

## Growth Rate Potential of Juvenile Chum Salmon on the Eastern Bering Sea Shelf: an Assessment of Salmon Carrying Capacity

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**Abstract:** Spatial and temporal variation in growing conditions for juvenile salmon may determine the survival of salmon after their first year at sea. To assess this aspect of habitat quality, a spatially explicit bioenergetics model was used to predict juvenile chum salmon (*Oncorhynchus keta*) growth rate potential (GRP) on the eastern Bering Sea shelf during years with cold and warm spring sea surface temperatures (SSTs). Annual averages of juvenile chum salmon GRP were generally lower among years and regions with cold spring SSTs. In addition, juvenile chum salmon GRP was generally higher in offshore than in nearshore regions of the eastern Bering Sea shelf during years with warm SSTs; however, the distribution (catch per unit effort) of juvenile chum salmon was not significantly ( $P < 0.05$ ) related to GRP. Shifts from warm to cold SSTs in the northern region do not appear to affect summer abundance of juvenile Yukon River chum salmon, whereas the abundance of juvenile Kuskokwim River chum salmon drops precipitously during years with cold SSTs. From this result, we hypothesize that size-selective predation is highest on juvenile Kuskokwim chum salmon during cold years, but that predation is not as great a factor for juvenile Yukon River chum salmon. Although not addressed in this study, we also hypothesize that the smaller Yukon River chum salmon captured during years with cold SSTs likely incur higher size-selective mortality during winter.

**Keywords:** Bering Sea, juvenile chum salmon, growth rate potential, climate variability

### INTRODUCTION

Larger juvenile Pacific salmon (*Oncorhynchus* spp.) during their first year at sea have a survival advantage over smaller juvenile salmon from the same cohort (Farley et al. 2007a). 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 (Beamish and Mahnken 2001). Farley et al. (2007b) suggested that bottom-up control of the trophic structure on the eastern Bering Sea (EBS) shelf affected the size and condition of juvenile sockeye salmon (*O. nerka*). Moss et al. (2005) found that juvenile pink salmon with an above-average growth trajectory during their first summer at sea had higher marine survival rates. Presumably, the above-average growth for juvenile pink salmon would occur during years with higher marine productivity. Thus, linking salmon prey demand to prey supply and their dependence on habitat could provide insight into the complex dynamics among marine productivity and growth and survival of salmon.

A leading hypothesis for ocean productivity on the EBS

shelf suggests that spring sea surface temperature (SST) affects prey availability to pelagic consumers. Specifically, cold spring temperatures negatively affect the productivity of prey (Hunt and Stabeno 2002), which will potentially impact salmon growth and survival. Seasonal sea ice extent and timing of ice retreat are believed to affect the timing, magnitude, and persistence of the spring phytoplankton bloom. When sea ice extends to the southern EBS shelf during March and April, an early and short-lived spring phytoplankton bloom occurs in cold water. Cold SST limits copepod growth (Coyle and Pinchuk 2002), thus much of the annual phytoplankton production sinks to the bottom of the ocean. Alternatively, when sea ice is absent during March and April, the bloom occurs substantially later in the season (May and June). The warmer temperatures and later bloom timing allow copepods to graze on phytoplankton, such that secondary production remains in the pelagic system. According to this hypothesis, zooplankton production during years with reduced sea ice (warm spring SST) is not limited by food availability, providing abundant prey for pelagic fish consumers.

To develop an understanding of the link between juvenile chum salmon prey demand and supply, we used a bioen-

ergetics model to estimate growth rate potential (GRP) over a 4-year period within the EBS shelf as a measure of habitat quality for juvenile chum salmon. The utility of applying bioenergetics models to examine juvenile salmon GRP in marine waters was discussed in Farley and Trudel (2009). Data on juvenile chum salmon and ocean conditions come from BASIS surveys conducted along the EBS shelf during mid-August to early October 2004 to 2007. Sea temperatures and ice extent on the shelf varied during this time period, with warm spring and summer SSTs and reduced sea ice extent during 2004 and 2005 and colder spring and summer SSTs and increased sea ice extent during 2006 and 2007.

Prior information on juvenile chum salmon size and diet data collected during research surveys along the EBS shelf (mid August to October 2000 to 2006) were reported in Farley et al. (in press). The results suggested that shifts in diet and size of juvenile chum salmon occurred between years with warm and cold spring SSTs. The juvenile chum salmon size and diet data presented here include one more year (2007) and are the focal data for the GRP models. We focus on 2004 to 2007 because during these years, the EBS shelf was consistently surveyed during the same time period, sampling the same station grid in the southern and northern EBS (Fig. 1). The EBS shelf was separated into northern and southern regions in order to address stock-specific differences in juvenile chum salmon because Yukon River juvenile

chum salmon are distributed in the northern EBS and juvenile Kuskokwim River chum salmon are distributed in the southeastern Bering Sea during fall (Farley et al. 2005). We report the diet and size data for these years; however, the objectives of this study were to compare juvenile chum salmon GRP among years with warm and cold spring SSTs and to examine whether GRP is a useful index of habitat quality for juvenile chum salmon on the EBS shelf. A bioenergetics model was used to test whether (1) GRP was significantly higher during years with warm spring sea temperatures; (2) salmon densities were positively related to GRP; and (3) larger, faster growing salmon occurred during years with higher GRP.

**MATERIALS AND METHODS**

**Study Area and Sampling Protocols**

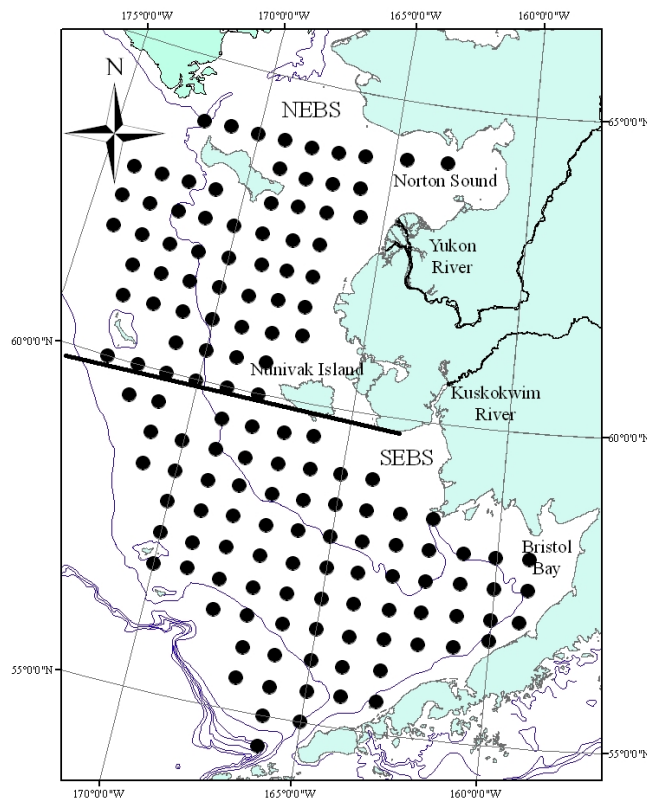
Stations along the EBS shelf were sampled during August–September, 2004–2007 (Fig. 1). Juvenile chum salmon were collected following methods described in Farley et al. (2005). Fish were collected using a mid-water rope trawl that was 198 m long, with a typical spread of 55 m horizontally and 15 m vertically. The trawl is constructed with hexagonal mesh in the wings and body, and a 1.2-cm mesh liner in the codend. Trawl stations were located along longitudinal meridians spaced every 55.6 km (i.e., along longitudinal meridians at stations spaced every 30 degrees of latitude). The rope trawl was towed at 6.5 to 9.3 km/h with the head rope at or near the surface. Trawl stations were sampled during daylight hours (0730–2100, Alaska Daylight Savings Time) and all tows lasted 30 min and covered 2.8 to 4.6 km. A Seabird SBE-911 conductivity-temperature-depth (CTD) device was deployed at each station to measure the vertical profiles (from near bottom to surface) of ocean temperature. Observed SSTs at 5 m depth taken from CTD profiles were used for bioenergetics modeling. At each trawl station, juvenile chum 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) were measured on board.

Regions along the EBS shelf were defined as northern (stations sampled north of 60N, including stations sampled along 60N) and southern (stations sampled south of 60N).

**Bioenergetics Model**

GRP of juvenile chum salmon over the EBS shelf was estimated using the bioenergetics model developed by Ware (1978) with incorporated modifications to the model developed by Trudel and Welch (2005). This model was parameterized for sockeye salmon and accounts for optimal cruising speed:

$$G_{i,s} = \tau \cdot I_{i,s} - (SMR_{i,s} + ACT_{i,s}) \tag{1}$$



**Fig. 1.** Area surveyed for juvenile chum salmon during August–September 2004 to 2007, Bering-Aleutian Salmon International Survey (BASIS) research cruises.

where  $G_{i,s}$  is the GRP (cal/s) for juvenile chum salmon during year  $i$  at station  $s$ ,  $\tau$  is the proportion of food that can be metabolized (Trudel and Rasmussen 2006),  $I_{i,s}$  is the feeding rate (cal/s),  $SMR_{i,s}$  and  $ACT_{i,s}$  are, respectively, the standard metabolic rate (cal/s) and activity costs (cal/s). For simplicity, we assumed that  $\tau$  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 (Trudel and Rasmussen 2006).

The relationship between salmon feeding rate and prey density was assumed to be described by a type II functional response (Holling 1965; Ware 1978):

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

where  $\rho$  is prey density (g/cm<sup>3</sup>),  $\gamma$  is the cross-sectional area of the reactive field (cm<sup>2</sup>),  $U$  is the optimum swimming speed (cm/s),  $h$  is handling time of prey (s/g), and  $ED$  is sum of prey caloric content (cal/gwet), and was estimated as:

$$ED_{i,s} = \sum_{z=1}^p ED_{i,s,z} \quad (3)$$

where  $p$  = the number of prey species  $z$ . Consumption rates were equal to zero when no prey were available. The equations for handling time were developed in Farley and Trudel (2009):

$$h = \alpha_4 \bar{W}_i^{CB-1} \quad (4)$$

$$\alpha_4 = \frac{1}{CA \cdot f(T)} \quad (5)$$

where  $\bar{W}_i$  is the average chum salmon weight (g),  $CA$  and  $CB$  are, respectively, the weight coefficient and exponent for maximum feeding rate for chum salmon, and  $f(T)$  is the Thornton and Lessem (1978) temperature-dependence function for cold-water fish species (see Table 1 for definition and parameters).

The energetic costs associated with the standard metabolic rates and activity costs of juvenile chum salmon were modeled using the empirical models derived by Trudel and Welch (2005). Specifically, standard metabolic rates were modeled as a function of weight and water temperature (°C):

$$SMR_{i,s} = \alpha_1 \bar{W}_i^\beta e^{\phi T_{i,s}} \quad (6)$$

where  $\alpha_1$ ,  $\beta$ , and  $\phi$  are regression coefficients (Table 1). Activity costs were modeled as a function of weight and swimming speed:

$$ACT_{i,s} = \alpha_0 \bar{W}_i^\delta U_{i,s}^\lambda \quad (7)$$

where  $\alpha_0$ ,  $\delta$ , and  $\lambda$  are regression coefficients (Table 1). We used the optimal cruising speed model derived by Trudel and

Welch (2005) to estimate the swimming speed of juvenile chum salmon (Table 1).

## Prey Biomass

Gut contents from subsamples of juvenile chum salmon at each trawl station were analyzed to characterize prey consumption (Fig. 2). Prey analyses determined that the following prey items were important for juvenile chum salmon (those with percent wet weight greater than 5%): pagurids (northern region only), *Oikopleura* spp., euphausiids, cnidaria, brachyura, amphipods, and fish including age-0 wall-eye pollock (*Theragra chalcogramma*) and Pacific sand lance (*Ammodytes hexapterus*). The typical size ranges of age-0 pollock and sand lance in the diets of juvenile chum salmon were between 28 to 67 mm total length (TL) and 55 to 80 mm fork length (FL), respectively. Prey that were less than 5% wet weight were lumped into "other fish" and "other zoop" categories.

Fish prey density (g/cm<sup>3</sup>) at each station was determined as:

$$\rho_{i,s} = \sum_{z=1}^f \frac{N_{i,s,f} \cdot \theta \cdot \bar{W}_f}{\phi \cdot V_{i,s}} \quad (9)$$

where  $N_{i,s,f}$  is the number of prey ( $f$  = age-0 pollock or sand lance) caught in the trawl at each station,  $\theta$  is the proportion of prey items captured in trawls that fell within the size range that juvenile chum salmon fed upon (dimensionless),  $\bar{W}_f$  is the average weight (g) for each prey item,  $\phi$  is the catchability coefficient (dimensionless), and  $V_{i,s}$  is the volume sampled at each station (cm<sup>3</sup>). 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 ( $\phi = 0.016$ ) for age-0 pollock and sand lance was determined following methods described in Farley and Trudel (2009).

The average weight of these prey was 1.7 g for age-0 pollock and 1.2 g for sand lance. Laboratory analyses of subsamples of age-0 pollock taken during the 2005 survey indicated that the average caloric content was 4,424 cal/gdry; caloric content for Pacific sand lance (4,209 cal/gdry) was obtained from Robards et al. (1999). The estimates of catchability, proportion of prey items, caloric content, and weight were held constant for each station, among years.

Zooplankton prey were collected using a 65-cm bongo sampler with 505-micron mesh net. The net was towed obliquely to near bottom (max 200 m depth) and the volume of water flowing through the net was measured using a General Oceanics 2030R flowmeter. Zooplankton samples were preserved in a buffered-formalin (5%) solution and processed at the University of Alaska Fairbanks laboratory.

Zooplankton prey density (g/cm<sup>3</sup>) at each station was determined as:

**Table 1.** Definitions of symbols used in the text. Note that subscripts *i* and *s* represent year (*i* = 2004 to 2007) and station and overbars denote mean quantities within the definitions of *i*.

Symbol	Parameter description	Value	Source
<i>ACT</i>	Activity costs (cal/s)		
<i>E</i>	Total energy content of juvenile chum salmon (cal)		
<i>ED<sub>f</sub></i>	Caloric content of juvenile salmon (cal/g <sub>wet</sub> )	1,176	2
<i>ED<sub>1</sub></i>	Caloric content of age-0 pollock (cal/g <sub>wet</sub> )	885	2
<i>ED<sub>2</sub></i>	Caloric content of sand lance (cal/g <sub>wet</sub> )	842	2
<i>ED<sub>is</sub></i>	Weighted average of caloric content of juvenile salmon prey at year <i>i</i> and stations <i>s</i> (cal/g <sub>wet</sub> )		
<i>G</i>	Growth rates (cal/s)		
<i>I</i>	Feeding rates (cal/s)		
<i>N</i>	Number of prey caught at a station		
<i>SMR</i>	Standard metabolic rates (cal/s)		
<i>T</i>	Sea surface temperature (°C; 5m below surface)		
<i>V</i>	Volume sampled by the net (cm <sup>3</sup> )		
<i>W</i>	Chum salmon weight (g)		
<i>W<sub>p</sub></i>	Prey weight (g)		
<i>ϕ</i>	Catchability coefficient of the net (dimensionless)	0.016	7
<i>τ</i>	Proportion of food that can be metabolized (dimensionless)	0.7	1
<i>θ</i>	Proportion of prey items captured in the net that is within the size range that juvenile salmon fed upon (dimensionless)		
<b>Consumption:</b>			
$I = \frac{\rho\gamma U}{1 + \rho\gamma h U}$			
<i>ρ</i>	Prey density (cal/cm <sup>3</sup> )		
<i>γ</i>	Cross-sectional area of the reactive field (cm <sup>2</sup> )		
<i>U</i>	Swimming speed (cm/s)		
<i>h</i>	Handling time (s/cal)		
<b>Cross-sectional area of the reactive field:</b>			
$\gamma = \alpha_3 \cdot W^{\beta_3}$			
<i>α<sub>3</sub></i>	Intercept (cm <sup>2</sup> )	1	1
<i>β<sub>3</sub></i>	Coefficient, <i>γ</i> versus <i>W</i>	0.69	1
<b>Handling time:</b>			
$h = \frac{W^{CB-1}}{ED_p \cdot CA \cdot f(T)}$			
<i>CA</i>	Intercept for maximum feeding rates (g/s)	4.56 E-06	5
<i>CB</i>	Allometric exponent of maximum feeding rate	-0.275	5
<i>f(T)</i>	Temperature adjustment for maximum food consumption rates		

Table 1 (continued).

Symbol	Parameter description	Value	Source
<b>Temperature adjustment function:</b>			
$f(T) = K_a \cdot K_b$			
$K_a = \frac{(0.58 \cdot L1)}{1 + 0.58 \cdot (L1 - 1)}$			
$L1 = \exp(G1 \cdot (T - 3))$			
$G1$			
$K_b = \frac{(0.5 \cdot L2)}{1 + 0.5 \cdot (L2 - 1)}$			
$L2 = \exp(G2 \cdot (24 - T))$			
$G2$			
<b>Standard metabolic rates*:</b>			
$SMR = \alpha_1 \cdot W^\beta \cdot e^{\varphi \cdot T}$			
$\alpha_1$	Intercept (cal/s)	$4.76 \times 10^{-5}$	4
$\beta$	Coefficient, SMR versus $W$	0.87	4
$\varphi$	Coefficient, SMR versus $T$ (1/°C)	0.064	4
<b>Swimming costs*:</b>			
$ACT = \alpha_0 \cdot W^\delta \cdot U^\lambda$			
$\alpha_0$	Intercept (cal·s <sup>-1</sup> )	$1.74 \times 10^{-6}$	4
$\delta$	Coefficient, ACT versus $W$	0.72	4
$\beta_3$	Coefficient, ACT versus $U$	1.6	4
<b>Swimming speed:</b>			
$U = \omega \cdot W^v \cdot \exp(\kappa \cdot T)$			
$\omega$	Intercept (cm/s)	11.1	4
$v$	Coefficient, U versus $W$	0.097	4
$\kappa$	Coefficient, U versus $T$ (1/°C)	0.040	4

1. Ware (1978); 2. This study; 3. Beauchamp et al. (1989); 4. Trudel and Welch (2005); 5. Davis et al. (1998); 6. Moss and Farley (unpubl. data); 7. Farley and Trudel (in press).

\*The oxygen consumption rates were converted from mg O<sub>2</sub>/h to cal/s using an oxy calorific equivalent to 3.24 mg O<sub>2</sub>/cal (Elliott and Davison 1975).

$$\rho_{i,s} = \sum_{z=1}^p N_{i,s,z} \cdot \bar{W}_{i,s,z} \tag{10}$$

where  $N_{i,s,z}$  and  $\bar{W}_{i,s,z}$  are the number and average weight of zooplankton species  $z$  ( $z = 1$  to  $p$ ) at station  $s$  during year  $i$ .

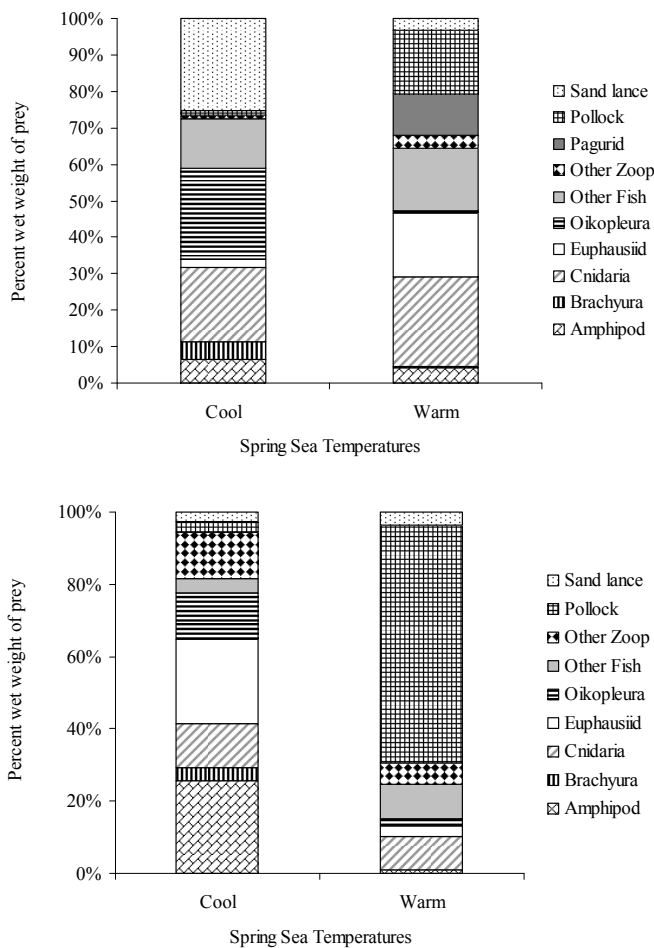
GRP (cal/s) was converted to cal/d by multiplying  $I_{i,s}$  by the number of seconds in a 15-hour day (estimated time juvenile chum salmon spend feeding per day during August and September) and by multiplying  $SMR_{i,s}$  and  $ACT_{i,s}$  by the

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. (1996):

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

where  $\bar{E}_{i,s}$  is the average total energy per fish (cal),  $ED_f$  is the



**Fig. 2.** Juvenile chum salmon prey composition (percent wet weight) in the northern (upper) and southern (lower) regions of the eastern Bering Sea shelf during warm (August to October, 2004 and 2005) and cold (August to October 2006 and 2007) years.

caloric content in juvenile chum salmon ( $\text{cal/g}_{\text{wet}}$ ), and  $\bar{W}_i$  is the average weight (g) of juvenile chum salmon. Annual averages of juvenile chum 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 chum salmon were caught. The caloric content of juvenile chum salmon was determined from subsamples of the juvenile chum salmon caught during the 2004 and 2005 (no data available for 2006 and 2007) surveys using bomb calorimetry and averaged  $5,107 \text{ cal/g}_{\text{dry}}$ . (There was no significant difference in average caloric content of juvenile chum salmon between years; ANOVA- Fixed effect,  $F = 1.0, P = 0.32$ ). The units ( $\text{cal/g}_{\text{dry}}$ ) were converted to ( $\text{cal/g}_{\text{wet}}$ ) by multiplying  $5,107 \text{ cal/g}_{\text{dry}}$  by 23% ( $W_{\text{dry}}/W_{\text{wet}}$ ), the average value obtained from the subsample (2004 to 2005) of juvenile chum salmon dried for the bomb calorimetry process. These estimates of growth (% body weight/d) were considered to be juvenile chum salmon GRP on the EBS shelf and were the primary statistic used in subsequent models.

*Spring SSTs*

Spring SSTs ( $^{\circ}\text{C}$ ) during May 2002 to 2008 in the southeastern Bering Sea are shown in Fig. 3. Mean May SSTs were averaged over  $54^{\circ}18' \text{ N}$  to  $60^{\circ}0' \text{ N}$ ,  $161^{\circ}12' \text{ W}$  to  $172^{\circ}30' \text{ W}$  (data from [www.beringclimate.noaa.gov](http://www.beringclimate.noaa.gov)). Index values were calculated as the deviations from the mean May SST value ( $2.33^{\circ} \text{ C}$ ) for the 1970–2000 period divided by the standard deviation ( $0.76^{\circ} \text{ C}$ ). Years with cold SSTs were defined as those years when the index values of SSTs were at or below 0 (2006 to 2008); years with warm SSTs were defined as those years when the index values of SSTs were above 0 (2002 to 2005).

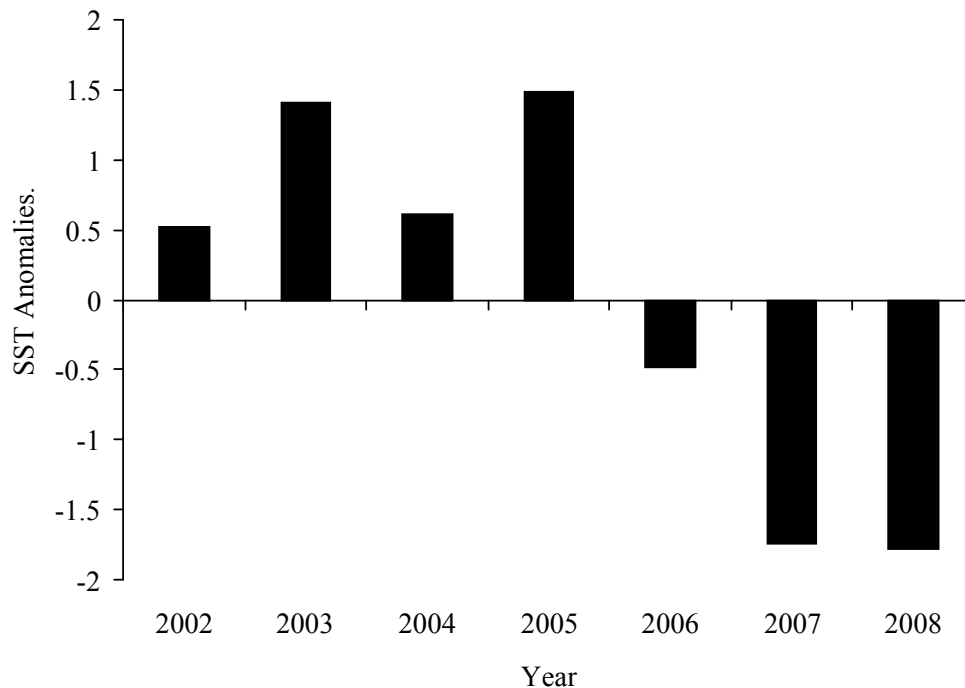
**Model Applications**

The bioenergetics model was used to test the following hypotheses:

*Hypothesis 1: GRP is significantly higher during years with warm spring temperatures.* This hypothesis was tested using two-way analysis of variance (ANOVA-Fixed Effect) with S-plus software (Insightful 2001) where year (2004 to 2007) and region (northern and southern) were the categorical variables and GRP was the dependent variable. These data were also pooled by oceanographic domain (see Kinder and Schumacher 1981) and two-way ANOVA was used to test for significant differences between nearshore (coastal domain – depths  $< 50 \text{ m}$ ; well-mixed vertical structure, low salinity, warm water temperature, low stratification) and off-shore (middle domain – depths  $> 50 \text{ m}$  and  $< 100 \text{ m}$ ; strong two-layer vertical structure, moderate salinity, high stratification) domains within each region (northern and southern) among years. If a significant difference ( $P < 0.05$ ) occurred, a Sidak 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 (Insightful 2001). The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of alpha.

*Hypothesis 2: Juvenile chum salmon are distributed in areas of high GRP on the EBS shelf.* Within each region, regression analysis was used to examine the relationship between  $\text{GRP}_{i,s}$  and catch per unit effort ( $\text{CPUE}_{i,s}$  – defined as the number of juvenile salmon caught during a 30-min trawl haul during year  $i$  at station  $s$  and hereon referred to as relative abundance). The natural logarithm of ( $\text{CPUE}_{i,s} + 1$ ) was used to reduce the wide variability in  $\text{CPUE}_{i,s}$ . Year was used as a factor within the regression analysis and an interaction between relative abundance and year was included to account for year effects. Juvenile chum salmon GRP and relative abundance were also compared graphically by year to provide perspective on the distribution of juvenile chum salmon in relation to regions of high and low GRP on the EBS shelf.

*Hypothesis 3: Juvenile chum salmon size and growth*



**Fig. 3.** Anomalies of sea surface temperatures (bar, SSTs, °C) during May 2002 to 2008 in the southeastern Bering Sea (data obtained from <http://www.beringclimate.noaa.gov>). 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 National Centers for Environmental Protection and the National Center for Atmospheric Research (NCEP/NCAR) reanalysis project (Kalnay et al. 1996). The 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).

rates were significantly higher during years with higher GRP. Differences in annual length within region were determined using two-way ANOVA where year was the categorical variable and length was the dependent variable. Because GRP was generally higher during years with warm spring SST (2004 and 2005) than during years with cold SST (2006 and 2007), the length data were pooled into warm and cold years within each region. Growth rate (mm/day) within each region for warm and cold years was estimated from the slope of the regression of Day of Year on length (dependent variable). The difference in slopes between warm and cold years within each region was determined using analysis of covariance.

## RESULTS

### Hypothesis Tests

*Hypothesis 1:* In general, mean annual GRP was positive during 2004 and 2005 and negative during 2006 and 2007 in both regions (Table 2). Juvenile chum salmon GRP differed significantly among years in the northern (ANOVA;  $f_{[3,154]} = 43.31$ ,  $P < 0.001$ ) and southern (ANOVA;  $f_{[3,331]} = 40.09$ ,  $P < 0.001$ ) regions. In the northern region, the pairwise comparison among years indicated that average GRP was significantly higher during 2004 than 2006 and 2007 ( $P < 0.001$ ) and GRP was higher during 2005 than 2006 ( $P <$

0.001) and 2007 ( $P < 0.01$ ). Average GRP was also higher during 2004 than 2005 ( $P < 0.001$ ). In the southern region, GRP was significantly higher during 2004 and 2005 than during 2006 and 2007 ( $P < 0.001$ ). These analyses indicate that juvenile chum salmon GRP was higher during warm than cold years in both regions of the EBS.

In the northern region, juvenile chum salmon GRP was positive in the middle domain during all years except 2007 and negative during all years except 2004 in the coastal domain (Table 3). Juvenile chum salmon GRP differed significantly among domains (ANOVA;  $f_{[7,288]} = 1814.1$ ,  $P < 0.001$ ), year (described above) and the interaction between domain and year in the southern region ( $P < 0.001$ ), whereas only the domain (ANOVA;  $f_{[7,150]} = 520.6$ ,  $P < 0.001$ ) and year (described above) were significant and not the interaction term ( $P = 0.40$ ) in the northern region. In the southern region, the middle domain had significantly higher GRP than the coastal domain during all years (2005 and 2006,  $P < 0.001$ ; 2007,  $P < 0.05$ ) except 2004. Juvenile chum salmon GRP in the coastal domain of the southern region was significantly higher during 2004 than all other years ( $P < 0.001$ ). In the middle domain of the southern region, juvenile chum salmon GRP was significantly higher during 2004 and 2005 than 2006 and 2007 ( $P < 0.001$ ).

*Hypothesis 2:* Relative abundance of juvenile chum salmon was highest during the warm years of 2004 and 2005 in the southern region, whereas relative abundance increased

**Table 2.** Annual averages ( $\pm$ SE) of juvenile chum salmon growth rate potential (GRP; % body weight per day) during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of stations (N) is included.

Year	Northern			Southern		
	N	GRP	SE	N	GRP	SE
2004	42	2.90	0.18	82	3.37	0.20
2005	38	0.58	0.44	81	3.01	0.45
2006	42	-1.04	0.32	89	-0.17	0.30
2007	37	-1.78	0.30	83	-0.25	0.25

**Table 3.** Annual averages ( $\pm$ SE) of juvenile chum salmon growth rate potential (GRP; % body weight per day) within the coastal and middle domains during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of stations (N) is included.

Region	Year	Coastal			Middle		
		N	GRP	SE	N	GRP	SE
Northern							
	2004	33	2.65	0.21	9	3.81	0.18
	2005	27	-0.16	0.40	11	2.39	0.97
	2006	35	-1.39	0.28	6	0.99	1.21
	2007	32	-1.95	0.25	5	-0.72	1.61
Southern							
	2004	28	2.95	0.37	47	3.75	0.18
	2005	25	-0.12	0.73	46	4.49	0.48
	2006	23	-2.00	0.22	56	0.75	0.40
	2007	27	-1.06	0.31	44	0.55	0.36

**Table 4.** Annual averages ( $\pm$ SE) of juvenile chum salmon length (mm) during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of juvenile chum salmon sampled (N) is included.

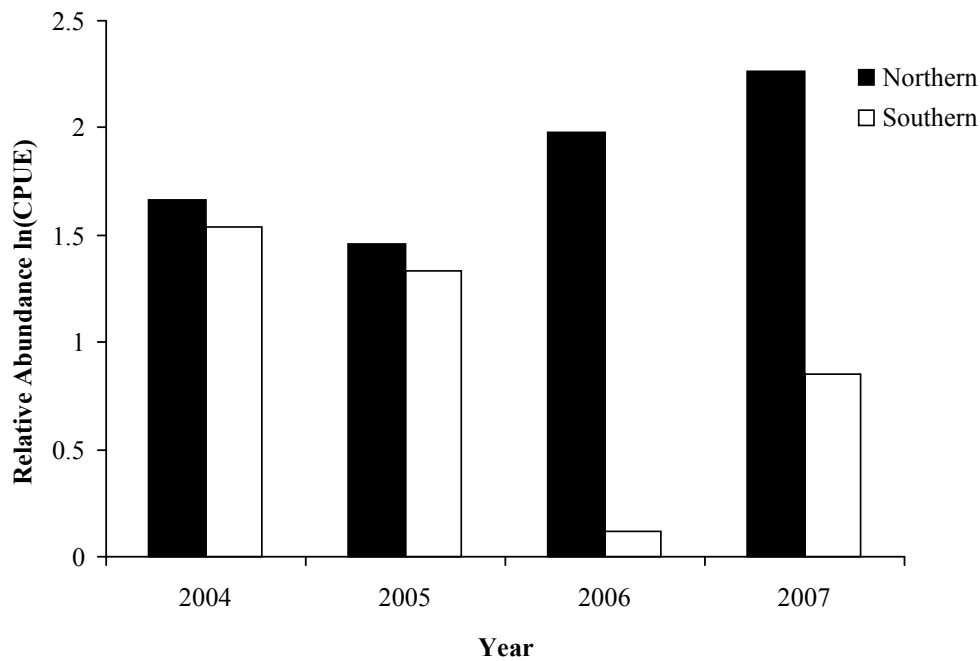
Year	Northern			Southern		
	N	Length	SE	N	Length	SE
2004	471	205.6	0.97	844	179.9	0.79
2005	253	199.6	1.11	649	172.5	0.88
2006	576	156.2	0.57	30	179.9	3.02
2007	755	193.5	0.90	577	178.1	1.57

during the cold years of 2006 and 2007 in the northern region (Fig. 4). The regression of GRP and relative abundance indicated that the relationship was not significant in either the northern ( $P = 0.30$ ) or southern regions ( $P = 0.30$ ). These results show that juvenile chum salmon were not distributed in areas of highest GRP during any year. As shown in Fig. 5, the highest catch of juvenile chum salmon generally occurred in water depths  $< 50$  m (coastal domain), an area where GRP was generally at or below zero (Table 3). Areas with the highest GRP occurred offshore in deeper water during each year (middle domain; Table 4); however, the offshore area tended not to have many juvenile chum salmon, especially

during the cold years of 2006 and 2007.

*Hypothesis 3:* Juvenile chum salmon length differed significantly among years in the northern (ANOVA;  $f_{[3,2051]} = 623.13$ ,  $P < 0.001$ ) and southern (ANOVA;  $f_{[3,2096]} = 9.32$ ,  $P < 0.001$ ) regions (Table 4). In the northern region juvenile chum salmon were significantly larger during 2004 and 2005 than during 2006 and 2007 ( $P < 0.001$ ). In addition, juvenile chum salmon were significantly larger during 2004 than 2005 ( $P < 0.01$ ) and during 2007 than 2006 ( $P < 0.001$ ). In the southern region, juvenile chum salmon were significantly smaller during 2005 than during 2004 ( $P < 0.001$ ) and 2007 ( $P < 0.01$ ). These results indicate that juvenile chum





**Fig. 4.** Relative abundance (natural logarithm of catch per unit effort defined as the number of juvenile chum salmon captured in a 30-min surface trawl) of juvenile chum salmon in the northern (solid bar) and southern (clear bar) regions of the eastern Bering Sea during 2004 to 2007.

salmon were significantly larger during warm years within the northern region, but not within the southern region.

Juvenile chum salmon growth rates were significantly lower ( $P < 0.001$ ) in the northern region during warm years (slope = 0.27 mm/day; regression statistics:  $F = 5.73$ , deg (1, 722),  $P = 0.02$ ) as opposed to cold years (slope = 2.53 mm/day; regression statistics:  $F = 1384$ , deg (1, 1329),  $P < 0.001$ ). Growth rates of juvenile chum salmon in the southern region were also significantly higher ( $P < 0.001$ ) during cold years (slope = 1.27 mm/day; regression statistics:  $F = 1533$ , deg (1, 1491),  $P < 0.001$ ) than warm years (slope = 1.53 mm/day; regression statistics:  $F = 978.3$ , deg (1, 605),  $P < 0.001$ ).

A schematic of these results is shown in Table 5 for reference.

## DISCUSSION

Our findings suggest a possible connection between GRP of juvenile chum salmon during late summer - early fall and spring SSTs along the EBS shelf. On average, salmon GRP was lower during years with cold rather than warm spring SSTs (supporting Hypothesis 1). However, juvenile chum salmon were not distributed in areas of highest GRP on the EBS shelf. In the southern region, many juvenile chum salmon were distributed in water depths  $< 50$  m (coastal domain), areas on the shelf with significantly lower GRP (opposing Hypothesis 2). Juvenile chum salmon were larger during years with warm rather than cold SSTs in the northern region, but not so in the southern region. In addition, growth rate of juvenile chum salmon was significantly higher during

cold rather than warm years in both regions (opposing Hypothesis 3). Juvenile chum salmon were also more abundant during cold years in the northern region, but relative abundance in the southern region declined dramatically during cold years.

The critical-size and critical-period hypothesis for juvenile salmon suggests two periods of high mortality linked to the size (growth rate) of juvenile salmon. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker 1968; Willette et al. 1999). The second stage is thought to occur following the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter conditions (Beamish and Mahnken 2001). In our study, juvenile chum salmon were collected at the end of the first summer's growing season. We found that in the southern region, juvenile chum salmon were similar in size among years but their relative abundance dropped dramatically during cold years. These results suggest that perhaps smaller, slower growing individuals during years with lower GRP experienced higher size-selective mortality early in their marine residence. In the northern region, size-selective mortality does not appear to take place during early marine residence. In this case, years with lower GRP had higher relative abundance, suggesting that predation is minimal in the northern regions during years with cold SSTs. However, it is possible that these smaller individuals may experience higher size-selective mortality during their first winter at sea, thus reducing survival later in their marine life history (see Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007b).

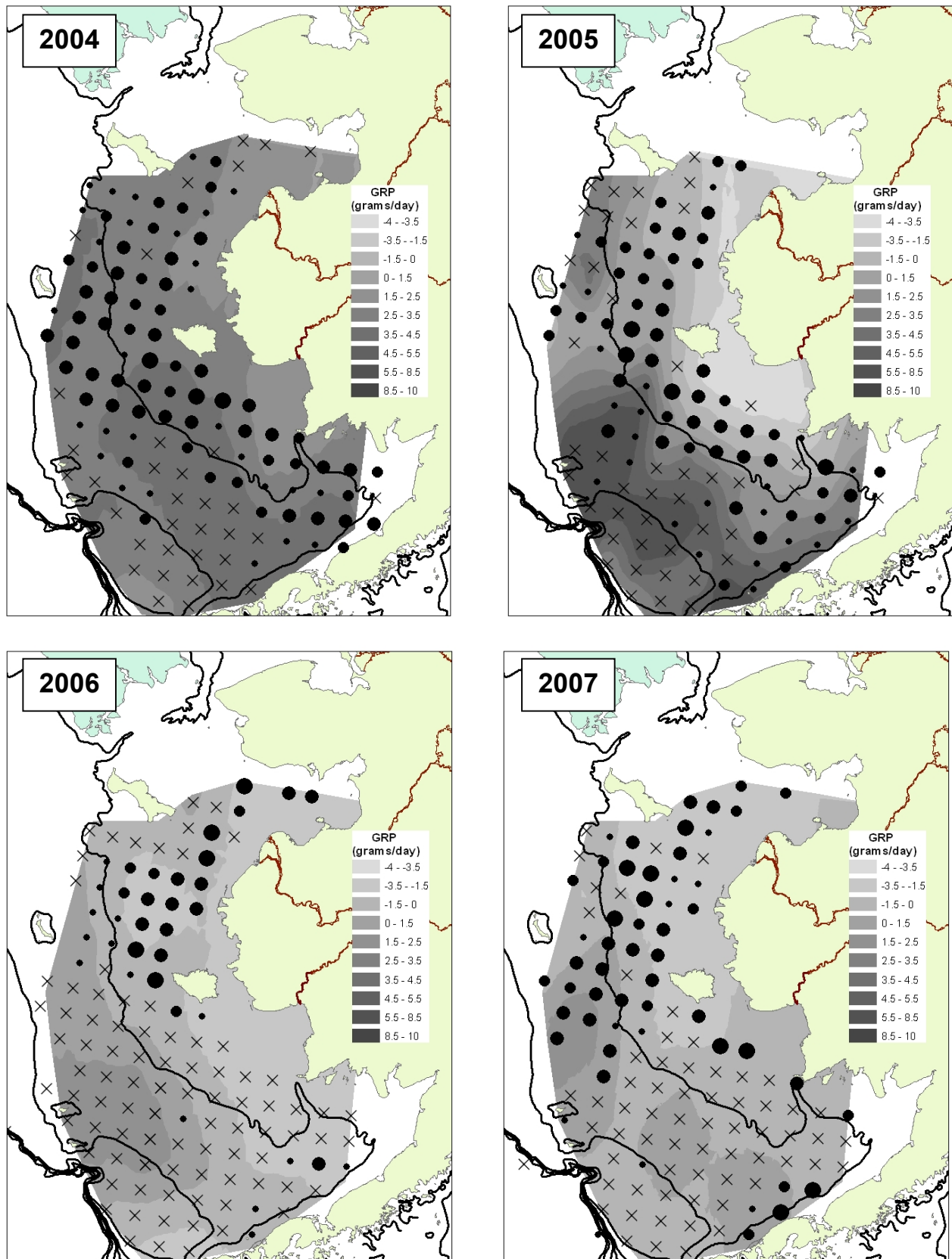


Fig. 5. Contour plot of juvenile chum salmon growth rate potential (GRP; % body weight per day) in relation to the natural logarithm of catch per unit effort of juvenile chum salmon captured in 2004 - 2007.

**Table 5.** Summary of the hypothesis tests for juvenile chum salmon growth rate potential (GRP), catch per unit effort (CPUE), fork length (FL), and growth rate (GR) within the northern and southern regions of the Bering Sea during years with warm (2004 and 2005) and cold (2006 and 2007) sea surface temperatures. Dash (-) indicates no difference in hypothesis test between warm and cold years.

Region	Hypothesis	Warm	Cold
Northern	GRP	High	Low
	CPUE	Low	High
	FL	Small	Large
	Growth Rate	Low	High
Southern	GRP	High	Low
	CPUE	High	Low
	FL	-	-
	Growth Rate	Low	High

We found that juvenile chum salmon growth rates were higher in both regions during years with cold SSTs and reduced GRP. These results appear to be at odds with similar studies of juvenile chum salmon in coastal waters that found that higher growth rates occurred during years with warmer SSTs (Karpenko 1987; Kawamura et al. 2000). We note that juvenile chum salmon were significantly larger during warm years than cold years in the northern region. As marine survival is a function of size for juvenile salmon, perhaps the smaller juvenile salmon dedicated more energy to growth during the latter part of their first summer's growing season. In the southern region, it is likely that smaller, slower growing juvenile chum salmon were not surviving, thus only the faster growing individuals of the population were surveyed. This result is supported by the fact that the relative abundance of juvenile chum salmon in the southern region was much less during years with cold SSTs when compared to years with warm SSTs.

Our goal was to use GRP as an indicator of habitat quality during years with cold and warm spring SSTs rather than to provide precise quantitative estimates of growth rates for juvenile chum salmon. For instance, juvenile chum salmon GRP was negative during some years and shelf habitats indicating that these salmon may be losing rather than gaining weight. The annual estimates of juvenile chum salmon average GRP varied from -1.78% to 3.37% body weight per day for fish that ranged in length between 156 mm to 205 mm FL. Smaller juvenile chum salmon (41 mm FL) fed a varying ration of prey items in an experimental holding tank gained an average of 5.4% body weight (g) per day (LeBrasseur 1969). Larger juvenile chum salmon (90 mm to 160 mm FL) captured in coastal waters off Vancouver Island, British Columbia, Canada, attained daily growth rates between 0.34% to 3.28% (Perry et al. 1996). Juvenile salmon growth rate is size-dependent, and daily growth rate decreases as the fish get larger (Brett 1974). Thus, our highest GRP estimates may not be out of line with experimental estimates, and seem to be in line with marine research estimates of juvenile chum salmon daily growth rate.

Bioenergetics models are particularly sensitive to changes in energy density, composition of stomach contents, and biomass of potential prey (Beauchamp et al. 1989). 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 pollock and Pacific sand lance) available to juvenile chum salmon on the EBS shelf. For instance, euphausiids make up 20% of juvenile chum salmon diet by wet weight in the southern EBS during cold SST years, yet the bongo nets used to sample these important prey items typically underestimate euphausiids (Ken Coyle, University of Alaska Fairbanks, Fairbanks, AK, pers. comm.), thereby lowering biomass estimates of euphausiids used in GRP models. 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 chum salmon GRP among the years examined.

Juvenile chum salmon GRP was estimated using average caloric content of juvenile chum salmon collected during 2004 and 2005 (warm years). Caloric content of juvenile chum salmon was not available during 2006 and 2007 (cold years). Decreasing the caloric content of juvenile chum salmon increases their estimated GRP. Thus, if caloric content of juvenile chum salmon were lower during cold years, our estimates of juvenile chum salmon GRP could be biased low. However, a recent paper comparing differences in caloric content of age-0 fish on the EBS found that the caloric content of these fish was significantly higher during years with cold SSTs (Moss et al. 2009). Thus, it is likely that juvenile chum salmon caloric content could have been higher during years with cold SSTs, suggesting that our estimates of juvenile chum salmon GRP are biased high.

Our study provides evidence that energetic limitation influences habitat quality on the EBS shelf for juvenile chum salmon during years with cold spring SSTs. Declining GRP in coastal waters is one possible reason why juve-

nile chum salmon begin to migrate offshore and away from shelf habitats. Our study also highlights differing responses of Yukon vs. Kuskokwim River juvenile chum salmon to changing ecosystem states. For instance, shifts from warm to cold SSTs in the northern region do not appear to affect summer abundance of juvenile Yukon River chum salmon, whereas the abundance of juvenile Kuskokwim River chum salmon drops precipitously during years with cold SSTs. From this result, we hypothesize that size-selective mortality from marine entry to late summer is highest in juvenile Kuskokwim chum salmon during cold years, but that size-selective mortality during early marine life is not a factor for juvenile Yukon River chum salmon. Although not addressed in this study, we hypothesize that the smaller Yukon River chum salmon captured during years with cold SSTs and lower GRP likely incur higher size-selective mortality during winter. 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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