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Research Article

Growth Rate Potential of Juvenile Sockeye Salmon in Warmer and Cooler Years on the Eastern Bering Sea Shelf

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A spatially explicit bioenergetics model was used to predict juvenile sockeye salmon *Oncorhynchus nerka* growth rate potential (GRP) on the eastern Bering Sea shelf during years with cooler and warmer spring sea surface temperatures (SSTs). Annual averages of juvenile sockeye salmon GRP were generally lower among years with cooler SSTs and generally higher in offshore than nearshore regions of the eastern Bering Sea shelf during years with warmer SSTs. Juvenile sockeye salmon distribution was significantly ($P < .05$) related to GRP and their prey densities were positively related to spring SST ($P < .05$). Juvenile sockeye salmon GRP was more sensitive to changes in prey density and observed SSTs during years when spring SSTs were warmer (2002, 2003, and 2005). Our results suggest that the pelagic productivity on the eastern Bering Sea shelf was higher during years with warmer spring SSTs and highlight the importance of bottom-up control on the eastern Bering Sea ecosystem.

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1. Introduction

Interannual differences in growth conditions in the ocean likely translate into annual variations in survival of juvenile, immature, and maturing Pacific salmon *Oncorhynchus* spp. For juvenile salmonids, increased growth during the first year at sea confers a survival advantage with respect to predator avoidance [1, 2] and better condition of the fish during late fall and winter [3, 4]. Ocean conditions are believed to play a pivotal role in constraining early marine growth of juvenile salmon. For instance, sized-based natural mortality of juvenile coho salmon *O. kisutch* was hypothesized to be linked to available nutrients regulating the food supply and hence competition for food [4]. Previous work on juvenile sockeye salmon *O. nerka* along the eastern Bering Sea shelf also suggested that smaller fish had lower survival [5] and that size, condition and offshore distribution of these fish were connected to bottom-up control of the trophic structure on the eastern Bering Sea shelf [6]. Thus, linking salmon prey demand to prey supply and their dependence

on habitat could provide insight into the complex dynamics between marine productivity and growth and survival of salmon.

Bioenergetics models that incorporate the spatial distribution of fish, their prey, and the physical conditions that affect foraging and growth are valuable for investigating the underlying basis for differences in habitat suitability [7]. Bioenergetics models stem from a species- and size-specific energy balance equation that describes the energy budget for a characteristic individual of a particular species [8]. Individual species characteristics are generally expanded to the stock or population level by multiplying single fish dynamics by estimates of the population size and cohort mortality rate [9, 10]. Linking the stock or population bioenergetics models to temporally and spatially explicit habitat features (i.e., water temperature and potential prey) can lead to estimates of fish growth potential and/or habitat quality [7, 11–13].

Bioenergetics models that examine growth rate potential (GRP) for salmonids have been developed within streams

[7], large freshwater lakes [14–16], and marine ecosystems [17]. These studies have shown that salmon in freshwater occupy habitats that support positive growth and that there are clear linkages between prey biomass and salmonid recruitment success. For juvenile salmonids during their first year in the ocean, energetics models have been used to investigate the effects of distribution or physiological and biological variables on salmon growth [18] and survival [19]. GRP models have also been used to explain migratory behavior of immature and maturing salmonids in the marine environment and to describe regions where salmonids would experience higher or lower GRP in both space and time.

To develop an understanding of the link between juvenile sockeye salmon prey demand and supply, we estimated GRP over a 7-year period within the eastern Bering Sea shelf as a measure of habitat quality for juvenile sockeye salmon. Data on juvenile sockeye salmon and ocean conditions come from surveys conducted along the eastern Bering Sea shelf during mid August to early September from 2000 to 2006. A leading hypothesis for ocean productivity on the eastern Bering Sea shelf suggests that spring ocean sea temperature affects prey availability to pelagic consumers; cooler spring temperatures negatively affect available prey productivity and abundance [20], potentially impacting salmon growth and survival. The objectives were thus to compare juvenile sockeye salmon GRP between years with warmer and cooler spring sea surface temperatures (SSTs) and to examine whether GRP is a useful index for habitat quality for juvenile sockeye salmon on the eastern Bering Sea shelf. The model was used to test whether (1) GRP was significantly higher during years with warmer spring sea temperatures, and (2) salmon densities were positively related to GRP. A sensitivity analysis was used to evaluate whether observed (August–September) SST (sea temperatures collected during the surveys and used in GRP models) or prey density had the strongest influence on model estimates of juvenile sockeye salmon GRP.

2. Methods

2.1. Study Area and Sampling Protocols. Stations ($n = 50$) along the eastern Bering Sea shelf from longitudinal meridians $161^{\circ}00' W$ to $166^{\circ}00' W$ and from the Alaska Peninsula to $60^{\circ}00' N$ at Nunivak Island were sampled during August–September 2000–2006 (Figure 1). Juvenile sockeye salmon were collected following methods described in Farley et al. [21]. Fish were collected using a mid-water rope trawl that was 198 m long, with a typical spread of 55 m horizontally and 15 m vertically. The trawl is constructed with hexagonal mesh in wings and body, and included a 1.2-cm mesh liner in the codend. Trawl stations were located along longitudinal meridians spaced every 27.8 km during 2001 to 2003 and every 55.6 km during 2000, and 2004 to 2006. Thus, survey data were consistently collected at stations spaced every 55.6 km (i.e., along longitudinal meridians at stations spaced every 30 degrees of latitude) during each year of the survey, and only data collected at

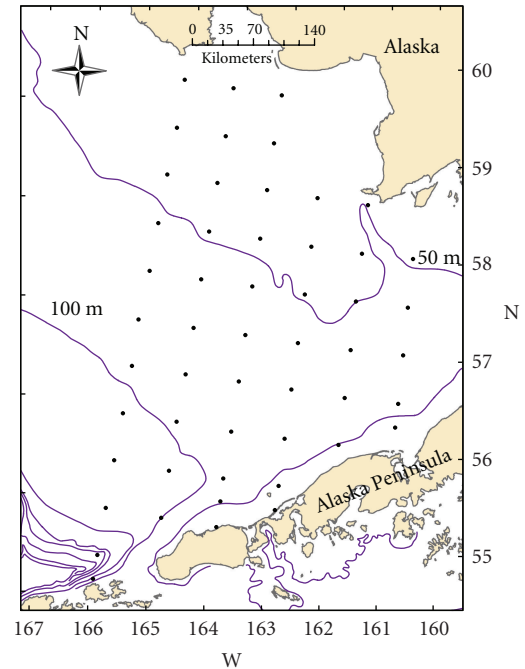


FIGURE 1: Approximate station locations where trawl sampling for juvenile sockeye salmon occurred during August–September from 2000 to 2006 Ocean Carrying Capacity, BASIS research cruises.

these stations were used in bioenergetics models for juvenile sockeye salmon. The survey area was fully sampled during all years, except 2001, when sampling occurred within the survey area from the Alaska Peninsula to $58^{\circ}00' N$. The rope trawl was towed at 6.5 to 9.3 km/h with the head rope at or near surface. Trawl stations were sampled during daylight hours (0730–2100 hours, Alaska Daylight Savings Time) and all tows lasted 30 minutes and covered from 3.25 to 4.6 km. A Seabird SBE-911 conductivity-temperature at depth (CTD) device was deployed at each station to measure the vertical profiles (from near bottom to surface) of ocean temperature. (Use of tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.) Temperatures ($^{\circ}C$) taken from CTD profiles at 5 m depth (further referred to as observed sea surface temperatures or OSSTs) were used for bioenergetics modeling. At each trawl station, juvenile sockeye salmon were selected at random (maximum 50) and standard biological attributes, including fork length (nearest 1.0 mm) and body weight (nearest 1.0 g) of juvenile sockeye salmon were measured onboard.

2.2. Bioenergetics Model. GRP of juvenile sockeye salmon over the eastern Bering Sea shelf was estimated using the bioenergetics model developed by Ware [22] and incorporating modifications to the model developed by Trudel and Welch [23]. This model was parameterized for sockeye salmon and accounts for optimal cruising speed:

$$G_{i,s} = \tau \cdot I_{i,s} - (\text{SMR}_{i,s} + \text{ACT}_{i,s}), \quad (1)$$

TABLE 1: Equations and parameter description of the sockeye salmon bioenergetics model. Note that subscripts i and s represent year ($i = 2000$ to 2006) and station, and overbars denote mean quantities within the definitions of i .

Symbol	Equation and parameter description	Value	Source
Growth: $G_{i,s} = \tau \cdot I_{i,s} - (\text{SMR}_{i,s} + \text{ACT}_{i,s})$			
G	Growth rates (cal/s)		
τ	Proportion of food that can be metabolized (dimensionless)	0.7	1
I	Feeding rates (cal/s)		
SMR	Standard metabolic rates (cal/s)		
ACT	Activity costs (cal/s)		
Consumption: $I = \text{ED}_{i,s} \cdot (\rho \cdot \gamma \cdot U / (1 + \rho \cdot \gamma \cdot h \cdot U))$			
ED	Prey energy density (cal/g _{wet})		
ρ	Prey density (g/cm ³)		
γ	Cross-sectional area of the reactive field (cm ²)		
U	Swimming speed (cm/s)		
h	Handling time (s/g)		
Cross-sectional area of the reactive field: $\gamma = \alpha_3 \cdot W^{\beta_3}$			
α_3	Intercept (cm ²)	1	1
β_3	Coefficient, γ versus W	0.69	1
W	Sockeye salmon weight (g)		
Handling time: $h = W^{\text{CB}-1} / (\text{CA} \cdot f(T))$			
CA	Intercept for maximum feeding rates (g/s)	3.51×10^{-6}	3
CB	Allometric exponent of maximum feeding rate	0.275	3
$f(T)$	Temperature adjustment for maximum food consumption rates		
T	Sea surface temperature (°C; 5 m below surface)		
Temperature adjustment function: $f(T) = K_a \cdot K_b$			
	$K_a = (0.58 \cdot L1) / (1 + 0.58 \cdot (L1 - 1))$		3
	$L1 = \exp(G1 \cdot (T - 3))$		3
	$G1 = (1/(20 - 3)) \cdot \ln((0.98 \cdot (1 - 0.58)) / (0.58 \cdot 0.02))$		3
	$K_b = (0.5 \cdot L2) / (1 + 0.5 \cdot (L2 - 1))$		3
	$L2 = \exp(G2 \cdot (24 - T))$		3
	$G2 = (1/(24 - 20)) \cdot \ln((0.98 \cdot (1 - 0.5)) / (0.5 \cdot 0.02))$		3
Standard metabolic rates*: $\text{SMR} = \alpha_1 \cdot W^\beta \cdot e^{\varphi \cdot T}$			
α_1	Intercept (cal/s)	4.76×10^{-5}	4
β	Coefficient, SMR versus W	0.87	4
φ	Coefficient, SMR versus T (1/°C)	0.064	4
Swimming costs*: $\text{ACT} = \alpha_0 \cdot W^\delta \cdot U^\lambda$			
α_0	Intercept (cal · s ⁻¹)	1.74×10^{-6}	4
δ	Coefficient, ACT versus W	0.72	4
λ	Coefficient, ACT versus U	1.6	4
Swimming speed: $U = \omega \cdot W^\nu \cdot \exp(\kappa \cdot T)$			
ω	Intercept (cm/s)	11.1	4
ν	Coefficient, U versus W	0.097	4
κ	Coefficient, U versus T (1/°C)	0.040	4

(1) Reference [22]; (2) this study; (3) reference [27]; (4) reference [23].

*The oxygen consumption rates were converted from mg O₂/h to cal/s using an oxycaloric equivalent to 3.24 mg O₂/cal [30].

where $G_{i,s}$ is the GRP (cal/s) for juvenile sockeye salmon during year i at station s , τ is the proportion of food that can be metabolized [24], $I_{i,s}$ is the feeding rate (cal/s), $\text{SMR}_{i,s}$ and $\text{ACT}_{i,s}$ are, respectively, the standard metabolic rate (cal/s) and activity costs (cal/s). For simplicity, we assumed that τ was constant and not affected by water temperature (Table 1), as the sum of fecal and urinary losses and specific

dynamic action is often nearly constant in bioenergetics models [24].

Feeding rate is likely a function of prey density [22]. Unfortunately, no empirical studies have been performed to date to examine the relationship between salmon feeding rate and prey density in natural conditions [25], probably due to the difficulty in estimating in situ food consumption rates.

Thus, the relationship between salmon feeding rate and prey density was assumed to be described by a type II functional response [22, 26]:

$$I_{i,s} = ED_{i,s} \cdot \frac{\rho_{i,s} \cdot \gamma_{i,s} \cdot U_{i,s}}{1 + \rho_{i,s} \cdot \gamma_{i,s} \cdot h_{i,s} \cdot U_{i,s}}, \quad (2)$$

where $\rho_{i,s}$ is prey density (g/cm^3) during year i and station s , $\gamma_{i,s}$ is the cross-sectional area of the reactive field (cm^2), $U_{i,s}$ is the optimum swimming speed (cm/s), $h_{i,s}$ is handling time of prey (s/g), and $ED_{i,s}$ is weighted average of prey caloric content during year i at station s ($\text{cal}/\text{g}_{\text{wet}}$), and was estimated as

$$ED_{i,s} = \frac{N_{i,s,1} \cdot ED_1 + N_{i,s,2} \cdot ED_2}{N_{i,s,1} + N_{i,s,2}}, \quad (3)$$

where $N_{i,s,1}$ and $N_{i,s,2}$ are the number of age-0 walleye pollock and Pacific sand lance caught at each station and ED_1 ($\text{cal}/\text{g}_{\text{wet}}$) and ED_2 ($\text{cal}/\text{g}_{\text{wet}}$) are the caloric contents of age-0 walleye pollock and Pacific sand lance. The weighted average of prey caloric content was set to 0 when $N_{i,s,1} + N_{i,s,2} = 0$. As a result, consumption rates were equal to zero when no prey were available. Equation (2) reaches an asymptote at

$$I_{\max} = \lim_{\rho \rightarrow \infty} \frac{\rho \cdot \gamma \cdot U}{1 + \rho \cdot \gamma \cdot h \cdot U} = \frac{1}{h}, \quad (4)$$

where I_{\max} is the maximum feeding rate (g/s). We used the equation derived by Beauchamp et al. [27] for the maximum feeding rate (g/day) for sockeye salmon to parameterize the handling time:

$$I_{\max} = CA \cdot \bar{W}_i^{1-\text{CB}} \cdot f(T), \quad (5)$$

where W is the average sockeye salmon weight (g), CA and CB are, respectively, the weight coefficient and exponent for maximum feeding rate, and $f(T)$ is the Thornton and Lessem [28] temperature dependence function for cool- and cold-water fish species (see Table 1 for definition and parameters). Thus, we substituted $1/h$ for I_{\max} in (5):

$$h = \alpha_4 \cdot \bar{W}_i^{\text{CB}-1}, \quad (6)$$

where

$$\alpha_4 = \frac{1}{CA \cdot f(T)}. \quad (7)$$

The energetic costs associated with the standard metabolic rates and activity costs of juvenile sockeye salmon were modeled using the empirical models derived by Trudel and Welch [23]. Specifically, standard metabolic rates were modeled as a function of weight and water temperature ($^{\circ}\text{C}$):

$$\text{SMR}_{i,s} = \alpha_1 \cdot \bar{W}_i^{\beta} \cdot e^{\varphi T_{i,s}}, \quad (8)$$

where α_1 , β , and φ are regression coefficients (Table 1). Activity costs were modeled as a function of weight and swimming speed:

$$\text{ACT}_{i,s} = \alpha_0 \cdot \bar{W}_i^{\delta} \cdot U_{i,s}^{\lambda}, \quad (9)$$

where α_0 , δ , and λ are regression coefficients (Table 1). We used the optimal cruising speed model derived by Trudel and Welch [23] to estimate the swimming speed of juvenile sockeye salmon (Table 1).

2.3. Prey Abundance. Gut contents from subsamples of juvenile sockeye salmon at each trawl station were analyzed to characterize prey consumption [6, 29]. Prey analyses determined that fish, including age-0 walleye pollock (*Theragra chalcogramma*) and Pacific sand lance (*Ammodytes hexapterus*) dominated (60% to 70%) the percent wet weight of stomach contents. The other dominant prey item was Euphausiidae spp. (approximately 20% wet weight during 2006 only); however, biomass estimates for these species were not available, thus only age-0 walleye pollock and Pacific sand lance were considered the primary ‘‘prey’’ for bioenergetics models. The typical size ranges of age-0 walleye pollock and Pacific sand lance in the diets of juvenile sockeye salmon were between 28 and 67 mm (total length) and 55 to 80 mm (FL), respectively [6].

Prey density (g/cm^3) at each station was determined as:

$$\rho_{i,s} = \sum_{p=1}^2 \frac{N_{i,s,p} \cdot \theta \cdot \bar{W}_p}{\phi \cdot V_{i,s}}, \quad (10)$$

where $N_{i,s,p}$ is the number of prey ($p = \text{age-0 walleye pollock or Pacific sand lance}$) caught at each station, θ is the proportion of prey items captured in trawls that fell within the size range that juvenile sockeye salmon fed upon (dimensionless), \bar{W}_p is the average weight (g) for each prey item, ϕ is the catchability coefficient (dimensionless), and $V_{i,s}$ is the volume sampled at each station (cm^3). Volume sampled at each station was estimated by multiplying the distance trawled (cm) by the vertical (cm) and horizontal (cm) spread of the net opening.

The catchability coefficient of age-0 walleye pollock was determined by comparing catches during the Bering-Aleutian Salmon International Surveys (BASISs) research cruises to hydroacoustic survey estimates [31]. The BASIS research cruises cover a large area of the eastern Bering Sea shelf, and age-0 walleye pollock and Pacific sand lance are typically captured [6]. The average density of age-0 walleye pollock in BASIS surveys conducted along the eastern Bering Sea shelf during 2000 to 2006 was $0.003/\text{m}^3$ compared to $0.191/\text{m}^3$ during acoustic surveys near the Pribilof Islands during August 1996-1997 [31]. These differences in number of age-0 walleye pollock per m^3 could be due to inter-annual variability (1996 and 1997 versus 2000 to 2006), different area surveyed (transects offshore of the Pribilof Islands versus stations covering a much broader area of the eastern Bering Sea shelf), gear type (acoustic measurements designed to target age-0 walleye pollock versus pelagic trawl designed to capture small salmon), and depth (acoustic estimates were from near surface to near bottom depths whereas the trawl fished from near surface to approximately 15 m depth).

Because the abundance of age-0 walleye pollock sampled along transects in the vicinity of the BASIS surveys was similar to that near the Pribilof Islands during 1999 [32], area effects were discounted. In addition, average pollock recruitment to age 1 from acoustic surveys conducted during 1997 and 1998 was similar to that for 2001 to 2005 (23.6 million versus 18.7 million; Jim Ianelli, personal communication). The vertical distribution of age-0 walleye

pollock during summer can range from surface to bottom depths on the eastern Bering Sea shelf [32]. Studies on vertical distribution of age-0 walleye pollock at oceanic fronts near the Pribilof Islands [33] suggest that highest densities of these fish occur below 30 m during the day, however dense aggregated fish shoals can be found above 20 m depth during day. In addition, the highest densities of age-0 walleye pollock occur above 20 m during night, indicating that these fish vertically migrate to the near surface waters during night [33]. But the diel vertical migration in age-0 walleye pollock was found to be a function of size, with smaller (<60 mm TL) fish occurring above the thermocline and generally not vertically migrating over the day [34].

Juvenile sockeye salmon feed during daylight hours and data from our survey indicate that their stomachs are generally fullest during afternoon and evening hours. The size range of age-0 walleye pollock in juvenile sockeye salmon stomachs analyzed during these surveys ranged between 28 to 67 mm TL [6] indicating that these fish are feeding on a subset of age-0 walleye pollock that are found in the surface layers. A comparison between lengths for age-0 walleye pollock (TL) and Pacific sand lance (FL) captured in the trawl net and in gut contents of juvenile sockeye salmon indicated that approximately 68% of age-0 walleye pollock and 59% of the Pacific sand lance caught in the trawl were within the size range that juvenile sockeye salmon fed upon (typical size range for age-0 walleye pollock and Pacific sand lance in the trawl samples was between 45 and 95 mm TL and 77 to 150 mm TL; [6]). So, a catchability coefficient of 0.016 for the BASIS pelagic trawl was determined by dividing the average number of age-0 walleye pollock per m³ caught during BASIS cruises by the average number of age-0 walleye pollock per m³ determined by Swartzman [31] multiplied by 1, the fraction of age-0 walleye pollock in the size range that juvenile sockeye salmon feed upon is available in the upper 15 m of the water column (i.e., 0.003/(0.19 · 11)). Similar comparisons for juvenile Pacific sand lance could not be made due to lack of published abundance estimates on the eastern Bering Sea shelf; the catchability coefficient for this prey item was assumed to be the same as age-0 walleye pollock.

The average weight of this prey was 1.7 g for age-0 walleye pollock and 1.2 g for Pacific sand lance. Laboratory analyses of subsamples of age-0 walleye pollock taken during the 2005 survey indicated that the average caloric content was 885 cal/g_{wet}; caloric content for Pacific sand lance (842 cal/g_{wet}) was obtained from Robards et al. [35]. The estimates of catchability, proportion of prey items, caloric content, and weight were held constant for each station, among years.

GRP (cal/s) was converted to cal/d by multiplying $I_{i,s}$ by the number of seconds in a 15.5-hour day (assumed time that juvenile sockeye salmon spend feeding per day during August and September) and by multiplying $SMR_{i,s}$ and $ACT_{i,s}$ by the number of seconds in a 24-hour day.

Estimated daily GRP (cal/d) at each station s was then expressed as a percentage of body weight (% body weight/d)

for each station s by dividing estimated daily GRP (cal/d) by the total energy per fish (cal) as in Perry et al. [18]:

$$\bar{E}_{i,s} = ED_f \cdot \bar{W}_i, \quad (11)$$

where $\bar{E}_{i,s}$ is the average total energy per fish (cal) during year i and at station s , ED_f is the caloric content in juvenile sockeye salmon (cal/g_{wet}), and \bar{W}_i is the average weight (g) of juvenile sockeye salmon during year i . Annual averages of juvenile sockeye salmon weight were used as opposed to average weight of these fish at each station because there were stations within a year where no juvenile sockeye salmon were caught. The caloric content of juvenile sockeye salmon was determined from subsamples of the juvenile sockeye salmon caught during the 2002 to 2005 surveys using bomb calorimetry and averaged 1,176 cal/g_{wet}. (There was no significant difference in average caloric content of juvenile sockeye salmon among years; (ANOVA- Fixed effect, $F = 5.3$, $P = .08$). Caloric content of juvenile sockeye salmon was not available for 2000, 2001, or 2006.) These estimates of growth (% body weight/d) were considered to be juvenile sockeye salmon GRP on the eastern Bering Sea shelf and were the primary statistic used in subsequent models.

2.4. Spring SSTs. Spring SSTs (°C) during May 2000 to 2006 in the southeastern Bering Sea are shown in Figure 2. Mean May SSTs were averaged over 54°18' N to 60°00' N, 161°12' W to 172°30' W (data from <http://www.beringclimate.noaa.gov/>). The SST anomalies were calculated as the deviations from the mean May SST value (2.33°C) for the 1970–2000 period divided by the standard deviation (0.76°C). Years with cooler SSTs were defined as those years with negative anomalies (2000, 2001, and 2006); years with warmer SSTs were defined as those years with positive anomalies (2002 to 2005).

2.5. Model Applications. (H1) *GRP is Significantly Higher during Years with Warmer Spring Temperatures*—This hypothesis was tested using two-way analysis of variance (ANOVA-Fixed Effect) with S-plus software [36] where year (2000 to 2006) was the categorical variable and GRP was the dependent variable. If a significant difference ($P < .05$) occurred, a Tukey multiple comparison test was used to calculate the 95% ($\alpha = 0.05, 0.01, 0.001$) confidence intervals for all pairwise differences between the dependent variable means [36]. The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of α .

(H2) *Juvenile Sockeye Salmon Are Distributed in Areas of High GRP on the EBS Shelf*—Regression analysis was used to examine the relationship between GRP and catch per unit effort (CPUE _{i,s} —defined as the number of juvenile salmon caught during a 30 minute trawl haul during year i at station s). The natural logarithm of (CPUE _{i,s} + 1) was used to reduce the wide variability in CPUE _{i,s} . Sea temperature is believed to influence the seaward migration pathway and offshore distribution of juvenile sockeye salmon [21]. Thus, the juvenile sockeye salmon CPUE and GRP data were

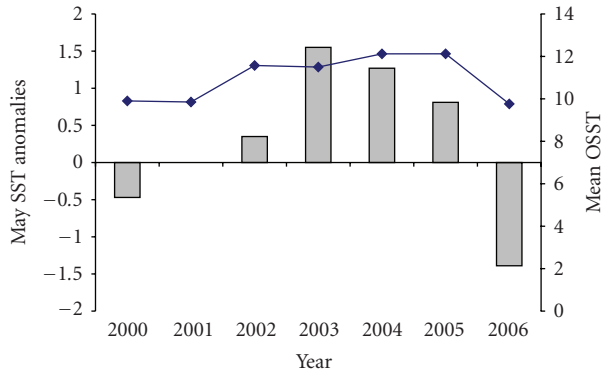


FIGURE 2: May sea surface temperature (SST) anomalies (bar, °C) during 2000 to 2006 in the southeastern Bering Sea (data obtained from <http://www.beringclimate.noaa.gov/>) and annual averages (line) of observed SSTs (OSST, °C) collected during August to early September surveys. Mean May SSTs are averaged over the area 54° 18' N to 60° 0' N, 161° 12' W to 172° 30' W using data from the NCEP/NCAR reanalysis project [37]. The May SST anomalies are the deviations from the mean May SST value (2.33°C) for the 1970–2000 period normalized by the standard deviation (0.76°C). Mean OSSTs (°C) are the averages of observed SSTs at 5 m depth taken at stations conducted within the survey area of Figure 1.

pooled into cooler years (2000, 2001, and 2006) and warmer years (2002 to 2005) to test this hypothesis.

(H3) *Prey Density and Spring SSTs Are Positively Correlated*—A leading hypothesis for ocean productivity on the eastern Bering Sea shelf suggests that spring ocean sea temperature affects prey availability to pelagic consumers; cooler spring temperatures negatively affect available prey productivity and abundance, whereas warmer spring temperatures have the opposite effect [20]. To test this hypothesis, regression analysis was used to examine the relationship between average annual prey density and the May SST anomalies. Average annual prey density was defined as:

$$\overline{PD}_t = \frac{\sum_{s=1}^n \text{CPUE}_{s(\text{age0pollock})} + \text{CPUE}_{s(\text{sandlance})}}{n}, \quad (12)$$

where n = the number of stations (s) in year t (t = 2000 to 2006), and $\text{CPUE}_{s(\text{age0pollock})}$ and $\text{CPUE}_{s(\text{sandlance})}$ are the catch per unit effort in a 30-minutes-trawl haul at each station (within a year) for age-0 walleye pollock and Pacific sand lance. The natural log of the average \overline{PD}_t was taken to reduce the wide variability in average \overline{PD}_t among years.

2.6. Sensitivity Analysis. The sensitivity of the model's estimates of GRP was estimated by varying OSST and prey density (number/cm³) by $\pm 20\%$ at each station during year i . The objective was to examine to what extent sea surface temperatures affect GRP for juvenile sockeye salmon as opposed to observed prey abundance. The variability of $\pm 20\%$ was chosen because this difference was close to the average difference in the OSST between years with cooler (2000, 2001, and 2006: 9.8°C) and warmer (2002 to 2005: 11.8°C) spring SSTs (Figure 2). For each analysis, one of the

TABLE 2: Annual averages (\pm SE) of juvenile sockeye salmon growth rate potential (GRP; % body weight per day) during August–September 2000 to 2006 along the eastern Bering Sea shelf. The number of stations (n) are included.

Year	n	GRP	SE
2000	34	−0.34	0.10
2001	32	−0.24	0.09
2002	43	−0.08	0.12
2003	41	0.17	0.14
2004	44	0.69	0.17
2005	45	0.32	0.15
2006	40	−0.39	0.09

inputs was held constant while adjusting the other by $\pm 20\%$. A sensitivity value of 0.0 or 1.0 means (for example) that a 20% increase in OSST or prey abundance resulted in no increase or a 20% increase in estimated GRP for juvenile sockeye salmon.

3. Results

3.1. Hypothesis Tests. (H1) In general, mean annual GRP was near 0 and was negative for all years except 2003 to 2005 (Table 2). Juvenile sockeye salmon GRP differed significantly among years (ANOVA; $f_{[6,272]} = 9.05$, $P < .001$). Years with warmer spring SSTs had higher GRP than those with cooler spring SSTs. The pairwise comparison among years indicated that average GRP was significantly higher during 2004 than 2000 to 2002 and 2006 ($P < .001$), higher during 2005 than 2000 ($P < .05$) and 2006 ($P < .01$), and higher during 2003 than 2006 ($P < .05$).

(H2) The regression of GRP and $\ln(\text{CPUE}_{i,s})$ pooled by warmer and cooler years indicated that the relationship was significant during cooler ($P = .03$) and warmer ($P = .002$) years. On average, the highest GRP occurred along the Alaska Peninsula and within the deeper waters between the 50 m and 100 m depth contours along the eastern Bering Sea shelf (Figures 3(a) and 3(b)). However, GRP was negative over much of the area on the eastern Bering Sea shelf during cooler years. Even so, juvenile sockeye salmon tended to be distributed south of 58° N in areas of higher GRP during cooler years. Whereas, juvenile sockeye salmon were broadly distributed during warmer years and their distribution appears to reflect the fact that GRP was higher over a much broader area than during cooler years.

(H3) Prey density was positive and significantly ($P = .02$) related to spring SST indices (Figure 4). The relationship appears to be linear, with increasing juvenile sockeye salmon prey density as spring SSTs increase.

3.2. Sensitivity Analysis. In general, adjusting either prey density or OSST by 20% leads to greater than 20% change in GRP during all years except 2004 and 2006 (Table 3). When prey density was held constant, increasing OSST by 20% had a negative effect on GRP whereas when OSST was held constant, increasing prey density by 20% had a positive

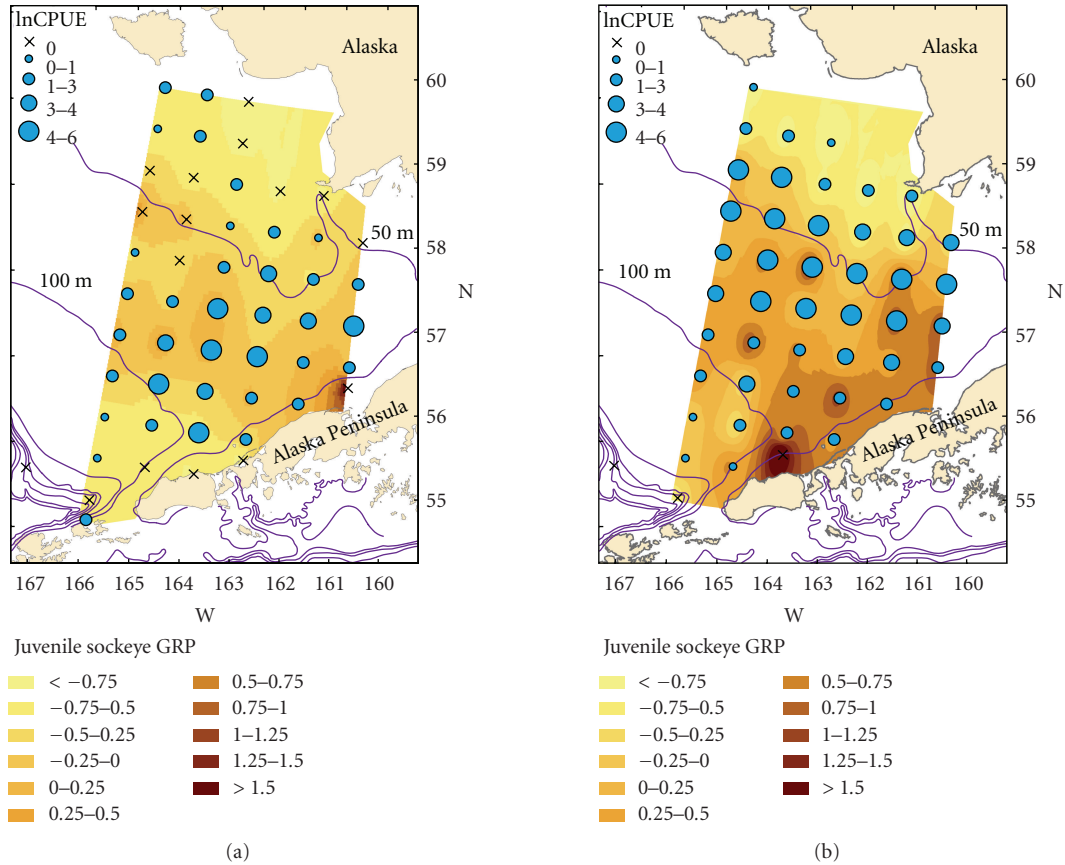


FIGURE 3: (a) Contour plot of the average juvenile sockeye salmon growth rate potential (GRP—% body weight per day) in relation to the natural logarithm of catch per unit effort of juvenile sockeye salmon capture during cooler years (2000, 2001, and 2006). (b) Contour plot of the average juvenile sockeye salmon growth rate potential (GRP—% body weight per day) in relation to the natural logarithm of catch per unit effort of juvenile sockeye salmon capture during warmer years (2002 to 2005).

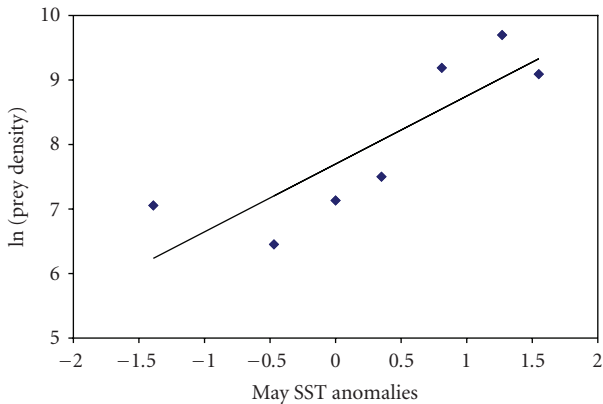


FIGURE 4: The relationship between the natural logarithm of prey density and indices of May sea surface temperatures (SST) anomalies.

effect on GRP. Adjusting either prey density or OSST had the greatest effect on GRP during warmer years (2002 and 2003) with the largest change occurring during 2002 for OSST and prey density.

4. Discussion

Our findings suggest a possible connection between GRP of juvenile sockeye salmon during late summer—early fall and spring SSTs along the eastern Bering Sea shelf. On average, juvenile sockeye salmon GRP was lower during years with cooler rather than warmer spring SSTs (supporting (H1)). We found a positive, significant relationship between annual averages of observed prey density and spring SSTs (supporting (H3)). Finally, juvenile sockeye salmon GRP was significantly related with lnCPUE during both cooler and warmer years (supporting (H2)).

Upon entering marine waters, juvenile sockeye salmon utilize eastern Bering Sea shelf as corridor for seaward migration to the offshore waters of the Bering Sea and North Pacific Ocean. When juvenile sockeye salmon first enter the marine waters of the eastern Bering Sea, they generally remain nearshore but begin to move offshore as they grow [21, 38]. Our results provide a snapshot of juvenile sockeye salmon distribution and GRP on the shelf during late summer and indicate that GRP is higher across a broader area of this juvenile sockeye salmon migration corridor during years with warmer spring SSTs. However, juvenile sockeye

TABLE 3: Sensitivity of bioenergetic model estimates of juvenile sockeye salmon growth. For each analysis, one of the inputs (OSST ($^{\circ}\text{C}$) or prey density (number/ cm^3)) was held constant while adjusting the other by $\pm 20\%$. A value of 1.0 means that a 20% increase in a value of SST or prey density from its nominal value caused a 20% increase in growth rate potential.

Year	Temperature ($^{\circ}\text{C}$)		Prey Density (number cm^{-3})	
	-20%	+20%	-20%	+20%
2000	0.9	-1.2	-0.9	0.8
2001	1.0	-1.2	-1.4	1.2
2002	3.4	-4.9	-4.7	4.0
2003	1.6	-2.6	-2.2	1.8
2004	0.1	-0.4	-0.5	0.4
2005	0.9	-1.6	-1.4	1.1
2006	0.8	-1.0	-0.6	0.5

salmon do not appear to aggregate in regions with high GRP during any year, likely due to the fact that they have a finite amount of time to migrate offshore of the eastern Bering Sea shelf before winter.

Our goal was to use GRP as an indicator of habitat quality during years with cooler and warmer spring SSTs, rather than to provide precise quantitative estimates of growth rate for juvenile sockeye salmon. For instance, juvenile sockeye salmon GRP was negative during all years except 2003 to 2005 indicating that these salmon are losing rather than gaining weight in 4 of the 7 years studied. The annual estimates of juvenile sockeye salmon average GRP varied from -0.39% to 0.69% body weight per day. Juvenile salmon growth rate is size dependent, and daily growth rate decreases as the fish get larger [39]. The average weight (g) of all juvenile sockeye salmon collected along the eastern Bering Sea shelf over the 7 year period was 74.0 g; the growth rate of “wild” juvenile sockeye salmon raised experimentally in salt water tanks and fed until satiated twice a day was approximately 1.01% per day for 110 g fish [39]. Thus, our estimates may not be out of line with experimental estimates of juvenile sockeye salmon daily growth rate because our juvenile sockeye salmon were collected in the wild under varying OSSTs and prey densities.

The previous investigations on the size and condition of juvenile Bristol Bay sockeye salmon indicated that juvenile sockeye salmon had full stomachs, were larger, and in better condition during 2002 and 2003 compared to previous years (2000 and 2001; [6]). Bioenergetics models are particularly sensitive to changes in energy density, composition of stomach contents, and biomass of potential prey [27]. Our estimates of available prey biomass were generated using a number of assumptions that could potentially lead to a bias of under/over estimating the number of dominant prey (age-0 walleye pollock and Pacific sand lance) available to juvenile sockeye salmon on the eastern Bering Sea shelf. There were no available data on abundance estimates of other prey items that made up to 30% of the stomach contents for juvenile sockeye salmon during some years. Thus, the most plausible

explanation for negative GRP is that our estimates of prey biomass were biased low. However, because we maintained these assumptions for all years, comparisons of the relative differences in juvenile salmon GRP would likely provide robust estimates of changes in juvenile sockeye salmon GRP among the years examined.

The bioenergetics model indicated that juvenile sockeye salmon GRP was more sensitive to changes in OSST and prey density during warmer years. Increasing OSST by 20% in the model resulted in decreasing juvenile sockeye salmon GRP from 8% to 98%, with the largest percent decrease occurring during years when OSSTs were warmest (2002, 2003, and 2005; see Figure 2). These results may herald negative consequences for juvenile sockeye salmon on the eastern Bering Sea shelf in the future. It is generally agreed that the climate in the Arctic and Bering Sea is warming [40]. Although warmer spring SSTs have been hypothesized to increase pelagic productivity on the eastern Bering Sea shelf [20], physical changes in the Bering Sea under a global warming scenario are expected to reduce the supply of nutrients to the shelf region [41]. Thus, productivity on the eastern Bering Sea shelf could be negatively impacted, in turn, lowering abundance of potential prey for juvenile sockeye salmon. Increasing SSTs and lower abundance of potential prey would negatively impact juvenile sockeye salmon GRP, potentially leading to smaller size and lower marine survival for juvenile Bristol Bay sockeye salmon.

Our study provides evidence that energetic limitation influences habitat quality on the eastern Bering Sea shelf for juvenile sockeye salmon during years with cooler spring SSTs. Abundance of the primary prey for juvenile sockeye salmon is higher during years with warmer spring SSTs, and the abundant prey was likely due to increased primary and secondary productivity in the pelagic ecosystem during these years [20]. In addition, warmer spring temperatures lead to earlier lake-ice break-up and, in turn, juvenile sockeye salmon smolt generally begin their seaward migration within days of ice break-up [42]. Thus, it appears that juvenile sockeye salmon gain a survival advantage during years with warmer spring temperatures due to an extended early marine period with increased productivity (bottom-up control) on the eastern Bering Sea shelf. As such, this work is an instructive case study and is a framework for future research on juvenile salmon energetics in large marine ecosystems.

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