

Energy Density and Length of Juvenile Pink Salmon *Oncorhynchus gorbuscha* in the Eastern Bering Sea from 2004 to 2007: a Period of Relatively Warm and Cool Sea Surface Temperatures

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Abstract: Juvenile pink salmon (*Oncorhynchus gorbuscha*) were examined in the eastern Bering Sea from 2004 to 2007 to assess the influence of ocean temperature on whole body energy content (WBEC), length, and diet. Fish were collected during the United States Bering-Aleutian Salmon International Study (U.S. BASIS) surveys in the eastern Bering Sea. Warmer spring and summer sea surface temperatures prevailed from 2004 to 2005 on the eastern Bering Sea shelf, whereas cooler spring and summer sea surface temperatures occurred from 2006 to 2007. Juvenile pink salmon changed diet between the warm and cool years. Walleye pollock *Theragra chalcogramma* dominated the diet (> 50% wet mass) in warm years, while walleye pollock were nearly absent from the diet in cool years. Juvenile pink salmon lengths were significantly longer in warm years but WBEC was significantly lower. We interpret our results to indicate that length is not always a reliable measure of energy status.

Keywords: pink salmon, *Oncorhynchus gorbuscha*, Bering Sea, energy density, whole body energy content (WBEC), diet, growth

INTRODUCTION

Juvenile Pacific salmon (*Oncorhynchus* spp.) early marine survival has been linked to early marine growth rate within nearshore environments (Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007). Size-selective mortality of juvenile salmon is believed to occur during two time periods. The first period occurs after entering the nearshore marine environment and is attributed to predation (Parker 1968; Willette et al. 1999). The second period is during the first winter at sea and is attributed to size and energy reserves (Beamish et al. 2004; Moss et al. 2005). The growth rate of juvenile salmon is linked to climate-driven processes that regulate ocean productivity (Farley et al. 2007). Thus, early marine survival of Pacific salmon is thought to be a reflection of the carrying capacity of the ecosystem they inhabit.

In the eastern Bering Sea, ocean productivity is hypothesized to oscillate, benefitting either pelagic or benthic habitats (Hunt et al. 2002; Mueter et al. 2007). The oscillating control hypothesis (OCH) predicts that the timing of the ice retreat and spring sea surface temperatures (SST) will dictate how ocean productivity is distributed between pelagic

and benthic environments in the southeastern Bering Sea. Early ice retreat and higher spring SSTs will lead to higher pelagic production during warm years, and conversely, late ice retreat and lower spring SSTs will lead to lower pelagic production and higher benthic production during cool years (Hunt et al. 2002). Research on salmon ecology indicates that juvenile salmon growth and early marine survival are regulated by bottom-up control in the eastern Bering Sea ecosystem (Straty 1974; Farley et al. 2007; Farley et al. in press).

In this paper, we test the impact of warm versus cool oceans on the condition of juvenile pink salmon (*O. gorbuscha*). The data are from trawl surveys conducted on the eastern Bering Sea shelf during late August to early October 2004 through 2007. A previous study on juvenile pink salmon suggests that their size was significantly different, being larger in warm spring SSTs and smaller in cool spring SSTs, and that diet and relative abundance shifted between spring SST states (Farley et al. in press). Our analysis expands on previous work by adding data for another year and includes energy density measurements of juvenile pink salmon.

MATERIAL AND METHODS

Field Methods

Fisheries and oceanographic data were collected during the U.S. BASIS trawl surveys conducted from 2004 to 2007 (Fig. 1). Salmon and other fish species were collected following methods described in Farley et al. (2005). At each station, diet analysis was performed on a random sample of up to 10 juvenile pink salmon for each of the following size bins: < 100 mm, 100–200 mm, and 200–300 mm. Contents of the stomachs in each size bin were pooled and then sorted to the lowest taxonomic group. The resulting prey groups were weighed (nearest 0.001 g). At each station, pink salmon were weighed (nearest 1.0 g) and measured (fork length to nearest 1.0 mm; hereafter referred to as length) on board, and the first two juvenile pink salmon from each trawl haul were labeled and frozen whole for laboratory analyses. This systematic sampling allowed us to obtain a representative sample of the juvenile pink salmon captured in our trawl.

Laboratory Methods

Juvenile pink salmon energy densities were determined using bomb calorimetry. Prior to bomb calorimetry analysis we obtained a whole fish wet weight (g), and removed oto-

liths and stomach contents. Fish were dried in a VWR 1324 convection oven at 60–65°C until a constant weight (within 0.005 g) was obtained; dried fish were stored in a desiccator until further processing. We homogenized individual fish using a pulverizer for 30 s then transferred the sample to a mortar and pestle and pulverized further until a uniform powder was obtained. For each sample, we pressed pellets weighing approximately 0.15 g and stored them in a desiccator until further processing. These pellets were then combusted in a Parr 1425 Semimicro calorimeter to determine whole body energy content (WBEC). The values generated by the calorimeter were converted from Cal g⁻¹ dry weight to J g⁻¹ dry weight. Total energy (J) represents the calculated energy for the entire fish and was calculated by multiplying WBEC by the dry weight of the fish.

Statistical Methods

The eastern Bering Sea was split into two areas north and south of 60°N latitude, based on the potential for pink salmon to be from different stock groups and to minimize the effects of survey timing between the two areas. For example, the southern area was surveyed earlier in the field season while the northern area was completed in the fall. Also, the southern area was intended to more closely match the area discussed by Hunt et al. (2002) with regards to the OCH. We defined the southeastern Bering Sea (SEBS) to include all stations to the south of 59.75°N and the northeastern Bering Sea (NEBS) to include all stations to the north of 59.75°N.

Earlier studies have determined the size and prey of juvenile salmon in the eastern Bering Sea (Farley et al. 2005; Farley et al. in press). In an effort to test the effects of the OCH we pooled our sampling years into warm and cool years. We defined warm and cool years based on whether they had positive or negative spring SST anomalies (www.beringclimate.noaa.gov). Warm years are represented by 2004 and 2005; cool years are represented by 2006 and 2007 (Fig. 2).

Juvenile pink salmon diet data were split by cool and warm years into the two regions, NEBS and SEBS. Prey items were pooled into common groups and expressed as percent wet weight. Dominant prey categories included: walleye pollock (*Theragra chalcogramma*), squid and octopus, pteropod, Pacific sand lance (*Ammodytes hexapterus*), other, other fish (ofish), larvacea, euphausiid, decapoda, copepod, capelin (*Mallotus villosus*), and amphipoda. The group ‘other’ represents: cnidaria, mysida, *Evadne* sp., insecta, polychaeta, bivalvia, cumacea, haploids, and chaetognatha. The group ‘ofish’ represents: hexagrammidae, cottidae, pleuronectidae, *Pleurogrammus monopterygius*, *Gadus macrocephalus*, *Clupea pallasii*, *Lumpenus fabricii*, teleostei, and *Sebastes* sp.

We tested for differences in juvenile pink salmon lengths between cool and warm years (i.e. spring SSTs) for the NEBS and SEBS regions. In an effort to account for the effect of growth during the survey we fitted a series of length models as a function of Day of Year by region (i.e. SEBS

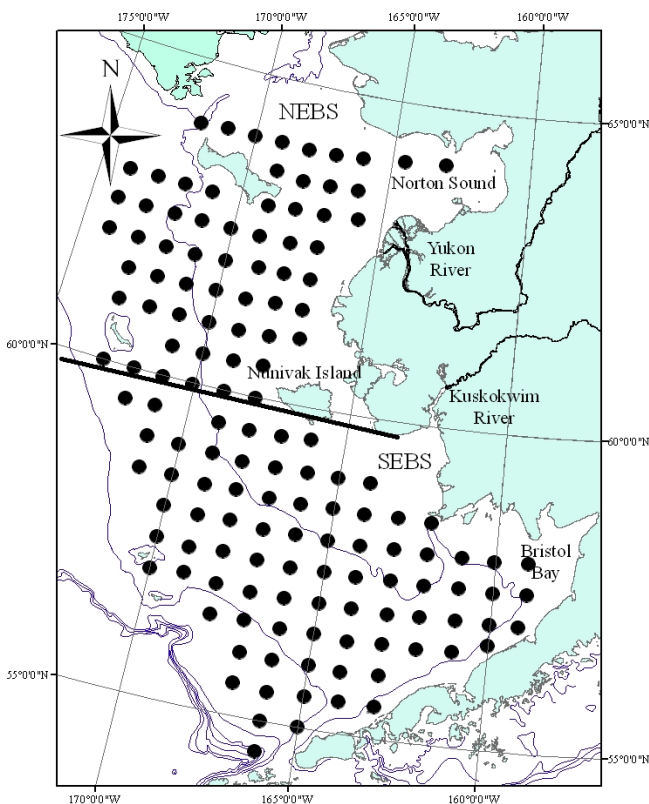


Fig. 1. Study area in the eastern Bering Sea. Solid line demarks the area where the northeastern Bering Sea (NEBS) and the southeastern Bering Sea (SEBS) were split for our statistical analyses.

and NEBS) and selected the best fitting models using F-tests and the Akaike Information Criterion (AIC) (Tables 1 and 2). The first model tested for the effect of Day of Year, the second model tested for the effect of Day of Year and spring SST, and the third model included an interaction term to test for variable slope. We evaluated whether the interaction between Day of Year and spring SST was significant to determine if the slopes were different. If the interaction term was not significant, we compared the remaining two models

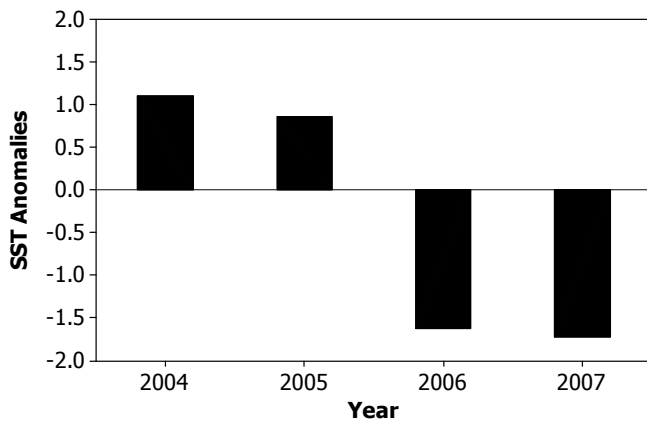


Fig. 2. Sea surface temperature anomalies based on mean May SSTs for the southeastern Bering Sea from 1948 to 2008. Mean May SSTs were averaged over the area 54°18'N to 60°00'N;161°12'W to 172°30'W using data from the NCEP/NCAR project (Kalnay et al. 1996). The SST anomalies are deviations from the mean May SST value (2.33°C) for the 1970–2000 period normalized by the S.D. (0.76°C). Warm years are represented by 2004 and 2005 while cool years are represented by 2006 and 2007.

to determine whether there was a significant difference in length between cool and warm years (spring SST effect).

Similarly, we tested for differences in total energy between cool and warm years for the NEBS and the SEBS regions. We fitted a series of three energy content models as a function of length between cool and warm years for each region (Tables 3, 4). The first model tested for the effect of length, the second model tested for the effect of length and spring SST, and the third model included an interaction term to test for variable slope. Each model was evaluated using the *p*-values and models were selected using the results of F-tests and the AIC. We used log transformed (total energy) and log transformed (length (mm)). First, we tested whether the slopes were constant by evaluating whether the interaction effect between spring SST and length was significant. If slopes were not significantly different, we compared the remaining models for the best performance. If the interaction term was significant, then differences in lengths were evaluated using an ANOVA.

RESULTS

Diet

Diets of juvenile pink salmon differed between warm and cool years in the eastern Bering Sea (Fig. 3). Walleye pollock were a major diet component in warm years and nearly absent in cool years; walleye pollock made up over 50% of the diet by wet weight of juvenile pink salmon in the SEBS during warm years. Overall, fish (i.e. walleye pollock, Pacific sand lance, capelin, and ofish) were larger compo-

Table 1. Series of models testing the effect of day of year and ocean condition on lengths in the SEBS. Model performance was evaluated using the results of F-tests and the AIC.

SEBS Fork Length Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β1	β2	β3						
M1: $y = \beta_0 + \beta_1 \cdot x_1 + \text{error}$	< 0.001			2325	1,003,564				20,727
M2: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \text{error}$	< 0.001	< 0.001		2324	855,534	M1&M2	401.9	< 0.001	20,357
M3: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \beta_3 \cdot (x_1 \cdot x_2) + \text{error}$	< 0.001	0.172	0.942	2323	855,532	M2&M3	0.005	0.942	20,359

y is fork length; *x*₁ is day of year; *x*₂ dummy variable for ocean condition; β₀, β₁, β₂, and β₃ are regression coefficients.

Table 2. Series of models testing the effect of day of year and ocean condition on lengths in the NEBS. Model performance was evaluated using the results of F-tests and the AIC.

NEBS Fork Length Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β1	β2	β3						
M4: $y = \beta_0 + \beta_1 \cdot x_1 + \text{error}$	< 0.001			2764	1,223,348				24,706
M5: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \text{error}$	< 0.001	< 0.001		2763	1,193,424	M4&M5	74.6	< 0.001	24,639
M6: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \beta_3 \cdot (x_1 \cdot x_2) + \text{error}$	< 0.001	< 0.001	< 0.001	2762	1,107,779	M5&M6	213.5	< 0.001	24,435

y is fork length; *x*₁ is day of year; *x*₂ dummy variable for ocean condition; β₀, β₁, β₂, and β₃ are regression coefficients.

Table 3. Series of models testing the effect of length and ocean condition on energy content in the SEBS. Model performance was evaluated using the results of F-tests and the AIC.

SEBS Energy Content Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β_1	β_2	β_3						
M7: $y = \beta_0 + \beta_1 x_1 + \text{error}$	< 0.001			167	0.61				-463.5
M8: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \text{error}$	< 0.001	0.003		166	0.58	M7&M8	8.94	0.003	-470.3
M9: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 x_2) + \text{error}$	< 0.001	0.116	0.093	165	0.57	M8&M9	2.86	0.093	-471.2

y is log transformed total energy content; x1 is log transformed fork length; x2 dummy variable for ocean condition; β_0 , β_1 , β_2 , and β_3 are regression coefficients.

Table 4. Series of models testing the effect of length and ocean condition on energy content in the NEBS. Model performance was evaluated using the results of F-tests and the AIC.

NEBS Energy Content Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β_1	β_2	β_3						
M10: $y = \beta_0 + \beta_1 x_1 + \text{error}$	< 0.001			120	0.45				-331.3
M11: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \text{error}$	< 0.001	0.030		119	0.43	M10&M11	4.77	0.031	-334.1
M12: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 x_2) + \text{error}$	< 0.001	0.934	0.893	118	0.43	M11&M12	0.02	0.893	-332.1

y is log transformed total energy content; x1 is log transformed fork length; x2 dummy variable for ocean condition; β_0 , β_1 , β_2 , and β_3 are regression coefficients.

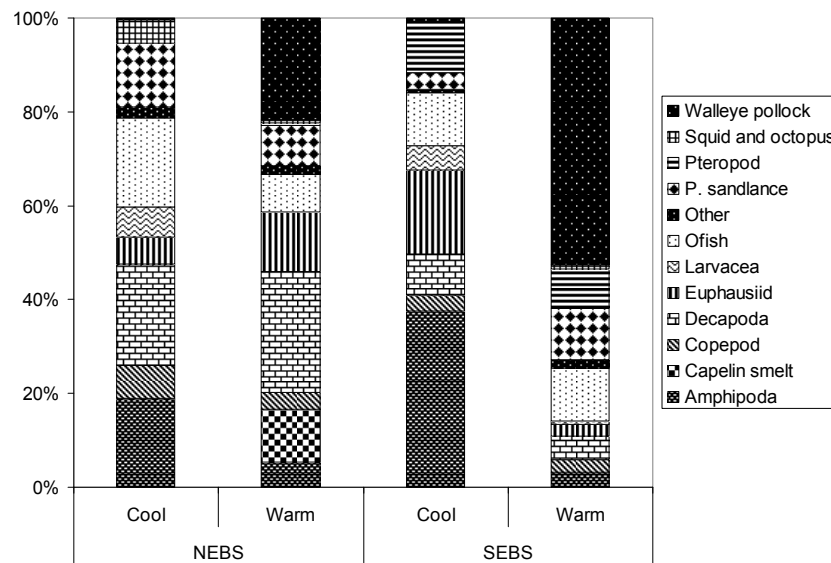


Fig. 3. Comparison of juvenile pink salmon diets in the northeastern Bering Sea (NEBS) and the southeastern Bering Sea (SEBS) during warm (2004 and 2005) and cool (2006 and 2007) years.

nents of the diet in warm years than in cool. In cool years, amphipoda, copepod, decapoda, euphausiids and larvacea comprised from 60 to 70% of the diet. Interestingly, larvacea were present in the diets during cool years and nearly absent in warm years.

Diets were also different between the NEBS and SEBS. Although amphipoda, decapoda, and copepods were important diet components in both regions, decapoda were three times higher in the NEBS. Overall, fish comprised a larger

percentage of the diet in the SEBS, with walleye pollock dominating the fish component. Capelin and squid and octopus were present in the diets in the NEBS and nearly absent in the SEBS, while pteropods were present in the SEBS and nearly absent in the NEBS.

Length Comparison

Juvenile salmon were significantly longer during the

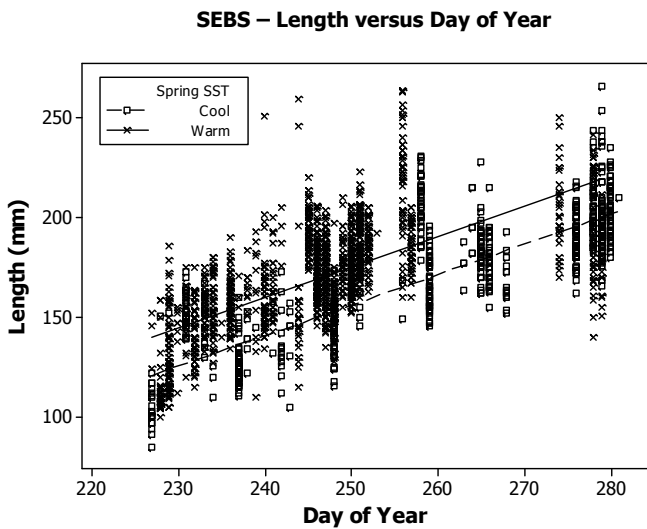


Fig. 4. Plot of juvenile pink salmon lengths versus Day of Year from fish collected in the southeastern Bering Sea (SEBS). Results of an analysis of covariance (ANCOVA) showed that on a given sampling day (Day of Year) juvenile pink salmon are significantly larger during warm years than cool years ($P < 0.01$).

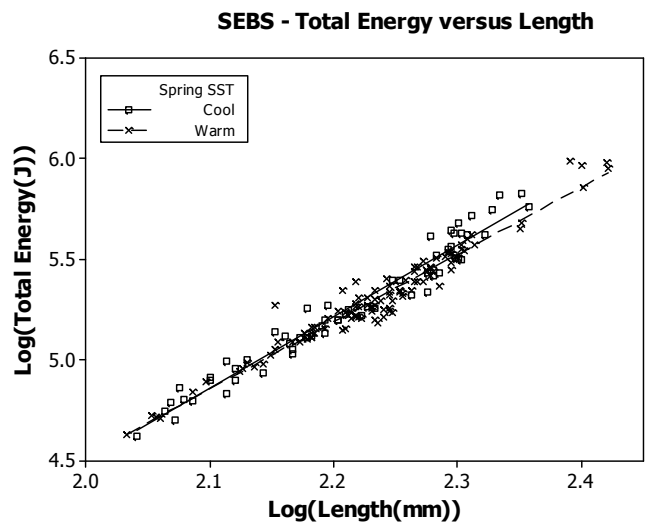


Fig. 6. Plot of log transformed (total energy (J)) versus log transformed (length (mm)) from juvenile pink salmon collected in the southeastern Bering Sea. Results of an analysis of covariance (ANCOVA) showed that total energy is significantly higher during cool years in the SEBS.

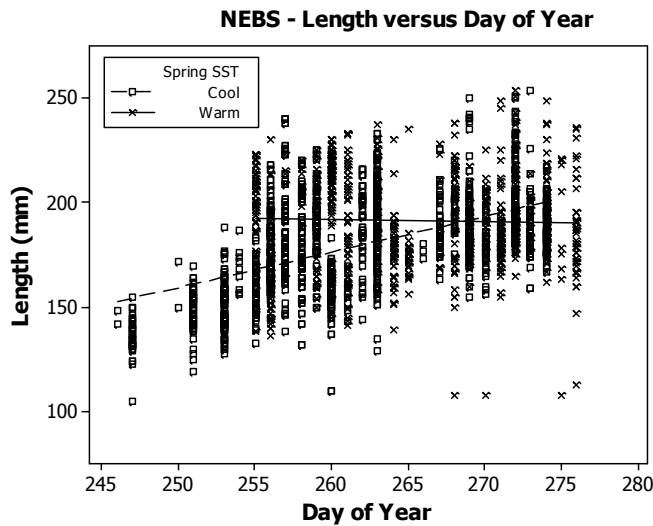


Fig. 5. Plot of juvenile pink salmon lengths versus Day of Year from fish collected in the northeastern Bering Sea (NEBS). Results of an analysis of covariance (ANCOVA) showed that there is significant interaction ($P < 0.01$) between climate and Day of Year reflecting that the slopes are different.

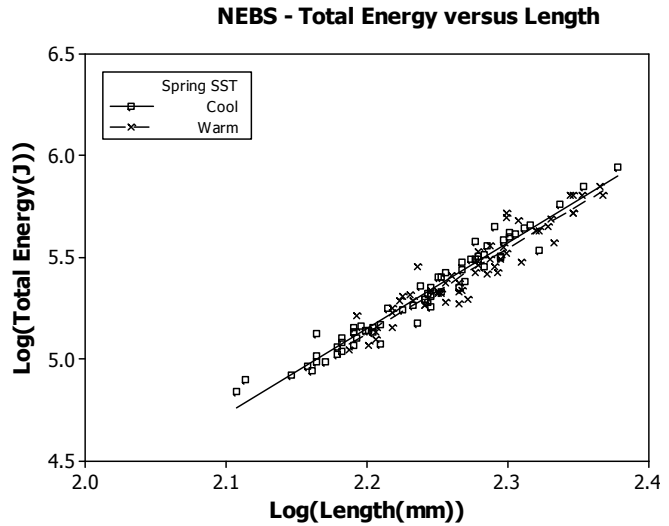


Fig. 7. Plot of log transformed (total energy (J)) versus log transformed (length (mm)) from juvenile pink salmon collected in the northeastern Bering Sea. Results of an analysis of covariance (ANCOVA) showed that total energy is significantly higher during cool years in the NEBS.

warm years in both regions. In the SEBS, we determined that the interaction term between spring SST and Day of Year was not significant (Table 1, M3: $P = 0.942$), which allowed us to assume constant slopes and to test M1 and M2 for best performance. M2 was significantly different from M1 ($P = 0.003$) and had a lower AIC value. We selected M2 which included both an effect for Day of Year and spring SST and determined that, for a given Day of Year, juvenile pink salmon were 19 mm longer in warm years (Fig. 4). In the NEBS, the interaction between spring SST and Day of

Year was significant (Table 2, M6: $P < 0.001$), indicating that the slopes were not constant (Fig. 5). This prevented us from testing for differences in lengths between cool and warm years using the general linear models. Using an analysis of variance (ANOVA), we tested for differences in lengths on a dataset that constrained the sampling days to include Day of Year between 255 and 275; this was the period of greatest overlap between cool and warm years in the NEBS. In the NEBS, we found that fish were significantly longer ($P < 0.01$) in warm years; mean length was 184.0 mm in cool

years and mean length was 191.8 mm in warm years.

Total Energy Comparison

Juvenile pink salmon had higher total energy during cool years in both the SEBS and NEBS (Figs. 6, 7). We determined that the interaction between spring SST and log transformed (length (mm)) was not significant in the SEBS (Table 3, M9: $P = 0.093$) or the NEBS (Table 4, M12: $P = 0.893$). We compared the remaining two models in each region and found similar results with M8 and M11 being the most parsimonious models. These models included a term for length as well as a term for spring SST. Spring SST was significant in the SEBS ($P = 0.003$) and the NEBS ($P = 0.030$), where fish total energy content values in cool years had consistently higher predicted values in both regions. Using the best models (i.e. M8 and M11) we calculated the predicted total energy for a 200-mm fish and determined that there is a difference of 23.0 kJ in the SEBS and 21.7 kJ in the NEBS, between cool and warm years.

DISCUSSION

Our results highlight a possible uncoupling between length and total energy content for juvenile pink salmon captured on the eastern Bering Sea shelf. Previous studies indicated that larger juvenile Pacific salmon during their first year at sea have a survival advantage over smaller conspecifics (see Farley et al. 2007). Presumably, larger juvenile salmon after their first year at sea would be better fit (higher lipid reserves) to survive their first winter at sea. This study found that juvenile pink salmon were significantly longer in warm years but, for a given size, had significantly lower total energy. Higher marine growth has been linked with higher adult salmon survival (Beamish et al. 2004; Moss et al. 2005) and higher energy reserves in some fish (Eurasian perch, *Perca fluviatilis*) are thought to be important for winter survival (Huss et al. 2008). Thus, a critical aspect of our results is what biological characteristic of juvenile pink salmon will best represent their ability to survive the first winter at sea.

On the eastern Bering Sea shelf, juvenile pink salmon were able to store more energy in cool years than in warm years. A similar study that compared age-0 walleye pollock diet, length, energy density and overwinter survival between cool and warm SST states found that age-0 walleye pollock captured during warm years were significantly larger, but had significantly lower energy density and reduced overwinter survival (Moss et al. 2009). Although more work is needed to determine the biological significance of having higher energy reserves, it may mean these fish can avoid starvation and death during their first winter at sea while fish with lower energy content cannot. Thus, studies that focus only on length as a measure of energetic status may increase the probability of incorrectly forecasting adult returns or recruitment, as over-winter mortality of juvenile fish is likely

a function of a combination of factors including energy reserves prior to winter.

Energy density of juvenile pink salmon is likely a function of prey quality, prey quantity, and temperature. Different prey items can have very different WBEC values and presumably individual prey species can have variable energy content depending on season and geographical region. Fish and squid tend to have relatively high WBEC when compared with copepods, euphausiids, hyperiid amphipods, pteropods, and larvacea (Davis et al. 1998). Juvenile pink salmon diets contain more fish in warm years and predominantly contain amphipods, copepods, decapods, euphausiids and larvacea in cool years. It appears that salmon have diets with higher energy content during warm years, yet have lower total energy. In Prince William Sound and the Gulf of Alaska, juvenile pink salmon survival and growth were positively correlated with pteropod dominated diets and high gut fullness (Armstrong et al. 2008). Pteropods have lower WBEC than many of the common diet items (Davis et al. 1998) consumed by juvenile pink salmon suggesting that perhaps prey quantity is more important than prey quality. If prey densities are insufficient during warm years on the eastern Bering Sea shelf, density-dependent factors between juvenile pink salmon and their prey could be a factor limiting WBEC. Water temperature may also play an important role in fish energy density. A laboratory study where juvenile coho salmon (*O. kisutch*) were fed *ad libitum* in two temperature treatments found that the fish in the cooler temperature treatment had higher WBEC than the fish in the warmer temperature treatment (Heintz 2009). The hypothesis for this result is that fish allocate more energy to storage when sea temperatures are cooler. Perhaps this observation helps partially explain the higher WBEC in juvenile pink salmon during the cool years.

Our findings show that juvenile pink salmon were significantly longer in warm years. However, based on the constant slopes illustrated in Fig. 4 the apparent growth rates in the SEBS were not significantly different during our sampling period. This suggests that either these fish must have had different growth rates prior to our sampling, or the outmigration timing was different. Although it is unknown what growth rates were prior to our survey it is very likely that earlier outmigration during warm years could have given these juvenile pink salmon a jump on growth that was difficult to overcome by the juveniles in the cool years. In the spring in the eastern Bering Sea, fish may be benefitting from higher pelagic productivity during years with warm SSTs, as predicted by the OCH.

Broad-scale climate changes in the Bering Sea could have far-reaching impacts on the marine ecosystem and the fisheries that it supports (Grebmeier et al. 2006; Mueter et al. 2007). The OCH describes a mechanism that may drive the flow and magnitude of primary production between the pelagic and benthic communities. In the summer and fall, juvenile pink salmon occupy the pelagic zone of the east-

ern Bering Sea and provide insights into the effects of this changing environment. The linkage between the “critical size and period” hypothesis (Beamish and Mahnken 2001) and the OCH (Hunt et al. 2002) could explain the variability of juvenile pink salmon populations as well as many other commercially important species that inhabit the eastern Bering Sea. However, the impact on survival of pink salmon being longer and leaner is unknown and will require future research on threshold requirements of WBEC during the physiologically stressful winter months.

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REFERENCES

- Armstrong, J.L., K.W. Myers, D.A. Beauchamp, N.D. Davis, R.V. Walker, J.L. Boldt, J.J. Piccolo, L.J. Haldorson, and J.H. Moss. 2008. Interannual and spatial feeding patterns of hatchery and wild juvenile pink salmon in the Gulf of Alaska in years of low and high survival. *Trans. Am. Fish. Soc.* 137: 1299–1316.
- Beamish, R.J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog. Oceanogr.* 49: 423–437.
- Beamish, R.J., C. Mahnken, and C.M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Trans. Am. Fish. Soc.* 133: 26–33.
- Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey composition. *N. Pac. Anadr. Fish Comm. Bull.* 1: 146–162. (Available at www.npafc.org).
- Farley, E.V., Jr., J.M. Murphy, B.W. Wing, J.H. Moss, and A. Middleton. 2005. Distribution, migration pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf. *Alaska Fish. Res. Bull.* 11: 15–26.
- Farley, E.V., J.M. Murphy, M. Adkison, and L. Eisner. 2007. Juvenile sockeye salmon distribution, size, condition and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf. *J. Fish Biol.* 71: 1145–1158.
- Farley, E.V., Jr., J.M. Murphy, J.H. Moss, A.M. Feldman, and L.B. Eisner. In press. Marine ecology of western Alaska juvenile salmon. *In Pacific salmon: ecology and management of western Alaska’s populations. Edited by C.C. Krueger and C.E. Zimmerman. Am. Fish. Soc. Symp.* 70.
- Grebmeier, J.M., J.E. Overland, S.E. Moore, E.V. Farley, E.C. Carmack, L.W. Cooper, K.E. Frey, J.H. Helle, F.A. McLaughlin, and S.L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. *Science* 311: 1461–1464.
- Heintz, R.A. 2009. Effects of adult salmon carcasses on the energy allocation strategies of juvenile salmonids. Doctoral dissertation. University of Alaska Fairbanks, Fairbanks, Alaska. 47 pp.
- Hunt, G.L., Jr., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II* 49: 5821–5853.
- Huss, M., P. Bystrom, A. Strand, L.O. Eriksson, and L. Persson. 2008. Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. *Can. J. Fish. Aquat. Sci.* 65: 2149–2156.
- Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, A. Leetmaa, B. Reynolds, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K.C. Mo, C. Ropelewski, J. Wang, R. Jenne, and D. Joseph. 1996. The NCEP/NCAR 40-year reanalysis project. *B. Am. Meteorol. Soc.* 77: 437–471.
- Moss, J.H., D.A. Beauchamp, A.D. Cross, K.W. Myers, E.V. Farley, J.M. Murphy, and J.H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Trans. Am. Fish. Soc.* 134: 1313–1322.
- Moss, J.H., E.V. Farley, Jr., A.M. Feldman, and J.N. Ianelli. 2009. Spatial distribution, energetic status, and food habits of eastern Bering Sea age-0 walleye pollock. *Trans. Am. Fish. Soc.* 138: 497–505.
- Mueter, F.J., J.L. Boldt, B.A. Megrey, and R.M. Peterman. 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. *Can. J. Fish. Aquat. Sci.* 64: 911–927.
- Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. *J. Fish. Res. Board Can.* 25: 757–794.
- Straty, R.R. 1974. Ecology and behavior of juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay and the eastern Bering Sea. *In Oceanography of the Bering Sea with Emphasis on Renewable Resources. Edited by D.W. Hood and E.J. Kelley. University of Alaska, Fairbanks, AK.* pp. 285–320.
- Willette, T.M., R.T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Can. J. Fish. Aquat. Sci.* 56: 364–376.