Size-Selective Mortality of Chinook Salmon in Relation to Body Energy after the First Summer in Nearshore Marine Habitats

Kathrine G. Howard[1], James M. Murphy[2], Lorna I. Wilson[3], Jamal H. Moss[2], and Edward V. Farley, Jr.[2]

[1]*Alaska Department of Fish and Game, Division of Commercial Fisheries,*
333 Raspberry Road, Anchorage, AK 99518, USA
[2]*Auke Bay Laboratories, Alaska Fisheries Science Center, NMFS, NOAA,*
17109 Point Lena Loop Road, Juneau, AK 99801-8344, USA
[3]*Alaska Department of Fish and Game, Mark, Tag and Age Laboratory,*
P.O. Box 115526, Juneau, AK 99811-5526, USA

Abstract: The probability of size-selective mortality (SSM) after the first summer of marine residency (i.e., the second critical period [SCP]) was evaluated for Yukon River Chinook salmon (*Oncorhynchus tshawytscha*). Size distributions of fish sampled as juveniles and back-calculated from adults were compared to evaluate SSM. Size distribution for juvenile samples at SCP was estimated from fork length (FL) of fish collected in the northeastern Bering Sea. Scale radii distributions for adult samples at SCP were estimated using the mean early marine circuli count from available juvenile scales, and back-calculating FL at SCP using a linear regression between juvenile FL and scale radius. A second regression was used to estimate body weight at FL. Size at SCP in the average adult sample (95% confidence interval of the mean = 163–178 g) was greater than that in the juvenile sample (95% confidence interval of the mean = 134–140 g), indicating SSM between SCP and sexual maturity. A generalized additive model (GAM) indicated a significant relationship between weight or energy density at SCP and the probability of SSM. These results support the theoretical mechanism of SCP: that SSM in salmon could be attributed to energy density after the first summer in nearshore habitats.

Keywords: Bering Sea, Chinook salmon, size-selective mortality, energy density, growth

INTRODUCTION

Size-selective mortality (SSM) is believed to be an important factor of the juvenile salmon life stage that links ecosystem processes to salmon mortality (Healey 1982; Sogard 1997; Moss et al. 2005; Farley et al. 2007; Cross et al. 2009; Miller et al. 2013). While SSM during the first critical period (FCP) of the critical period-critical size hypothesis (estuarine and early marine residence) is predicted to be predation-dependent, the second critical period (SCP; summer growth prior to the first winter at sea) is expected to be energy status-dependent (Beamish and Mahnken 2001). Mortality during SCP is generally considered to be a function of total energy storage, with larger juveniles typically having a higher probability of surviving. Energy allocation patterns in juvenile salmon, to growth or storage, and these relationships to nearshore rearing conditions are poorly understood.

High mortality is expected for juvenile stages of salmon (Hartt 1980), and only a portion of a brood is expected to attain adequate size and energetic status to survive the SCP

(Beamish and Mahnken 2001). Juvenile Yukon River Chinook salmon enter marine waters in late May through August (Martin et al. 1987), and utilize habitats in the northeastern Bering Sea during their first summer in the ocean, prior to winter ice formation (Farley et al. 2005; Murphy et al. 2009). Most Yukon River Chinook salmon are "stream-type", migrating to the ocean after rearing for one year in-river as fry. Smaller proportions of "ocean-type" (freshwater residency of months; age-0.X), and freshwater residency of two years (age-2.X) are also observed in returning adults (JTC 2015). "Ocean-type" adults are particularly uncommon. It is unknown how freshwater life-history characteristics, out-migration timing, and environmental conditions interact to influence size, growth, and mortality of these stocks.

Previous size and growth studies of Yukon River Chinook salmon have focused on different reference points throughout their life from historic scale collections of adult salmon (Ruggerone 2009a, b; Myers et al. 2010). It is important, however, to recognize that the life history of size and growth for individual Chinook salmon are back-calculated
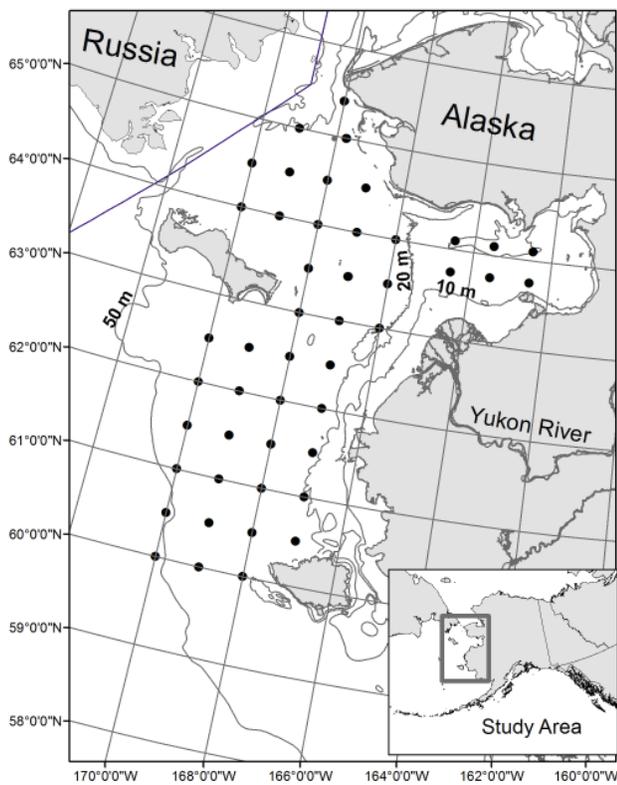
Fig. 1. Typical station coordinates (black dots) of surface trawl surveys in the northeastern Bering Sea.

of a grid-based sampling design with stations spaced at each degree of longitude and 30 minutes of latitude (Fig. 1). Surface rope trawls (Cantrawl Pacific Limited, Richmond, British Columbia) were fished for 30 minutes at each station, during daylight hours (0730–2100, Alaska Daylight Savings Time), and covered a distance of approximately 3.2–4.2 km. Trawls were fished to sample the top 20 m of the water column, encompassing the entire water column in some shallower areas (Farley et al. 2007, 2009; Murphy et al. 2009).

Individual FL (to nearest mm) and weight (to nearest g) were recorded for up to 50 juvenile Chinook salmon at each station sampled. Scales were collected when present in the preferred area (the second to the seventh rows of scales above the lateral line diagonal from the back of the dorsal fin), and placed on gummed cards for later processing (Mosher 1963). Most salmon were largely descaled by the trawl gear, particularly the smallest sized fish, limiting the available scales obtained in a given year. Hatchery fish were rarely encountered, presence of adipose fin clips associated with coded wire tags was noted, and these fish were excluded from this study.

To define total Yukon-origin juvenile Chinook salmon size distributions at SCP of each of the 2002–2007 juvenile years, length and weight frequencies of juvenile Chinook salmon captured in 2002–2007 northeastern Bering Sea marine trawl surveys were assessed. At least 60% of juveniles captured north of 60°N originate in the Yukon River based on mixed stock genetic analysis, with the remaining 40% containing Yukon stocks that cannot be definitively differentiated from other coastal western Alaskan stocks using current genetic markers (Murphy et al. 2009). Because the Yukon River represents over 90% of the total Chinook salmon

from adult salmon scales. Therefore, the back-calculated size and growth characteristics represent Chinook salmon that survived from egg to adult and therefore are subject to the combined effects of growth and SSM.

Recent dramatic productivity declines in western Alaska Chinook salmon, Yukon River Chinook salmon in particular, has prompted considerable research into mechanisms that may structure productivity trends in these stocks (ADF&G 2013; Schindler et al. 2013). Our primary objective was to evaluate the role of size and energetic status at SCP in structuring Yukon River Chinook salmon survival. This study attempts to determine if significant SSM is present in juvenile Yukon River Chinook salmon after SCP, and to evaluate how SSM varies with energetic condition of juvenile Chinook salmon.

MATERIALS AND METHODS

Juvenile Sampling: Defining Total Juvenile Size Distribution

The Bering Aleutian Salmon International Survey (BASIS) and later surface trawl surveys in the northeastern Bering Sea captured juvenile Yukon River Chinook salmon in September of their first year in the ocean. Surveys have been conducted since 2002, excluding 2008. Surveys consisted

Table 1. Adult scale samples digitized and used for growth analysis are shown by age class and return year that are proportional to actual ages returning from 2002-2007 juvenile years. Scales sampled from Pilot Station, Yukon River. Age is shown using the European notation, with the numeral before the decimal indicative of the number of winters the fish spent in fresh water before outmigration, and the numeral after the decimal indicative of the number of winters the fish spent in salt water before returning to the river (Koo 1962).

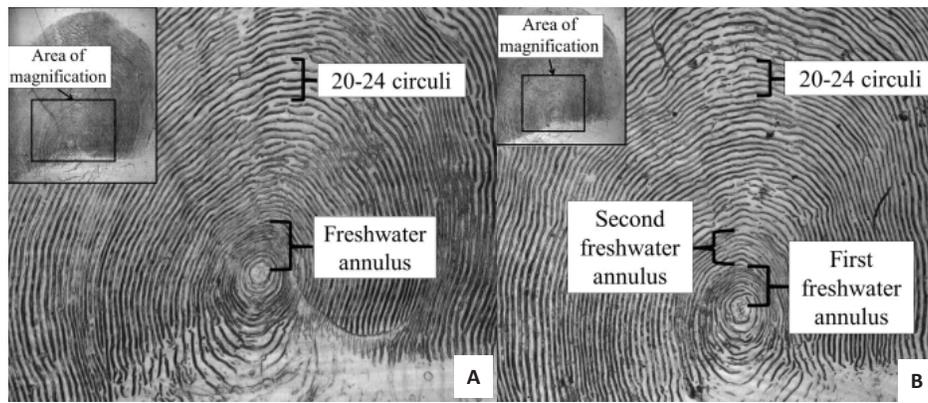| Return year	Age class							Total
	1.1	1.2	1.3	1.4	1.5	2.3	2.4	
2004	1	27						28
2005		15	61					76
2006		16	63	30		3		112
2007		13	61	52	1	1	1	129
2008		7	77	47	15		3	149
2009		30	67	54	4	1	2	158
2010			88	54	5	1	1	149
2011				28				28
Total	1	108	417	265	25	6	7	829

Fig. 2. Digitized scales from a freshwater age-1 adult (A), freshwater age-2 adult (B). The mean ± 1 SD (20–24 circuli) is identified and corresponds to the SCP reference point sample area for most back-calculated adult scales. Samples collected from Pilot Station, Alaska, for this study. Images from ADF&G MTA Laboratory.

production for rivers entering the northeastern Bering Sea, it can be assumed that the remaining 40% of juveniles that cannot be genetically discriminated are primarily of Yukon origin, and the size distribution of juveniles in this region is representative of the size distribution of Yukon-origin juvenile Chinook salmon in a given year. Juvenile size data at SCP were standardized to an average capture date of 20 September (2002–2007), based on an assumed growth rate of 1 mm/day (Farley et al. 2009) or 1.2% body weight g/day (Walker et al. 2013). Fork length and weight distributions from the juvenile samples represented the portion of the juvenile population that survived to the end of their first summer in salt water and represented the candidate adult population at the SCP.

Juvenile Sampling: Energy Density

Energy density is a measure of nutritional condition and was estimated from a subset of juvenile Chinook salmon captured since 2005 (typically two juveniles from each sta-

tion) using standard bomb calorimeter methods (Fergusson et al. 2010). Fish were dried to a stable weight ($\leq$ 5 mg change), homogenized with a Waring pulverizer, and ground to a fine powder with a mortar and pestle prior to analysis with a 1425 Parr micro-bomb calorimeter. Energy density estimates (kJ/g) from the calorimeter were rescaled to wet weight energy density by the percent water content (ratio of dried weight to initial body weight).

Adult Sampling and Scale Digitization

Scales from the adult Chinook salmon represented the portion of the juvenile population that survived past the SCP to adulthood. A target subsample of 150 scales was collected from adult Chinook salmon at Pilot Station, Alaska, in the lower Yukon River for each of the 2002–2007 juvenile years (adult return years = 2004–2011). The Pilot Station test fishery was chosen because it uses a suite of gill-net mesh sizes (7 to 21.6 cm stretched mesh) and modeling efforts demonstrate the overall catch to be relatively unbi-
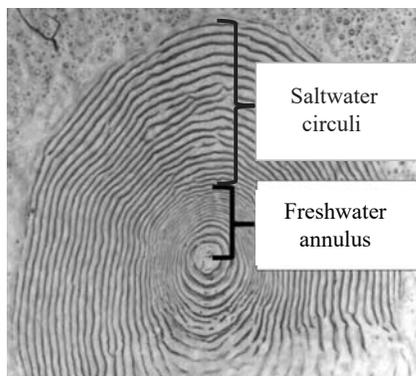

Fig. 3. Digitized juvenile scale demonstrating the freshwater annulus and saltwater circuli (age 1.0) present at capture. Juvenile Chinook salmon was sampled in 2005 on the eastern Bering Sea shelf and was 277 mm and 270 g at capture. Image from ADF&G MTA Laboratory.

Table 2. Mean and standard deviation of circuli counts and summed circuli distance for freshwater and first-year saltwater growth observed in juvenile scales (by date of capture) used for length-scale radius linear regression, and for adult scales used in the scale back-calculation analysis. SW1 measurements for juvenile scales represents a partial year while those for adults scales represents the full SW1 year.

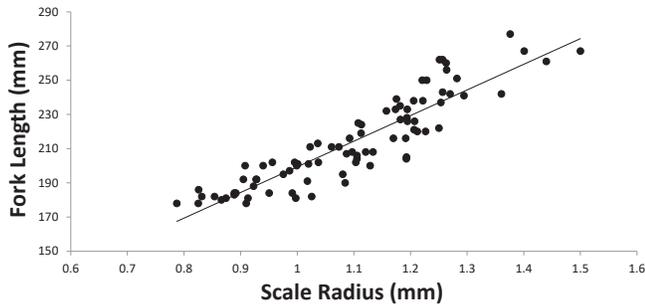| Scale growth zone	Juvenile scales (n = 84)		Adult scales (n = 829)	
	Circuli count (SD)	Circuli distance, μm (SD)	Circuli count (SD)	Circuli distance, μm (SD)
FW0	NA	NA	NA	NA
FW1	7.2 (1.8)	0.3 (0.04)	9.6 (2.2)	0.3 (0.06)
FW2	NA	NA	9.5 (2.0)	0.2 (0.04)
SW1	22 (1.98)	0.8 (0.1)	29.7 (4.6)	1.3 (0.2)

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Fig. 4. Relationship between scale radius (distance from focus to scale edge in mm) and fork length (mm) of juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea (Myers et al. 2010). Line represents a linear regression model: y = 150.0x + 49.4, r^2 = 0.82.

ased to the size and age composition of returning adult fish (Bromaghin et al. 2011). All adult scales were taken from the preferred area and only clean, readable scales without regeneration were used. Scales were cleaned, mounted on gummed cards, heated, and hydraulically pressed on acetate cards.

Adult Chinook salmon scales were selected to be included in the subsample to best match the age composition of each juvenile Chinook salmon year of return, as well as the run timing and sex composition of the run. Adult scales were sampled proportional to brood-year age structure and aggregated across return years by juvenile year. Within-age scale sampling was completed proportionally to the size-at-age and sex distribution occurring within each age stratum of returns. For example, if 40% of the fully returned 2002 juvenile cohort matured as age-1.3 fish, then a target of 60 adult scales representing the 2002 juve-

nile cohort would be selected from the 2005 adult return, and those samples would span the sex, size, and run timing distributions of age-1.3 returns observed in 2005. Due to their rarity in returns, no freshwater age-0 adults were sampled (Table 1).

Scale digitization followed procedures described by Hagen et al. (2001). Scales were scanned using Indus 4601-11 Screen Scan and a fixed 22 mm optical lens producing a high-resolution image (3360 x 4426 pixels, 400 dpi). Scales were measured using Image Pro Plus image analysis software, version 7.01, and the Otolith and Fish Scale Analysis macro, version 2.17, at the Alaska Department of Fish and Game (ADF&G) Mark, Tag and Age (MTA) Laboratory in Juneau. Measurements were made along a transect from the focus (initial growth) to the furthest edge of the scale margin. Distances between circuli (growth rings) were measured to the nearest 0.1 micrometer and circuli measurements were summed for each growth zone (fresh- and saltwater annuli, Fig. 2A, B). MTA Lab technicians were trained by experienced Yukon River agers to identify marine transition points and freshwater plus growth patterns unique to Yukon River Chinook salmon. To test for the effect of reader on scale growth zone measurement, a subset of scales was re-measured and compared using multiple analysis of variance (MANOVA) with independent variable reader on multiple dependent variables (growth zone measurements) and no significant differences were found ($p > 0.05$ for all growth zones) suggesting no difference in growth zones due to reader. Scale images were saved as uncompressed tiff files to archive scale appearance and measurements were stored in an Oracle database and summarized using Microsoft Access PL/SQL queries.
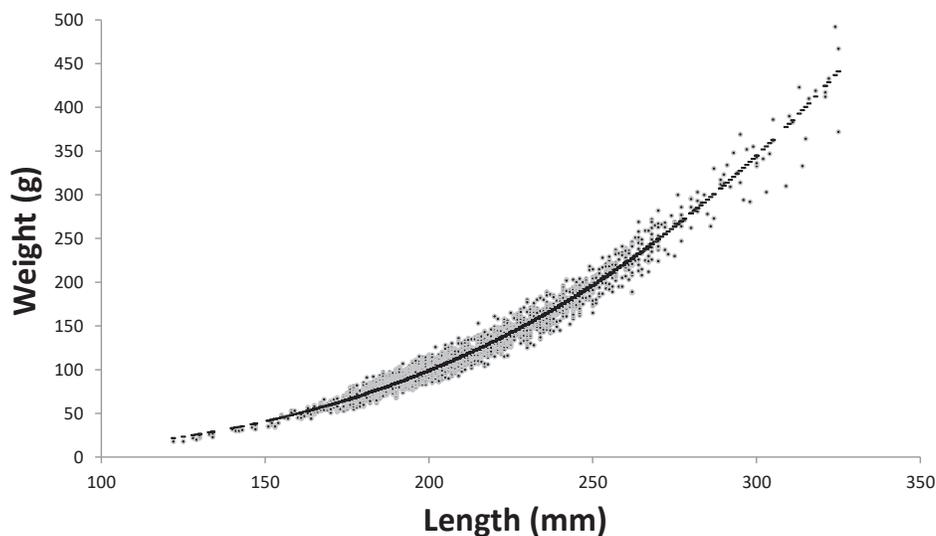

Fig. 5. Relationship between fork length (mm) and fresh weight (g) of juvenile Chinook salmon captured in the northern Bering Sea during surface trawl surveys in the northern Bering Sea (Murphy et al. 2013). Grey points are individual fish measurements, black points are from the fitted allometric growth model ln(weight) = 3.08 · ln(length) - 11.7.

Table 3. Juvenile sample catch characteristics, 2002–2007. Mean length and weight standardized to 20 September catch date also provided.

Year	Sample size	Mean date of capture	Mean FL, mm (SD)	Mean standardized FL, mm (SD)	Mean weight, g (SD)	Mean standardized weight, g (SD)
2002	126	26 September	229 (33)	223 (36)	156 (59)	149 (57)
2003	232	15 September	201 (32)	207 (29)	102 (49)	116 (44)
2004	175	17 September	221 (26)	224 (25)	136 (56)	146 (53)
2005	136	22 September	225 (21)	223 (18)	139 (42)	140 (38)
2006	104	9 September	188 (16)	199 (15)	77 (22)	99 (22)
2007	267	19 September	236 (25)	237 (12)	169 (57)	171 (50)

Identification of the Second Critical Period Reference Point on Adult Samples

The reference point on adult scales estimating growth prior to SCP was defined by the sampling distribution of total marine circuli counts on available juvenile scales sampled and standardized to 20 September (Fig. 2). As trawl-caught fish are largely descaled, a subsample of juvenile Chinook salmon scales available from eastern Bering Sea samples in 2002–2007 were digitized and scale growth increments analyzed (n = 84; Myers et al. 2010). When standardized, mean juvenile marine circuli was a count of 22, variance of 4: this does not yield a SCP saltwater circuli range different from the unstandardized circuli distribution (Fig. 3; Table 2). Scale measurements for each adult scale at the estimated SCP reference point were randomly assigned based on circuli numbers drawn from a normal probability distribution defined by this juvenile circuli distribution. Each adult in the sample was randomly assigned a circuli count and radius measurement once in each simulation of the adult population, and 1000 simulations were performed. Simulations represent possible realities of the true size distribution at SCP for those salmon that survived and returned as adults.

Back-Calculation of Weight at the Second Critical Period from Adult Samples

Several studies have documented clear relationships between scale radius and fish body length (Francis 1990; Ricker 1992), enabling back calculation of previous fish size using scale radius length. The subsample of paired juvenile length and scale radius measurements was used to determine relationships between body size and scale radius (n = 84; Myers et al. 2010). Scale radius measurements at SCP of adult fish were converted to fork length (FL, mm) based on the following scale radius (S, mm) to length relationship ($r^2 = 0.82$; n = 84; $p < 0.001$; Fig. 4):

$$FL = 150.0(S) + 49.4. \tag{1}$$

Reconstructed FL was converted to weight (WT, g) based on the following length-weight relationship for juvenile Chinook salmon (Fig. 5):

$$\ln(WT) = 3.08 \cdot \ln(FL) - 11.7. \tag{2}$$

Scale radius measurements from adult sample simulations were converted to weights to allow for comparisons to the weights of the juvenile sample at SCP.
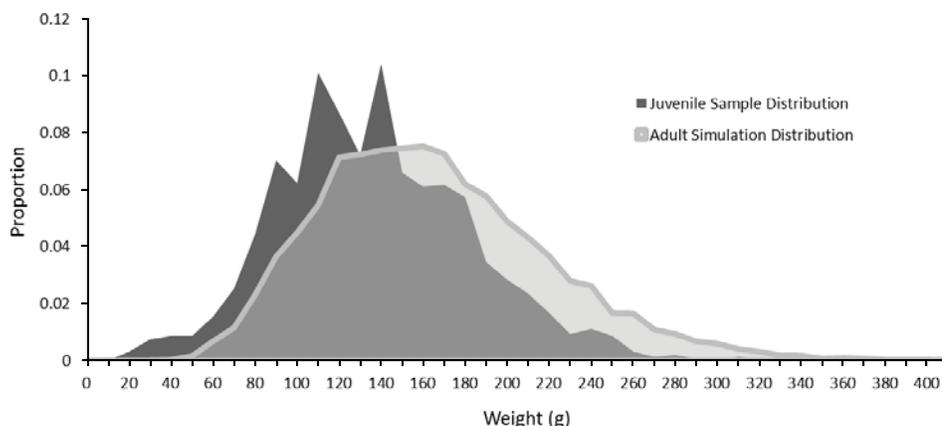

Fig. 6. Average weight distribution of simulated back-calculated adult weights at SCP (grey), compared to weight distribution of the total juvenile population at SCP (black).

Size-Selective Mortality Modeling

Weight models, rather than length models, were used to describe size-selective mortality at SCP as it is believed to be primarily a function of available energy reserves required to survive the first winter in the ocean (Yerokhin and Shershneva 2000; Beamish and Mahnken 2001). Weight can be used as proxy for energy storage for juvenile Yukon River Chinook salmon (Murphy et al. 2013). Weight distributions of the total observed juvenile population at SCP and the average of the simulations of back-calculated size of the adult survivor population at SCP, standardized to 20 September, were used to examine mortality probabilities. Size-selective mortality probabilities, ρ_i, were estimated from the proportion of juvenile, j_i, and surviving adults, a_i, within each weight interval, i, as:

$$\rho_i = \frac{j_i / a_i}{\left(\dfrac{j_i}{a_i} + 1\right)}. \tag{3}$$

Generalized additive models (GAM; Chambers and Hastie 1992) were fit to mortality probabilities and used to describe size-selective mortality in juvenile Chinook salmon.

RESULTS

Size Comparisons at the Second Critical Period

Yearly size distributions of juvenile Chinook salmon varied within and among years (Table 3). The smallest size classes captured in marine surveys overlap with outmigrating smolt sizes documented in the Yukon River Delta (mean smolt FL (SD) = 94 (12) mm in 1986, 2014, and 2015), while the largest individuals were roughly three times larger than outmigrating smolt sizes (Martin et al. 1987; K. Howard, unpublished data).

Size distribution differences, as measured in either FL or weight, are evident between the total juvenile population and the survivor population reconstructed from adult scales. In each of the simulations of adult size distribution at SCP, the mean (± 95% confidence interval) was larger than the distribution of the juvenile samples (simulation with the smallest adult sample mean = 167 ± 4 g; juvenile sample mean = 137 ± 3 g). The smallest sized juveniles were notably absent in the back-calculated sizes of adults at SCP, while a higher proportion of the adult samples were in the largest size classes at SCP (Fig. 6; Table 4). The total juvenile population had a lower minimum weight (18 g) than back-calculated adult samples at SCP (56 ± 4 g averaged across simulations) from 2002 to 2007.

Although juvenile salmon were not aged in this study, freshwater life-history differences were evident in the back-calculated sizes of adult samples at SCP, with freshwater age-2 fish being significantly larger than freshwater age-1 fish by 20 September (mean (SD) = 239 g (57) and 168 g (45), respectively; Welch's two sample *t*-test: $p < 0.001$).

Size-Selective Mortality Modeling and Juvenile Energy Density

The mortality GAM model for Yukon River Chinook salmon indicates that mortality is very high for the smallest juveniles, but rapidly declines to the point of neutral selec-

Table 4. Observed juvenile weight distribution, averaged back-calculated adult weight distribution at SCP, and size-selective mortality probabilities averaged across 1000 simulations.

| Weight bin (g)	Juvenile weight distribution	Back-calculated adult weight distribution	Size-selective mortality probability
10–20	0.00	0.00	1.00
21–30	0.00	0.00	1.00
31–40	0.01	0.00	1.00
41–50	0.01	0.00	0.98
51–60	0.01	0.00	0.86
61–70	0.02	0.01	0.70
71–80	0.03	0.01	0.69
81–90	0.04	0.02	0.66
91–100	0.07	0.04	0.66
101–110	0.06	0.04	0.58
111–120	0.10	0.05	0.65
121–130	0.09	0.07	0.55
131–140	0.07	0.07	0.50
141–150	0.10	0.07	0.59
151–160	0.07	0.07	0.47
161–170	0.06	0.08	0.45
171–180	0.06	0.07	0.46
181–190	0.06	0.06	0.48
191–200	0.03	0.06	0.38
201–210	0.03	0.05	0.37
211–220	0.02	0.04	0.36
221–230	0.02	0.04	0.32
231–240	0.01	0.03	0.25
241–250	0.01	0.03	0.30
251–260	0.01	0.02	0.35
261–270	0.00	0.02	0.16
271–280	0.00	0.01	0.11
281–290	0.00	0.01	0.18
291–300	0.00	0.01	0.10
301–310	0.00	0.01	0.00
311–320	0.00	0.00	0.26
321–330	0.00	0.00	0.18
331–340	0.00	0.00	0.20
341–350	0.00	0.00	0.20
350–360	0.00	0.00	0.00
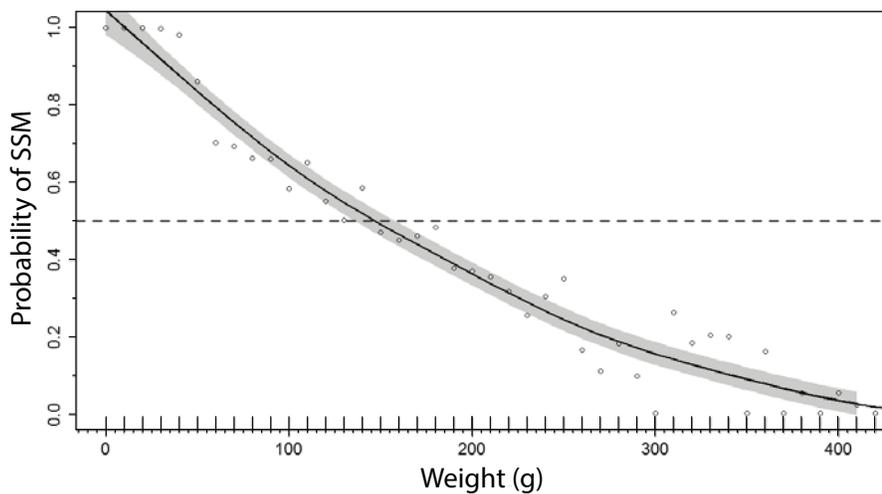
Fig. 7. Generalized additive model (thick solid black line) fit to size selective mortality (SSM) probabilities of juvenile Yukon River Chinook salmon based on differences between actual juvenile weights and the average of simulated back-calculated weights of adults at SCP. The horizontal dashed 0.5 probability line identifies the reference point of neutral selection on the GAM model; a selective disadvantage is expected for weights smaller than this point, a selective advantage is expected for weights larger than this point. Shaded area represents GAM model confidence intervals.

tion (mortality probability of 0.5) at approximately 145 g (Fig. 7; Table 4). Chinook salmon smaller than 145 g weight or 227 mm length would be expected to experience higher mortality rates at SCP, and larger fish to experience a survival advantage due to size.

Much of the variability in energy density can be explained by weight alone and, consequently, weight can be used as a surrogate for identifying energy storage patterns in juvenile Yukon River Chinook salmon (Fig. 8). Given this relationship, it would be expected that energy storage of 4.96–5.16 kJ/g (95% CI, defined by the GAM model) would be needed at neutral selection and individuals with energy stores less than this would incur a survival disadvantage while fish with additional energy stores would gain a survival advantage at SCP. The average energy density for the juvenile sample was 4.98 ± 0.41 kJ/g, indicating that fish with below average energy density would be subject to SSM at SCP.

DISCUSSION

Our analyses suggest that size-selective mortality (SSM) of juvenile Yukon River Chinook salmon at the second critical period (SCP) is evident. Juvenile Chinook salmon that attain a size of 227 mm or larger and a caloric content of 4.96 to 5.16 kJ/g or higher before the end of September are expected to have a greater chance of surviving their first winter at sea. These late summer size and energetic reference points for juvenile Yukon River Chinook salmon come from a time series of data collected over a period of varying climate states that had an impact on ecosystem production (see Hunt et al. 2011). Consequently, we also found the juvenile Chinook salmon late summer size and energetic data contained interannual variability

that may be attributed to environmental conditions (see Farley et al. 2011) or to variation in growth during their freshwater life-history stage.

While we see evidence of SSM for juvenile Yukon River Chinook salmon during the SCP, there are other factors influencing freshwater and FCP survival that may be more influential on cohort strength. Juvenile Yukon River Chinook salmon abundance before SCP has been demonstrated to be a good predictor of future adult run size and indicator of productivity (Murphy et al. in press). If SSM at SCP and mortality processes in later marine life were more significant in defining cohort strength, then abundance measured prior to SCP would not be a good predictor of adult run size. For the juvenile years examined in this study, the stock group for which a juvenile survival index has been developed (Cana-
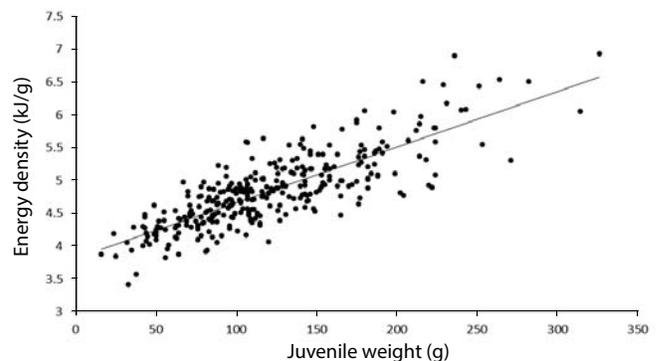

Fig. 8. Relationship between weight (g) and energy density (kJ/g) for juvenile Chinook captured during surface trawl surveys in the northeastern Bering Sea (2005–2011). Line represents linear regression model: y = 0.0085x + 3.8165, r^2 = 0.67
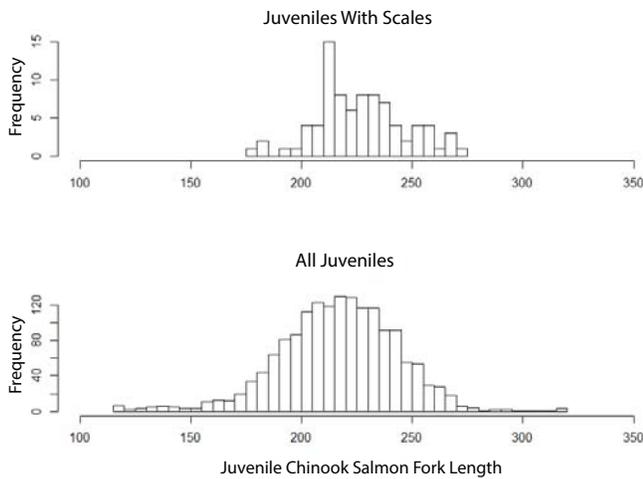
Fig. 9. Size distributions of juvenile fish sampled from the eastern Bering Sea shelf that retained scales from the preferred region and were available for digitization, and total juvenile Chinook salmon sampled in marine surveys (2002–2007).

dian-origin Yukon River Chinook salmon) does not demonstrate a relationship between relative juvenile survival (adult return abundance/juvenile abundance index) and average juvenile size in that year. The lowest average juvenile weight by September (2006; 99 g), was associated with the highest juvenile survival index (0.08; Murphy et al. 2013). Consequently, SSM at SCP does not appear to substantially explain adult return strength beyond what would be predicted by juvenile abundance alone prior to SCP for Yukon River Chinook salmon.

Research on other Chinook salmon stocks suggest the FCP may be more influential than the SCP in defining cohort strength. Rapid growth and size by July were found to be important to marine survival in Puget Sound Chinook salmon, but size differences after September (SCP) were less related to marine survival (Duffy and Beauchamp 2011). Likewise, size during the first month at sea appeared to be highly influential to Central Valley Chinook salmon survival and adult return abundance in a year when ocean productivity was poor (Woodson et al. 2013). It is likely a combination of processes that structures Yukon River Chinook salmon cohort survival and adult returns, but it is important to understand the relative magnitude of mortality processes in shaping overall stock productivity.

Although abundance information prior to SCP suggests SSM at SCP may be less influential in structuring cohort strength in Yukon River Chinook salmon than earlier mortality processes, SSM may nevertheless introduce important constraints on juvenile life-history. Due to the presence of SSM, faster growth rates, larger juvenile sizes, and increased energy storage will improve survival. Neutral selection (size at which there is no survival advantage or disadvantage) appears to occur at approximately the average juvenile Chinook salmon energy density across all years sampled.

It should be noted that there are several limitations and potential biases that may limit interpretation of SSM at SCP with the data available for this study. The trawl gear used to sample the juvenile population typically descales all fish sampled, particularly from the preferred area, limiting the scale samples available. While a subset of scales was available (n = 84), larger fish tended to retain scales, and the smallest individuals were not represented in the scale sampling (Fig. 9). Using this subset of fish with scales alone would have artificially limited the range of sizes, excluded small-sized fish, and inflated the mean size of juveniles compared to the sampled population (Welch's two sample *t*-test: $p < 0.001$). These limitations necessitated that back-calculated adult scale radii measurements be converted to FL and weight using linear regression, rather than a direct comparison of scale radius measurements between the adult and juvenile samples. This approach, however, introduces its own biases because the linear regression to convert scale radius to FL has a tendency to underestimate the slope of the relationship (i.e., underestimate the FL values of back-calculated adult samples at SCP that are larger juveniles, and overestimate the FL values of back-calculated adult samples at SCP that are smaller juveniles). The same underestimate of slope would be true in the linear regression relationship converting FL to weight. As both linear regression relationships have a high correlation coefficient (0.91 and 0.96 for scale radius-FL and FL-weight relationships, respectively), the potential bias introduced with these linear regression conversions is likely relatively small. However, it should be noted that if the size of smaller fish are overestimated in back-calculated adult samples, this bias could give the appearance of SSM existing at SCP when it does not. It does not, however, explain the presence of back-calculated fish that are larger than juveniles observed in the surveys. If a more representative scale sample were available, then a more straightforward relationship between samples that was not contingent on a linear regression conversion could have been performed.

It is also possible that sampling error of reconstructed size of juveniles and/or the effect of combining multiple juvenile years into a single probability model is biasing the true underlying mortality curve. It is reasonable to assume the true relationship has a higher level of non-linearity than we can estimate with this model. The presence of non-linearity in the relationship between size and survival is important when attempting to reconstruct juvenile size distributions from back-calculated adult scales as it will reduce the variation in size of back-calculated adults at SCP relative to the true size of juveniles and subsequently between low and high growth periods. Caution is needed when attempting to reconstruct body size and growth rates from scale back-calculations during life stages with size-dependent survival.

Other biases related to sampling were minimized to the greatest extent possible, but should be considered. Sampling bias may occur in years when more juvenile Chinook salm-

on are in shallow nearshore areas and unavailable to sampling gear. If smaller Chinook salmon preferentially use nearshore areas inaccessible to sampling gear, then these fish may be under sampled in the juvenile survey and the relative role of SSM at SCP may be underestimated by this model. While it is possible that larger juveniles could be deeper in the water column than sampling gear can accommodate, features of the northern Bering shelf are expected to sharply limit the vertical distribution of juvenile salmon. The northern Bering shelf exhibits a highly stratified two-layer water column with a well-mixed layer at the surface and a cold (< 2°C) dense bottom layer known as the "cold pool" (Danielson et al. 2011; Lauth 2011). It is believed that this colder bottom layer is unsuitable for juvenile salmon (Brett 1952). Shallow bottom depths and temperatures within the cold pool limit the vertical distribution and permit surface trawls to effectively sample much of the vertical habitat of juvenile salmon (Murphy et al. in press). If a portion of the juvenile population were inaccessible to sampling and were exclusively the largest individuals, then it may explain why the largest sized individuals of back-calculated adults at SCP were larger than the largest sized individuals in the juveniles sampled in the survey.

Increased energetic demand for overwinter survival is expected in high latitude stocks of salmon and is evident in the contrast between the energy density-weight relationships of juvenile Chinook salmon in the northern Bering Sea and those in the Gulf of Alaska (Moss et al. 2016), where the allometric energy density-weight relationship for juvenile Chinook inhabiting the northern Bering Sea is greater than that for those inhabiting the Gulf of Alaska. The average energy density in the Gulf of Alaska juvenile Chinook salmon samples is less than what would be expected to meet the neutral selection reference point for northern Bering Sea juvenile Chinook salmon. Differences in the energy density-weight relationship between the northern Bering Sea and Gulf of Alaska are believed to reflect counter-gradient variation in juvenile energy allocation (Conover et al. 2009). As Yukon River Chinook salmon are among the most northerly stocks of this species, research into the role of environmental disruptions, such as climate change and the loss of sea ice, as drivers of growth and size-selective mortality is needed. This study provides an important first step in understanding energy storage needs in northerly juvenile Chinook salmon stocks.

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