrinsic mortality per se (i.e., condition-independent) versus the degree of condition dependence in mortality. We did so by examining rates of senescence in sockeye salmon subject to predation by brown bears. If extrinsic mortality per se is most important (i.e., the classic ETS), senescence should be slower in salmon populations experiencing lower rates of predation. If, instead, condition-dependent mortality is most important (henceforth the "condition-dependent ETS"), senescence should be slower in salmon populations where bears selectively kill fish at more advanced stages of senescence. This last prediction arises because such populations would experience direct selection against senescence (Abrams 1993); i.e., individuals with less senescence at a given age will be favored by selection.

Pacific salmon have several features that commend them to the study of senescence in nature. First, they show true senescence in the form of a rapid physical deterioration from the time they start breeding until their death several weeks later (Hendry *et al.* 2004; Morbey *et al.* 2005). Second, they do not feed while breeding, and instead rely entirely on stored energy reserves. This "capital breeding" sets up a trade-off between energy saved as somatic stores to fuel metabolism versus that invested into gonads (females) or secondary sexual traits (males). Differential selection on the elements of this trade-off can then cause adaptive variation in senescence (Hendry *et al.* 1999; Hendry *et al.* 2004). Third, the start of breeding reliably demarcates the physiological starting point for assessing senescence (Hendry *et al.* 2004; Morbey *et al.* 2005).

Pacific salmon can also yield insights into the evolutionary importance of extrinsic mortality – because breeding adults are often subject to bear predation (Quinn and Kinnison 1999; Reimchen 2000; Ruggerone et al. 2000; Quinn and Buck 2001; Quinn et al. 2001a; Quinn et al. 2001b; Quinn et al. 2003; Gende and Quinn 2004; Gende et al. 2004). Moreover, this predation varies in intensity ("predation rate") and the degree to which it is condition-dependent ("predator selectively"). With regard to the former, bears kill up to 89 % of breeding salmon in some creeks but only 10 % in other creeks (Quinn *et al.* 2001b). With regard to the latter, bears selectively kill fish that have just started breeding ("little senescence") in some streams, but selectively kill fish that are about to die ("advanced senescence") in other streams (Gende *et al.* 2004). Fish showing little senescence should always be preferred because they have twice the energy density of fish showing advanced senescence (Hendry and Berg 1999; Gende et al. 2004). And yet fresh fish are more vigorous (Quinn and McPhee 1998) and therefore harder for bears to catch. Bears therefore kill salmon showing little senescence in streams where they are easy to catch (small and shallow creeks with few refuges for the fish) but salmon showing advanced senescence in streams were they are hard to catch (large and deep creeks with many refuges).

Our goal was to determine whether variation in senescence rates among salmon populations is associated with rates of extrinsic mortality or with the degree of condition-dependent mortality. We therefore selected sockeye salmon populations that varied in these aspects of predation, but little else; eventually settling on six creeks in the Wood

River Lakes system in southwestern Alaska (Figure 2.1). The fish in all of these populations return from the ocean at approximately the same time of year (Hodgson and Quinn 2002), and have easy upstream migrations (Burgner 1991). They also show evidence of local adaptation for some traits that might influence susceptibility to bear predation, such as body size and body depth (Quinn *et al.* 2001b). This adaptive divergence is facilitated by restrictions in gene flow among the populations (pair-wise FSTs based on microsatellites for three of our study populations range from 0.045 to 0.067, (Lin *et al.* In review). The presence of variation in selection imposed by bears, of limited gene flow among populations, and of local adaptations to bear predation, led us to predict local adaptation in senescence rates.

Our analyses were based on two data sets. The first was used to estimate predation rates and thereby extrinsic mortality rates. This data set was based on five decades of surveys that estimated the numbers of breeding salmon in each creek in each year. Starting in 1990, these surveys recorded the proportion of fish killed by bears (Quinn *et al.* 2001b). The second data set was used to estimate senescence rates and predator selectivity. This data set was based on 6,867 individually-tagged breeding salmon, with data for at least two years from each of the six creeks. Tagged fish were monitored from the day they started breeding until the day they died, an interval that defined their “reproductive lifespan” (Table 2.1). We also recorded the mode of death: senescence (n = 1,327) or predation by bears (n = 4,222). This combination of data sets allowed a direct test of the importance of the classic (condition-independent) versus a condition-dependent theory of senescence in driving senescence variation in natural populations.

Materials and Methods

Field sampling

Wood River sockeye salmon return from the ocean in late June, and then aggregate off the mouths of their natal creeks. They mature within a few weeks, enter the creek, and almost immediately start breeding (McPhee and Quinn 1998; Hendry et al. 1999). To ensure we monitored individuals from the onset of breeding, we capturing them in beach seines as they shoaled off the creek mouths (after which they entered the creeks volitionally), or with landing nets as they entered the creek. Each captured fish was tagged with an individually-coded, external disk tag (3 cm diameter), a procedure that does not have noticeable effects on subsequent survival or breeding behavior (McPhee and Quinn 1998; Hendry et al. 1999). We then determined the start of breeding for each fish (the day it entered the creek), and whether it was still present in the creek on each subsequent day. This was possible because all of the study creeks have very clear and often shallow water (Figure 2.2C), and are short enough that they can be surveyed completely in just a few hours.

Reproductive lifespan was calculated for each tagged fish as the number of days between creek entry and death. Death was assumed to occur the day after a fish was last seen alive, which was also typically coincident with the recovery of its carcass. Recovered carcasses manifest obvious indicators of the mode of death (McPhee and Quinn 1998; Hendry et al. 1999; Quinn and Kinnison 1999; Quinn et al. 2001a; Carlson et al. 2004; Hendry et al. 2004). *Gull-killed* salmon have distinctive radial chiseling wounds that penetrate the body cavity near the gill plates, vent, or pectoral fins. *Stranded* salmon lack penetrating wounds, show little signs of senescence, and are found in shallow areas of the creek (Figure 2.2B). *Bear-killed* salmon have large wounds and pieces of missing flesh (Figure 2.2C). *Senescent* salmon are emaciated, have frayed fins and rough skin, and lack penetrating wounds (Figure 2.2D). Based on these criteria, the mode of death could be unambiguously assigned to each tagged fish whose carcass was recovered. Tagged fish whose carcasses were not recovered were assumed to be bear-killed because bears frequently carry fish out of sight into the riparian zone (Reimchen 2000; Gende *et al.* 2004). Very few of the missing carcasses would be fish that died of senescence because the creeks have almost no areas where such carcasses would be obscured.

Data for Bear and Yako creeks were collected by SMC (Bear: 2003, *n* = 387; 2004, *n* = 542; Yako: 2003, *n* = 364; 2004, *n* = 599). Data for A and C creeks were collected by RH (A: 1998, *n* = 318; 2001, *n* = 225; 2004, *n* = 453; 2005, *n* = 439; C: 1998, *n* = 595; 2001, *n* = 381; 2004, *n* = 422; 2005, *n* = 300). Data for Pick Creek were collected by APH (1995, *n* = 247; 1996, *n* = 347). Data for Hansen Creek were collected by TPQ (1999, *n* = 126; 2000, *n* = 174; 2001, *n* = 173; 2002, *n* = 168; 2003, *n* = 205; 2004, *n* = 161; 2005, *n* = 241). The data for all creeks and years are directly comparable because the methods were identical, and because all investigators were trained by the same person (TPQ).

Predation rate (extrinsic mortality rate)

The annual predation rate for a creek (percentage of all breeding adults killed by bears) can be reliably estimated based on a single survey during the peak of the breeding season ((Quinn *et al.* 2001b); Figure 2.3). This estimate is obtained as the average of two proportions: (1) the total number of salmon killed by bears divided by the cumulative number of dead salmon (bear-killed + senescent dead), and (2) the cumulative number salmon killed by bears divided by the sum of the total number of live salmon and the cumulative number of dead salmon (Figure 2.3). We used this established method to estimate annual predation rates for each creek (Table 2.2).

Predator selectivity (condition-dependent mortality)

Sockeye salmon usually enter a given creek over a period of 2 to 5 weeks (Hendry *et al.* 1999). On most days, bears are therefore presented with a range of fish of different "in-stream ages". A fish's "in-stream age" on any given day was the number of days since it had entered the creek, a length of time that accurately reflects that individual's stage of senescence. We estimated predator selectivity based on the number of salmon of varying in-stream ages that were killed by bears. This method allowed estimation of the probability of being killed as a function of the number of days spent in the stream (i.e., in-stream age), *given* survival up to that day. Details of the method are provided in Gende et al. (2004), and its application to the present data is described in the appendix. The results were then combined for each stream into an overall index of the degree to which predators select fish showing little senescence. This index was the average predation rate on individual fish during their first three days of breeding in the creek (Table 2.3). It would also be possible to generate an index based on the degree to which predators select fish showing *advanced* senescence, but the former index is preferable because it is based on many more fish (Gende *et al.* (2004). Note that salmon showing little and advanced senescence are simultaneously present on each day throughout much of the season (Gende *et al.* 2004), and we here examined to what extent bears select between fish of different in-stream ages on a given date.

Senescence rates

Senescence rates were evaluated by modeling survival probabilities with respect to in-stream age. We used the Weibull model (Crawley 2002) for this purpose according to the convention of several recent studies (Tatar et al. 1997; Dudycha and Tessier 1999; Hendry et al. 2004). This model is particularly appropriate for comparisons among populations because the rate of senescence parameter (ω, described below) is independent of extrinsic mortality (Ricklefs and Scheuerlein 2002). The Weibull model has two parameters that define the hazard function (the probability of dying given that the individual survived up to that time): α, which represents the shape of the function, and λ, which represents the magnitude of the hazard given its shape.

In the Weibull model, the *survivor function* is the proportion of individuals from the initial cohort that is still alive at some future time, *t* (Crawley 2002):

$$(1) \qquad S(t) = e^{-\lambda t^{\alpha}}$$

The *density function* is the probability of dying in any interval (i.e., in-stream age) (Crawley 2002):

$$(2) \qquad f(t) = \alpha \lambda t^{\alpha - 1} e^{-\lambda t^{\alpha}}$$

The *hazard function* is then the probability of dying given that the individual survived up to that time (Crawley 2002):

(3) $$h(t) = \frac{f(t)}{S(t)} = \alpha\lambda t^{\alpha-1}$$

When $\alpha = 1$, the Weibull distribution simplifies to the *exponential* (constant hazard) *distribution*, wherein hazard is equal to λ and does not increase with age (i.e., no senescence). When $\alpha > 1$, hazard increases with age and represents true senescence (Tatar et al. 1997; Ricklefs and Scheuerlein 2001, 2002). We therefore compared the fit of a model in which $\alpha = 1$ to models where it was estimated from the data.

Because α and λ are not independent, Ricklefs (1998) introduced a new parameter, ω (see also (Ricklefs and Scheuerlein 2001, 2002)), that provides a shape-adjusted index of the rate of senescence. This parameter has units of time^{-1} and is calculated as:

(4) $$\omega = \lambda^{\frac{1}{\alpha+1}}.$$

Models of senescence must account for individuals whose date of senescent death is not known. Data for tagged individuals therefore included uncensored observations (senescent carcass recovered) or censored observations (bear-killed, gull-killed, stranded or still alive at the end of the study). When dealing with censored data, the appropriate likelihood function is (Allison 1995; Crawley 2002):

(5) $$L = \prod_{i=1}^{n} \left[f(t_i) \right]^{w_i} \left[S(t_i) \right]^{1-w_i}$$

where *f(t)* represents the probability density function of choice, *S(t)* represents the associated survivor function, *w* represents the censoring indicator, *i* represents the individual, and *n* represents the total number of individuals. Below, we have substituted the Weibull density and survivor functions into the likelihood:

(6) $$L = \prod_{i=1}^{n} \left[\alpha \lambda t_i^{a-1} e^{-\lambda t_i^{a}} \right]^{w_i} \left[e^{-\lambda t_i^{a}} \right]^{1-w_i}$$

The censoring indicator can take on values of one (not censored) or zero (censored).

For the subset of individuals recovered as senescent carcasses (i.e., not censored, $w = 1$), the likelihood function simplifies to the density function, *f(t)*. For individuals that died of other causes (i.e., censored, $w = 0$), the likelihood function simplifies to the survival function, *S(t)*. Thus, if an individual has died of senescence, we gain information regarding the density function, whereas if the individual has died of other causes, we gain information about the survivor function (Allison 1995; Crawley 2002). The total negative likelihood (NLL) for a given model can then be computed by taking the negative of the likelihoods summed across all individuals.

Senescence rates were compared among populations by examining models that included or excluded creek-specific α and λ parameters (Table 2.3). These models also included “day of entry” parameters because early breeders senesce slower than late breeders (Hendry *et al.* 2004). The “day of entry” factor (*R*) for individual *i* was:

(7) $$R_i = e^{\left(b_{c_i} \lfloor E_i - \overline{E}_{c_i} \rfloor \right)}$$

where the subscript *c* indicates creek-specific parameter values, b_{c_i} determines how day of entry affects the probability of senescence, E_i is the day of entry for individual *i*, and $\overline{E}_{c_i}$ is the average day of entry for all individuals in the creek of the focal (i^{th}) individual. In the simplest model, we estimated a single lambda for all populations. In the most complex model, lambda was calculated as:

(8) $$\lambda_i = \lambda_{c_i} R_i \,.$$

The fit of alternative models to the data were formally compared based on Akaike's Information Criterion (AIC) (Hilborn and Mangel 1997; Burnham and Anderson 2002):

(9) $$AIC_i = 2NLL(Y \mid M_i) + 2P_i$$

where *NLL* is the negative log likelihood for a given model (M_i) given the data (*Y*), and *P* is the number of parameters in that model. We compared seven models to test for a) evidence of senescence, b) the influence of day of entry within a creek on senescence, and c) variation among populations in the rate of senescence. AIC values for our alternative models always differed by at least 15 (Table 2.3), which indicates much stronger support for the model with the lower AIC value (Burnham and Anderson 2002).

Results

The six populations differed markedly in predation rate, estimated as the average annual percentage of breeding salmon killed by bears, and predator selectively, estimated as the average predicted daily predation rate for individual salmon during their first three days in the stream (Table 2.2). Predation rate was lowest for Bear, Pick, and Yako creeks, intermediate for Hansen Creek, and highest for "A" and "C" creeks. Based on this variation, the classic ETS would predict that senescence should be slowest in Bear, Pick, and Yako creeks, intermediate in Hansen Creek, and fastest in A and C creeks. On the other hand, predator selectivity for salmon showing little senescence was lowest for Pick Creek, intermediate for Bear, C, and Yako creeks, and highest for Hansen and A creeks (Table 2.2; Figure 2.4). Based on this variation, the condition-dependent ETS would predict that senescence should be slowest in Pick Creek, intermediate in Bear, C, and Yako creeks, and fastest in Hansen and A creeks.

Comparisons of senescence models (Table 2.3) yield the following conclusions. First, our populations manifest true senescence; because models II – VII, in which α was estimated to be greater than unity (true senescence), fit the data much better than did model I, in which α was set to unity (no senescence). Second, fish that entered a stream later in the breeding season showed more rapid senescence because models III – VII, which included day of entry parameters, always fit the data much better than did models I – II, which did not include these parameters. Third, senescence rates varied dramatically among populations because models V – VII, in which α and/or λ parameters varied among populations, always fit the data much better than did models I – IV, in which these parameters did not vary among populations.

Model VII, in which both α and λ varied among the populations, was the best model (Table 2.3) and its likelihood function was:

$$L = \prod_{i=1}^{n} \left[\alpha_{c_i} \lambda_i t_i^{\alpha_{c_i}-1} e^{-\lambda_i t_i^{\alpha_{c_i}}} \right]^{w_i} \left[e^{-\lambda_i t_i^{\alpha_{c_i}}} \right]^{1-w_i} \quad (10)$$

where α_{c_i} represents the α parameter in the creek of the ith individual, λ_i is determined as in equation 8, t_i represents the age at death (in days) of the ith individual, and w_i represents the censoring indicator.

Age-specific hazards based on this model for individual i at time x were then calculated as:

$$h(x) = \alpha_{c_i} \lambda_i x^{\alpha_{c_i}-1} \quad (11)$$

Parameter values from this model were used in generating population-specific hazards (Figure 2.5) and in calculating the index of senescence rates (ω in Table 2.4). This index revealed that senescence was slowest in Pick Creek, intermediate in A, Yako, Bear, and C creeks, and fastest in Hansen Creek (Table 2.4; Figure 2.6). Although we focus on model VII as it was the best model, estimates from models V (only α varies among populations) and model VI (only λ varies among populations) yielded similar conclusions (Table 2.5).

We next formally tested whether variation in senescence rates among populations was better explained by the classic ETS or the condition-dependent ETS. To do so, we regressed ω against predation rate (Figure 2.6A) or predator selectivity (Figure 2.6B). Contradicting the classic ETS, senescence was unrelated to predation rate ($r^2 = 0.040$, $p = 0.704$, Figure 2.6A). Supporting the condition-dependent ETS, senescence was faster in populations where bears selectively kill salmon showing little senescence ($r^2 = 0.819$, $p = 0.0131$, Figure 2.6B). These results held using alternative metrics for senescence: population-specific α's assuming a constant λ (model V, rate: $r^2 = 0.036$, $p = 0.721$; selectivity: $r^2 = 0.817$, $p = 0.0134$) or population-specific λ's assuming a constant α (model VI, rate: $r^2 = 0.036$, $p = 0.720$; selectivity: $r^2 = 0.823$, $p = 0.0125$).

Discussion

We have demonstrated that variation in predation by brown bears is closely associated with senescence rates in natural populations of sockeye salmon. The classic evolutionary theory of senescence would predict that the cause of this relationship was variation in rates of extrinsic mortality (i.e., Williams' hypothesis (Williams 1957)). And yet this was not the case because senescence rates were not associated with overall predation rates. The condition-dependent theory of senescence would predict that the cause of this relationship was variation in the degree to which bears select salmon that show different degrees of senescence (Abrams 1993; Williams and Day 2003). This does seem to be the case because senescence rates were positively correlated with the degree to which bears selectively kill salmon showing little senescence. This finding supports previous suggestions that senescence rates should decrease when predators directly select against individuals exhibiting advanced senescence (Abrams 1993).

An outstanding question is whether the observed patterns of senescence are the result of genetic differences or phenotypic plasticity? The typical approach to addressing this question in other taxa might be a common-garden experiment (Tatar et al. 1997; Dudycha and Tessier 1999; Dudycha 2001; Bryant and Reznick 2004), which is not feasible in sockeye salmon due to their large body size (~ 2-4 kg) and late maturity (~ 4-6 years). We have instead taken the approach of examining senescence rates in nature (Austad 1993; Bryant and Reznick 2004; Hendry et al. 2004; Morbey et al. 2005), while controlling or testing for possible effects of environmental effects.

This approach demonstrated that environmental factors other than bear predation did not drive the observed senescence rate variation in our study. First, regional environmental factors, such as day length, parasites, and water chemistry, vary little among our populations owing to their geographical proximity (Figure 2.1). Second, the timing of entry into fresh water does not vary appreciably among these populations (Hodgson and Quinn 2002). Third, environmental conditions that do vary among populations are not correlated with senescence: ω versus water temperature ($r^2 = 0.28$, $p = 0.281$; Table 2.2), migration distance ($r^2 = 0.25$, $p = 0.315$; Table 2.2), and elevation (r^2

= 0.23, $p = 0.338$; Table 2.2). Fourth, other forms of mortality, such as predation by gulls or "stranding", account for relatively few of the deaths (6.3%, Table 2.1), and so we attribute variation in extrinsic mortality to variation in the intensity of bear predation among populations. Finally, the one environmental feature (water depth) that did correlate with senescence ($r^2 = 0.58$, $p = 0.081$) was the likely driver of variation in condition-dependent mortality (Gende *et al.* 2004). That is, it is easier for bears to catch fish in shallow streams (Quinn *et al.* 2001b) and so it is here that they can express selectivity for salmon showing little senescence (Gende *et al.* 2004). We therefore expect that the observed differences among populations reflect genetically-based evolutionary responses to condition-dependent mortality imposed by bears.

Why do some studies provide strong support for the classic ETS (Austad 1993; Tatar et al. 1997; Dudycha and Tessier 1999; Dudycha 2001; Reznick et al. 2001; Bryant and Reznick 2004), whereas others do not (Williams and Day 2003; Reznick et al. 2004). Among several possibilities, our results yield insight into the role of condition-dependent mortality. Specifically, we suggest that rates of extrinsic mortality may vary in parallel with the degree of condition-dependent mortality in some systems but not others. For example, when few individuals are killed, those showing advanced senescence may be most vulnerable, but when many individuals are killed, those showing less senescence may be accessible. In our case, the two aspects of predation were not correlated ($r^2 = 0.28$, $p = 0.276$). For example, the rate of predation is much lower in Hansen Creek (49%) than in C Creek (79%), but predator selectivity is much higher in Hansen Creek (0.175) than in C Creek (0.087). This decoupling of predation rate and predator selectivity shows the greater importance of the latter. Perhaps the previous studies providing support for the classic ETS were dealing with systems where extrinsic mortality rates were correlated with the degree of condition-dependent mortality. Further empirical data from natural systems, combined with theoretical models incorporating condition-dependent extrinsic mortality, are needed to test the above idea and reconcile recent exceptions to the classic ETS.

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Table 2.1. Sample sizes and reproductive lifespans in relation to mode of death and population. The mode of death "other" includes individuals that died owing to gull predation or that stranded in areas of low water. Censored individuals either died prematurely (i.e., from predation or stranding) or were still alive at the end of the study.

	Mode of death (N)			Reproductive lifespan (average ± S.D.)			Censored
Creek	Senescent	Bear-killed	Other	Senescent	Bear-killed	Other	N
A	248	828	65	12.65 ± 3.64	4.36 ± 3.57	6.02 ± 4.4	294
Bear	164	718	28	13.43 ± 4.01	8.40 ± 5.03	7.29 ± 4.31	19
C	261	889	30	12.9 ± 3.86	7.36 ± 5.06	5.57 ± 4.12	518
Hansen	226	753	258	10.72 ± 2.84	3.47 ± 2.82	2.18 ± 1.89	11
Pick	276	263	31	18.46 ± 5.12	11.98 ± 6.77	8.71 ± 5.96	24
Yako	152	771	24	11.59 ± 2.84	7.16 ± 4.29	7.08 ± 3.28	16

Table 2.2. Physical habitat attributes, predation rate, and predator selectivity for each creek. Creek temperatures were measured during the breeding period via hand-held thermometers and data loggers. Values are the average and SD across days within a year. Migration distances were measured as the shortest straight-line water distance from the mouth of each focal creek to the ocean. Migration elevation gain was measured as meters above sea level for the lake into which the focal creek drains (Burgner 1991). Predation rate represents the average of the yearly percent of breeding salmon killed by bears. The standard deviation represents the among year variation in the percent of salmon killed by bears. Predator selectivity for salmon showing little senescence represents the average predicted predation rate for the first full three days in-stream (± SD, *n* = 3).

Creek	Width	Depth	Creek temperature (ºC)	Migration distance	Migration elevation gain	Predation rate (%)		Predator selectivity for salmon showing little senescence
	(m)	(cm)	mean ± S.D.	(km)	(m)	mean ± S.D.	N	mean ± S.D.
A	1.4	10.0	5.93 ± 0.63	106	23	88.42 ± 14.57	5	0.165 ± 0.005
Bear	5.1	19.3	9.28 ± 0.92	44	10	29.8 ± 12.35	16	0.067 ± 0.008
C	2.1	10.0	7.21 ± 0.89	106	23	78.72 ± 24.82	5	0.087 ± 0.004
Hansen	3.9	9.8	10.83 ± 1.01	42	10	48.56 ± 20.00	18	0.175 ± 0.006
Pick	7.6	37.9	7.36 ± 0.88	98	21	34.56 ± 15.93	17	0.024 ± 0.001
Yako	4.2	22.6	7.79 ± 0.44	39	10	29.58 ± 12.38	15	0.091 ± 0.010

Table 2.3. Candidate models for explaining variation in senescence. Listed is the general model structure, the negative log-likelihood (NLL), the number of parameters (No. parameters), and Akaike's Information Criterion (AIC).

Model	NLL	No. Parameters	AIC
I. α = 1, same λ for all creeks	6,211.50	1	12,425.00
II. Same α and λ for all creeks	4,807.23	2	9,618.47
III. Same day of entry (b), α, λ parameter for all creeks	4,698.21	3	9,402.42
IV. Different b for each creek, same α and λ	4,684.57	7	9,383.14
V. Different b and α parameters for each creek, same λ	4,382.78	12	8,789.56
VI. Different b and λ parameters for each creek, same α	4,375.23	12	8,774.46
VII. Different b, α, and λ parameters for each creek	4,359.71	17	8,753.41

Table 2.4. Parameter estimates for α, λ, and ω (with 95% confidence bounds based on likelihood profiles (Hilborn and Mangel 1997)) derived from our best model (i.e., model VII, Table 2.3).

Population	α	λ	ω
A	4.73	2.57E-06	0.102 ≤ 0.106 ≤ 0.110
Bear	3.93	9.45E-06	0.092 ≤ 0.096 ≤ 0.100
C	4.33	3.61E-06	0.092 ≤ 0.095 ≤ 0.099
Hansen	4.55	1.03E-05	0.121 ≤ 0.126 ≤ 0.131
Pick	5.50	5.48E-08	0.074 ≤ 0.076 ≤ 0.079
Yako	5.05	1.12E-06	0.100 ≤ 0.104 ≤ 0.108

Table 2.5. Parameter estimates for *α*, *λ*, and *ω* derived from the second- and third-best models: model V (constant *λ*, population-specific *α*'s) and model VI (constant *α*, population-specific *λ*'s). Variation among populations in *ω* is here due entirely to variation in *α* (model V) or variation in *λ* (model VI).

	Model V			Model VI		
Population	*α*	*λ*	*ω*	*α*	*λ*	*ω*
A	4.717	2.66E-06	0.106	4.61	3.54E-06	0.107
Bear	4.383	2.66E-06	0.092	4.61	1.45E-06	0.091
C	4.445	2.66E-06	0.095	4.61	1.7E-06	0.094
Hansen	5.062	2.66E-06	0.120	4.61	8.75E-06	0.125
Pick	4.220	2.66E-06	0.085	4.61	7.99E-07	0.082
Yako	4.710	2.66E-06	0.106	4.61	3.37E-06	0.106

Figure 2.1. Locations of the six study populations in the Wood River Lakes, southwest Alaska, USA.

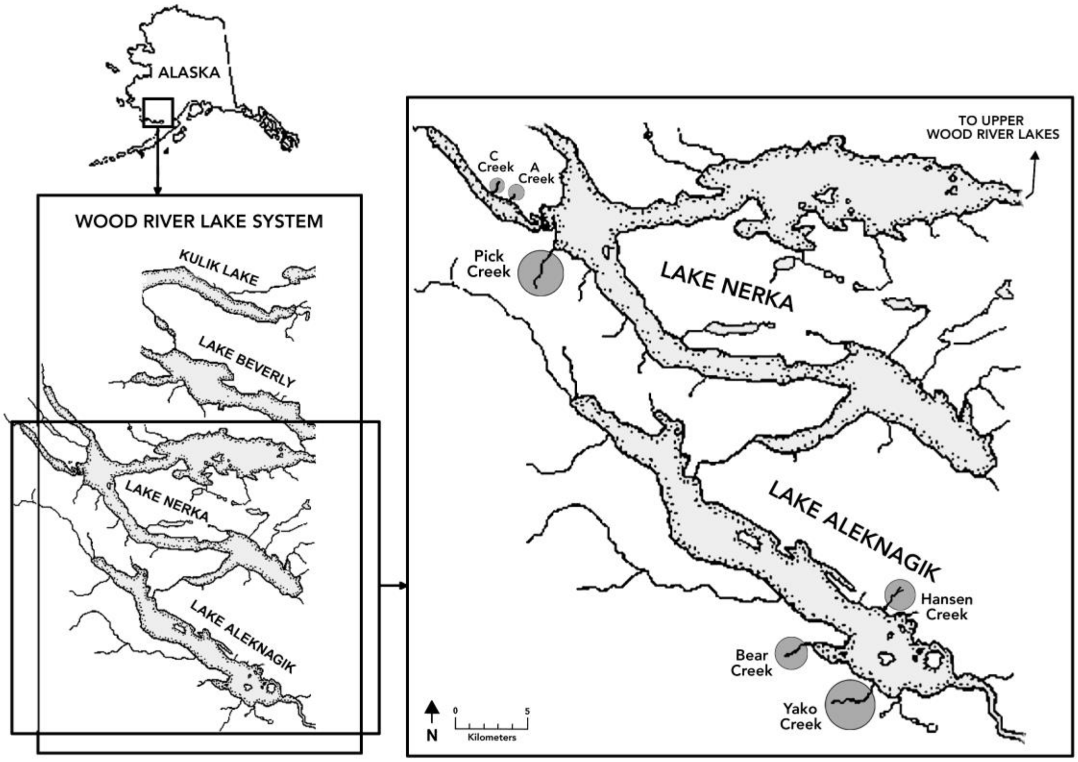


Figure 2.2. Photographs showing breeding sockeye salmon in various states. Panel (*a*) shows newly arrived sockeye salmon that show little senescence. Note their bright red coloration. Panel (*b*) shows salmon that have stranded in an area of low water (bottom left corner of panel *b*). Panel (*c*) shows a bear-killed male salmon. Panel (*d*) shows a senescent male (top) and female (bottom) salmon. Note their frayed fins, drab coloration, and general emaciated appearance relative to the newly arrived fish. Photographs by Ranae Holland (A, B) and Stephanie Carlson (C, D).

Figure 2.3. An illustration of the accuracy of our predation rate estimation method. The annual percentage of salmon killed by bears was estimated in each creek based on a single mid-season survey in which the total live and dead (partitioned by mode of death) fish were enumerated. This method was validated by reference to Hansen Creek, where these surveys are performed on each day of the breeding season. Panel (*a*) shows the daily predation rate estimates (black circles) calculated as the average of two quantities on that day: (1) the cumulative number of bear-killed salmon divided by the cumulative number of dead salmon (open circles), and (2) the cumulative number of bear-killed salmon divided by the sum of the cumulative number of dead salmon plus the live salmon on that day (grey circles). Note how stable the estimates are over the season and that they closely approximate the actual percentage of bear-killed fish over the entire breeding season (the final points). Panel (*b*) shows how a single daily estimate from August 6th each year is highly correlated with the actual percent of salmon killed over the entire breeding season in Hansen Creek ($r^2 = 0.88$; $n = 16$ years).

Figure 2.3. continued

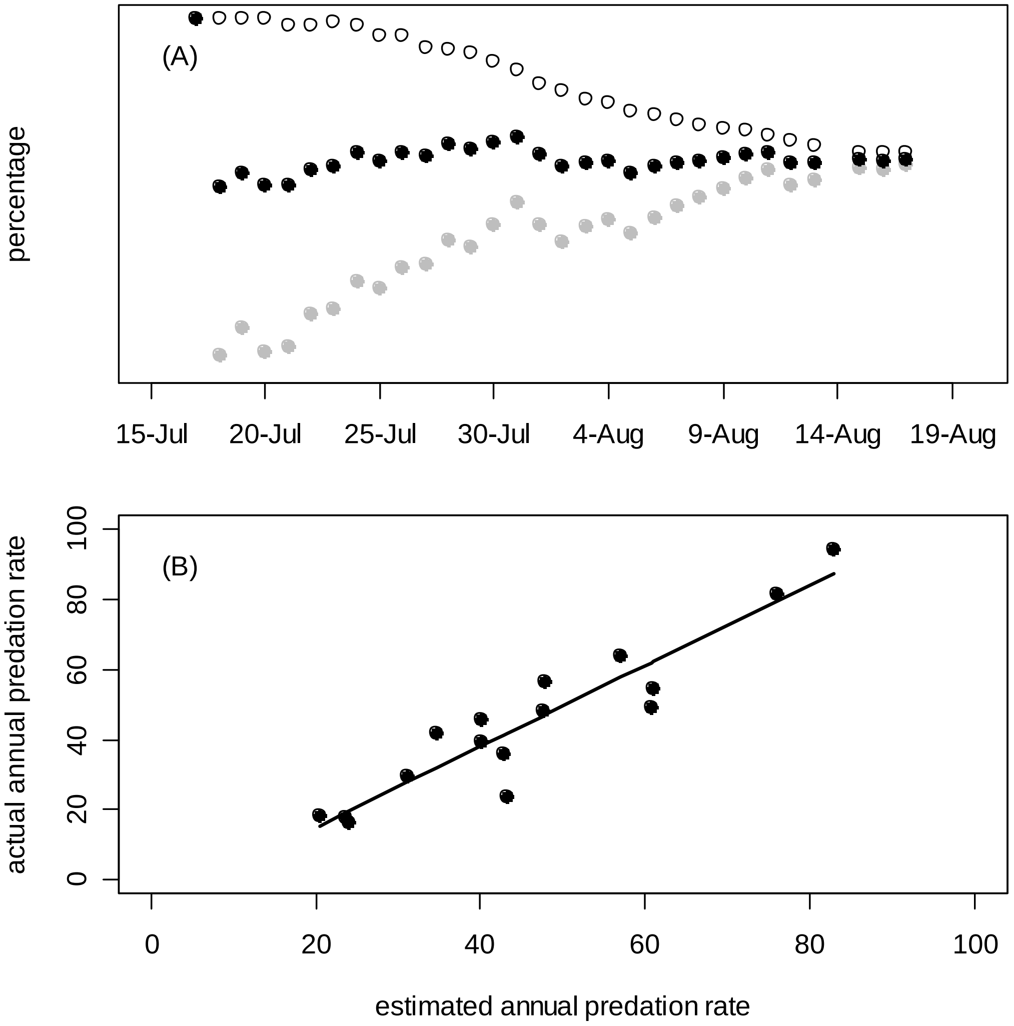


Figure 2.4. Population-specific predator selectivity for fish of different in-stream ages. Shown are proportions of the available fish of a given in-stream age (i.e., individuals that survived to day *d*) that are killed by bears in each creek. Our estimate of predator selectivity was the average of the predation rates on the first three days in the stream (i.e., the first three points in each panel). Note that the probability of being killed decreases within increasing age in Hansen and A creeks (i.e., bears selectively kill salmon showing little senescence), but increases to varying degrees in Bear, Hansen, Pick, and Yako creeks (i.e., bears selectively kill salmon showing more advanced senescence).

Figure 2.4. continued

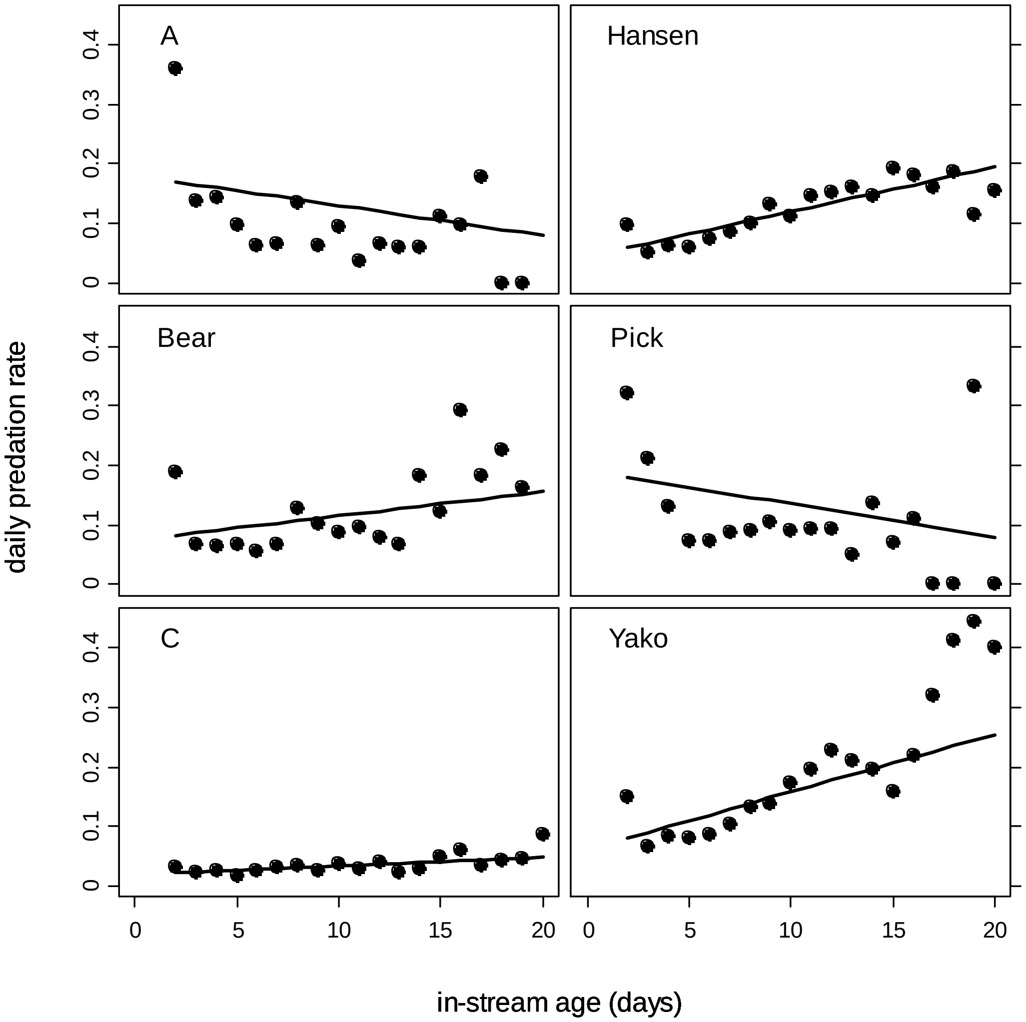


Figure 2.5. Population-specific hazard functions (y-axis) plotted against in-stream age (x-axis). These functions are based on a mean day of entry and on population-specific day of entry parameters. The higher the hazard for a given in-stream age, the greater the senescence rate at that age. The slopes of these lines represent variation in the shape of the hazard function (α) and the elevation of the lines represent variation in their magnitude given the shape (λ).

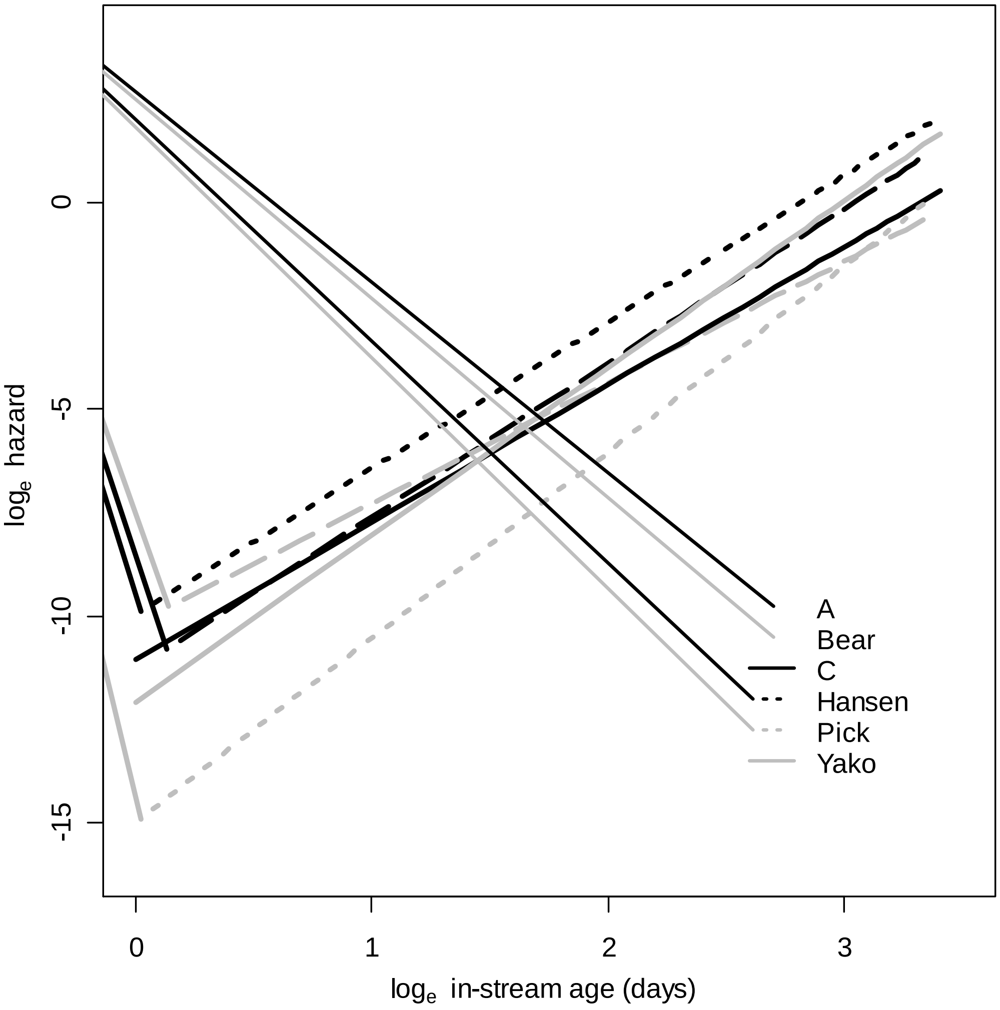
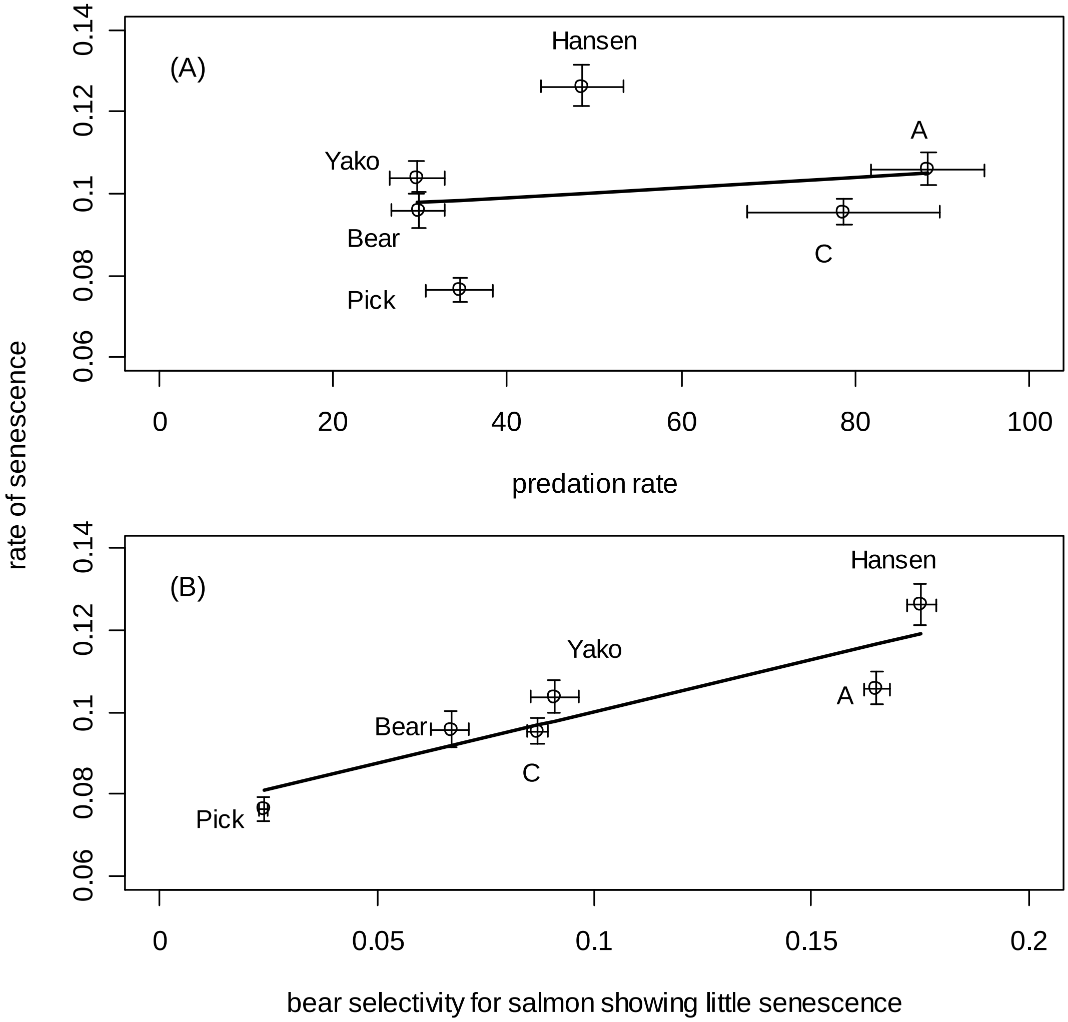


Figure 2.6. Senescence rates (ω ± 95% confidence intervals generated from likelihood profiles) (Hilborn and Mangel 1997) plotted against (*a*) predation rate (± SE across years) and (*b*) predator selectivity for salmon that show little senescence (± SE across the first three days in the stream).



Appendix

We used the method of Gende *et al*. (2004) to model predator selectivity (i.e., condition-dependent mortality) based on the number of salmon of different in-stream ages (*d* days) that were killed by bears. The observed predation rate (y_d) for individuals of a given in-stream age (*d*) was first calculated for each creek as:

$$(1) \qquad y_d = \frac{k_d}{a_d}$$

where k_d is the observed number of fish killed by bears of in-stream age of *d*, and a_d is the total number of fish of in-stream age of *d* that were available to the bears (i.e., the number of fish that had survived at least *d* days in the stream). The predicted predation rate ($\hat{y}_d$) on fish of a given in-stream age of *d* is then:

$$(2) \qquad \hat{y}_d = md + b$$

where *m* is the slope and *b* is the intercept of a linear regression between observed predation rates and in-stream age for a given creek. These predicted daily predation rates are shown in Figure 2.4.

As in Gende *et al*. (2004), we employed the negative binomial distribution to calculate the likelihood (*L*) of the predicted number of fish killed by bears given the observed number of kills and the overdispersion parameter, *p*.

$$(3) \qquad L(k_d \mid \hat{k}_d, p) = \left(\frac{\Gamma(p + k_d)}{\Gamma(k_d + 1)\Gamma(p)} \right) \left(\frac{\hat{k}_d}{\hat{k}_d + p} \right)^{k_d} \left(\frac{p}{p + \hat{k}_d} \right)^{p}$$

$$(4) \qquad \Gamma(x) = \int_0^{\infty} t^{x-1} e^{-t} dt$$

where k_d is the observed number of fish killed by bears of in-stream age of *d*, $\hat{k}_d$ is the predicted number of fish killed by bears of in-stream age of *d*, and *p* is the overdispersion parameter. The Γ function is another probability density function invoked when using the negative binomial distribution (Hilborn and Mangel 1997).

We next generated for each creek an estimate of overall "predator selectivity" with respect to in-stream age (i.e., state of senescence). This index was designed to avoid potential biases associated with (1) mortality before we were able to observe a fish (in its first day in the creek), and (2) variation among creeks in the availability of fish of different in-stream ages (owing to different rates of extrinsic mortality) (Gende *et al.* 2004). Specifically, we averaged the predicted age-specific predation rates across the first full three days in the stream (i.e., we excluded the day of stream entry). Thus, higher values of predator selectivity indicate stronger selection for fish showing little senescence.

Chapter 3: Senescence variation in natural populations of salmon: the role of energy reserves and energy allocation

Synopsis

Pacific salmon are renowned for the precipitous physical deterioration they undergo while spawning. Because Pacific salmon are capital breeders (cease feeding while breeding) and also semelparous (single breeding bout), they rely on stored energy to fuel their single reproductive season. Recent research has demonstrated that senescence rates differ among conspecific populations but whether these populations also differ in mass-specific energy of the somatic tissue, total energy (body mass × mass-specific energy), or whether a trade-off exists between energy devoted to current reproduction (i.e., to gonadal stores) versus energy devoted to future metabolism (i.e., somatic stores) all remain unknown. We tested these ideas by sampling males from four natural populations of sockeye salmon (*Oncorhynchus nerka*). Specifically, we quantified inter-population variation in 1) age- and size-at-maturity, 2) somatic tissue proximate composition (% ash, lipid, protein, water), 3) energy density (as partitioned between somatic tissues and testes), 4) energy reserves (energy density × mass), and 5) rates of senescence. We found that age- and size-at-maturity as well as percent lipid in the somatic tissues varied among natural populations of salmon. Inter-population variation in somatic energy paralleled variation in both body size and energy density of the somatic tissues. Of the populations we sampled, the population characterized by the most rapid senescence was also the population with the smallest body sizes, the lowest somatic energy density, the lowest total somatic energy but the highest gonadal energy density. Conversely, the population with the slowest rates of senescence were large, had higher

somatic energy density but less gonadal energy density. Our results thus suggest that senescence variation among natural populations of salmon was driven by both variation in total somatic energy as well as a trade-off between energy allocated to gonadal versus somatic tissues

Introduction

Senescence, the post-maturation physiological deterioration associated with the process of aging, is among the most fundamental life history traits. Two genetic mechanisms have been proposed by which senescence can evolve. The first, mutation accumulation (MA), suggests that mutations that are deleterious only in late-life will accumulate because few individuals will reach advanced ages precluding the removal of these deleterious mutations through selection (Medawar 1952). The second, antagonistic pleiotropy (AP), instead suggests that some of the mutations that are deleterious late in life will be favored by selection if they also improve early-life performance (Williams 1957). This occurs because early-life fitness contributes disproportionately more to overall fitness than late-life fitness. In general, studies that document a trade-off between early and late life performance (i.e., increased senescence) are interpreted as evidence of AP (Partridge and Gems 2002). Results of laboratory studies on *Drosophila melanogaster* tend to support AP rather than MA (reviewed in (Partridge 2001; Partridge and Gems 2002); but see (Hughes et al. 2002)).

Extensive variation in the senescence rates exist among conspecific populations in nature (Austad 1993; Tatar et al. 1997; Dudycha and Tessier 1999; Dudycha 2001; Reznick et al. 2001; Bryant and Reznick 2004; Reznick et al. 2004; Carlson et al. In review-a). Despite this variation, only two studies have attempted to test for a trade-off between current reproduction and future survival in nature. Dudycha and Tessier (1999) studied natural populations of zooplankton (*Daphnia pulex-pulicaria* species complex) existing on a habitat permanence gradient. Consistent with AP, they found that populations from ephemeral ponds (risky environments) had shorter life spans and steeper declines in fecundity than populations from more permanent lakes (safe environments) (Dudycha and Tessier 1999). Likewise, Hendry *et al*. (2004) asked whether AP could explain the observed variation in senescence rates within a population of semelparous sockeye salmon (*Oncorhynchus nerka* W.) by testing for a trade-off between energy devoted to future metabolism versus current reproduction. They found that early arriving females lived longer and commenced breeding with more somatic energy than their late-arriving counterparts but that the late arrivers allocated a relatively larger proportion of their total energy to their gonadal tissues. We here take a complementary approach to test whether population-specific energy allocation patterns between somatic and gonadal tissues differ among populations of sockeye salmon known to differ in their rates of senescence (Carlson et al. In review-a).

Pacific salmon are emerging as a model system for studying the evolutionary theory of senescence (Hendry et al. 2004; Morbey et al. 2005; Carlson et al. In review-a). This research has demonstrated that senescence rates vary both within populations (late arriving individuals senesce more rapidly their early arriving counterparts, (Hendry et al. 2004)) and among populations (Carlson et al. In review-a). Most relevant to this study, Carlson *et al*. (In review-a) demonstrated that rates of senescence varied among six spatially proximate populations of sockeye salmon and ascribed the differences to variability in the intensity of predation from brown bears (*Ursus arctos*). The question remains, however, whether the differences in senescence rates among populations represent a population-specific balance between energy devoted to future metabolism and energy devoted to current reproduction. Such trade-offs due to energy limitation are common and widespread in diverse organisms (Roff 1992; Stearns 1992).

Pacific salmon are renowned for the precipitous physical deterioration that they undergo while spawning, and consequently, they are also a model system for studying the physiological mechanisms of senescence. Mechanisms often invoked to explain the rapid deterioration of Pacific salmon include the depletion of energy stores (reviewed in (Dickhoff 1989)), elevated cortisol levels (e.g., (Barry et al. 2001)), and oxidative stress (e.g., (Sawada et al. 1993)). With regards to energy stores, previous work has shown that salmon lose up to 80% of their stored energy reserves during the migration and breeding period (Gilhousen 1980; Brett 1995; Hendry and Berg 1999). However, the amount of energy expended varies considerably among conspecific populations and is related to the difficulty of the migration (in terms of total distance migrated and/or elevation gain; e.g., (Hendry and Berg 1999; Kinnison et al. 2003; Crossin et al. 2004). Here, we controlled for this known source of inter-population variation by studying four proximate populations of salmon that all have relatively easy migrations from the ocean (Table 3.1).

We tested the following predictions regarding the role of energy reserves and energy allocation to rates of senescence in natural populations of salmon. First, because lipid can be readily mobilized as an energy source (Jobling 1994; Brett 1995), we predicted that lipid content varied among populations and was positively correlated with energy density (i.e., mass-specific energy, $kJ \bullet g^{-1}$). Second, we predicted that inter-population variation in rates of senescence were inversely related to inter-population variation in somatic energy density, body size, and total energy (energy density × somatic mass). Inter-population variation in total energy could arise for one of three reasons: 1) both somatic energy density and somatic mass varied among populations, 2) somatic energy density but not somatic mass varied among population (i.e., variation in *somatic energy density* drives differences in senescence), or 3) somatic mass but not somatic energy density varied among populations (i.e., variation in *somatic mass* drives differences in senescence). By measuring both body size and energy density of the somatic tissues, we were able to discriminate between these three alternatives. Finally, we predicted that senescence rates would be positively related to total and mass-specific gonadal energy, consistent with the AP theory of senescence.

Materials and methods

Study system

Sockeye salmon are semelparous; they cease feeding prior to breeding (capital breeders) and die after their single season of breeding in streams, rivers, or along the beaches of lakes. Juveniles typically rear in a lake for 1 or 2 years prior to migrating to the North Pacific Ocean where they spend another 1-3 years, gaining over 99% of their total body mass, before returning to freshwater to breed and die (Burgner 1991; Quinn 2005). Adults migrate back into freshwater during early summer, complete maturation near their natal sites, enter the breeding grounds where females compete for and prepare nest sites and males compete for access to females. In the absence of a premature death (e.g., due to predation), sockeye salmon undergo a rapid physical deterioration associated with senescence and die within 1-3 weeks (e.g., (McPhee and Quinn 1998; Hendry et al. 1999; Carlson et al. 2004)).

Study sites

We sampled four populations in the Wood River Lakes system of southwestern Alaska (Figure 3.1). Three of these populations breed in tributaries of Lake Aleknagik (Bear, Hansen, and Yako creeks), the southernmost lake in the Wood River Lakes system. The remaining population breeds in Pick Creek, draining into Lake Nerka, directly north of Lake Aleknagik. The senescence rates and energy reserves of individuals spawning in these populations are directly comparable because the populations are geographically proximate, the sockeye returning to these populations migrate from the ocean at approximately the same time of the year (late June – early July, (Hodgson and Quinn 2002), and these populations have non-arduous migrations from the ocean (both in terms of distance and elevation gain, Table 3.1) relative to conspecific populations (Burgner 1991).

Sample collection and processing

In 2004, 20 of the earliest arriving males reaching each stream to breed were captured in the stream and killed (total N = 80 males). All sampling occurred between the 15th and 19th of July (15 July: Yako; 17 July: Bear; 19 July: Hansen and Pick). We sampled the earliest arriving individuals from each population to standardize arrival timing to the breeding grounds as previous research has demonstrated that later arriving individuals have a shorter breeding lifespan than their early arriving counterparts (Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; Carlson et al. 2004) and that later arriving individuals commence breeding with reduced somatic energy stores relative to earlier arriving individuals (Hendry et al. 1999). Characteristics of these 80 fish are presented in Table 3.2. Each carcass was divided into somatic tissues (all body parts excluding the testes) and testes, and then shipped, frozen, back to Seattle, WA, USA for subsequent analyses. At the NOAA/NMFS facilities in Seattle, the fish (minus gonads) were ground in a meat grinder after which a subsample was dried at 105° C to constant weight. The gonad was small enough so that we could dry the entire gonad at 105° C. The dried samples were then further processed until a finely ground homogenate remained.

Proximate composition, in which the main chemical constituents were estimated (% ash, lipid, protein, and water), was determined for subsamples of the finely ground somatic and gonadal homogenates using standard approaches. In particular, nitrogen was determined using the combustion method with a Leco FP-2000 (Leco Corp., St Joseph, MI). Protein was then calculated as Nitrogen x 6.25 (Jones 1931). Lipid content was determined using a 1 h extraction in a Soxhlet device with dymethyline chloride as the solvent. Ash was determined gravimetrically after combustion at 550° C for 16h. Carbohydrates were not measured as they constitute < 0.5% of the somatic tissue of salmonid fishes (e.g., (Jonsson et al. 1991, 1997). Energy density was measured using a isoperibol calorimeter (model 1266, Parr Instrument Company, Moline, Illinois).

Total somatic energy is calculated as: mass of the somatic tissues × energy density of the somatic tissues. Because we sampled such a small subset of each population (20 individuals each) and our goal was to characterize the average total somatic energy for each population, we multiplied the population-specific energy density × an estimate of the population-specific average mass based on more extensive data. Data on body mass were collected in at least two years in each creek (Bear: N = 661, 2003-04; Hansen: 834, 1999-2002 and 2004-05; Yako: N = 531, 2003-04; Pick: N = 382, 1995-96), and was collected over the entire breeding season. To estimate each individual's somatic mass, we subtracted the gonad mass from the total body mass (for Bear, Hansen, and Yako, gonad mass was estimated from gonad mass versus body length relationships presented in (Carlson et al. In review-b); for Pick Creek: gonad mass was instead estimated based on a gonad versus length relationship generated from the 20 individuals sacrificed for this study). We then multiplied this somatic mass by the corresponding energy density to determine population-specific estimates of total energy. Because body size differs among populations, mass-specific metabolic rates will also differ. To account for this size-dependence of metabolic rate, we also present our total energy results after correcting for differences in body size among populations. To do this, we used the "teleost average" scaling coefficient of 0.79 (Clarke and Johnston 1999). To do this, we calculated: (somatic mass ^ 0.79) × somatic energy density. We present the total somatic energy results both uncorrected and corrected for body size (and thus metabolic rate).

Estimating senescence rates

Age-specific survival was modeled using the Weibull distribution following the statistical convention of recent studies of senescence in nature (Tatar et al. 1997; Dudycha and Tessier 1999; Hendry et al. 2004). Details of the method are provided in

Carlson *et al*. (Carlson et al. In review-a) and its application to the present data is described below. The Weibull distribution is characterized by two parameters: α (determines the shape of the hazard function) and λ (determines the magnitude of hazard for a given function shape) (Crawley 2002). When $\alpha = 1$, the Weibull distribution simplifies to the exponential (constant hazard) distribution, wherein hazard does not increase with age (i.e., no senescence). When $\alpha > 1$, hazard increases with age (i.e., true senescence) (Tatar et al. 1997; Ricklefs 1998; Dudycha and Tessier 1999). To infer senescence, we compared a model in which $\alpha = 1$ to models where it was estimated from the data. Senescence rates were then compared among populations by examining models including or excluding creek-specific α and λ parameters (Carlson et al. In review-a). These models also included "day of entry" parameters because early breeders senesce slower than late breeders (Hendry et al. 2004).

We compared a range of models with creek- and individual-specific parameters to models with parameters fixed among creeks and individuals via Akaike's information criterion (Hilborn and Mangel 1997; Burnham and Anderson 2002). This criterion revealed that the best model had creek-specific day of entry (*b*), α , λ parameters (Carlson et al. In review-a). For each individual, we calculated a λ based on the creek-specific value and the day of creek entry:

(1) $$R_i = e^{\left(b_{c_i}\left[E_i - \bar{E}_{c_i}\right]\right)}$$

(2) $$\lambda_i = \lambda_{c_i} R_i$$

The subscript *c* denotes creek-specific parameter values, R_i is a day of entry factor on senescence for individual *i*, b_{c_i} is a parameter that determines how entry day affects the probability of senescence and may differ between creeks, E_i is the day of entry for individual i, $\overline{E}_{c_i}$ is the average day of entry in the creek of the ith individual.

The likelihood function for this model is:

$$L = \prod_{i=1}^{n} \left[\alpha_{c_i} \lambda_i t_i^{\alpha_{c_i} - 1} e^{-\lambda_i t_i^{\alpha_{c_i}}} \right]^{w_i} \left[e^{-\lambda_i t_i^{\alpha_{c_i}}} \right]^{1-w_i} \qquad (3)$$

Where t_i is the days after creek entry that animal i died, w_i is the censoring indicator for individual i, which can take on values of one (not censored; i.e., senescent) or zero (censored; i.e., still alive at the end of the study or non-senescent death).

Ricklefs (1998) and Ricklefs and Scheuerlein (2001; 2002) introduced a derived parameter, ω, that provides a shape-adjusted index of the rate of senescence in a Weibull model because α and λ are not independent. This parameter has units of time^{-1} and is calculated as:

$$\omega = \lambda^{\frac{1}{\alpha + 1}}. \qquad (4)$$

We present population-specific senescence rates (ω) and associated 95% confidence intervals generated from likelihood profiles (Hilborn and Mangel 1997).

Statistical analysis and interpretation

To determine whether proximate composition differed among the four populations, we employed a MANOVA. Because proximate composition data are compositional (for a given fish, % lipid + % protein + % water + % ash = 1), the recommended method of analysis is to: 1) pick one of the constituents as a control (here, we chose % water since it constitutes so much of each fish, Table 3.3), 2) take the $\log_{10}$ of the ratio of each of the remaining three constituents relative to the % water (y1 = log[%lipid / % water], y2 = log [% protein / % water], y3 = log [% ash / % water]), 3) perform a MANOVA using the log ratios generated above to test for differences in composition among populations. This approach yields a multivariate vector which minimizes the amount of redundant information (Aitchison 1986).

We employed ANOVA to establish whether total energy (somatic and gonadal) or energy density (somatic and gonadal) differed among populations. When population means differed significantly, a post-hoc Tukey's test was used to determine which means differed from each other (Zar 1999).

We used ordered-heterogeneity (OH) tests (Rice and Gaines 1994c, 1994b, 1994a) to test the hypotheses that total energy and energy density of the soma and testes can be predicted from observed senescence rates. This approach allowed us to test ordered hypotheses. We predicted that somatic energy (both total and mass-specific) and that gonadal energy (both total and mass-specific) would be would be positively related to senescence rates (a positive relationship would be congruent with AP). Ordered-heterogeneity tests generate a composite test statistic incorporating information on both the rank order of the parameter estimates as well as the magnitude of the variation among the parameter estimates. Specifically, this composite test statistic is calculated as:

(5) ordered-heterogeneity test statistic = $r_s * P_c$

where r_s is the Spearman's rank correlation between the observed and expected rankings (here, observed rankings of energy means and the rankings of the senescence rates). P_c is determined as:

(6) $$P_c = 1 - P_{ANOVA}$$

where P_{ANOVA} represents the P-value from the nondirectional heterogeneity test. Critical values are provided in Rice & Gaines (1994c).

Results

Proximate composition

The proximate composition of somatic tissue differed significantly among our four focal populations (MANOVA, Pillai's Trace $P < 0.001$), including differences in both protein ($P = 0.001$) and lipid content ($P = 0.004$). Differences in ash content among populations were less pronounced ($P = 0.09$). Differences in water content could not be tested because water was used as the control constituent but water content varied little among populations (mean = 78.43%, SD = 0.22%, Table 3.3). For protein, Yako Creek fish did not differ from Hansen Creek fish, and individuals breeding in these two populations had significantly more protein than individuals returning to Bear Creek (Table 3.3). Pick Creek individuals had significantly less protein than individuals returning to Hansen Creek but did not differ from either Bear or Yako creek fish (Table 3.3). For lipid, Bear Creek did not differ from any of the other three creeks, Yako and Pick also did not differ from each other, but the lipid content of Hansen Creek individuals was significantly less than that of individuals breeding in either Pick of Yako creeks.

Energy reserves and energy density

Total somatic energy and total gonadal energy differed among populations ($P < 0.001$ in both cases). Hansen Creek fish had significantly less total somatic energy than the other three populations. Pick and Bear Creek had the most total somatic energy and did not differ statistically from each other. Yako Creek fell intermediate with less total somatic energy than either Bear or Pick creeks but more total somatic energy than Hansen Creek (Table 3.4). Results were similar with regards to total energy in the testes. Specifically, Tukey's post hoc tests revealed that Hansen had the lowest total gonadal energy followed by Yako Creek (Table 3.4). The total gonadal energy of Bear and Pick Creeks again did not differ significantly (Table 3.4) and was elevated relative to Hansen and Yako (Table 3.4).

The differences in total energy reflected in part the differences among populations in body mass (Pick and Bear fish tend to be older and thus larger than fish returning to Yako, which in turn tend to be older and larger than fish returning to Hansen Creek; Figure 3.2). However, the energy density of somatic and gonadal tissues also differed significantly among populations ($P = 0.001$ and $P = 0.033$, respectively). Tukey's post hoc tests revealed that the energy density of somatic tissues was lower in Hansen Creek than in Pick and Yako creeks (Table 3.4). In contrast, Hansen Creek salmon had higher energy density in gonadal tissues than Pick Creek salmon. No other differences were apparent (Table 3.4). Thus, the only consistent differences between the two tissue types were that 1) Hansen and Pick creek always differed (somatic energy density: Pick > Hansen; gonadal energy density: Pick < Hansen; Table 3.4) and that 2) Bear Creek never differed from the other populations. Finally, as expected, lipid content was highly and significantly related to energy density ($P < 0.001$, $R^2 = 0.90$, $N = 80$).

Senescence, energy reserves, and energy allocation

The total energy and energy density of both the somatic tissue and testes generally varied among populations in a manner consistent with expectations based on variation in senescence rates among populations. As predicted, total somatic energy and somatic energy density were both inversely related to senescence rates (total somatic energy both corrected and uncorrected for body size: $r_sP_c = 0.80$, $k = 4$, $P < 0.01$; somatic energy density: $r_sP_c = 0.40$, $k = 4$, $P \approx 0.12$ as estimated from Figure 3.1, (Rice and Gaines 1994a)). Moreover, as predicted, inter-population variation in gonadal energy density was positively related to variation in senescence rates (gonadal energy density: $r_sP_c = 0.77$, $k = 4$, $P < 0.025$). However, total gonadal energy was not positively related to senescence rates as predicted ($r_sP_c = - 0.80$, $k = 4$, $P > 0.99$). Rather, total gonadal energy tracked variation in overall body size (i.e., Hansen fish are the smallest and have the least total gonadal energy), which is not surprising given that larger males have larger testes (Carlson et al. In review-b).

Discussion

We propose that variation in rates of senescence among natural populations of sockeye salmon reflects a reproductive trade-off due to energy limitation. Our rationale is as follows. First, sockeye salmon are semelparous capital breeders. They cease feeding at entry into fresh water on their breeding migration from the marine environment. This energy limitation (no future feeding) sets up an energy allocation trade-off between gonadal stores (for current reproduction) and somatic stores (to fuel future metabolism). Second, natural populations of sockeye salmon vary with regards to rates of senescence (Table 3.1), apparently reflecting the intensity and timing of predation by bears (Carlson et al. In review-a). Third, these same populations vary in proximate composition (percent lipid, protein, ash, and water; Table 3.3), body size- and age-at-maturity (Figure 3.2), and energy density of both the somatic and gonadal tissues (Table 3.4). Fourth, senescence rates are inversely related to somatic energy stores (total energy: $P < 0.01$; mass-specific energy: $P \approx 0.12$). Finally, senescence rates are positively related to the energy density of gonadal tissues ($P < 0.025$), indicating a population-specific balance in the trade off between current reproduction and future survival. Specifically, of the populations we sampled, Hansen Creek salmon have the most rapid senescence, the smallest body size (Figure 3.2), the highest gonadal energy density, the lowest somatic energy density, and the lowest total somatic energy (Table 3.4). Pick Creek salmon are larger, have a longer reproductive lifespan, and have higher energy density in their bodies but less in their testes.

Total somatic energy differed among populations, and the difference parallels differences among populations in rates of senescence. Interestingly, the difference in total energy was not due simply to differences in body size but also to differences in somatic energy density (i.e., mass-specific energy). Long-term sampling by the Fisheries Research Institute at the University of Washington has revealed significant differences in body size, age-at-maturity, and length-at-age in the focal populations (Quinn et al. 2001b). Knowing that these populations vary in body size (Figure 3.2), we were specifically interested in testing whether body size alone or combinations of body size and energy density accounted for the differences in senescence rates among populations. If energy density did not differ among populations, differences in senescence could be attributed to differences in body size. If energy density differed among populations, this would suggest a more complicated relationship between body size, energy density, and rates of senescence. We have found the latter. This is not simply due to larger individuals having higher somatic energy densities because somatic mass explained very little of the variation in somatic energy density ($R^2 = 0.09$, $N = 80$).

Because total energy is a product of mass and energy density, it is not surprising that the variation in total gonadal energy stores among populations parallels the variation in total somatic energy (because populations with bigger fish in general have more somatic energy but also larger gonads, on an absolute basis). However, variation in gonadal energy density does not parallel variation in somatic energy density. For instance, Hansen Creek salmon displayed the most rapid senescence, the highest gonadal energy density but lowest somatic energy density. To examine this trade-off properly, one would also want to measure the energy cost of building secondary sexual characters but measuring these costs is not a trivial endeavor. Previous work has focused on trait size as a proxy for energy invested. For instance, Kinnison *et al*. (2003) compared two populations of chinook salmon (*Oncorhynchus tshawytscha*) that faced different migratory costs and found that the population with the longer migration developed less exaggerated secondary sexual characters (e.g., body depth and jaw length). Similarly, Crossin *et al*. (2004) found Fraser River sockeye populations with more arduous migrations tended to be smaller and generally more fusiform than populations with easier migrations.

We took a similar approach to the aforementioned studies and examined variation in trait size (standardized for overall body length) among populations and found substantial inter-population variation with regards to secondary sexual characters. For instance, Bear and Pick creek fish were deeper bodied (Figure 3.3A) and heavier (Figure 3.3B) for their length than males breeding in Hansen or Yako creeks. No clear differences among populations emerged with regards to jaw length (Figure 3.3B) or gonad mass (Figure 3.3D). Thus, when considering proximate populations (i.e., similar migrations), among population variation in secondary sexual characters tended to parallel overall differences in body size and not differences in energy allocation. Moreover, the migrations to Bear, Hansen and Yako are essentially identical (Table 3.1). The migration to Pick Creek is slightly farther with slightly more elevation gain (Table 3.1), but these fish had the highest somatic energy density, strengthening our argument that among population differences represent spawning ground, not migration route, processes.

Only two studies of natural populations have previously attempted to discriminate between the mutation accumulation and antagonistic pleoitropy mechanisms of senescence (Dudycha and Tessier 1999; Hendry et al. 2004). The former examined the balance between current reproduction and subsequent survival in multiple populations that existed across a simple habitat permanence gradient (ephemeral ponds versus permanent lakes; (Dudycha and Tessier 1999). The latter examined the trade-off within a population between early and late breeders (Hendry et al. 2004). Here we build on these studies by examining the trade-off between current reproductive effort and future survival among populations that exist along a gradient of habitats, and thus predation intensities from brown bears (Quinn et al. 2001b), which then yields a gradient of senescence rates (Carlson et al. In review-a). Thus, AP was supported in all three studies that focused on natural populations. Similarly, the laboratory evidence from *Drosophila melanogaster* strongly supports AP as well (reviewed in (Partridge 2001; Partridge and Gems 2002); for a notable exception see (Hughes et al. 2002)). Future work on a more diverse array of organisms is necessary to test the generality of these findings.

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Table 3.1. Population, migration distance, elevation gained during migration, senescence rates, and the proportion of males in each population that spent three years in the ocean.

Population	Migration distance[1] (km)	Migration elevation gain[2] (m)	Senescence rates[3]	Proportion 3-ocean individuals[4]
Bear	44	10	$0.092 \leq 0.096 \leq 0.100$	0.50 ± 0.27 (1950 – 2005; N = 56)
Hansen	42	10	$0.121 \leq 0.126 \leq 0.131$	0.31 ± 0.26 (1947 – 2005; N = 59)
Pick	98	21	$0.074 \leq 0.076 \leq 0.079$	0.42 ± 0.24 (1947 – 2005; N = 59)
Yako	39	10	$0.100 \leq 0.104 \leq 0.108$	0.33 ± 0.19 (1993, 2003 – 2005; N = 4)

[1] Distances migrated were measured as the shortest straight-line water distance from the mouth of each focal creek to the ocean.
[2] Elevation gained was measured as meters above sea level for the lake in which the focal creek drains.
[3] For details regarding the senescence model and determination of population-specific senescence rates, see (Carlson et al. In review-a).
[4] Average long-term proportion of males returning to each stream that spent three years in the ocean. Each year, ocean age was determined for a fraction of the individuals returning to each population (~ 100 males) from which we determined the annual proportion of 3-ocean males. We here report the average proportion 3-ocean males across years (the number of years is indicated in parentheses) as well as the standard deviation, which represents the among-year variation in the proportion of males spending three years in the ocean.

Table 3.2. Population, sample sizes, and characteristics of male sockeye salmon sampled for proximate composition and bomb calorimetry. Values are presented as mean ± standard deviation. Note that these values represent raw trait values, see figure 3.2 for length-standardized comparisons of body depth and jaw length.

Population	N	Body length (mm)	Body depth (mm)	Jaw length (mm)	Somatic mass (kg)	Gonadal mass (g)
Bear	20	509.65 ± 20.64	187.30 ± 11.08	99.05 ± 6.27	3.89 ± 0.43	60.81 ± 15.27
Hansen	20	466.05 ± 30.08	135.65 ± 11.25	85.90 ± 7.89	2.48 ± 0.51	45.66 ± 10.84
Pick	20	460.60 ± 51.39	157.65 ± 25.04	85.3 ± 14.48	2.62 ± 1.10	60.49 ± 13.22
Yako	20	502.85 ± 30.05	168.55 ± 14.51	91.65 ± 9.14	3.22 ± 0.68	68.19 ± 14.24

Table 3.3. Proximate composition (by wet mass) of male sockeye salmon from four proximate populations in southwestern Alaska. Values are presented as mean ± standard deviation for subsamples of somatic homogenate. Superscripts denote significant differences among populations based an ANOVA followed by a Tukey's post hoc significance test ($\alpha = 0.05$).

Population	Water (%)	Ash (%)	Protein (%)	Lipid (%)
Bear	78.75 ± 0.78	2.19^{a} ± 0.12	15.75^{a} ± 0.76	$2.59^{a,b}$ ± 0.62
Hansen	78.32 ± 1.02	2.27^{a} ± 0.09	17.04^{c} ± 0.83	2.17^{a} ± 0.75
Pick	78.33 ± 1.28	2.22^{a} ± 0.15	$16.24^{a,b}$ ± 0.92	2.91^{b} ± 0.76
Yako	78.33 ± 1.28	2.20^{a} ± 0.09	$16.48^{b,c}$ ± 0.70	3.04^{b} ± 0.91

Table 3.4. Energy density of the somatic tissue and gonadal tissue of male sockeye salmon from four proximate populations. Results are reported as mean ± standard deviation, below which the sample sizes are indicated in parentheses. Superscripts denote significant differences among populations based an ANOVA followed by a Tukey's post hoc significance test ($\alpha = 0.05$).

Population	Gonad		Soma		
	energy density (kJ/g)	total energy (kJ)	energy density (kJ/g)	total energy (kJ)	total energy scaled by somatic mass* (kJ)
Bear	21.23^{a,b} ± 0.29	1,322.11^{c} ± 171.89	22.68^{a,b} ± 0.56	64,538.56^{c} ± 17,352.00	12,072.78^{c} ± 2,580.46
	(N = 20)	(N = 661)	(N = 20)	(N = 661)	(N = 661)
Hansen	21.24^{b} ± 0.29	1,053.75^{a} ± 95.15	22.17^{a} ± 0.64	54,667.13^{a} ± 15,332.41	10,553.26^{a} ± 2,350.47
	(N = 20)	(N = 834)	(N = 20)	(N = 834)	(N = 834)
Pick	20.98^{a} ± 0.27	1,319.15^{c} ± 71.75	22.81^{b} ± 0.63	63,683.87^{c} ± 16,024.94	11,971.27^{c} ± 2,377.56
	(N = 20)	(N = 382)	(N = 20)	(N = 382)	(N = 382)
Yako	21.13^{a,b} ± 0.34	1,188.71^{b} ± 93.72	22.99^{b} ± 0.75	60,608.62^{b} ± 19,179.80	11,494.95^{b} ± 2,892.17
	(N = 20)	(N = 531)	(N = 20)	(N = 531)	(N = 531)

* Because these populations differ in size (Figure 3.2), they will also differ in metabolic rate. Here we have scaled total energy by body size (and thus metabolic rate) using the "teleost average" scaling coefficient of 0.79 (Clarke and Johnston 1999). Note that the inter-population differences in total energy are apparent even after accounting for the inter-population differences in somatic mass.

Figure 3.1. Locations of the four study populations in the Wood River Lakes, southwest Alaska, USA.

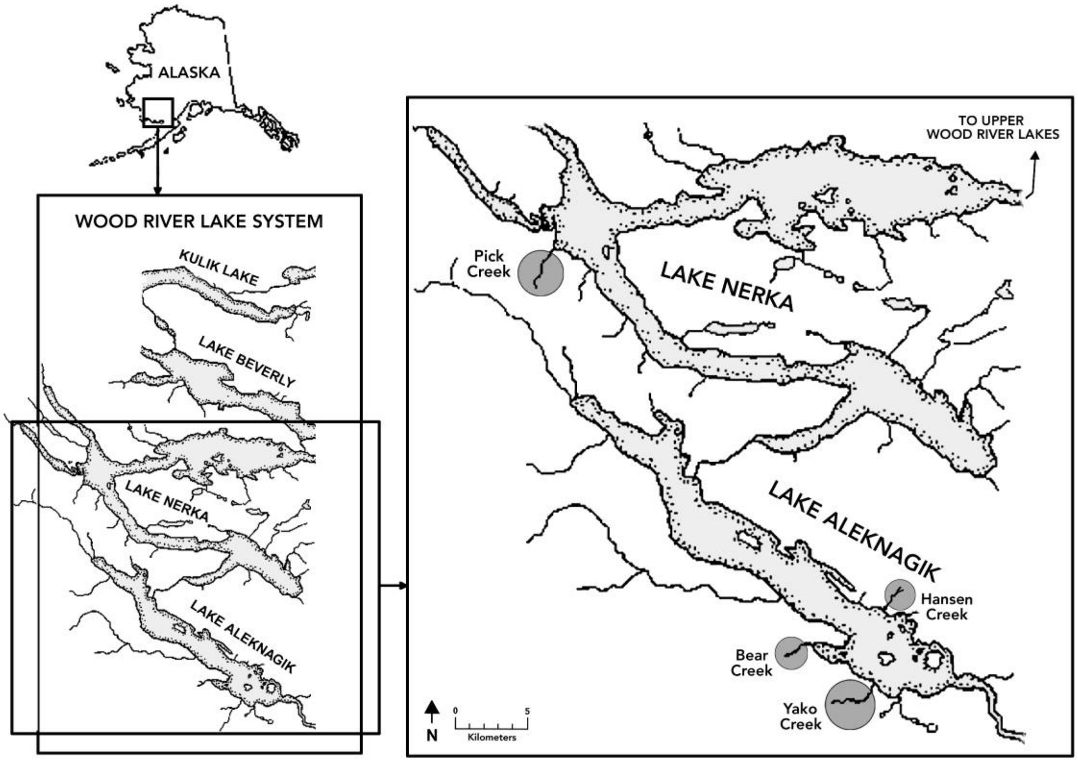


Figure 3.2. Population-specific frequency distributions for length-at-age (right-panels; two years in the ocean: ▨, three years in the ocean: ▧) and body mass (left-panels) based on historical data collected in each of our four focal populations. Note that the populations are arranged by rates of senescence (Hansen > Yako > Bear > Pick).

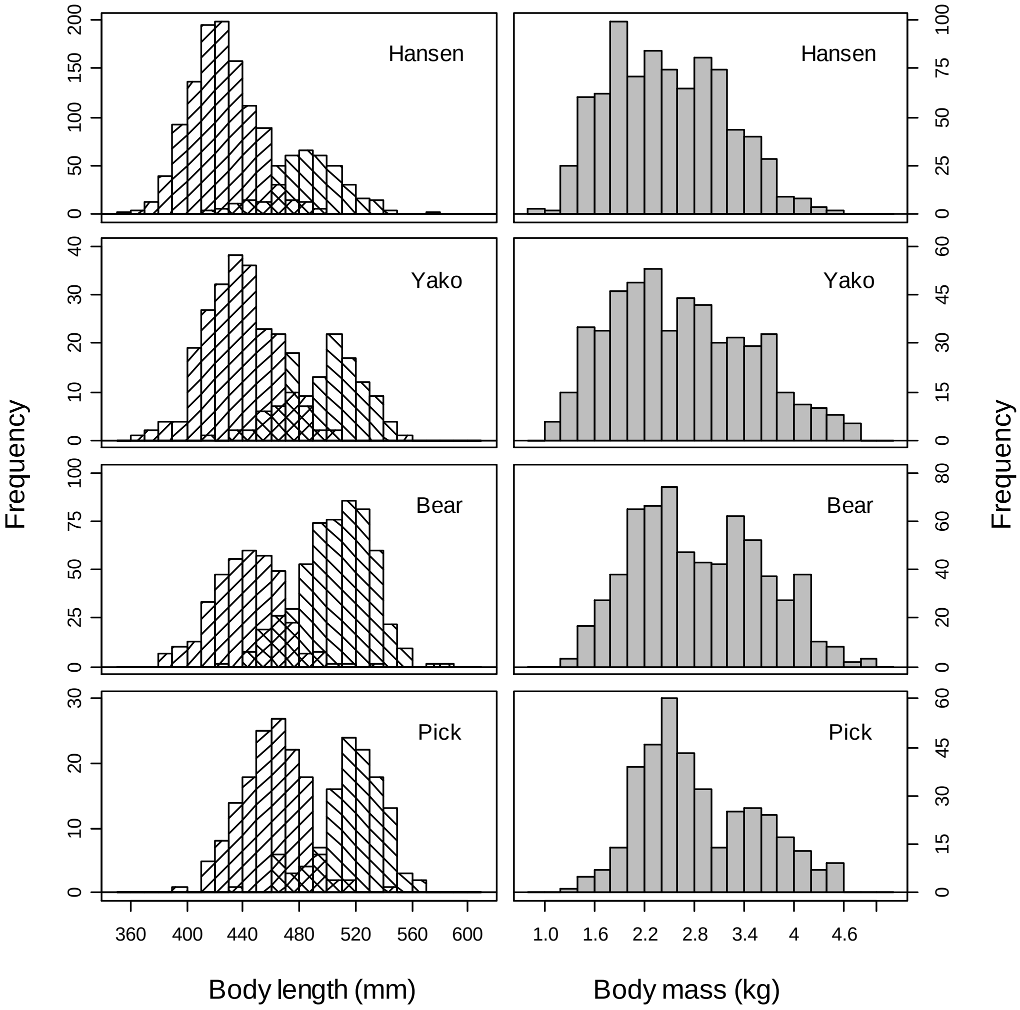
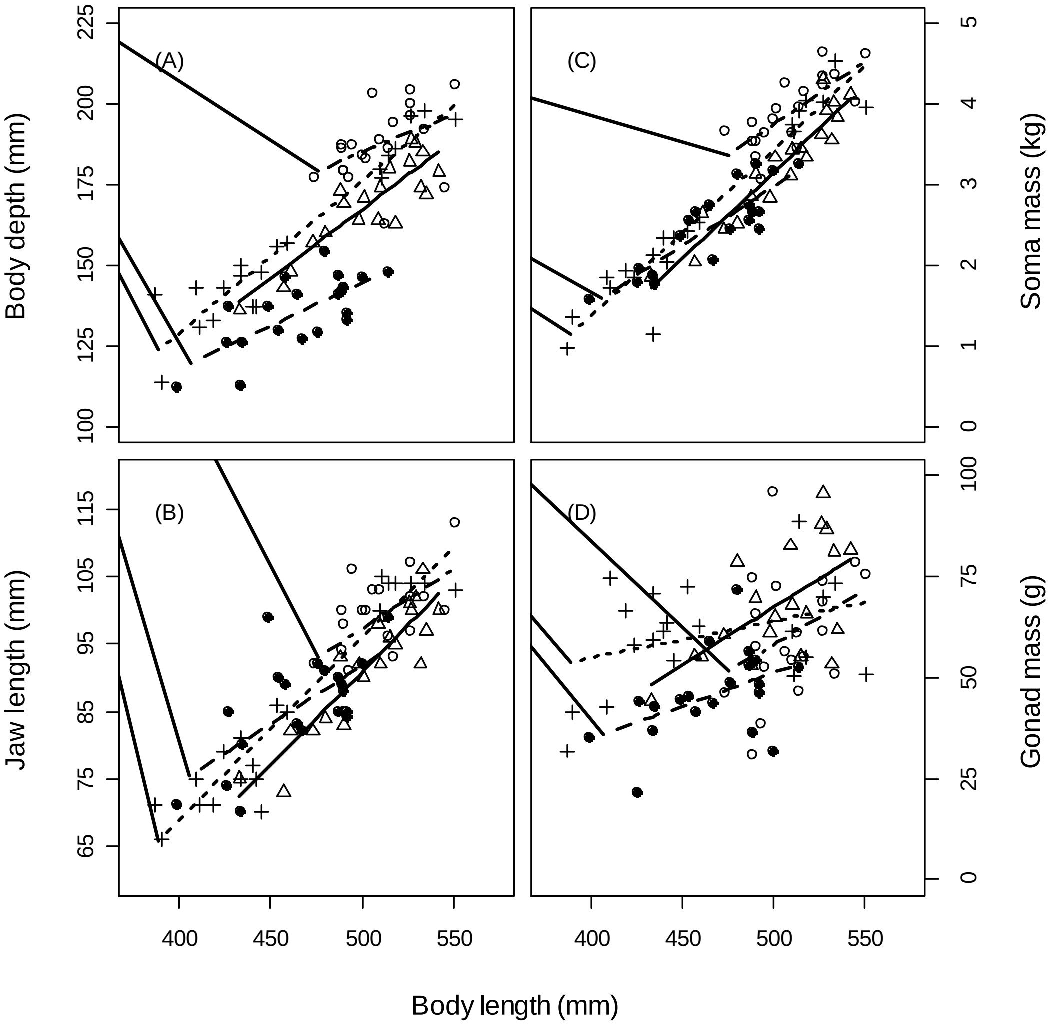


Figure 3.3. Length-standardized comparisons of body depth (A), jaw length (B), soma mass (C), and gonad mass (D). Results partitioned by population: Bear Creek (open circles, dot-dashed line), Hansen Creek (closed circles, dashed line), Pick Creek (crosses, dotted line), and Yako Creek (triangles, solid line).



Chapter 4: Does variation in selection imposed by bears drive divergence among populations in the size and shape of sockeye salmon?

Synopsis

Few studies have determined whether formal estimates of selection explain the patterns of trait divergence among populations yet this approach is critical for evaluating the possibility that the populations are in equilibria. If adaptive divergence is complete, then directional selection should be absent and stabilizing selection on trait means should be present. We estimated natural selection, due to predation from brown bears (*Ursus arctos*), acting on the body size and shape of male sockeye salmon (*Oncorhynchus nerka*) in three discrete breeding populations that experience differing selective regimes. Our approach was to 1) estimate the shape and form of selection acting within each population on each trait based on an empirical estimate of reproductive activity, 2) test for trait divergence among populations, and 3) test whether selection coefficients were correlated with trait divergence among populations. Stabilizing selection was never significant, indicating that these populations have yet to attain equilibria. Furthermore, the sign and magnitude of directional selection varied among populations in a manner consistent with the trait divergence among populations, indicating that population differentiation is ongoing. Specifically, the rank order of the creeks in terms of intensity and selectivity of bear predation mirrored the order in terms of 1) the average size and shape: males were shortest and least deep-bodied in the creek with the most intense predation and 2) the patterns of selection: the shortest and least deep-bodied males had the highest reproductive activity in the creek with intense predation and the long, deep-bodied males were favored in the creek with the least predation risk. Our results thus demonstrated that selection due to predation can drive adaptive population divergence in

phenotypic traits. Finally, we discuss reasons why these self-sustaining populations are not in equilibria.

Introduction

The importance of divergent selection in driving phenotypic differentiation among conspecific populations and among species has long been recognized (Darwin 1859; Simpson 1953; Schluter 2000); yet, the mechanisms of divergent selection are rarely identified (Schluter 2000). Most research has focused on the role of resource competition in driving divergence (Schluter and Grant 1984; Schluter 2000; Benkman 2003). Recent work has also linked sexual selection (Svensson *et al.* 2006) and predation (Nosil and Crespi 2006) to adaptive population divergence by demonstrating a correlation between the strength of divergent selection and trait divergence. Schluter (2000) suggested that studies designed to test the hypothesis of divergent natural selection should attempt to both demonstrate that selection is truly divergent, and identify the mechanism of selection. This latter goal has been particularly difficult to meet in natural systems and the mechanisms identified typically “represent an educated guess” (Schluter 2000, p. 106). We accomplish both of these tasks in the present study.

Qualitative differences in predation have repeatedly been shown to influence trait divergence. For instance, life history traits (Reznick 1982; Reznick and Endler 1982; Reznick et al. 1996; Reznick et al. 2004), locomotor performance(O'Steen et al. 2002; Ghalambor et al. 2004), and color patterns (Endler 1978, 1980; Houde 1987, 1997) of guppies, *Poecilia reticulata*, vary among sites with different levels of predation. Threespine stickleback, *Gasterosteus aculeatus*, populations vary in life-history traits, armor, and size as a function of predation intensity (Reimchen 1991, 1994). However, no study has determined whether formal estimates of selection due to predation explain the observed patterns of trait divergence in a natural system. The additional value of this latter approach is that it provides a greater ability to evaluate the possibility of evolutionary equilibrium. Populations in equilibrium should experience stabilizing selection around mean trait values but if equilibrium has not been attained, each population should experience directional selection to move its mean towards the adaptive peak (Schluter 2000).

Numerous studies have quantified selection in nature (reviewed by (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004)) but few have done so in multiple populations (Kingsolver *et al.* 2001). Moreover, when investigators have attempted to determine how differences in selection drive phenotypic divergence, selection has often not actually been quantified. We here address these two issues in a natural system by quantifying natural selection due to brown bear (*Ursus arctos*) predation within multiple populations of sockeye salmon (*Oncorhynchus nerka*), allowing us to determine whether selection coefficients were correlated with inter-population trait divergence. Our work complements the recent work of Svensson et al. (2006) and Nosil and Crespi (2006) by linking variation in predation intensity and selectivity to phenotypic differentiation among populations that is consistent with the strength of directional selection on each population.

Pacific Salmon

Pacific salmon (*Oncorhynchus* spp.) present an excellent opportunity to study the importance of selection in driving phenotypic divergence because their homing behavior promotes reproductive isolation and the formation of numerous discrete breeding populations that experience different selective pressures (e.g., (Quinn 2005)). These populations have differentiated in many phenotypic traits (Taylor 1991), including body size, age and shape at maturity (Roni and Quinn 1995; Quinn et al. 2001b), and rates of senescence (Carlson *et al.* Submitted), all of which can influence individual fitness. Body size has many important influences on fitness of both females and males. Female size affects reproductive potential through positive correlations with fecundity and egg size (Beacham and Murray 1993; Quinn et al. 1995; Hendry et al. 2001), egg burial depth (Steen and Quinn 1999), and competition for nest sites (Foote 1990; Quinn and Foote 1994) (but see (Holtby and Healey 1986)). Male size correlates positively with mating success, at least in the absence of alternative mating tactics by small males (Gross 1985; Foote and Larkin 1988; Foote 1990; Fleming and Gross 1994; Quinn and Foote 1994; Quinn et al. 2001a; Hamon and Foote 2005).

Pacific salmon populations differ in many traits including the extent of sexual dimorphism (Quinn et al. 2001b). Previous work has indicated that bear predation is size selective (Quinn and Kinnison 1999; Ruggerone et al. 2000), and salmon populations experiencing high rates of bear predation tend to be smaller-bodied than those experiencing lower predation rates (Quinn et al. 2001b). However, the death of the salmon at the end of their first breeding season is inevitable, regardless of the bears, so the evolutionary effect of the bears depends on the extent to which reproductive opportunities are curtailed. The ability of bears to kill newly arrived salmon varies among creeks (Gende et al. 2004; Carlson et al. Submitted), and the extent of pre-reproduction mortality probably varies as well.

To determine the evolutionary effect of bears on salmon size and shape, we studied three proximate breeding populations that vary in the intensity of bear predation, and in the age at maturity, size-at-age, and shape of adult salmon (Quinn et al. 2001b). First, we quantified the intensity of predation from bears by estimating both the percent of salmon killed in each population and the tendency of bears to remove fish early in their stream life (i.e., individuals that had only recently started breeding). Second, we estimated the strength and form of selection acting on male body size and shape within these populations. Third, we quantified trait divergence among the populations. Fourth, we tested whether estimates of divergent selection corresponded with the observed trait variation among populations. We predicted that populations susceptible to bear predation would have the smallest body sizes (because bears are more likely to kill large than small salmon). Finally, we evaluated whether these populations are in evolutionary equilibria by comparing the strength and form of selection acting on each trait in each population with theoretical predictions (i.e., directional selection should be absent if adaptive divergence is complete).

Materials and methods

Study organism and sites

Sockeye salmon lay their eggs in the gravel of streams, rivers and lake beaches in late summer and fall. Embryos incubate for several months prior to hatching, complete yolk-absorption, emerge from the gravel in spring, and migrate to a lake where they feed for one or two years before migrating to sea (Burgner 1991). After 1, 2 or 3 years in the North Pacific Ocean, individuals migrate back to their natal lake system, often remaining in a lake for several weeks until they have fully matured, at which point they enter their natal site (stream, river, or beach), attempt to reproduce, and die.

The Wood River system in southwestern Alaska (Figure 4.1) has many populations of sockeye salmon breeding in creeks and rivers, where they are subject to predation from bears. Creek width explains over 50% of the variation among populations in the average annual percent of salmon killed within a population (henceforth “overall predation rate”; Quinn et al. 2001a); the wider the creek, the lower the predation rate. The three study sites (Bear, Hansen, and Yako creeks) are all tributaries of Lake Aleknagik, the southernmost lake in the Wood River Lakes system (Figure 4.1). Adult sockeye salmon in these populations return from the ocean at the same time of the year (Hodgson and Quinn 2002) and have similarly short migrations to their natal sites without substantial elevation gain (Table 4.1), so we could study the patterns of selection acting on these populations in the absence of these potentially confounding factors.

Predation rate

Carlson et al. (Submitted) employed the method of Quinn et al. (2001b) to estimate overall predation rate (average annual percent of salmon killed, based on counts of live, bear-killed and senescent dead salmon) and the method of Gende et al. (2004) to estimate the per day probability of predation on fish in each of the three focal creeks, based on daily observations of tagged fish. To generate an index of predator selectivity for newly arrived fish, Carlson et al. (Submitted) then averaged the probability of predation over the first three days of stream life for salmon in each creek. We here present the values provided in Carlson et al. (see Table 4.2) and refer the reader to Quinn et al. (2001b) and Gende et al. (2004) for a thorough description of these estimation methods.

Phenotypic traits, fitness, and selection

The reproductive success of male salmon was estimated as the difference between the expected pre-spawning gonad mass for a given body size (referred to as "reproductive potential") and the observed gonad mass at death (Schroder 1973; Semenchenko 1986, 1987; Fleming and Gross 1992). This difference accurately reflects the number of spawning events in which a male salmon participated (Fleming and Gross 1993). Moreover, this method is more integrative over the entire breeding period than the average of point estimates of social dominance (Quinn and Foote 1994), though the male's success in actually fertilizing eggs is not known in either case.

To use this approach, we first determined expected reproductive potential as a function of body length in each of the three study populations (Figure 4.2) by sacrificing males of varying lengths from each population prior to breeding and measuring their gonads via volume displacement ("pre-reproductive" males). We then sampled dead males on the spawning grounds, determined their gonad volume and mode of death, and estimated their reproductive activity as the difference between their gonad mass at death and their expected pre-reproductive gonad mass, given their length. We measured the male's body length (mid-eye to hypural plate), body depth (from the anterior insertion of the dorsal fin to the ventral surface of the fish), and jaw length (mid-eye to the tip of the upper jaw), as previous work has related these sexually dimorphic traits to male breeding opportunities (Fleming and Gross 1994; Quinn and Foote 1994). Data were collected in at least two years from each population (Bear and Yako: 2003-04; Hansen 2003-05) but were pooled to ensure adequate sample sizes for a robust analysis of selection (see Table 4.3 for total sample sizes).

We analyzed selection on body length, relative body depth, and relative jaw length. Consistent with previous work (Quinn et al. 2001a; Hamon and Foote 2005), relative jaw length and body depth were estimated as residuals from their relationship with body length (jaw length: Bear: $r^2 = 0.68$, $P < 0.001$, $n = 232$; Hansen: $r^2 = 0.53$, $P < 0.001$, $n = 201$; Yako: $r^2 = 0.66$, $P < 0.001$, $n = 164$; body depth: Bear: $r^2 = 0.74$, $P < 0.001$, $n = 140$; Hansen: $r^2 = 0.60$, $P < 0.001$, $n = 189$; Yako: $r^2 = 0.79$, $P < 0.001$, $n = 108$). As evident from variation in the above sample sizes, not all measurements could be obtained from all fish (e.g., owing to wounds from bear predation). We therefore performed two sets of selection analyses, one in which we estimated selection acting on length and relative jaw length and a second analysis in which we estimated selection acting on length and relative body depth.

Selection may act differently on bear killed and senescent salmon, and so selection on the entire population will depend on the relative frequencies of these two categories. The fish included in our selection analyses were a small proportion of the entire population (at least 2500 fish in each creek in each year, 2003 – 2004 data presented in Rich et al. (2006); 2005 data, Fisheries Research Institute, unpublished), and so may yield non-representative proportions of the two mortality categories. We therefore sub-sampled the fish in the selection analysis to more accurately represent the population as a whole. For instance, in the length and residual depth analysis for Bear

Creek, we sampled 56 bear-killed males and 84 senescent males. The average annual percent of bear killed fish in Bear Creek was 30% (Table 4.2). To generate a representative sample, we randomly selected 36 of the 56 bear-killed individuals and also included all 84 of the senescent individuals (Table 4.3). This yielded 120 individuals to be included in the selection analysis, 30% of which had been killed by bears (i.e., 36 / 120) with the remaining 70% representing senescent individuals (i.e., 84 / 120). Details on the number of bear-killed and senescent individuals included in each selection analysis can be found in Table 4.3. To quantify the error introduced by this sub-sampling, we randomly sampled (without replacement) the 56 bear-killed individuals 1000 different times, merged each of these data sets with the data corresponding to the 84 senescent individuals, and then performed selection analyses on each of the 1000 combined data sets. This yielded a total of 6000 selection analyses (1000 each for the residual depth and residual jaw data sets × 3 populations). We present the average (± S.D.) selection coefficients (see below) and standard errors associated with each coefficient as these parameters were normally distributed; however, the distribution of p-values was highly non-normal, and so we instead present the median p-value associated with each of the 1000 selection analyses.

In Hansen Creek, many fish were measured for length but neither body depth nor jaw length ($n = 140$). Therefore, these fish could not be used in any analyses requiring information on multiple traits (e.g., in multiple regressions to estimate the selection gradients and correlational selection, see below). However, we included these fish in all analyses in which only data on length were required (e.g., regressions for generating the linear and quadratic length differentials for Hansen Creek, see below).

Estimating selection

We used standard procedures for estimating the strength and form of selection (Lande and Arnold 1983; Brodie et al. 1995). Relative fitness was calculated as the absolute fitness (i.e., reproductive activity) of the individual divided by the mean absolute fitness of all individuals from that population and data set. The opportunity for selection (*I*), was estimated as the variance in the relative fitness for each population and data set (Brodie et al. 1995). We present the average opportunity for selection based on the 1000 selection analyses performed on each data set (see above). All traits, as well as squared and cross-product terms, were standardized to a mean of zero and a standard deviation of unity within a population. Because larger males have larger gonads (Figure 4.2), the maximum "reproductive activity" of large males exceeded that of small males. Examination of residual plots confirmed that the variance in residuals ($Y - \hat{Y}$) increased with increasing X values. To minimize bias in the regression coefficients due to this heteroscedasticity, we transformed the response variable prior to analyses (transformed Y = natural $\log_e$ (Y + 1), (Zar 1999)).

Selection coefficients were estimated using four sets of linear regressions of relative fitness on trait values in each population. The first set used simple linear regressions of relative fitness on the traits independently (length, relative jaw length, relative body depth). The resulting regression coefficients represent *linear selection differentials*, which estimate the total strength of selection (i.e., direct selection on a trait plus indirect selection through correlations with other traits). The second set used a multiple linear regression with both traits included (length and relative jaw length *or* length and relative body depth). These regression coefficients estimate *linear selection gradients*, representing the strength of directional selection acting directly on each trait (i.e., independent of correlations with the other trait in the analysis). The third set used multiple linear regressions for each trait independently, together with its corresponding squared term. Coefficients for the squared terms are *quadratic (non-linear) selection differentials*, which are often interpreted as representing the total strength of disruptive (when positive) or stabilizing (when negative) selection. The fourth set used a multiple linear regression including both traits, squared terms for each trait, and the cross-product term between the two traits. This final regression provided estimates of *univariate non-linear selection gradients* (squared terms) and *bivariate non-linear selection gradients* (cross-product terms), the latter representing correlational selection favoring combinations of traits that are similar (when positive) or dissimilar (when negative).

Coefficients derived from this selection analysis were then compared to results from other studies of selection in nature (i.e., the 749 estimates compiled by Kingsolver et al. (2001)). Univariate cubic splines (non-parametric regressions; (Schluter 1988)) were then used to visualize the form of selection acting on each trait in each population. For each trait and population combination, we used a normal model combined with a smoothing parameter (λ) to minimize the prediction error (body length: λ = 8 (Bear), λ = 6 (Hansen and Yako); jaw length: λ = 6 (Bear and Yako), λ = 4 (Hansen); relative depth: λ = 2 (Bear, Hansen, and Yako). We also used bivariate cubic splines (Schluter and Nychka 1994) to visualize correlational selection acting on combinations of body length and relative jaw length (Bear and Yako: λ = -10, Hansen: λ = 10) or body length and relative depth (λ = 10 for all three populations).

Trait divergence among populations

We employed analysis of variance (ANOVA) to test for differences in each of the mean trait values (body length, jaw length, or body depth) among populations. When population means differed significantly, a post-hoc Tukey's test was used to determine which means differed from each other. We also used ANCOVA to test for differences among populations in length-standardized traits because jaw length and body depth are strongly correlated with body length.

To determine whether estimates of divergent selection corresponded with the observed trait variation among populations, we used ordered-heterogeneity (OH) tests (Rice and Gaines 1994c, 1994b, 1994a). Ordered-heterogeneity tests generate a composite test statistic, which incorporates two sources of information: a) the rank order of the parameter estimates and b) the magnitude of the variation among the parameter estimates. The composite test statistic is calculated as:

(1) OH test statistic = $r_s * P_c$

where r_s is the Spearman's rank correlation between the observed and expected rankings (here, observed rankings of size/shape means and the expected rankings are based on the rankings of the selection coefficients for size/shape). P_c is determined as:

(2) $P_c = 1 - P_{ANOVA}$

where P_{ANOVA} represents the *P*-value from the nondirectional heterogeneity test. Critical values are provided in Rice and Gaines (1994c).

Results

The average annual percent of salmon killed by bears was highest in Hansen Creek (50%) and similar for Bear and Yako creeks (on average, 30% of the adult salmon are killed in these two populations; Table 4.2). The probability of being killed early in stream life also varied among populations and was highest in Hansen Creek, followed by Yako Creek, and then Bear Creek (Table 4.2). Taken together, these two indices suggest that the intensity of predation is highest in Hansen Creek, intermediate in Yako Creek, and lowest in Bear Creek. In all populations, gonad mass increased with body size in pre-reproductive males (Figure 4.2). Predation by bears tended to reduce male breeding opportunities, as evidenced by the larger gonad volumes at death of bear-killed males relative to similarly-sized senescent dead males (Figure 4.2). Thus bears were killing males before they had completed breeding.

Selection analyses

The average opportunity for selection (*I*) differed among creeks, being highest in Hansen Creek: *I* for both length and jaw length: Hansen = 1.43, Bear = 0.65, Yako = 0.58; *I* for body depth (smaller data set): Hansen = 1.43, Bear = 0.64, Yako = 0.57.

The strength and sign of the directional selection coefficients varied among populations (linear differentials and linear gradients, Table 4.4). Of the 18 coefficients (differentials and gradients), eight were positive, ten were negative. Of these, three were significant ($\alpha = 0.05$), and two others were marginally significant ($P = 0.118$, 0.113). Differentials and gradients were similar in sign and magnitude, suggesting that the use of residuals had effectively removed any correlation between body length and either of the two traits. In Bear Creek, directional selection favored longer individuals ($P < 0.001$ for both the differential and gradient; Table 4.4). In Yako Creek there was a weak tendency for longer males to be favored ($P > 0.10$ for both the differential and gradient; Table 4.4). On the other hand, in Hansen Creek, selection favored shorter males ($P < 0.01$ for the differential, $P > 0.1$ for the gradient; Table 4.4). These patterns were confirmed by cubic splines (Figure 4.4A).

Differences among populations in selection on body depth and jaw length, after accounting for the effects of body length, were suggestive but weak. Males with short jaws were favored in Bear and Yako creeks, whereas males with long jaws were favored in Hansen Creek; but none of the coefficients was significant ($\alpha = 0.05$; Table 4.4). Cubic splines confirmed the general interpretation of the jaw selection coefficients but also revealed some slightly more complex patterns. For instance, in Bear Creek, fitness decreased as relative jaw length increased for negative values of relative jaw length but not for positive values (Figure 4.4B). The opposite pattern was observed in Yako Creek – fitness was constant for negative values of relative jaw length but decreased as values of relative jaw length became increasingly positive (Figure 4.4B). In Hansen Creek, fitness increased as relative jaw length increased but at a decreasing rate (Figure 4.4B). Males with large dorsal humps tended to be favored in Bear Creek, whereas males with small dorsal humps were favored in Hansen and Yako creeks (Table 4.4). Again, cubic splines suggested more complicated relationships between fitness and relative body depth. For instance, while the general trend was positive in Bear Creek, the relationship between fitness and relative depth appeared bimodal, with individuals with average body depths (i.e., relative depth = 0) having reduced fitness relative to slightly shallower-bodied and slightly deeper-bodied males (Figure 4.4C). This bimodal pattern was also apparent in Yako Creek, although the overall trend was that fitness tended to decrease as relative depth increased (Figure 4.4C). Finally, in Hansen Creek, cubic splines revealed a fitness valley, associated with a sharp reduction in fitness for males with relative depths of 5 – 15 mm followed by a sharp increase in fitness with relative depths > 15 mm (Figure 4.4C).

There was little evidence of stabilizing or disruptive selection on size and shape in the populations (univariate quadratic coefficients, Table 4.5). Of the 24 coefficients (differentials and gradients), 13 were positive, 11 were negative, and none was significant ($\alpha = 0.10$). Length coefficients tended to be negative, suggestive of stabilizing selection, and were always negative after accounting for correlation with other traits (i.e., gradients, Table 4.5). Relative jaw length coefficients were consistently positive in Bear Creek but negative in Hansen and Yako Creeks; however, the coefficients were not significant ($P > 0.4$ in all cases; Table 4.5). The lack of quadratic selection acting on length and relative jaw length was supported by cubic splines (Figure 4.4A–4.4B). The relative body depth coefficients were variable in direction (half positive, half negative), small (average = -0.0012), and never significant ($P > 0.4$ in all cases; Table 4.5). Despite the lack of significant quadratic depth differentials, cubic splines revealed more complex patterns including bimodal fitness functions in Bear and Yako creeks and a fitness threshold in Hansen Creek (see above, Figures 4.4A – 4.4C)

Correlational coefficients, which reflect selection on combinations of traits, were remarkably consistent (bivariate quadratic coefficients, Table 4.5). All six correlational coefficients were positive, suggesting that selection favored fish with similar trait combinations (e.g., long fish with long jaws), but were never significant (Table 4.5).

Positive correlational coefficients for length × residual jaw length suggest that either long individuals with long jaws or short individuals with short jaws were favored. Bivariate cubic splines revealed the latter in Hansen Creek (i.e., relatively constant slope of increasing fitness from the lower right to the upper left of Figure 4.5B), but no clear pattern emerged in Bear (Figure 4.5A) or Yako (Figure 4.5C) creeks. However, some interesting patterns emerged regarding combinations of length and residual body depth. In particular, the directional selection coefficients for length and residual depth were both positive in Bear Creek, suggesting that long fish with deep bodies were favored (Table 4.4), and bivariate cubic splines confirmed this (i.e., relatively constant slope of increasing fitness from the lower left to the upper right of Figure 4.5D). In contrast, the directional coefficients for length and residual depth were both negative for Hansen Creek fish, suggesting that short fish with small dorsal humps for their length had the highest fitness (Table 4.4), and bivariate cubic splines again confirmed this (i.e., relatively constant slope of increasing fitness from the upper right to the lower left of Figure 4.5E). No pattern was evident from the correlational coefficients in Yako Creek, as this coefficient was positive (suggesting fish with similar trait values were favored) but directional coefficients differed in sign. However, bivariate cubic splines revealed that long fish with short jaws were favored (i.e., relatively constant slope of increasing fitness from the upper left to the lower right of Figure 4.5F)

Predicted divergence and observed trait variation among populations

The population means differed significantly for all three traits (body length, body depth and jaw length, $P < 0.001$; Figure 4.3). To test whether differences in shape were due to differences in body length among populations, we also tested for differences in size-standardized depth and jaw means. The interaction between jaw length and body length was not significant ($P = 0.630$), facilitating a comparison of length-standardized means. Comparisons of adjusted mean traits revealed that Hansen Creek males had shorter jaws than individuals from Bear ($P = 0.003$) and Yako ($P < 0.001$) creeks, which did not differ from each other ($P = 0.539$). The interaction between body depth and length was significant ($P = 0.007$) precluding a comparison of length-standardized body depths. However, over nearly the entire range of data, the rank order of body depths at any given body length did not differ – Bear Creek fish had deeper bodies at any length, followed by fish from Yako Creek, and then Hansen Creek.

Thus, Bear Creek fish were longer, deeper bodied, and had similarly-sized jaws compared to fish from Yako Creek, which were longer, deeper bodied, and had longer jaws than Hansen Creek fish (Figure 4.3). Ordered-heterogeneity (OH) tests revealed that body length and length-standardized depth differed among populations in a manner consistent with inter-population variation in selection differentials (body length: $r_sP_c = 1.0$, $k = 3$, $P < 0.001$; length-standardized body depth: $r_sP_c = 1.0$, $k = 3$, $P < 0.01$). Among-population variation in length-standardized jaw length, however, did not follow variation in the jaw length selection differentials ($r_sP_c = -0.5$, $k = 3$, $P > 0.90$) but instead followed inter-population differences in body size.

Discussion

The goal of this study was to predict population divergence based on quantitative estimates of natural selection, specifically predation – a task that has not previously been accomplished in natural populations. Our analysis yielded several general conclusions:

1) the opportunity for selection, determined as variance in relative fitness for each population, differed among populations and was highest in Hansen Creek, paralleling the elevated predation intensity from brown bears in this creek (Table 4.2).

2) patterns of selection acting on body length and length-standardized depth were congruent: big males (i.e., long and deep-bodied) were favored in Bear Creek, small males (short and shallow-bodied) were favored in Hansen Creek, and males of intermediate size and shape were favored in Yako Creek. Thus the combination of length and body depth, which would affect visibility to a predator and maneuverability in shallow water, were opposite in Bear and Hansen creeks, and intermediate in Yako Creek. These populations also differed in jaw length – males in Hansen Creek had shorter length-standardized jaws than males breeding in either Bear or Yako creeks.

3) quadratic selection (whether stabilizing or disruptive) varied in direction among traits and was never significant (Table 4.5).

4) correlational selection favored individuals that were both long and relatively deep-bodied in Bear Creek but individuals that were short and relatively shallow-bodied in Hansen Creek (Table 4.5, Figure 4.5).

5) the strength of directional selection varied in a manner consistent with body length and depth variation among these populations (Bear > Yako > Hansen; for both body length and length-standardized depth, $P < 0.001$). Differences in size-standardized jaw lengths among populations paralleled differences in overall body size and not the

variation in selection coefficients (relative jaw length: Hansen > Bear > Yako). This suggests that jaw length and body size may be pleiotropically linked and sets up the possibility of a constraint on adaptive evolution in jaw length that warrants further investigation.

Selection and population divergence

If evolutionary equilibria among populations have been reached, each population should experience stabilizing selection around its mean. Alternatively, if equilibria have yet to be reached, each population should experience directional selection pushing each population's mean towards its adaptive peak (e.g., (Schluter 2000)). We found no evidence of stabilizing selection on any trait in any population. Rather, we found contrasting patterns of directional selection acting among populations. These results thus indicate a lack of evolutionary equilibria in our study populations. Furthermore, these results demonstrate that variation in natural selection owing to bear predation can drive divergence among populations in the size and shape of sockeye salmon. These populations are self-sustaining and presumably well-adapted to their breeding environments, so why might they be out of equilibria? We here suggest several possibilities.

The first possibility is that selection is absent in these populations but we inadvertently sampled reproductively unsuccessful immigrants from other populations. This seems highly unlikely, however, given the strong natal homing in salmonids (Quinn et al. 1987; Quinn et al. 1999), and the consistent differences in size, shape and age among the populations (Quinn and Buck 2001; Quinn et al. 2001b). Precise estimates of straying rates are not available for these populations but are probably on the order of 1% of less. Such low rates of straying, combined with the numbers of spawning adults in the three focal populations (Table 4.1) make it unlikely that we measured a substantial number of immigrants.

A second possibility is migration with gene flow (i.e., reproductively successful strays). This would result in the production of offspring with maladapted phenotypes for the new environment and could thus be keeping the recipient population from attaining equilibrium. But, as stated above, straying rates are low and population sizes are large (Table 4.1), so this possibility also seems implausible. Further, Lin et al. (In review) demonstrated genetic isolation among sockeye salmon populations breeding in creeks elsewhere in the Wood River system that are much closer together (spatially) than the ones we studied, so migration between populations (whether successful or not) is probably not driving these populations out of equilibria.

A third possibility is opposing selection at some other life stage. The observed contemporary selection acting in these populations may be maintained in part by earlier episodes of selection favoring different values of size and shape (Schluter et al. 1991). One selective agent that can influence the evolution of fish populations is commercial fishing. Sockeye salmon returning to the Wood River Lakes system are subject to an intense commercial fishery using gillnets that are size-selective to some extent ((Burgner 1964; Bue 1986; Hamon et al. 2000); N. Kendall unpublished data; Alaska Department of Fish and Game unpublished data). The individuals we sampled in each population, therefore, represent only the subset of individuals that ‘escaped’ the fishery. The evolutionary effect of the fishery on these populations is currently unknown, but fishery selection is a plausible explanation for why these populations are not in equilibria.

Selection from fishing will act on all populations, but to varying extents depending on their size and shape. There are, however, other forms of size-selective mortality that affect the populations unequally. In Hansen Creek, many salmon strand at the shallow creek mouth and die prior to reaching the breeding grounds, and this stranding mortality is heavily selective against large males (Quinn and Buck 2001; Carlson and Quinn In review). Differences in the interface between the creek and the lake make this mortality especially severe at Hansen Creek, much less so at Yako Creek, and non-existent at Bear Creek. We did not incorporate stranded fish in our analysis but had we done so strength of selection against large males would have been greatly magnified in Hansen Creek, as the two sequential episodes of selection both favor short individuals, suggesting that this population is even further out of equilibrium than our selection differentials suggest. While we focused our analyses on males, large females are also killed by bears, and selection against large size in males is presumably correlated with selection against large size in females. Indeed, this has been shown to be true with regards to selection due to stranding (Carlson and Quinn In review).

A fourth possibility is fluctuating selection. Two studies using formal approaches have previously estimated selection acting on breeding male salmon (e.g., (Lande and Arnold 1983; Brodie et al. 1995)), both in Hansen Creek. Based on data from two breeding seasons, Hamon and Foote (2005) found that natural selection did not act on male length in one year (1994) but favored short males in the second year (1995). Quinn et al. (2001a) merged data collected from two breeding seasons (1999-2000) and found that small males had an overall fitness advantage. Our data from Hansen Creek, merged across three breeding seasons (2003-2005) also suggested a fitness advantage for small males. In combination with the consistent evidence of size-selective predation (Ruggerone et al. 2000; Quinn and Buck 2001) and size-selective stranding mortality (Quinn and Buck 2001; Carlson and Quinn In review), our present results indicate that natural selection does not favor large males in Hansen Creek, although the strength of selection favoring small males may vary among years.

A fifth possibility is shifting adaptive landscapes. Work on Darwin's finches has demonstrated that adaptive landscapes may not be static but rather can shift temporally as the abundance of seeds of varying sizes fluctuates. For example, large individuals of the medium ground-finch (*Geospiza fortis*) were favored in some years (following droughts when large seeds were abundant) whereas smaller birds were favored following wet years when small seeds were abundant (Grant and Grant 2002). In our system, the intensity and strength of selection may differ among years due to, for instance, the density of salmon and/or bears. No study has yet related year-specific quantitative estimates of selection within a system to the intensity of predation in that year, but this would certainly be a profitable area for future research. The density of breeding salmon varies greatly among years in each creek (Table 4.1) and the proportion of salmon killed decreases with density (Quinn et al. 2003). The strength of selection might covary positively with salmon density, if high salmon availability causes bears to preferentially remove large, energetically rewarding, individuals.

Despite the evidence that selection due to bear predation was correlated with divergence in this system, the selection was actually quite weak in comparison to other studies (i.e., compared to the studies included in Kingsolver et al. (2001)). For instance, our median body length differential (0.06), relative jaw length differential (0.038), and relative body depth differential (0.028) corresponded with the 30th, 20th, and 16th percentiles from Kingsolver's review (Kingsolver et al. 2001). Moreover, our quadratic coefficients were *never* significant but sometimes strong in comparison to other studies (median length^2 differential = 0.106, 59th percentile; median relative jaw length^2 differential = 0.012, 21st percentile; median relative depth^2 differential = 0.011, 21st percentile). This latter result is due to generally weak quadratic selection in wild populations (Kingsolver et al. 2001).

Thus, on the one hand, we found that natural selection due to predation can drive divergence among populations. On the other hand, selection tended to be weak in our study populations relative to other studies of selection (Kingsolver et al. 2001). We interpret this as evidence that even weak selection (if temporally consistent) can drive evolution. Indeed, this same point was made by Hoekstra et al. (2001), who concluded that persistent weak directional selection (median $|\beta| = 0.15$), could shift the mean trait value in a population by one standard deviation in as few as 16 generations assuming a trait heritability = 0.5. Moreover, stronger selection in other studies (i.e., Kingsolver's database) suggests that those populations were even further out of equilibrium. Indeed, Kingsolver et al. (2001) reported that quadratic selection tended to be weaker than linear selection in natural populations and that stabilizing selection was no more common than disruptive selection.

Conclusions

We advanced previous research estimating the strength and form of selection in nature by 1) identifying the agent of selection (bear predation), 2) including more spatial replicates than previous work (Kingsolver et al. 2001), 3) quantifying the percent of salmon killed in each population, 4) sub-sampling our dataset to ensure that the percent of salmon killed in our dataset paralleled the population level pattern (most studies simply assume no sampling bias), and 5) testing for a correlation between contemporary selection and trait divergence among populations. Furthermore, by using gonad depletion as a proxy for reproductive activity, the data we collected were independent of the problems and possible biases in observational studies of salmonid reproductive behavior (Mehranvar et al. 2004). We thus feel confident that we have presented a robust analysis of selection.

Our results suggest that natural selection, due to predation, can be an important driver of adaptive population divergence. Furthermore, the lack of stabilizing selection but presence of directional selection suggests that these populations are not in evolutionary equilibria. Results of the Kingsolver et al. (2001) review suggest that this is generally true of natural populations – stabilizing selection tends to be quite weak in self-sustaining, natural populations. Perhaps this is due to the non-static nature of adaptive landscapes. If adaptive landscapes shift regularly (e.g., in response to local environmental conditions), selection acting to push a population towards the current adaptive peak may be acting in the wrong direction based on the adaptive landscape that will be encountered by future generations. We might therefore expect that natural populations will rarely be in evolutionary equilibrium (and Kingsolver's review provides support for this assertion) and that directional selection should be common. Based on this view, the strength of directional selection would depend on the location in the adaptive landscape in the current generation, which is itself based on the response to selection acting on the previous generation, and the steepness of the adaptive peaks, which can be estimated as the opportunity for selection. Long-term studies estimating the temporal stability of fitness surfaces are needed to test the above ideas.

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Table 4.1. Average annual abundance and density of sockeye salmon (mean ± S.E., total number of years indicated in parentheses), physical habitat attributes including average stream width and depth, as well as the distance and elevation gained during the breeding migration for three sockeye salmon populations.

Population	Abundance mean ± S.E. *(n)*	Density fish / m^2 *(n)*	Width (m)	Depth (cm)	Migration Distance (km)	Migration Elevation Gain (m)
Bear	3796 ± 277 (59)	0.24 ± 0.02 (59)	5.1	19.3	44	10
Hansen	3699 ± 499 (50)	0.45 ± 0.06 (50)	3.9	9.8	42	10
Yako	2563 ± 309 (51)	0.11 ± 0.01 (51)	4.2	22.6	39	10

Table 4.2. Overall predation rate (average annual percent of salmon killed ± S.D., and number of years of data) and predator selectivity for newly arrived fish in Bear, Hansen, and Yako creeks, southwestern Alaska (see Carlson et al. submitted for details on the calculation of these two indices of predation intensity).

Population	Overall Predation Rate (%) mean ± S.D. *(n)*	Predator Selectivity For Newly Arrived Fish mean ± S.D.
Bear	29.80 ± 12.35 (16)	0.067 ± 0.008
Hansen	48.56[1] ± 20.00 (18)	0.175 ± 0.006
Yako	29.58 ± 12.38 (15)	0.091 ± 0.010

[1] Note that some salmon strand and die at the mouth of Hansen Creek. If we instead calculate the percent of salmon killed by bears as a function of only those fish that successfully ascended the mouth (as opposed to the total number of fish returning to Hansen Creek), overall predation rate increases to 64 %.

Table 4.3. Sample sizes for selection analyses reported by the trait(s) included in the focal analysis. We report both the total number of bear-killed or senescent individuals sampled for gonad depletion and morphology (“Total”) as well as the number of individuals from each mode of death category included in selection analyses (“Sub-sample”). The percentage of bear-killed and senescent individuals in the sub-sample reflects the long-term average annual percentage of bear-killed and senescent individuals at the population level.

		Total		Sub-sample	
Population	Traits	Bear-killed *(n)*	Senescent *(n)*	Bear-killed *(n)*	Senescent *(n)*
Bear	Body length & residual jaw length	93	139	60	139
Hansen	Body length & residual jaw length	51	150	51	29
Yako	Body length & residual jaw length	99	65	28	65
Bear	Residual depth	55	85	36	85
Hansen	Residual depth	46	143	46	26
Yako	Residual depth	53	55	24	55

Table 4.4. Directional selection acting on length, residual jaw, and residual depth. For both the selection coefficient (b) and associated standard error (SE), we present the average value of 1,000 analyses based on random sub-samples of our data (see Methods; standard deviation in parentheses below the average). Because the distribution of *P*-values was highly non-normal, we instead focus our interpretation on the median *P*-value.

		Linear selection differentials			Linear selection gradients		
Population		length	residual jaw	residual depth	length	residual jaw	residual depth[1]
Bear	b	0.06 (0.008)	-0.018 (0.001)	0.014 (0.002)	0.06 (0.008)	-0.019 (0.007)	0.015 (0.01)
	SE	0.016 (0.001)	0.016 (0.008)	0.02 (0.01)	0.016 (0.001)	0.016 (0.001)	0.02 (0.002)
	P	< 0.001	0.257	0.472	< 0.001	0.220	0.437
Hansen	b	-0.098[2] (0.013)	0.065 (0.001)	-0.045 (0.001)	-0.073 (0.021)	0.063 (0.024)	-0.068 (0.034)
	SE	0.037[2] (< 0.001)	0.054 (0.025)	0.067 (0.031)	0.054 (0.001)	0.054 (0.001)	0.068 (0.002)
	P	0.009[2]	0.225	0.511	0.177	0.242	0.326
Yako	b	0.02 (0.018)	-0.038 (0.004)	-0.028 (0.004)	0.022 (0.017)	-0.039 (0.02)	-0.031 (0.015)
	SE	0.024 (0.004)	0.023 (0.02)	0.026 (0.014)	0.023 (0.004)	0.023 (0.004)	0.026 (0.004)
	P	0.338	0.118	0.271	0.315	0.113	0.23

Table 4.4 continued

[1] Regressions included the subset of fish for which length and residual depth data were available. Only the residual depth coefficients are reported as the length coefficients closely corresponded to those generated from the regressions that instead included body length and residual jaw length.

[2] Regression included an additional 140 fish for which no jaw or depth information was available.

Table 4.5. Univariate selection acting on length (length × length), residual jaw (residual jaw × residual jaw), and residual depth (residual depth × residual depth); and bivariate selection acting on trait combinations (length × residual jaw; length × residual depth) in Bear Creek, Hansen Creek, and Yako Creek salmon. For both the selection coefficient (b) and associated standard error (SE), we present the average value of 1,000 analyses based on random sub-samples of our data (see Methods; standard deviation in parentheses below the average). Because the distribution of *P*-values was highly non-normal, we instead focus our interpretation on the median *P*-value.

Population		Quadratic selection differentials			Quadratic selection gradients				
		length × length	residual jaw × residual jaw	residual depth × residual depth	length × length	residual jaw × residual jaw	length × residual jaw	residual depth × residual depth[1]	length × residual depth[1]
Bear	b	0.025 (0.243)	0.009 (0.008)	-0.007 (0.014)	-0.027 (0.244)	0.002 (0.007)	0.187 (0.107)	-0.016 (0.015)	0.017 (0.101)
	SE	0.399 (0.03)	0.017 (0.001)	0.021 (0.002)	0.402 (0.03)	0.016 (0.001)	0.196 (0.015)	0.023 (0.003)	0.246 (0.026)
	P	0.720	0.570	0.583	0.671	0.760	0.325	0.415	0.739
Hansen	b	1.023[2] (0.235)	-0.029 (0.036)	-0.011 (0.035)	-0.188 (0.506)	-0.018 (0.03)	0.512 (0.323)	0.017 (0.037)	1.087 (0.583)
	SE	0.784[2] (0.027)	0.055 (0.002)	0.069 (0.002)	1.305 (0.085)	0.06 (0.002)	0.737 (0.049)	0.071 (0.004)	1.142 (0.126)
	P	0.190[2]	0.491	0.704	0.774	0.678	0.490	0.690	0.317
Yako	b	-0.106 (0.331)	-0.012 (0.015)	0.014 (0.014)	-0.089 (0.275)	-0.01 (0.015)	0.04 (0.26)	0.003 (0.016)	0.169 (0.164)
	SE	0.476 (0.077)	0.024 (0.004)	0.026 (0.004)	0.491 (0.082)	0.024 (0.004)	0.298 (0.051)	0.029 (0.005)	0.357 (0.062)
	P	0.719	0.572	0.527	0.707	0.618	0.518	0.659	0.648

Table 5 continued

[1] Regressions included the subset of fish for which length and residual depth data were available. Only the residual depth coefficients are reported as the length coefficients closely corresponded to those generated from the regressions that instead included body length and residual jaw length.

[2] Regression included an additional 140 fish for which no jaw or depth information was available.

Figure 4.1. Map of Lake Aleknagik and the three study sites (Bear Creek, Hansen Creek, and Yako Creek) relative to the Wood River Lakes, southwestern Alaska.

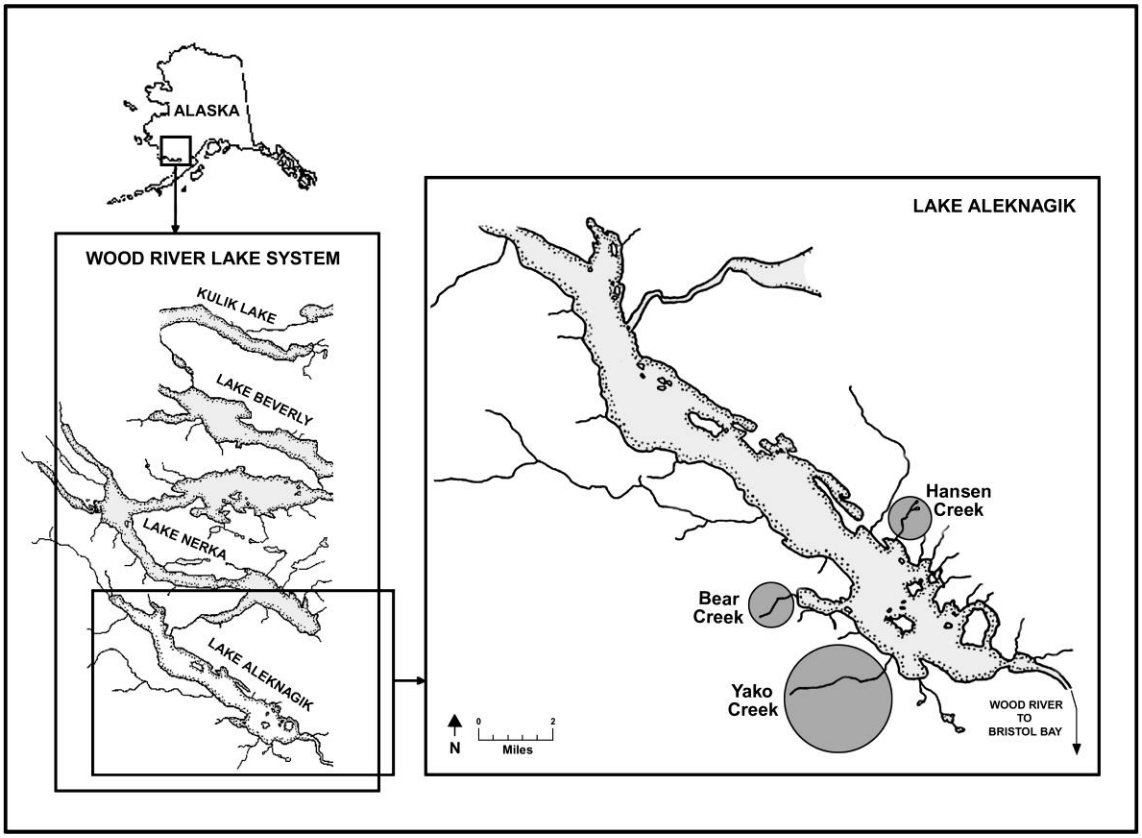

Figure 4.2. Gonad mass (y-axis) plotted against body length (x-axis). The results are grouped by status (pre-reproductive: sold black circles and regression line, bear-killed: open black triangles, senescent: crosses). Results are presented by population: (A) Bear, (B) Hansen, and (C) Yako.

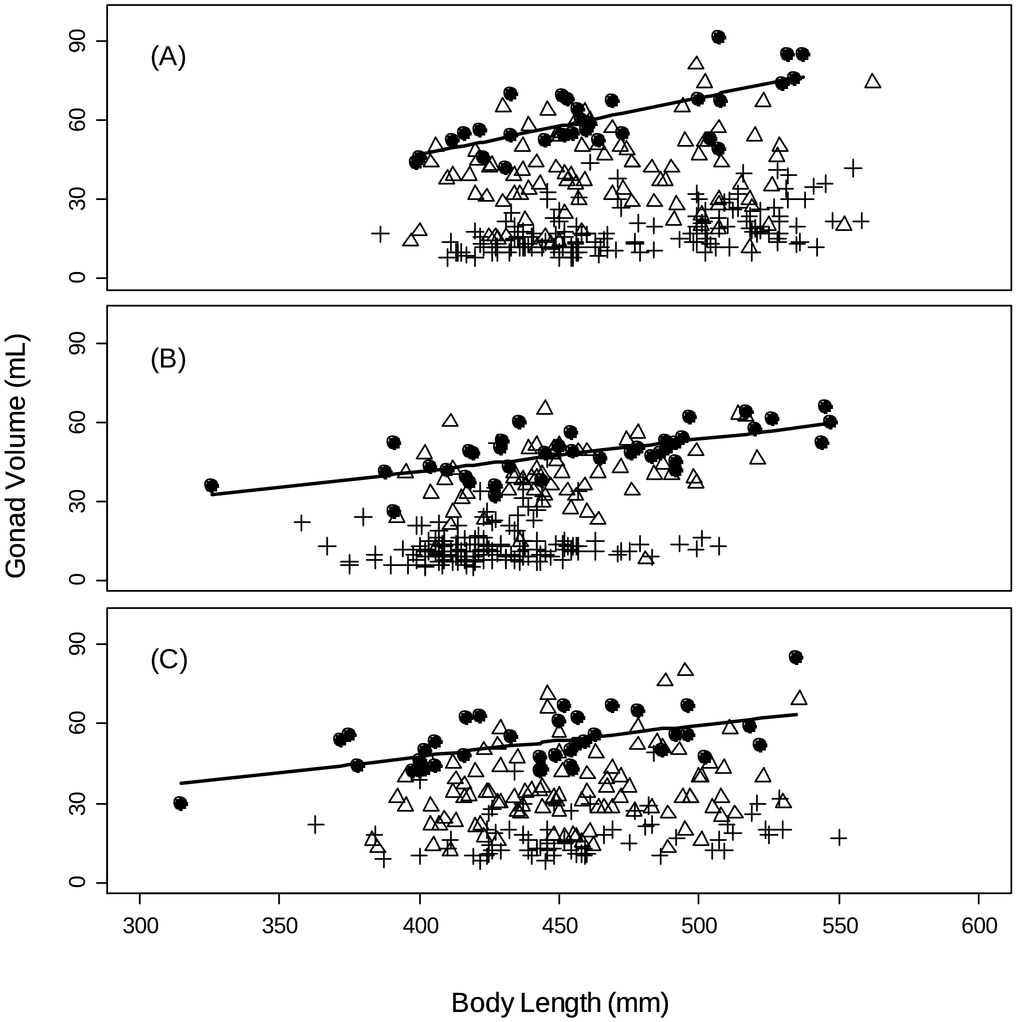

Figure 4.3. Frequency distributions of the focal traits grouped by population. Body length (A – C), jaw length (D – F), and body depth (G – I) for Bear Creek (top row), Hansen Creek (middle row), and Yako Creek (bottom row). Arrows indicate trait means (black arrow: raw trait mean; gray arrow: length-standardized trait mean).

Figure 4.3. continued.

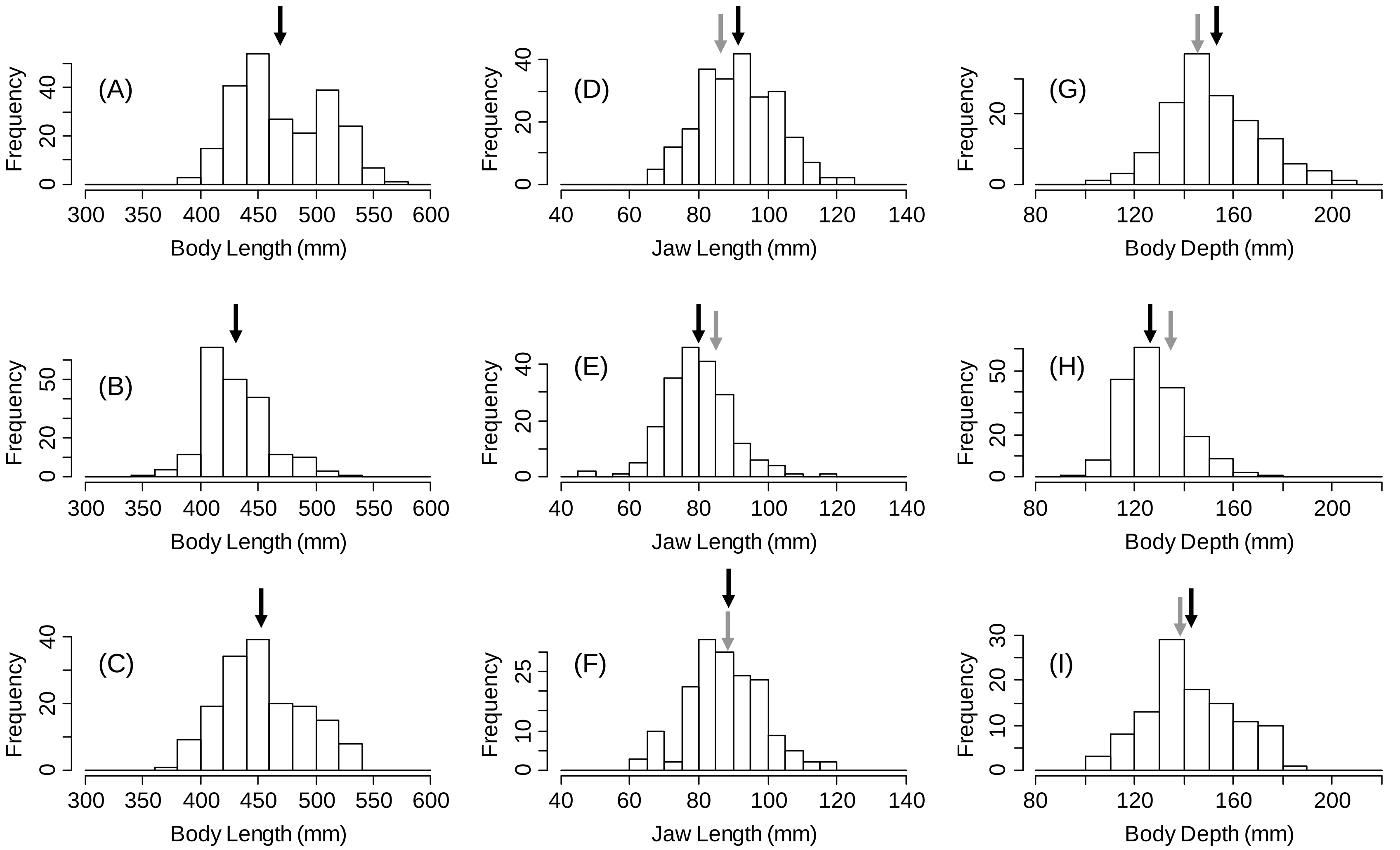

Figure 4.4. Relationship between body length (A), relative jaw length (B), and relative body depth (C) and an individual's absolute fitness for male sockeye salmon breeding in Bear (solid line), Hansen (dashed line), and Yako (dotted line) creeks. The lines represent univariate cubic splines (Schluter 1988).

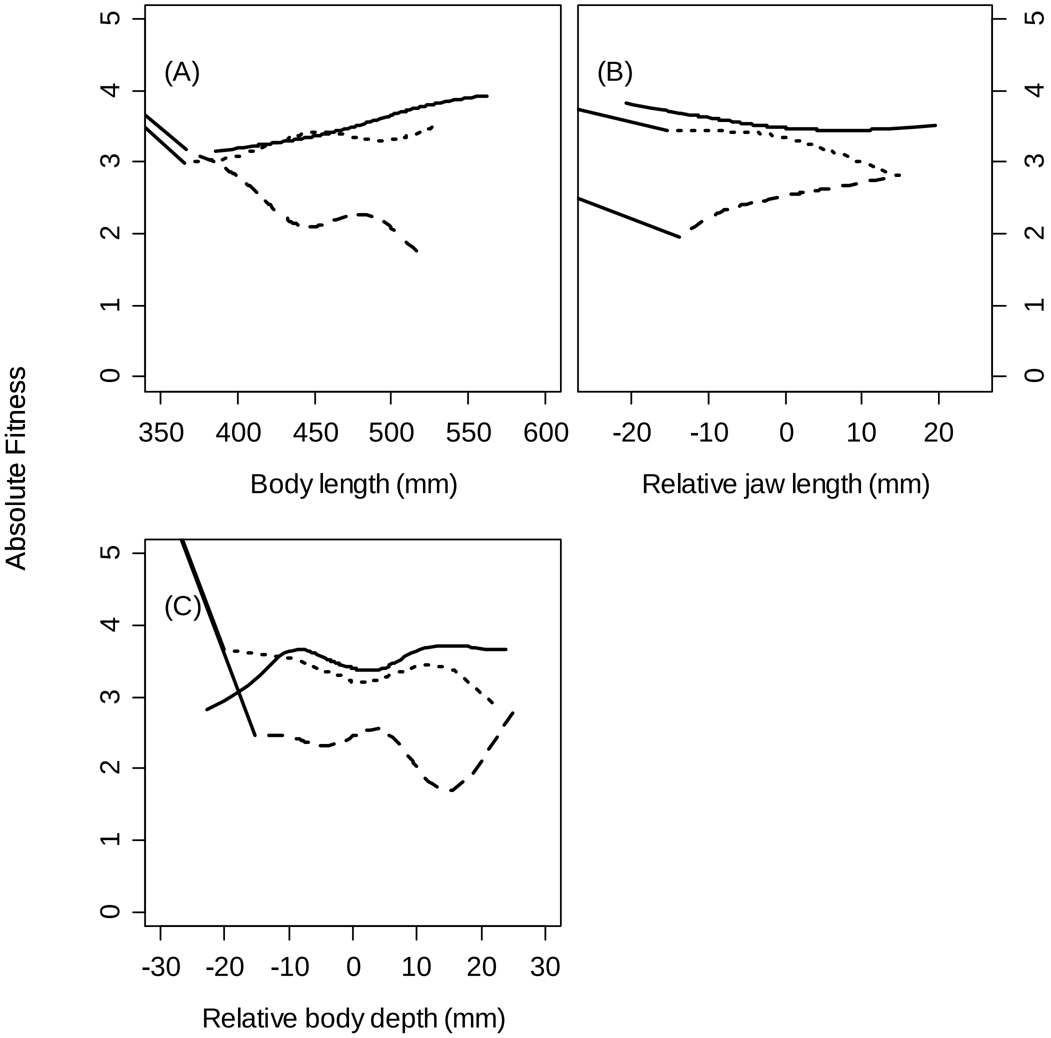

Figure 4.5. Bivariate spline estimation of the fitness surface relating standardized body length and either standardized jaw length (panels A-C) or standardized body depth (panels D-F) to an individual's absolute fitness in Bear (A, D), Hansen (B, E) and Yako (C, F) creeks. The contour lines represent an interpolated fitness surface, which was fit to the predicted fitness values generated using surface.exe (Schluter and Nychka 1994).