# Allometric Relationships between Body Size and Energy Density of Juvenile Chinook (*Oncorhynchus tshawytscha*) and Chum (*O. keta*) Salmon across a Latitudinal Gradient

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Abstract: Allocation of energy toward storage *versus* somatic growth by juvenile Pacific salmon during early marine residence is important because winter is a period when prey resources become scarcer, which increases the demand on energy reserves for satisfying basic physiological requirements. Energy allocation strategy differences along a latitudinal gradient may suggest counter-gradient variation in energy storage for juvenile salmon, where higher latitude populations allocate more energy to storage than growth to satisfy greater energetic demands during winter in more northerly regions relative to southerly locations. Region-specific patterns in the relationship between energy density and body size of juvenile Chinook (*Oncorhynchus tshawytscha*) and chum (*O. keta*) salmon from rivers in Oregon, Washington, and the Yukon River were investigated to identify if latitudinal position has an influence on the allometric relationship between energy density and body size. The allometric relationship between energy density and body size increased at a greater rate for both Chinook and chum salmon inhabiting higher latitudes, where longer, more severe winters occur. Juvenile Chinook had higher energy density than chum salmon across the latitudinal gradient, suggesting that energy stores may be more important for Chinook than for chum salmon. Gaining a better understanding of how spatially segregated populations of the same species are adapted to localized conditions can provide insight into how variability in environmental conditions and prey fields may act to improve or hinder growth and survival.

Keywords: Chinook salmon, chum salmon, energetic condition, over-winter survival

## INTRODUCTION

Numerous studies conducted on juvenile salmon support the concept that year-class strength is influenced by two factors, with the first being related to predation and the second to physiologically based mortality (Beamish and Mahnken 2001). Physiological mortality in juvenile salmon is believed to be a result of failing to acquire a critical body size by the end of fall (Beamish and Mahnken 2001; Moss et al. 2005; Farley et al. 2007), because winter is an energetically taxing time for salmon (Walker et al. 2013). Interannual variability in ocean conditions can affect the availability and quality of prey resources (Gladics et al. 2014), which may in turn influence the amount of growth and energy stores acquired during the first growing season. Regional differences in the timing and magnitude of primary and secondary production in the ocean can also affect growth (Ferriss et al. 2014) and survival (Brosnan et al. 2014), and may potentially influence the phenology of stocks inhabiting a particular region.

Countergradient variation is the variability in morphological or physiological traits between distinct populations that span an environmental gradient (Marcil et al. 2006; Conover and Present 1990; Conover et al. 2009). It is a response to environmental conditions (Mogensen and Post 2012; Hurst and Conover 2003) that describes how fish may be adapted to local conditions in order to maximize survival. Post and Parkinson (2001) observed that smaller juvenile fish at higher latitudes exhibited higher survival when energy was allocated primarily to somatic growth, while survival was comparable for intermediate sized fish whether they allocated energy toward somatic growth or lipid deposition. However, Post and Parkinson (2001) observed that relatively small fish which allocated most of their energy to lipid stores late in the growing season also experienced higher survival rates. It is believed that lipid stores are important for over-winter survival because food availability decreases while physiological stressors increase during winter (Beamish and Mahnken 2001). Therefore, greater energy stores may be beneficial for fish inhabiting

regions where winter is more severe (Mogensen and Post 2012; Conover et al. 2009).

We investigated differences in the allometric relationships between body size and energy density for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and juvenile chum salmon (*O. keta*) inhabiting the northern Bering Sea (NBS) and the eastern Gulf of Alaska (GOA). The NBS is characterized by long, severe winters and a short growing season; whereas the GOA has shorter, less severe winters and a longer growing season. We hypothesize that juvenile salmon inhabiting large marine ecosystems at higher latitudes allocate more energy to lipid stores at a smaller body size relative to those inhabiting lower latitudes, as a provisionary response to survive colder, longer winters. Gaining a better understanding how populations of Chinook and chum salmon that inhabit the northern versus southern regions of their range may respond to a spectrum of biophysical conditions is key to understanding how these species may be affected by changing ocean conditions.

## MATERIALS AND METHODS

### Specimen Collection

Juvenile Chinook and chum salmon were collected in the GOA and NBS aboard a chartered fishing vessel using a 198-m-long mid-water rope trawl with hexagonal mesh wings and body and a 1.2-cm mesh liner in the codend. The trawl was configured with three 60-m bridles (top, middle, and bottom) connecting the trawl to two steel alloy 5-m trawl doors. The mouth opening of the net had a horizontal spread ranging from 20 to 30 m and had a vertical spread ranging from 20 to 45 m. The head rope of the trawl was fitted with buoys in order for it to be towed at or near the surface. Each tow was conducted at a rate of 3.5–5.0 kn and the tow speed was adjusted to keep the trawl at the surface and the trawl doors in the water. All tows were 30 minutes in duration.

Surveys in the GOA were conducted during the month of July 2010–2014 and surveys in the NBS were conducted during the month of September 2003–2013. Juvenile Chinook and chum salmon sampled in the GOA during July were similar in size to those sampled in the NBS during September. Thus, we believed it was appropriate to make comparisons across populations and regions despite a 2-month difference in collection timing. Fishes collected by the trawl were sorted by species and age, counted, and measured on deck at each survey station (Fig. 1). Biological measurements on specimens included body weight (g) and fork length (tip of the snout to the fork of the tail, mm) for up to 50 individuals of each species. When more than 50 fish were captured at a station, excess fish were counted, weighed in bulk, and an average weight was calculated from the bulk sample. Two Chinook and two chum salmon were randomly selected and bagged whole for energy density analysis and up to 10 additional specimens of both species were randomly selected for diet analysis. These fish were frozen whole and transported to the Auke Bay Laboratories in Juneau, Alaska and processed within 8 months of the survey.

### Stock Identification

The stock of origin for juvenile Chinook salmon sampled in the NBS survey was determined by a combination of coded-wire tag recoveries and single nucleotide polymorphism (SNP) genetic markers. Coded-wire tags were assigned to freshwater origin using the Pacific States Marine Fisheries Commission coast-wide mark database (www. rmpc.org/). Nearly all Chinook salmon belonged to Yukon River stocks, including 45% upper Yukon River (Canadi-
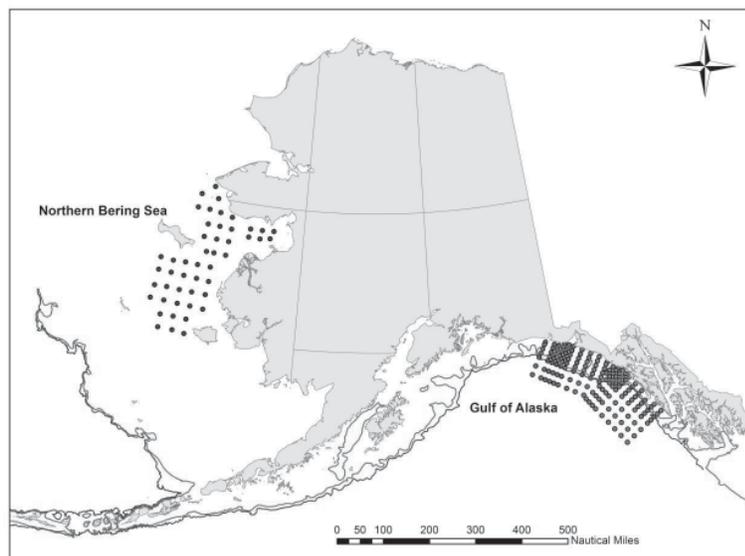


**Fig. 1.** Survey station locations for the Northern Bering Sea and Gulf of Alaska trawl surveys.

**Table 1.** Results from Analysis of Covariance (ANCOVA) on the relationship between body size and energy density for juvenile Chinook and chum salmon inhabiting the northern Bering Sea (NBS) and Gulf of Alaska (GOA). Statistical significance denoted by *.

| Location | Species | Parameter | Value | Std. error | *t*-value | *p*-value |
|----------|---------|-----------|-------|------------|-----------|-----------|
| NBS | Chinook | Intercept | 19.2 | 0.077 | 255.0 | 0.000* |
| GOA | Chinook | Intercept | 21.1 | 0.122 | 172.8 | 0.000* |
| NBS | Chinook | Slope | 0.020 | 0.001 | 25.4 | 0.000* |
| GOA | Chinook | Slope | 0.003 | 0.001 | 7.0 | 0.000* |
| NBS | Chum | Intercept | 19.6 | 0.206 | 95.1 | 0.000* |
| GOA | Chum | Intercept | 20.5 | 0.153 | 135.1 | 0.000* |
| NBS | Chum | Slope | 0.040 | 0.003 | 12.4 | 0.000* |
| GOA | Chum | Slope | 0.014 | 0.002 | 7.5 | 0.000* |

an) and 55% middle and lower Yukon River Stocks (U.S.) (Murphy et al. 2009; JTC 2015). The stock of origin for juvenile Chinook salmon sampled in the GOA surveys were based solely on coded-wire tag recoveries, which estimated that 90% of these fish belong to Oregon and Washington stocks with 10% belonging to southeast Alaska and British Columbia stocks (Celewycz et al. 2012). Juvenile chum salmon captured in the NBS were assumed to be western Alaska stocks based on stock mixture proportions estimated by Kondzela et al. (2009). Juvenile chum salmon captured the GOA were assumed to be from southeast Alaskan stocks (W. Templin, bill.templin@alaska.gov, pers. comm.).

**Sample Processing**

Juvenile Chinook and chum salmon were thawed in the laboratory and whole body wet weight measured to the nearest 0.0001g. Stomach contents were removed and the stomach lining returned to body cavity. Two Chinook and two chum salmon collected from each station were individually dried in a thermogravimetric analyzer until no change in body weight was detected, which indicated that the carcass was devoid of moisture. Fish were then ground into a fine homogenate using a mortar and pestle. Homogenous tissue was pressed into a pellet weighing 0.1–0.2 g and measured to the nearest 0.0001 g. A Parr Instruments (Moline, IL, USA) 6725 Semimicro Calorimeter was used to measure the energy released upon combustion of each sample which was then converted to wet weight energy density of the sample. A reference material (benzoic acid standard) and duplicate tissue samples were used to evaluate the precision of the machine.

Stomach contents for up to 10 fish per station were removed from the stomach cavity, pooled, and stored in 10% formalin until diet analysis. Diet analyses was performed on preserved prey items that were sorted into general taxonomic groups using a dissecting scope. These groups included: euphausiids, copepods, amphipods, gastropods, decapods, fish, and miscellaneous prey. Each prey group was weighed and reported as a percentage of the entire food bolus weight.

**Statistical Analysis**

Analysis of covariance (ANCOVA) was used to identify differences in the relationship between body weight and energy density for juvenile Chinook and chum salmon inhabiting the NBS and the GOA. Three linear models were evaluated for each species. The first model had a total of four parameters (full model), which included factors for slope and intercept for each region. The second and third models had three parameters. The second model had a common intercept for both regions and separate factors for slope for each region, and the third model had a common slope for each region but a different intercept for each region. Mallow's Cp statistic was used to assess the best least squares fit and the model having the lowest Cp statistic was determined to have the best fit to the data.

**RESULTS**

**Allometric Relationship between Body Weight and Energy Density**

The most parsimonious model for Chinook salmon was the full model (4 parameters) which included factors for slope and intercept for each region (Cp = 446.9). Cp statistics for the 3-parameter models were higher. The model with a common intercept for both regions and separate factors for slope had a Cp = 490.7 and the model with a common slope and separate factors for intercepts had a Cp = 575.5. The most parsimonious model for chum salmon was also the model that included separate factors for slope and intercept for each region (Cp = 142.6). The model with a common intercept for both regions and separate factors for slope had a Cp statistic = 146.8 and the model with a common slope and separate factors for the intercepts had a Cp statistic = 163.6.

All coefficients for Chinook and chum salmon models were highly significant ($p < 0.001$; Table 1). There was a greater difference in the intercept values for Chinook (GOA = 21.1, NBS = 19.5) relative to chum salmon (GOA = 20.5,
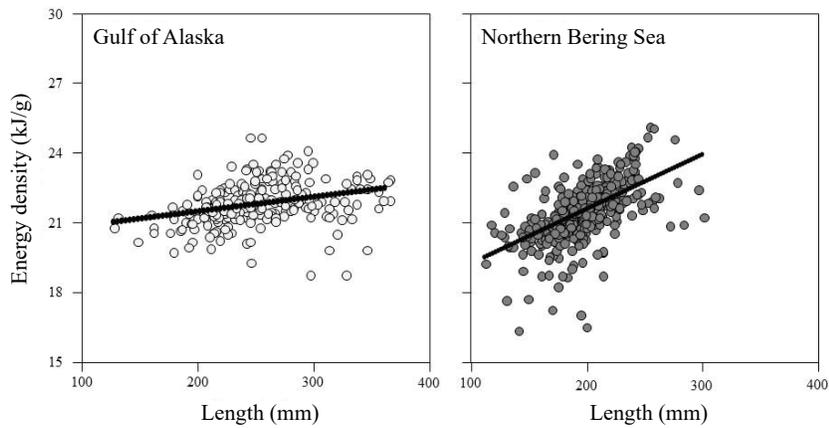
**Fig. 2.** Allometric relationship between energy density (kJ/g) and body size (g) for juvenile Chinook salmon inhabiting the Gulf of Alaska and northern Bering Sea during late summer and early fall.

NBS = 19.6).  A greater difference in the intercepts for Chinook salmon was likely due to a broader range in body size of Chinook relative to chum salmon, and less power to distinguish ecological differences between the intercepts of Chinook salmon by region.

The slope for Chinook salmon inhabiting the NBS was greater than for those inhabiting the GOA (Fig. 2) with the rate of change in energy density per gram body weight greater by a factor of 4.2 for juveniles inhabiting the NBS relative to the GOA (Table 1).  The slope for chum salmon inhabiting the NBS was also steeper (Fig. 3), with energy stores being accumulated by a factor of 2.7 times faster relative to those inhabiting GOA.  Chinook and chum salmon were not significantly longer and heavier in the GOA relative to those inhabiting the NBS (Table 2).

**Regional Differences in Diet Composition**

A large proportion of the prey consumed by Chinook salmon was fish.  Fish prey accounted for 87.5% of the diet by weight for Chinook salmon inhabiting the NBS and 46.8%

by weight for those inhabiting the GOA (Fig. 4).  Age-0 capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes hexapterus*) were the most common fishes consumed in the NBS, accounting for 42.0% and 20.5%, respectively (Fig. 4).  A large proportion of the fish prey in the diets of Chinook salmon inhabiting the GOA were too digested to identify to the species level, however, the largest proportion of identifiable fish prey was capelin, which accounted for 12.0% of the diet by weight (Fig. 4).  Chum salmon in the NBS and GOA fed largely upon zooplankton (Fig. 5).  Hyperiid amphipods comprised the largest proportion of prey in the diet of chum salmon inhabiting the NBS (37.0%) and large calanoid copepods comprised the largest proportion of those inhabiting the GOA (30.5%; Fig. 5).

**DISCUSSION**

Energy density reflects the amount of lipid stores in somatic tissue (Heintz et al. 2013), and comparing energy density differences of the same species and size range along
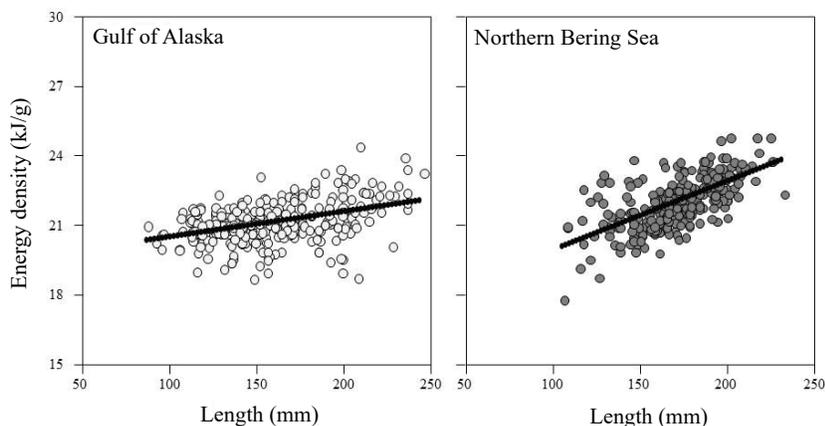


**Fig. 3.** Allometric relationship between energy density (kJ/g) and body size (g) for juvenile chum salmon inhabiting the Gulf of Alaska and northern Bering Sea during late summer and early fall.

**Table 2.** The average body size in fork length (mm) and weight (g), and energy density (kJ/g) for juvenile Chinook and chum salmon inhabiting the northern Bering Sea (NBS) and Gulf of Alaska (GOA).

| Location | Species | Average | | | Standard deviation | | |
|---|---|---|---|---|---|---|---|
| | | Length | Weight | kJ/g | Length | Weight | kJ/g |
| NBS | Chinook | 194 | 110.3 | 21.5 | 28.9 | 51.2 | 1.2 |
| GOA | Chinook | 240 | 226.3 | 21.8 | 37.6 | 91.0 | 0.8 |
| NBS | Chum | 177 | 63.3 | 22.0 | 16.1 | 19.2 | 1.0 |
| GOA | Chum | 182 | 79.2 | 21.5 | 23.1 | 32.2 | 0.9 |

a latitudinal gradient can potentially reveal differences in the energetic requirements of individuals inhabiting more northerly versus southerly ecosystems. Juvenile Chinook and chum salmon inhabiting the NBS had greater energy stores than those inhabiting the GOA suggesting that individuals inhabiting more northern latitudes may require greater lipid stores to survive in winter. Winters in the Bering Sea are longer and more extreme than those in the GOA (Stabeno et al. 2010, 2016). Most western Alaska Chinook salmon stocks spend their first winter in the Bering Sea whereas the majority of stocks from Oregon, Washington, British Columbia, and Southeast Alaska spend their first winter in the Gulf of Alaska (Myers et al. 2009). Therefore, it is likely that individuals inhabiting the NBS during summer were storing energy at a greater rate to offset future energy demands during winter. Previous investigations had not identified a consistent trend in energy accumulation with latitude for juvenile Chinook salmon, but hypothesized that regional differences in energy allocation were due to localized environmental differences (Trudel et al. 2007). However, despite no apparent relationship between energy accumulations with latitude, there was an increase in growth rate with latitude.

This pattern was true for all regions investigated with the exception of the southeastern Bering Sea, which exhibited higher growth rates than those in the NBS (Trudel et al. 2007).

Energy stores increased at a greater rate for Chinook than for chum salmon in the NBS, and the difference between the rates at which chum accumulated energy in the NBS versus the GOA was much less than for Chinook salmon. This decrease may be a response to requiring fewer energy stores by western Alaska juvenile chum salmon because a large proportion of them overwinter in the Gulf of Alaska (Fredin et al. 1977), where winter is shorter and less extreme. However, differences in the slopes and intercepts of the models representing the allometric relationship between energy accumulation and body size for either species may have been influenced by ecological processes or other factors not accounted for by the models.

These factors might include, but not be limited to, a high proportion of hatchery fish in the GOA that may have been larger relative to individuals inhabiting northern latitudes, which are mostly wild western Alaska stocks. The smallest Chinook and chum salmon inhabiting northern lat-
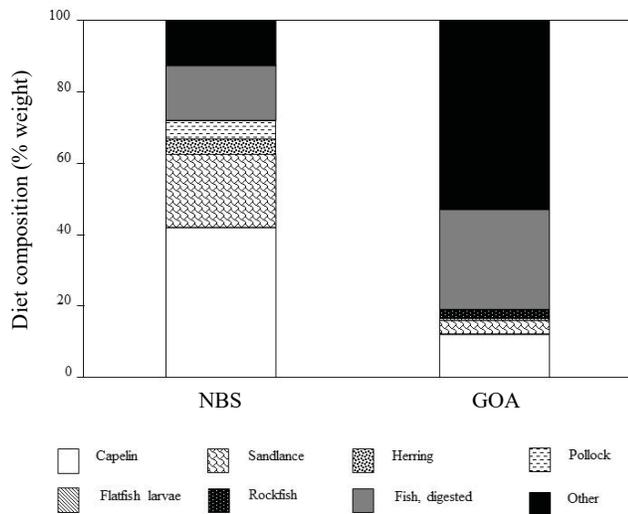


**Fig. 4.** Proportional contribution of prey in the diet by weight for juvenile Chinook salmon inhabiting the northern Bering Sea (NBS) and Gulf of Alaska (GOA) during 2004–2011. Figure created from information from Murphy et al. (2013).
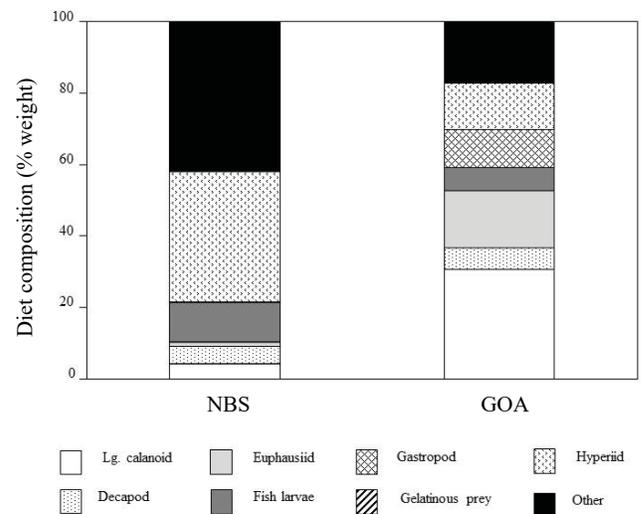


**Fig. 5.** Proportional contribution of prey by weight in the diet of juvenile chum salmon inhabiting the northern Bering Sea (NBS) and Gulf of Alaska (GOA) during 2011–2013.

itudes had slightly lower, and more highly variable energy density relative to those in more southern latitudes. This may have been due to environmental conditions or some other unidentified limiting factor(s). However, these fish may be destined to perish given that they are small and have low energy reserves to survive the winter. Juvenile Chinook and chum salmon sampled in the eastern GOA during July were within the same size range as those sampled in the NBS during September. However, a two-month time difference in sample collection timing may have confounded the true differences in size and energy density between populations. Previous studies have shown that energy is allocated toward somatic growth by young salmon inhabiting fresh water and marine waters during summer, with energy being used for somatic growth to presumably escape gape-limited predators; and energy used for lipid accumulation at the end of the summer before fall to presumably survive a period of food shortage (Biro et al. 2005; MacFarlane 2010). Similar processes are apparent in striped bass (Hurst and Conover 2003) and other species (Schultz and Conover 1997). A seasonal effect of greater lipid accumulation in response to winter may have been confounded with a regional effect of greater lipid accumulation at higher latitudes. Potential mechanisms influencing seasonal effects may be a decrease in photoperiod or temperature. Juvenile Chinook salmon from both regions are presumably increasing lipid stores as they grow in addition to increasing lipid stores as summer transitions into autumn. Therefore, despite a similar body size in the NBS and GOA, the seasonal effect may have influenced lipid storage, which was not accounted for in our models. Unfortunately such an effect could not be examined due to the difference in sample collection timing between regions.

Size-selective mortality exists for NBS juvenile Chinook salmon (Howard et al. 2016), which will also influence early marine survival. Therefore, accelerated growth is also important for juvenile Chinook salmon inhabiting the NBS. Larger fish are more capable of feeding on larger nekton prey. Juvenile Chinook primarily preyed upon sandlance and capelin in the NBS, while Pacific herring (*Clupea pallasii*) comprised a small proportion of the overall diet. Juvenile Chinook salmon are able to prey on all size ranges of age-0 capelin, but they are only able to capture and consume a portion of the age-0 year class of Pacific herring due to gape width limitation (Murphy et al. 2013). Increased growth rate and achieving an overall larger body size by early fall would increase the amount of age-0 Pacific herring that could be available to Chinook salmon, which could be important during years when age-0 capelin and sandlance abundance is low.

A balance must be struck between allocating energy to somatic body growth to increase the capacity for energy storage and sheltering against predation versus energy storage for periods when food availability is scarce (Heintz and Vollenweider 2010). Larger fish generally have a lower weight-specific metabolic rate than smaller fish (Brett 1970), and thus, acquiring a larger size may be a way to reduce

their overall energy demands, which may off-set lower lipid reserves. Juvenile Chinook salmon captured in the NBS in September were smaller on average than juvenile Chinook salmon captured in the GOA during July. Juvenile Yukon River Chinook stocks are typically located within the Yukon River delta and estuary where they feed primarily on insects and small copepods (K. Miller, katharine.miller@noaa.gov, pers. comm.). Thus, juvenile Chinook salmon from Washington and Oregon were presumably larger than those emigrating from the Yukon River during the month of September. Most of the juvenile Chinook salmon captured in the coastal GOA during summer months are of hatchery origin (Tucker et al 2011; Tucker et al. 2012) and are likely larger than their wild conspecifics, which may also partly explain the larger in size in the GOA. Washington and Oregon stocks may have also begun to allocate more energy toward lipid storage by September as well. Thus, there is a possibility that the observed differences may have been partially due to season and not entirely to latitude.

An alternative explanation to higher energy reserve storage in the NBS is that food quality, specifically the amount of lipid in the prey, in the NBS latitudes is greater than in the GOA. Juvenile chum salmon fed on zooplankton in both the NBS and GOA, but large calanoid copepods and euphausiids were fed upon most heavily in the GOA. Amphipods comprised the greatest proportion of the diet in the NBS. A more energetically rich prey field in northerly latitudes would give juvenile salmon a greater advantage to store lipid. Juvenile chum salmon inhabiting Kuskokwim Bay experienced a decrease in energy density with size, suggesting they were allocating more of their energy toward somatic tissue growth (Burril 2007) that may result from increasing water temperatures and energy demands not balanced by food supply as the season progressed (Hillgruber and Zimmerman 2009). However, more information is needed on the seasonal and regional differences in the energetic content of prey and effect of water temperature differences in the NBS and GOA to make such a determination.

## ACKNOWLEDGMENTS

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