2014 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Project Final Product[1]

Yukon River Juvenile Chinook Salmon Survey

by:

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INTRODUCTION

Significant harvest restrictions, including the closure of commercial fisheries and reductions in subsistence fisheries, have been implemented in response to declining production levels of Yukon River Chinook salmon stocks (Evenson et al. 2009). Although causes of their production decline are unclear, concurrent declines throughout the drainage (Schindler et al. 2013), production declines in other regions of Alaska (ADFG 2013), and the presence of bycatch in marine fisheries (Stram and Ianelli 2009) have placed emphasis on ocean conditions and the marine life-history stage of Chinook salmon.

Juvenile research directed at improving pre-season forecasts and our understanding of mechanisms impacting survival will help provide insight in the underlying production dynamics of Yukon River Chinook salmon. Juvenile research has provided unique insight into juvenile marine ecology and critical periods in the production of juvenile salmon (Orsi et al. 2000, Beamish and Mahnken 2001, Brodeur et al. 2003, Farley et al. 2007, Moss et al. 2009, Wertheimer et al. 2010, Miller et al. 2013). Stock origin is an important component of Chinook salmon in marine habitats due to their highly migratory behavior and is a key linkage between juvenile and adult population of Chinook salmon. Coded-wire tags and genetic stock structure are the two primary sources of stock origin for juvenile Chinook salmon (Teel 2003, Trudel et al. 2003, Fisher et al. 2007, Murphy et al. 2009, Templin et al. 2011a). Size-selective mortality and diet are important ecological features of the juvenile life-history stage of salmon that link ecosystem processes to salmon production dynamics (Healey 1982, Sogard 1997, Moss et al. 2005, Farley et al. 2007, Cross et al. 2009, Miller et al. 2013).

This report summarizes the research conducted as part of the Yukon River Juvenile Chinook Survey. The primary goals of this project were to support the 2011 pelagic trawl research survey in the northern Bering Sea and to provide a broad overview of the marine ecology of juvenile Chinook salmon in the northern Bering Sea to help provide a framework for evaluating causes of production declines in Yukon River Chinook salmon.

The proposed research included the following objectives:
1. Incorporate stock- and age-structure information into a juvenile abundance index for Yukon River Chinook salmon and define the relationship between juvenile abundance,

adult returns, and spawner abundance for Yukon River Chinook salmon (2002-2011 juvenile years).

2. Estimate the Chinook salmon stock mixtures present in the northern region of the eastern Bering Sea shelf (2002-2011 juvenile years).

3. Assess the energetic status of juvenile Yukon River Chinook salmon (2011).

4. Describe the distribution and abundance patterns of key forage fish species utilized by Chinook salmon in the northern region of the eastern Bering Sea shelf (2011).

5. Identify ecosystem indicators related to juvenile abundance and fitness for Yukon River Chinook salmon (2002-2011).

The following changes to the proposed objectives were made. Estimates of juvenile age-structure were not included with objective 1 due to complications associated with obtaining reliable age estimates from juvenile scale collections. Abundance estimates were not included for 2002 due to the different trawl gear used in 2002. Stock mixtures in 2002 were also not included. Objective 3 was broaden to address the general nutritional status of juvenile Yukon River Chinook salmon and a size-selective mortality model was developed, and the thiamine status of Yukon River juvenile Chinook salmon was explored. Funding support for the additional analyses included in objective 3 was provided by the project funds. Due to budget timing issues, it was not possible to purchase a new trawl in time for the 2011 survey with project funds. Subsequently, these project funds were redirected to expand the scope of objective 3. The proposed objectives are address in the following sections in this report:

1. Northern Bering Sea Coastal Habitat,
2. Northern Bering Sea Surface Trawl Surveys,
3. Juvenile And Adult Abundance
4. Juvenile Distribution and Temperature,
5. Size-Selective Mortality and Energy Density,
6. Juvenile Diet, Prey, and Thiamine.

Extended abstracts reported as part of the International Workshop on Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystem, April 25-26, 2013 are included as appendices. These abstracts address juvenile Chinook salmon abundance and survival (Murphy et al. 2013) (Appendix 1), marine habitat and juvenile salmon in the northern Bering Sea

(Gann et al. 2013) (Appendix 2), and juvenile salmon diets in the northern Bering Sea (Cook and Sturdevant 2013) (Appendix 3). Additional appendices include a preliminary review of the early marine ecology of juvenile Chinook salmon in the northern Bering Sea provided to the AYKSSI Chinook salmon expert panel in 2012 (Murphy et al. 2012) (Appendix 4), and a draft manuscript on the thiamine status of Yukon River Chinook salmon (Honeyfield et al. In Prep) (Appendix 5).

METHODS

Northern Bering Sea Coastal Habitat

The northern Bering Sea shelf is a shallow, vertically mixed coastal ecosystem. Significant freshwater inputs from the Yukon River and other major river tributaries in western Alaska produce result in warm, turbid, and low salinity habitats throughout much of the coastal region of the northern Bering Sea, which drives northward flowing currents along the coast (Gann et al. 2013) (Appendix 2). Surface and bottom temperatures decrease with distance from shore and nearshore temperature are typically in the range of 7-10 degrees C at the surface during the summer growing season for juvenile salmon (Figures 1 and 2). Salinities increase with distance from shore and nearshore salinities can range from a low of 20 PSU in inner Norton Sound to approximately 32 PSU in offshore habitats. Bottom temperatures are generally significantly lower than the surface, with subzero bottom temperatures (eastern Bering Sea cold pool) present in offshore habitats. The Yukon River and the shallow habitats of the Yukon River Delta have high turbidity levels (Figure 3). Northward advection of turbid waters of the Yukon River plume is evident in satellite images of the northern Bering Sea (Figure 4), and is consistent with the general northward flow of coastal currents in the northern Bering Sea (Figure 5). Coastal habitats of the northern Bering Sea are generally nitrogen limited with heavy or enriched nitrogen isotopes resulting from nitrogen recycling within the marine food web (Schell et al. 1998). Timing of ice break up on the Yukon River is variable, but has typically occurred between the 21st and 26th of May in recent years (Figure 6). Winter sea ice begins to form in nearshore regions of the northern Bering Sea in November and by January the entire shelf is covered with sea ice (Figure 7). The residence period of juvenile Chinook in the northern Bering Sea is believed to be limited to 4-5 months and defined by the time period between ice break up in the Yukon River and winter ice formation in the Bering Sea (Figure 8).
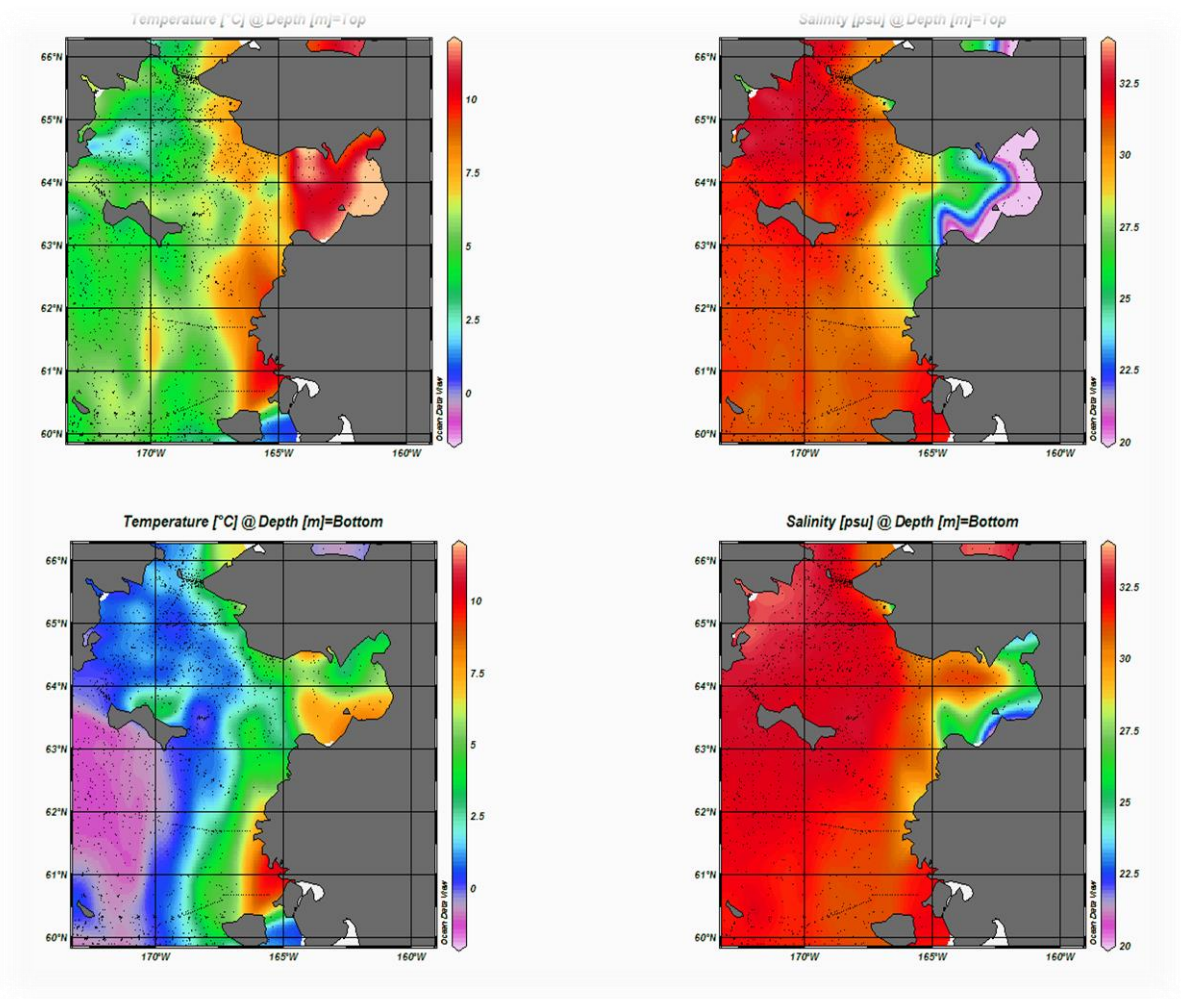
Figure 1. Surface and bottom temperature of the northern Bering Sea (May-July) (Gann et al. 2013).
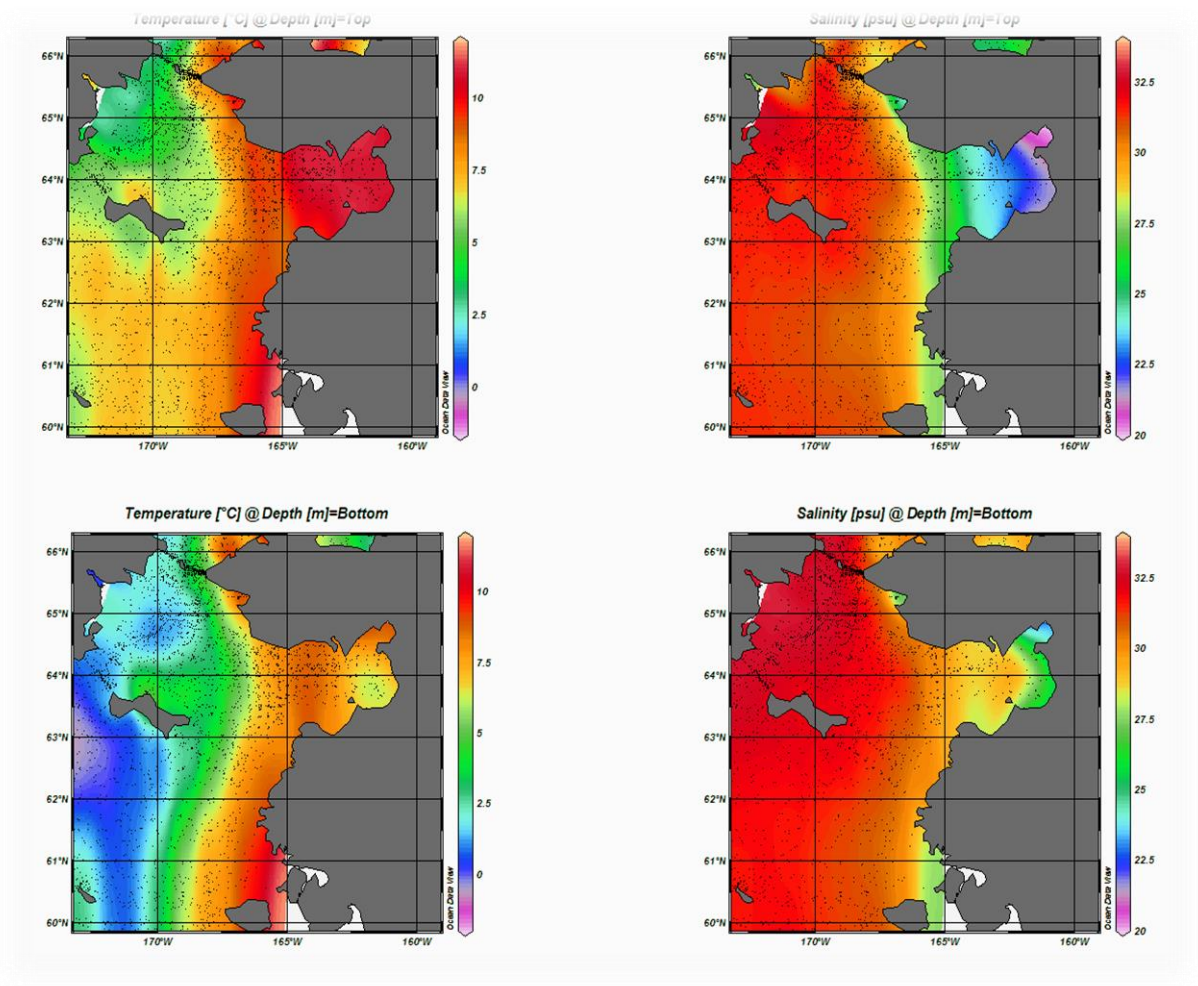
Figure 2. Surface and bottom temperatures of the northern Bering Sea (August-October) (Gann et al. 2013).

Figure 4. A natural color satellite image of the Yukon River delta from the NASA Earth Observing System (EOS) Landsat 7 satellite on September 22, 2002. The complex network of stream and channels of the Yukon River and the high turbidity of the Yukon River Delta is clearly shown in this image. This image was made available by Jesse Allen and Robert Simmon of the United States Geological Survey (image available at http://visibleearth.nasa.gov/view.php?id=72762).

Figure 3. A natural color satellite image of the northern Bering Sea from the NASA Earth Observatory System (EOS) Land Atmosphere Near Real-time Capability (LANCE) AQUA satellite on August 8, 2012. The image shows the high turbidity of nearshore marine habitats of the Yukon River and the northward displacement of the Yukon River plume (turbid, low salinity water). Turbid water of the Yukon River and its three primary outlets: south mouth (primary discharge), middle mouth, and north mouth, are shown in the image. The Yukon River plume is present throughout much of the southern half of Norton Sound (the embayment just north of the Yukon River), and extends north into the Bering Strait region just offshore of Norton Sound. This Image was made available by the Land Atmosphere Near-real time Capability for EOS (LANCE) system operated by the NASA/GSFC Earth Science Data and Information System (ESDIS) with funding provided by NASA/HQ.
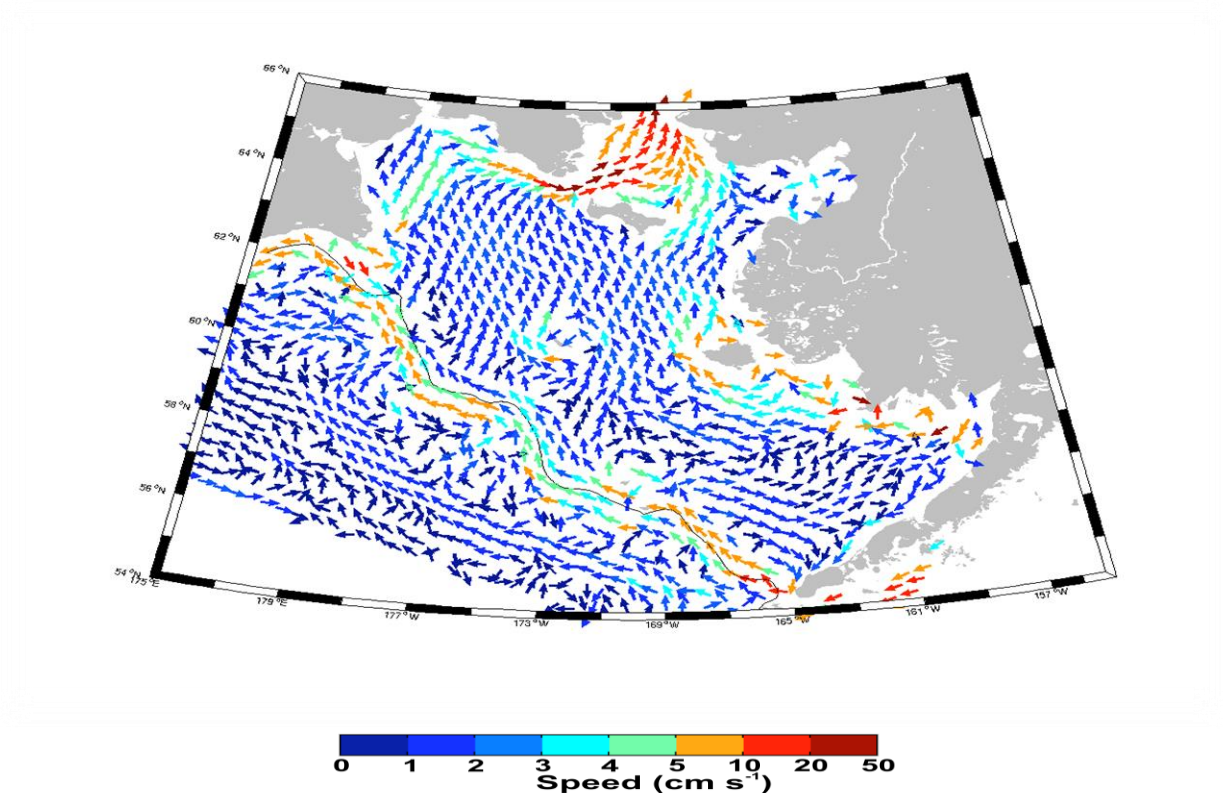
Figure 5. Average surface currents in the eastern Bering Sea (1987-2007) (Gann et al. 2013).
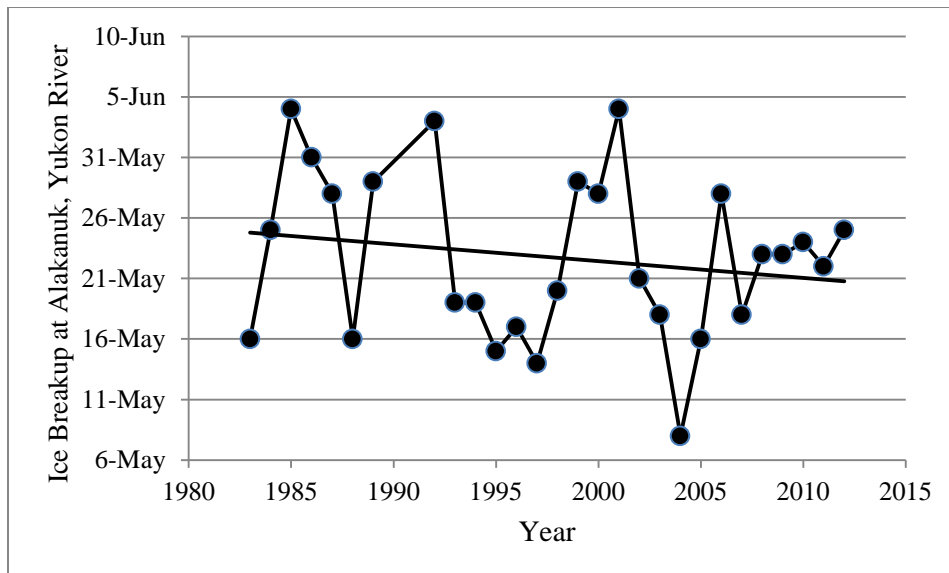
Figure 6. Date of ice breakup at Alakanuk, Yukon River by year. Data provided by the National Weather Service, Alaska-Pacific River Forecast Center (http://aprfc.arh.noaa.gov/php/brkup/getbrkup.php?riverbasin=Yukon&river=Yukon+River).
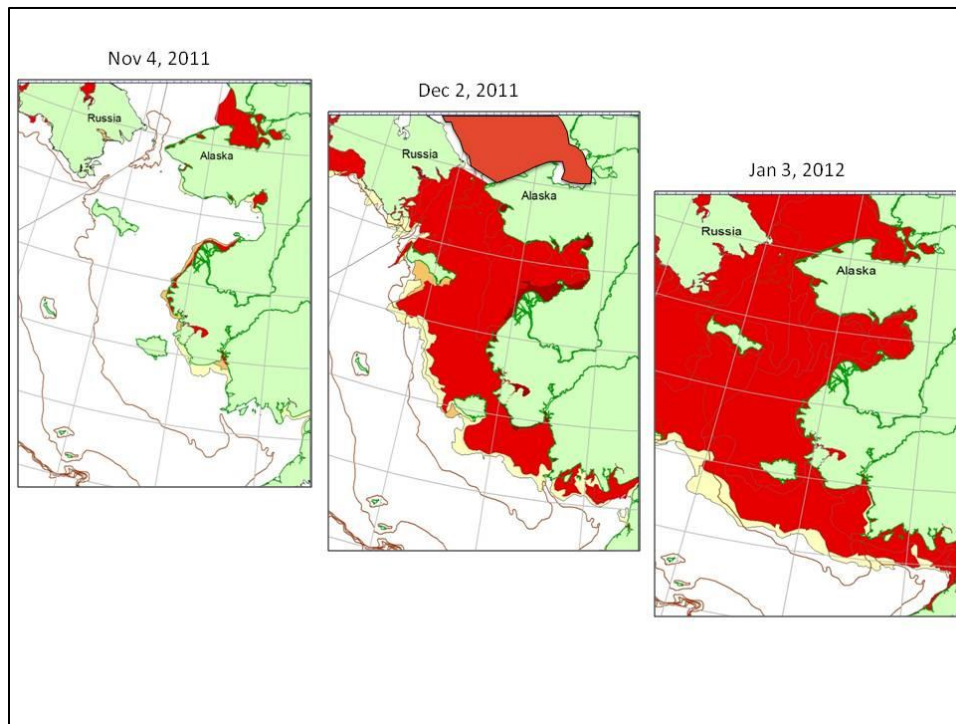
Figure 7. Sea ice cover in the northern Bering Sea during 2011-2012 winter season. Sea ice begins to form in low salinity nearshore habitats in November; sea ice covers nearly all water depths less than 50m by early December; and the entire northern Bering Shelf is covered in sea ice by early January. Data are provided by the National Ice Center's Bi-Weekly sea ice analysis for Alaska waters.
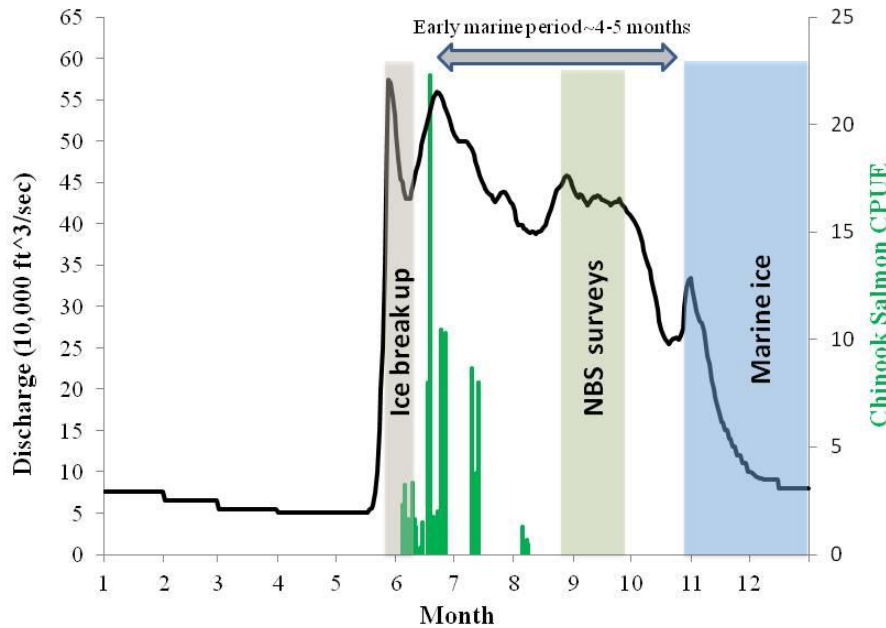
Figure 8. Yukon River discharge, timing of breakup, timing of the northern Bering Sea (NBS) marine survey, and timing of winter sea ice formation in relation to juvenile Chinook salmon catches at the mouth of the Yukon River. Green bars identify the daily CPUE (catch per km^2) of juvenile Chinook at the mouth of the Yukon River and the black line is the Yukon River discharge in 10,000 ft^3/sec at Pilot Station during 1986. Discharge data is provided by the National Weather Service, Alaska-Pacific River Forecast Center. CPUE data are from the south mouth of the Yukon River during smolt studies in 1986 (Martin et al. 1987).

Northern Bering Sea Surface Trawl Surveys

Surface trawl surveys have been conducted by NOAA in the northern Bering Sea since the start of the Bering-Aleutian Salmon International Survey (BASIS) research program in 2002 (NPAFC 2001). Although the focus of the BASIS research program was on the ocean ecology of salmon, surface trawl research surveys have expanded to include marine ecosystem research objectives since 2007. Surface trawl surveys by the Alaska Fisheries Science Center in the northern Bering Sea (approximately 60N-65.5N) has varied from year to year due to time constraints on available ship time, funding objectives, and sampling priorities and objectives in other regions, survey effort has primarily occurred within the inner shelf domain (water depths typically less than 50m). The 2011 survey on the eastern Bering Sea is typical of recent survey coverage in the northern

Bering Sea (Figure 9). Surveys in the southern Bering Sea are more extensive and include coverage across all oceanographic domains of the shelf (inner: 0-50m, middle: 50-100m, and outer: 100-200m shelf domains).

Sampling effort in the northern Bering Sea has centered on the month of September (Figure 10) with an average sampling date of September 16. Sampling dates have ranged from as early as Aug 21 and as late as Oct 8; however, this broad range of dates was due to an unusual survey design in a single year, 2003. During 2003, BASIS surveys began in Norton Sound in late August and sampled Kotzebue Sound before starting the southern Bering Sea survey. Trawl sampling in the northern Bering Sea resumed after completing the southern Bering Sea survey and finished just south of Norton Sound in early October. This atypical survey design is believed to have resulted in oversampling of Yukon River juvenile Chinook salmon due to their southward migration in the northern Bering Sea. Rather than remove this year from the short time series of juvenile abundance data, an ad-hoc correction was applied to juvenile Chinook catch data by subtracting peak catches offshore of the Yukon River during Sep 27-Oct 3 from peak catches in Norton Sound during Aug 21-23.

A Cantrawl model 400/601 (made by Cantrawl Pacific Ltd., Richmond, B.C.) midwater rope trawl (Figure 11) was modified to fish at the surface with adjustments to trawl setbacks and floats along the headrope was used to capture juvenile Chinook salmon in the Northern Bering Sea aboard chartered commercial fishing vessels for all survey years in the northern Bering Sea except 2002 (2003-2007, 2009-2011). Due to concerns with shallow bottom depths in the northern Bering Sea, a smaller trawl (Cantrawl model 300) was purchased for northern Bering Sea surveys 2002. However, once it was shown that the larger Cantrawl 400/601 that was chosen for the offshore BASIS research (Murphy et al. 2003) could be used in the northern Bering Sea, a Cantrawl 400/601 was used for all subsequent surveys in the northern Bering Sea. Without fishing power corrections for the smaller trawl, the 2002 survey data in the northern Bering Sea were not included. The Cantrawl 400/601 trawl has hexagonal mesh in the wings and body, is 198 m in length, a headrope length of 120 m, and a 12-mm mesh liner in the codend (Figure 11). The trawl was configured with three 60-m bridle legs (top, middle, and bottom) connecting the trawl to two steel alloy 5-m^2 fixed bail trawl doors from Noreastern Trawl (NETS) (Figure 12). Total weight of each door was approximately 613 kg and included a 91-kg steel plate added to the shoe of each door to increase vertical stability of the doors when trawling near the surface.

Bridal material was switched from ¾" wire rope to ¾" TSII jacketed spectra in 2009. The switch from wire to synthetic material was made to extend the usable life of the bridals (approximately 10+ years for synthetic bridals, and < 5 years for wire rope), to reduce bridal weight (making it easier to maintain the balance between the trawl and trawl doors at the surface, and making it easier for fishermen to deploy and retrieve the trawl), and to maintain consistency with industry standard. Three polyform floats (one 80-cm-A5 buoys and two 60-cm-A4 buoys) were attached to the headrope on both wingtips with ¾" c-links, and two F4 polyform floats were attached to either side of the net sonar kite at the headrope to help keep the headrope at the surface; a 120-kg chain was used to allocate the weight along the footrope. Main warp was set between 274 to 360 meters, and trawl speeds were approximately 4.0-4.5 knots.

Towing speeds and bridal setback chains have been adjusted to maintain a constant footrope depth optimized for mixed layer or bottom depth since 2009. Vertical opening of the trawl can generally be varied by 3-4 meters with minor adjustments to towing rpm and towing speeds while keeping the doors below the surface and headrope buoys at the surface. By reducing towing rpm and speed through the water when sampling in deeper water, the vertical opening of the trawl is allowed to open up and ensure as much of the mixed layer is sampled as possible. Increasing towing speeds or reducing the length of footrope and middle bridal setbacks chains will keep the trawl footrope off bottom when sampling at shallow stations. Bridal setback chains are a standard configuration of rope trawls and are added to the middle and bottom bridals of the Cantrawl 400/601 to increase its vertical opening. The Cantrawl 400/601 has a vertical opening of approximately 18 meters with standard setback lengths, which has generally limited trawling locations to water depths deeper than 20 meters. By removing or reducing setback chain lengths, the trawl can be used effectively in water depths shallower than 20 meters. These minor adjustments sampling protocols add flexibility to trawl sampling and are believed to improve consistency in trawl catch over attempts to maintain fixed trawl configuration parameters.

All surface trawls from 2003-2013 were set to a standard duration of 30 min and typically, three to four stations are sampled each day of the survey. Weather contributes significantly to the amount of work that can be accomplished in a single day, by shutting down survey operations once seas exceed 10 feet, or reducing transit speeds between stations when seas are below 10 feet. Trawl dimensions are monitored continuously at each trawl with a third wire net sonar system. Actual net sonar types have varied with different vessels that have been used in the northern

Bering Sea, but all provide accurate sonar estimates of trawl width and height. Logs of net sonar data and/or depth loggers (SBE39) have been placed on the trawl headrope and footrope to maintain permanent records of trawl dimension since 2009.

Catch of fish and jellyfish species are estimated by species and life-history stage (if appropriate) in number and weight. Shipboard weights are measured with either 60kg or 6kg motion compensated scales, and scales are calibrated to ship's motion at each station to optimize accuracy and precision of sampled weights. Individual lengths and weights are recorded from Chinook salmon for two life-history stages (juvenile and immature/maturing). As a general rule, a 325 mm length cutoff provides clear separation these two life-history stages. Visual inspection of body characteristics (caudal fin edges, etc.) are also used to help separate large, robust juveniles from small immature when they close to 325 mm, however, Chinook are rarely present in this size range. Specimen samples collected from juvenile Chinook salmon include: genetic tissues for stock information, scales and otoliths for age and growth studies, stomach samples for diet studies, and specimen samples for nutritional studies. Sampling protocols for all species collected during the survey are based on scientific sample requests; priority is given to requests consistent with the funding source; other requests are fulfilled as time and interest by participating scientists permit.

Oceanographic data are collected prior to the start of each trawl station. Oceanographic data include CTD data with a SBE9-11, or model SBE25 CTD used to describe water column profiles of temperature, salinity, and other oceanographic variables. Water samples are collected at discrete depth from a rosette sampler attached to the CTD. Zooplankton samples are collected with bongo and other zooplankton plankton nets. Acoustic data and mid-water trawls have also been used to collect information on mid-water fish and jellyfish in the northern Bering Sea since 2009. Acoustic data are recorded continuously throughout the survey; mid-water trawls are conducted adaptively based on the strength of the acoustic backscatter in the water column.
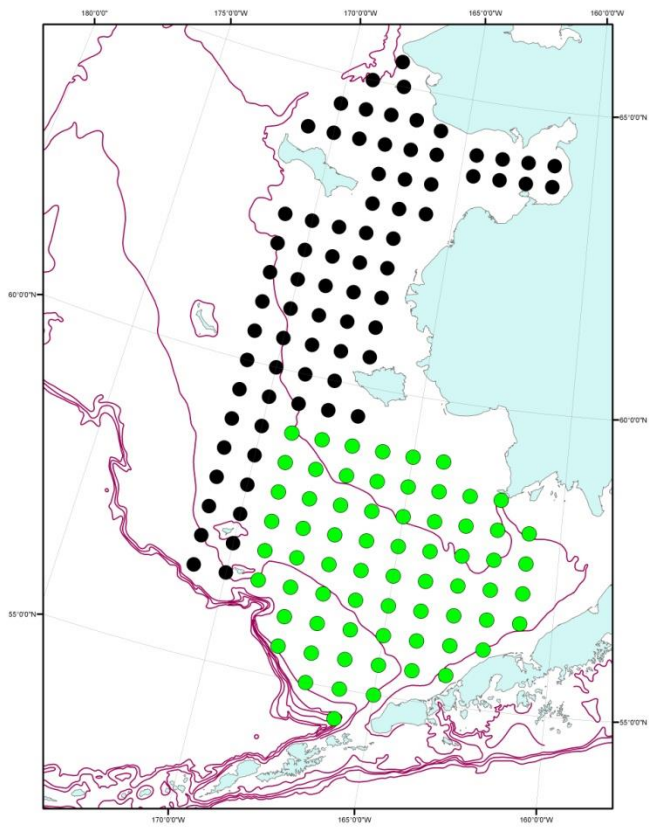
Figure 9. Station coordinates for the eastern Bering Sea surface trawl survey in 2011 by the *F/V Bristol Explorer* (black dots) and the NOAA Ship Oscar Dyson (yellow dots). Depth contours are shown for 50-400m at 50m intervals.
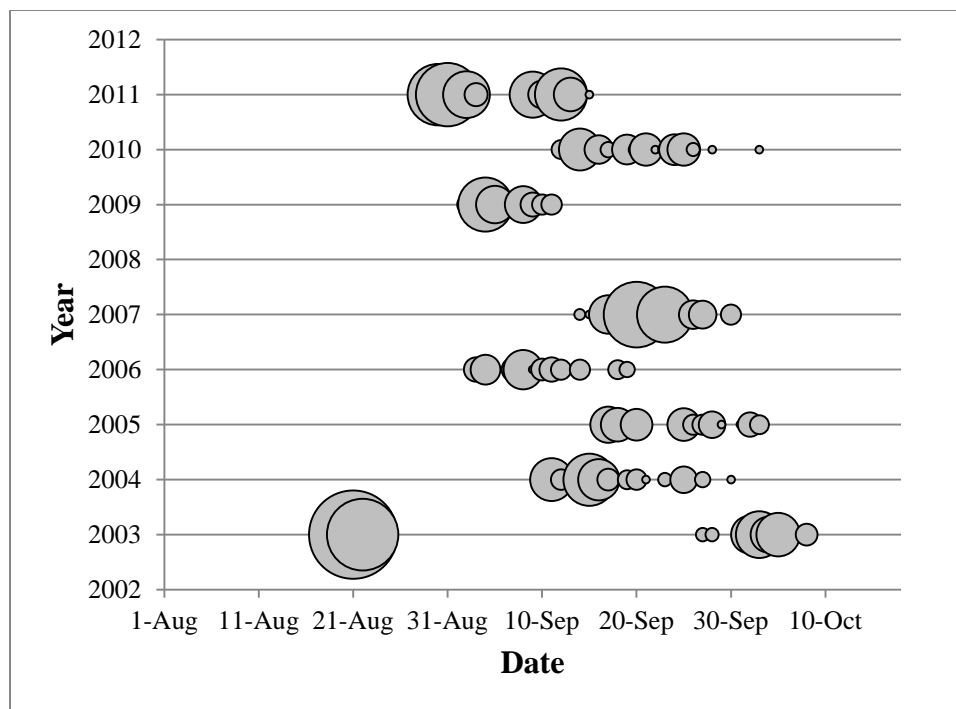
Figure 10. Capture dates of juvenile Chinook salmon during surface trawl operations in the northern Bering Sea (latitude 60N-65.5N) from 2003-2013. Circles are scaled to total catch of juvenile Chinook salmon during each survey day.
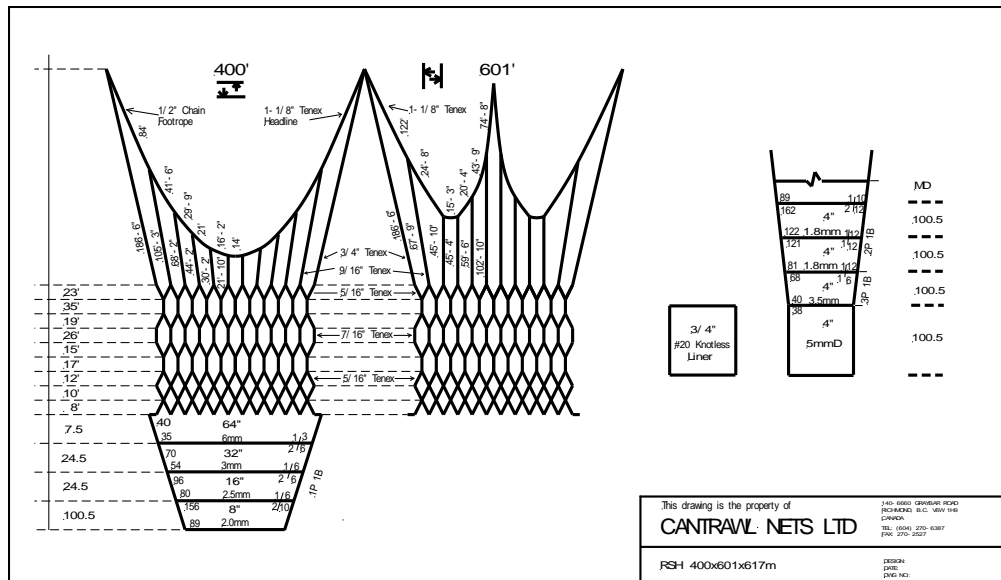
Figure 11. Net diagram of the Cantrawl 400/601 trawl used during NOAA surface trawl opertations (2003-2011).

A)   Trawl winch   B) Top roller   C) Warp 29 mm

D)   Steel alloy 5m² trawl doors (613 kg)

E)   Net bridle 19 mm diameter 60 m length x 3 x 2

F)   Wingtip bouyancy: 6 polyform floats (2 x 80 cm, 4 x 60cm)

G)   Net sounder bouyancy 6 x 31 cm center hole trawl floats

H)   Allocated footrope weight (120 kg)

Figure 12. Surface trawl bridal and trawl operations during the surface trawl survey aboard the *F/V Northwest Explorer* in the Bering Sea during 2002. This configuration is identical surface trawl operations in the northern Bering Sea (2003-2011) except for the replacement of center hole floats with two F4 polyform floats at the center of the headrope.

<u>Juvenile Abundance and Adult Abundance</u>

An abundance index was generated for Canadian-origin juvenile Chinook salmon based on surface trawl catch and effort data, mixed layer depth, and genetic stock composition of juveniles in the northern Bering Sea. Effort data are based on area swept by each trawl haul calculated from net sonar measurements of trawl width (km) and measurements of distance trawled (km) from gps coordinates of the start and end positions of the trawl haul using spherical earth coordinates as:

$$x = \cos^{-1}(\sin(lat_s)^2 + \cos(lat_e)^2 \cos(\Delta \text{lon})) * 6371,$$

where lat_s is the trawl start latitude position in radians, lat_e is the trawl end latitude position in radians, Δlon is the longitude distance between the start and end trawl positions in radians, and 6371 is the earth radius in kilometers.

Average juvenile Chinook salmon CPUE (catch per unit effort, catch/km^2) is expanded to an abundance index for the northern Bering Sea by the survey area and mixed layer depth. The northern Bering Sea was divided into four spatial strata: 60-62N, 62-64N, Norton Sound, and Bering Strait. The Norton Sound and Bering Strait stations were corrected for inconsistent survey effort over time. Variance and coefficients of variation were estimated for the juvenile abundance index from a bootstrap (Efron and Tibshirani 1986) resample distribution (1,000 bootstrap samples). Survey area was calculated by:

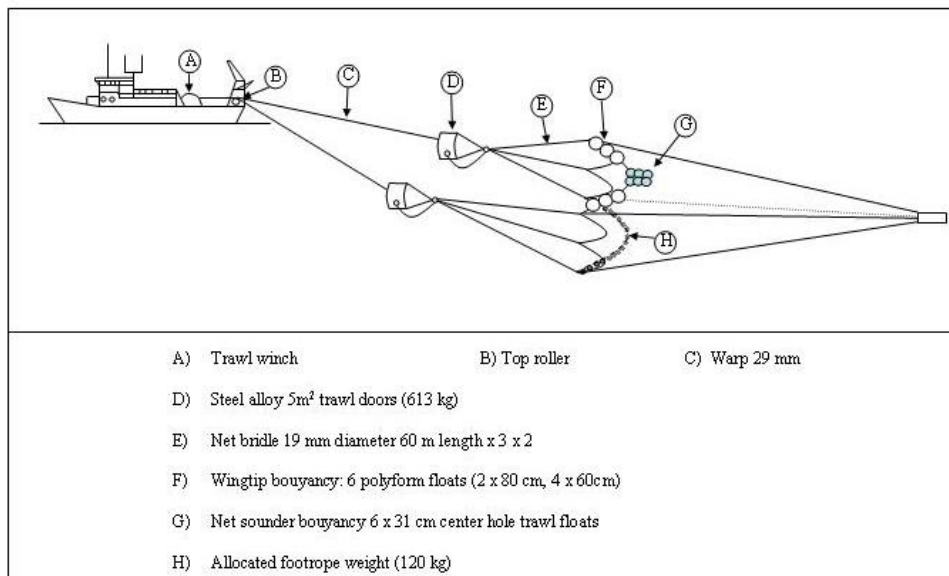$$A_{y,s} = \frac{G_{y,s}}{S_{y,s}} * n_{y,s},$$

where $A_{y,s}$ is the survey area in year y and strata s, $G_{y,s}$ is the average sample grid area (km^2), $S_{y,s}$ is the average area swept (km^2), and $n_{y,s}$ is the number of stations. The survey design used in the BASIS survey design for the northern Bering Sea is based on a latitude and longitude coordinate grid (0.5 degrees of latitude by 1 degree of longitude for all years except 2003), therefore the y-grid dimension (km) of the sample grid is a simple conversion of nautical miles to km (30 nm = 55.56 km). The average x-grid dimension (km) can be estimated from spherical earth coordinates based on average latitude.

Mixed-layer depth (MLD) is used to expand area swept estimates of abundance to volume to obtain an abundance index for juvenile Chinook. The formation of winter sea ice in the northern Bering Sea creates a dense, sub-zero pool of seawater that remains on the seafloor throughout the subsequent year, referred to as the Bering Sea cold pool, and is a dominate feature of the northern Bering Sea (Figure 13 and 14). Seawater temperatures below the surface mixed layer generally are below zero and therefore the mixed layer depth provides a reasonable approximation to juvenile Chinook salmon habitat and they are not adapted to survive in water temperature near zero for any length of time (Brett and Alderdice 1958). Corrections for mixed layer depth are applied to juvenile catch data based on the mixed layer and trawl depth at each station and assuming that juvenile Chinook salmon are randomly distributed within the surface mixed layer (a reasonable assumption as this layer is uniformly mixed through wind and waves). MLD is defined as the depth where seawater density increased by 0.10 kg/m^3 relative to the surface (Danielson et al. 2011). The MLD correction to trawl catch, θy, was estimated as:

$$\theta_y = \sum_j \frac{MLD_{j,y}}{TD_{j,y}} C_{j,y},$$

where $MLD_{i,y}$, $TD_{j,y}$, and $C_{j,y}$ are the mixed layer depth, trawl depth, and catch, respectively, at stations, j, where trawl depth is above the mixed layer and juvenile Chinook catch is positive, and year y. MLD trawl catchability correction, q_y, was estimated by:

$$q_y = \frac{\theta_y}{\sum_i C_{i,y}},$$

where $C_{i,y}$, is the total catch at the ith station in year, y.

A Canadian-origin juvenile abundance index was estimated from genetic stock mixtures present in the juvenile population. A single nucleotide polymorphism (SNP) genetic baseline (Templin et al. 2011a) was used to assign genetic stock origins through Bayesian mixed stock analysis (Pella and Masuda 2000). Juvenile stock proportions in the northern Bering Sea have been reported in (Murphy et al. 2009) and (Templin et al. 2011b).

The Canadian-origin juvenile index and Canadian-origin returns to the Yukon River (JTC 2014) and were used to define the relationship between juvenile and adult abundance. The number of Canadian-origin Chinook salmon returning to the Yukon River and the number of spawners

(escapement) were scaled to juvenile year based on the assumption that all juveniles were freshwater age1. The average number of 7-year old Canadian-origin Chinook was added to the return estimate for the 2009 juveniles reported in the JTC report (JTC 2014). Although multiple freshwater ages are present in the juvenile population (age0, age1, and age2), based on juvenile size distributions and freshwater age structure of returning adults, nearly all juveniles are expected to be freshwater age1 and the error introduced with this assumption is minor compared to the error in estimates of abundance. Available information on juvenile Chinook scale ages are summarized in a recent report submitted to AYKSSI on ocean and climate effects on Chinook salmon (Myers et al. 2010). Work is currently in progress to develop age estimates with otoliths (scale loss of juveniles during trawl capture prevents their use in estimating age composition of juveniles) but age composition data is primarily applicable to juvenile life-history studies, not abundance.
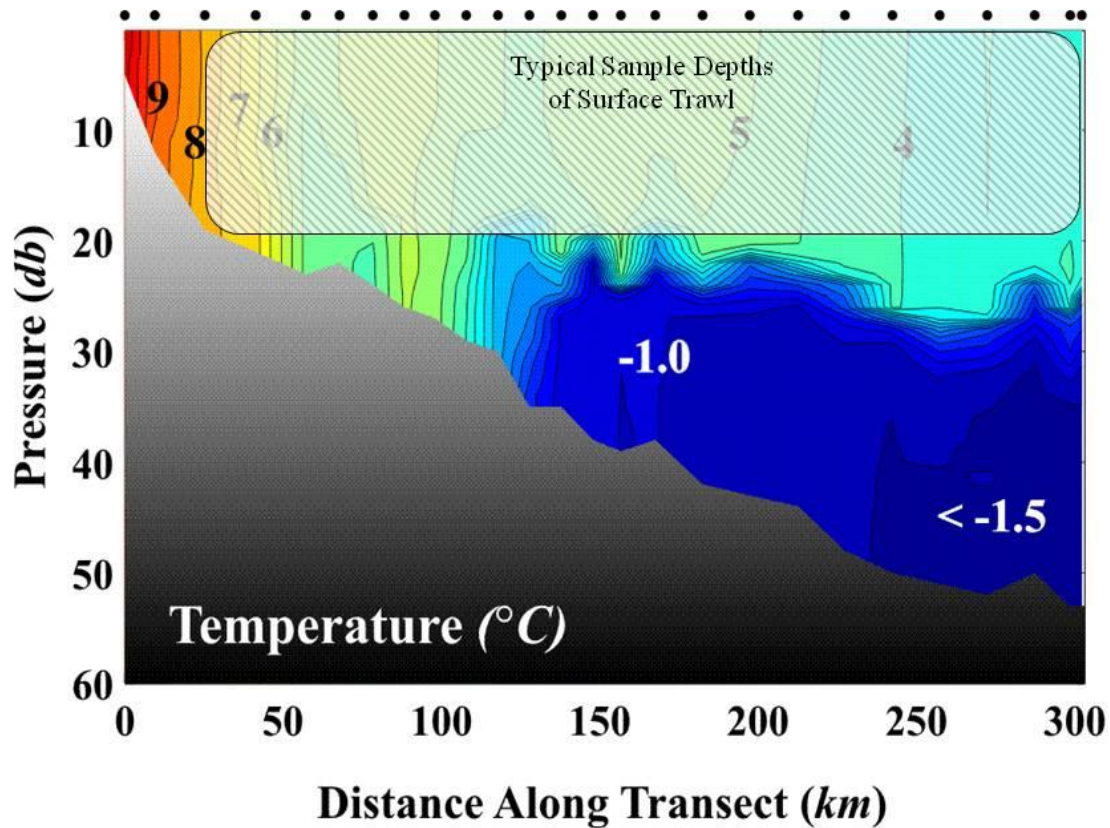
Figure 13. Typical sampling depths of the surface trawl and water column temperatures in the northern Bering Sea (temperature data is from 15-16 July, 2009 along latitude 62°N, figure adapted from Danielson et al. (2011)). Sample locations are indicated by black dots above the figure and bottom depths are the grey/black polygon indicates bottom depth. The eastern Bering Sea cold pool (sub-zero temperatures below 20-25m) is assumed to restrict the vertical distribution of juvenile salmon to the surface mixed layer and juvenile catches are expanded (average expansion is 13%) to the mixed layer when generating the juvenile abundance index.
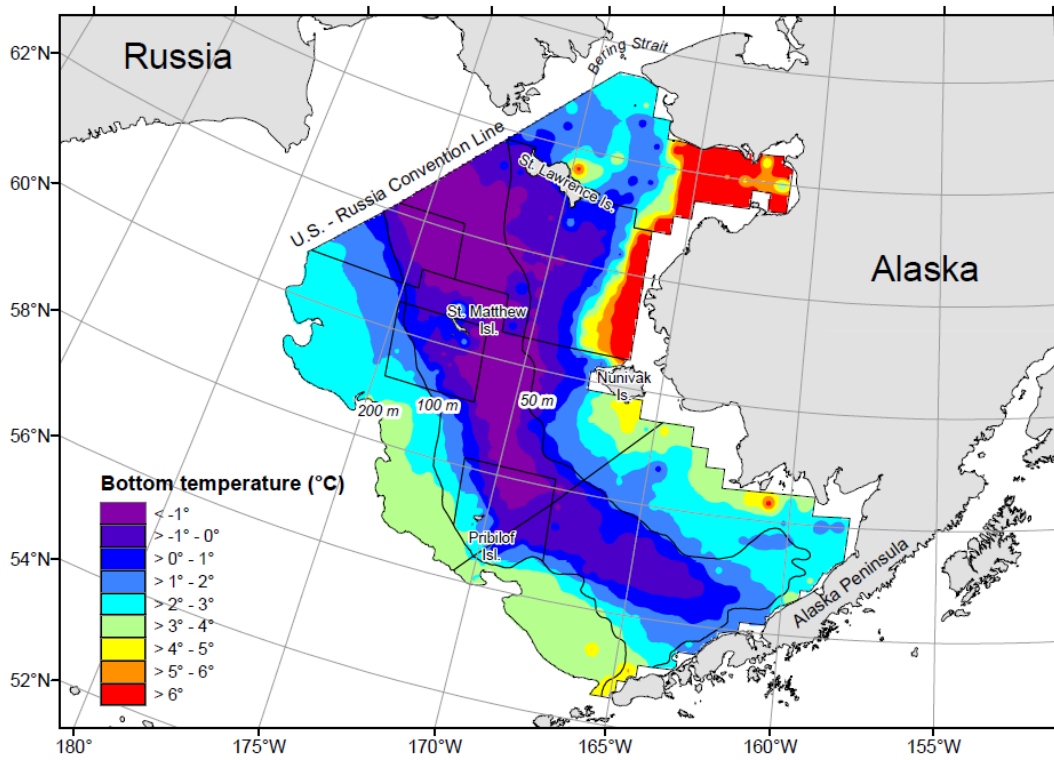
Figure 14. Map of the mean bottom temperatures from the 2010 eastern and northern Bering Sea shelf bottom trawl survey (Lauth 2011).

Juvenile Distribution and Temperature

Catch per unit of effort (CPUE) data are used to map juvenile Chinook densities over space using the start latitude and longitude position of each trawl sample location (station). Densities are pooled by year into the warm years (2002-2007, the original BASIS project years), and cold years (2009-2011). Catch distribution were standardized by effort as:

$$Catch_{i,y} = \frac{C_{i,y}}{E_{i,y}}\overline{E_y},$$

where $C_{i,y}$ is the number of juvenile Chinook captured at station i in time period y, $E_{i,y}$ is the area swept in km^2 and $\overline{E_y}$, is the average area swept during each time period, y. Zero catch boundary conditions were added to land mass, and the prediction surfaces were constructed with an exponential kernel function (spatial trend) and a local kriging model fit to trend residuals (ESRI 2001). A neighborhood search criteria was set with a minimum of 8 and a maximum of 20

datapoints within the covariogram sill range to the local kriging model, and cross-validation statistics were used to optimize the prediction surface to observed data.

Average seawater temperature within the mixed layer depth (MLD) from the BASIS surface trawl surveys were used to define inter-annual variability in seawater temperature of the northern Bering Sea shelf and juvenile distributions were pooled by warm (2003-2007) and cold (2009-2011) years. Inter-annual variability in migratory trajectories of juvenile Chinook salmon is described by average latitude position of juveniles (catch weighted average station latitude by year) and is compared with inter-annual variability in MLD temperatures. Winter sea ice cover is estimated by the average number of days of at least 15% ice cover at the NOAA M2, M4, and M5 moorings (data provided by Sigrid Salo PMEL/NOAA, personal communication). An index of the cold pool area was estimated by the area of the bottom trawl survey with temperatures less than 0° C (data provided by Bob Lauth AFSC/NOAA, personal communication).

Size-Selective Mortality and Energy Density

Juvenile size provides a key ecosystem indicator for juvenile Chinook salmon in the northern Bering Sea as it integrates bottom-up ecosystem processes impacting their survival. Energetic condition (energy density) adds another important dimension to bottom-up ecosystem processes and it is necessary to understand energy allocation patterns in juvenile fish (to growth and storage) when using size as an ecosystem indicator. Energetic condition is believed to be important to survival in juvenile salmon (Beamish and Mahnken 2001).

Energy density estimates were obtained from a subset of juvenile Chinook since 2005 (typically two juveniles from each station) using standard bomb calorimeter methods (Fergusson et al. 2010). Fish were dried to a stable weight (≤5 mg change), homogenized with a Waring pulverizer, and ground to a fine powder with a mortar and pestle prior to analysis with a 1425 Parr micro-bomb calorimeter. Energy density estimates (kJ/g) from the calorimeter were rescaled to wet weight energy density by the percent water content (ratio of dried weight to initial body weight).

Size-selective mortality of juveniles was modeled with data from juvenile scales and body size in the northern Bering Sea (2002-2007), and from age structure and scales of adult Chinook salmon

returning to the Yukon River (2004-2011). Juvenile size data were standardized to an average capture date of Sep 15 (2002-2007), based on an assumed growth rate of 1 mm/day. A target subsample of 150 scales was collected from adult Chinook salmon at Pilot Station in the lower Yukon River for each juvenile year. Scales were selected to match age composition of each juvenile year return as well as the run timing and sex composition of the run. Adult scales were digitized by the Mark, Tag, and Age Laboratory at the Alaska Department of Fish and Game. Marine scale circuli counts from juvenile scales collected during surface trawl surveys (mean circuli count of 22, standard deviation of 1.98) were used to define the sampling distribution of adult scale circuli. Scale measurements for each adult scale were based on circuli numbers drawn from a normal probability distribution defined by the juvenile scale circuli (avg=22, std=1.98). Scale radius measurements at each circuli were converted to length (mm) based on a scale radius (mm) to length model (Figure 15) from juvenile scale collections. Reconstructed lengths (mm) were converted to weight (g) based on the length-weight relationship for juvenile Chinook (Figure 16). Weight models were used to describe size-selective mortality as size-selective mortality at this life-history stage is believed to be primarily a function of energy storage (Beamish and Mahnken 2001) and juvenile energy density is linear with juvenile weight (Murphy et al. 2013).

Size selective mortality probabilities, ρ_i, were estimated from the proportion of juvenile, j_i, and surviving adults, a_i, within each weight interval, i, as:

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

Generalized additive models (Chambers and Hastie 1992) were fit to mortality probabilities and used to describe size-selective mortality in juvenile Chinook salmon.
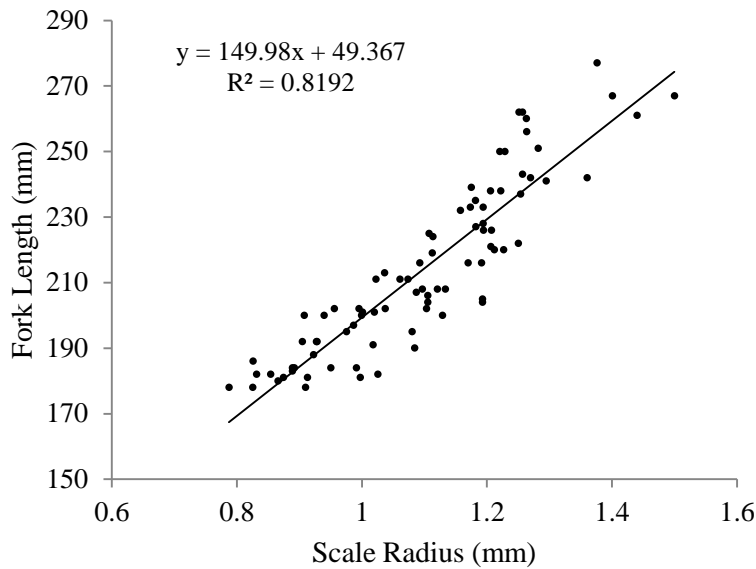
Figure 15. Relationship between scale radius (distance from focus to scale edge in mm) and fork length (mm) of juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea.
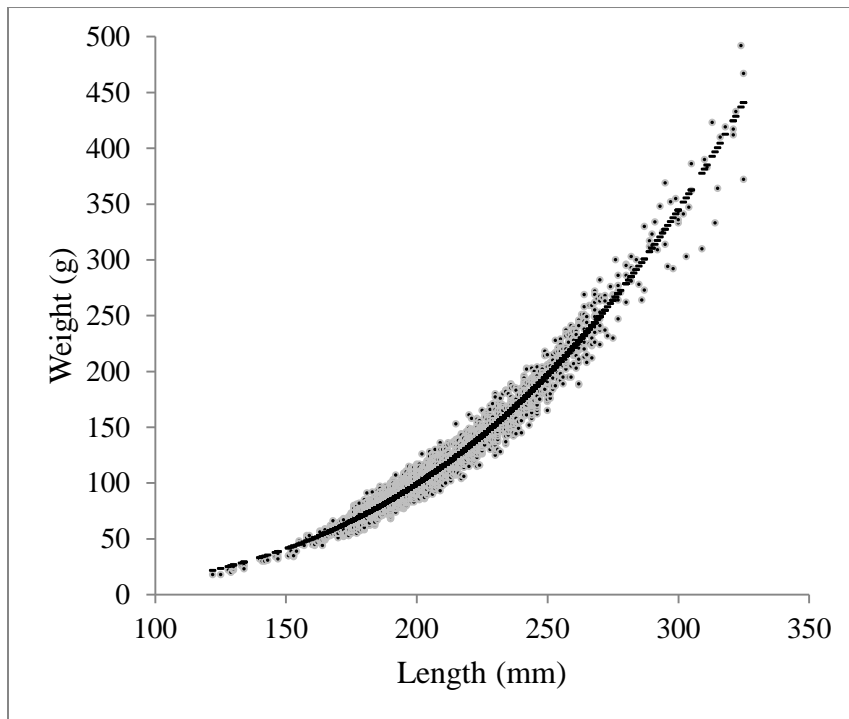
Figure 16. Relationship between fork length (mm) and fresh weight (g) of juvenile Chinook salmon captured in the northern Bering Sea during surface trawl surveys in the northern Bering Sea. Grey point are individual fish measurements, black points are from the fitted allometric growth model $\ln(\text{weight}) = 3.0816*\ln(\text{length})-11.735$.

Juvenile Chinook Diet, Prey Species, and Thiamine

Juvenile diets were estimated from onboard stomach content analysis. Up to ten stomachs of juvenile Chinook salmon were sampled and contents were pooled and weighed at each station. Species composition was estimated by volume or weight. Prey composition was estimated for each year by a catch weighted stomach content index (SCI). SCI values were estimated for each prey species as the ratio of prey weight to predator weight.

Juvenile Chinook salmon diet composition, D_j, was calculated from a catch weighted stomach content index ($SCIC_j$):

$$SCIC_j = \sum_i \frac{\sum_n Py_{j,i,n}}{\sum_n Pd_{j,i,n}} C_i,$$

where the stomach content index (ratio of prey weight $Py_{j,I,n}$ to predator weight $Pd_{j,I,n}$) for the prey species j is estimated by pooling n stomachs at station i and multiplying by the catch, C_i, at that station. Diet composition of the prey species j, $SCIC_j$, is expressed as a proportion of the total prey composition as:

$$D_j = \frac{SCIC_j}{\sum_j SCIC_j}.$$

Relative biomass (mt) of forage fish species (herring, capelin, sandlance, and age0 pollock) were estimated from trawl catch, effort, and the systematic spatial survey design grid as follows:

$$B_y = \frac{G_y}{S_y} * \sum_i C_{y,i}$$

Where B_y is the relative biomass in year y, G_y is the average sample grid area (km^2), S_y is the average area swept (km^2), and $C_{y,i}$ is the trawl catch (numbers or biomass) at station i in year y. Sample grid area was calculated using the same approach for juvenile Chinook salmon abundance estimates.

Length frequency data for herring and capelin were scaled to catch as:

$$C_{i,l} = \sum_j L_{i,j,l} \frac{C_{i,j}}{S_{i,j}},$$

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where $L_{i,j,l}$ is the number of lengths measured for species *i* at station *j* in the length bin *l*, $C_{i,j}$ is the catch of species *i* at station *j*, and $S_{i,j}$ is the number of lengths sampled for species *i* at station *j*.

Thiamine concentrations in eggs and juvenile muscle and liver tissue were examine to evaluate the potential for thiamine deficiency in Yukon River Chinook salmon (Honeyfield et al. In Prep) (Appendix 5). Thiamine levels were examined in Chinook salmon eggs collected from broodstock females at the Whitehorse Rapids Fish Hatchery and Fish Ladder (Upper Yukon, Canada), and from opportunistic collections during weir and carcass surveys from the Middle Yukon rivers: Chena, Salcha, and Goodpaster, and the Lower Yukon river: Andreafsky. Thiamine levels in juvenile muscle and liver tissue collected during the 2012 surface trawl survey were also evaluated as part of this study. Thiamine concentrations were measured by high pressure liquid chromatography following standard thiamine methods (Brown et al. 1998).

Threshold or critical thiamine concentrations of egg and muscle were drawn from studies conducted on fish populations in the Great Lakes region. Thiamine deficiency produces overt fry mortality (lethal concentrations of low thiamine) at egg thiamine levels less than 1.5 nmol/g (Fisher et al. 1996, Honeyfield et al. 2005, Fitzsimons et al. 2007). Secondary effects of thiamine deficiency in fry such as poor growth and immune dysfunction occur when egg thiamine levels are between 1.5 and 8.0 nmol/g (Honeyfield et al. 2005, Fitzsimons et al. 2009, Ottinger et al. 2012). Thiamine deficiency is not considered to be present when thiamine concentration in eggs is greater than 8.0 nmol/g. A reference value of 1.0 nmol/g in muscle tissue is generally used to identify thiamine deficiency in salmon (Brown et al. 2005); however, thresholds levels for thiamine concentration in muscle tissue are poorly understood and less well defined in the literature than eggs. The presence of secondary effects of thiamine deficiency to metabolic functions in fry at thiamine levels much higher than lethal limits would suggest that adverse effects (secondary effects) of low thiamine is likely to be present when muscle tissue thiamine is above 1.0 nmol/g.

RESULTS AND DISCUSSION

Juvenile and Adult Abundance

Information on juvenile abundance helps provide a framework for evaluating critical periods in production and can be used to help identify when and where production declines may be

occurring in Yukon River Chinook salmon. The juvenile abundance index for Canadian-origin Chinook salmon from the Yukon River varied from a high of approximately 2.3 million in 2003 to a low of 0.7 million in 2010 (Table 1, Figure 17). The juvenile index was approximately 1.5 million in 2011. The juvenile abundance index for the Canadian-origin stock group was positively correlated with adult returns (r = 0.89, p = 0.02, r2 = 0.72 n = 6; Table 2, Figure 18), emphasizing the importance of freshwater and estuarine (early marine) life history stages to inter-annual variability in recent adult returns. However, the average juvenile survival index is low (0.06) and, therefore, mortality after the juvenile stage is important to their overall production; an understanding of ecosystem and fishery effects on survival after the juvenile stage will be required to adequately address the overall production dynamics of Yukon River Chinook salmon. Average variance of the northern Bering Sea juvenile index (bootstrap coefficient of variation) is 23% and varies from 12% to 36% depending on the spatial distribution of juvenile Chinook.

Error in juvenile abundance estimates could be an important factor in the variance observed between juvenile and adult abundance; however, it is not possible to separate or identify the relative contribution of measurement and process error (survival) in the relationship between juvenile and adult abundance. Current surveys are not designed specifically for juvenile Chinook salmon; design changes to the survey could be made to improve precision in the juvenile Chinook salmon abundance index. Design changes will alter the interpretation of other fisheries and oceanographic data, therefore it is important to clearly understand sampling priorities and the impact of survey data with changes to survey design over time. Finer scale sampling would reduce uncertainty in abundance estimates, but will significantly increase the length and cost of the survey to maintain a similar sampling area.

Adaptive cluster sampling (Thompson and Seber 1996) is an alternative approach that could be used to achieve finer-scale sample data specific to juvenile Chinook salmon. In contrast to conventional sampling designs, where sampling is fixed prior to the survey, adaptive designs allow for increased sampling intensity depending upon observations made during the survey. Adaptive sampling techniques will provide the most efficient approach to reducing sampling variance for juvenile Chinook and can be scaled to meet whatever level of precision is desired for juvenile abundance and genetic assignment of stock origin.

Shallow bottom depths and presence of the eastern Bering Sea cold pool are important physical features of the northern Bering Sea shelf that restrict juvenile habitat to surface waters and

simplify expansions of surface trawl catch data to abundance. Mixed layer depth (MLD) corrections are applied to the surface trawl abundance data to expand survey data to juvenile habitat. MLD corrections varied from 1% to 29% with an overall average expansion of 13% (Table 1). The depth of the mixed layer, sampling depth of the surface trawl, and spatial distribution of Chinook salmon all contribute to the MLD correction. The large correction in 2005 (29%) was primarily due to the storm activity in 2005, which contributed to a much deeper mixed layer. The MLD correction is applied to the catch data based on the assumption that juvenile Chinook are randomly distributed throughout the surface mixed layer. Vertical distribution of juvenile Chinook in the northern Bering Sea is unknown, but this assumption was considered more appropriate than assuming all juveniles are distributed within the depths sampled by the trawl or other assumptions based on constant vertical distribution of juveniles over time and space. Additional research on vertical distribution of juvenile Chinook would provide valuable insight into surface trawl catchability for juvenile Chinook; however, it should be considered within the context of other factors that impact trawl catchability, such as trawl and boat avoidance. The relatively high trawling speeds (~4.5 knots) and long warp lengths (~ 300 meters) used during surface trawl surveys in the northern Bering Sea are believed to effectively herd juvenile salmon into the trawl and minimize trawl and boat avoidance; however, this has not been tested.

Stock composition of the Canadian-origin stock group has been relatively stable in the northern Bering Sea juvenile population. The proportion of Canadian-origin Chinook salmon varied from 42% to 52%, with an overall average of 46% during the 2003-2011 juvenile years (Table 1). The overall average is slightly below the typical stock proportions of Canadian-origin Chinook salmon in fishery harvests within the Yukon River (50%) (JTC 2014). It is possible that the minor difference between these two averages is simply due to the presence of Norton Sound Chinook salmon in the juvenile population of the northern Bering Sea; if so, this would indicate that the proportion of Canadian-origin Chinook in the juvenile population is very similar to the adult population in the Yukon River (Murphy et al. 2009). Stability in juvenile mixtures and consistency with stock proportions in adult returns is an important feature in the production dynamics of Yukon River Chinook salmon as it tends to implicate a common source of reduced productivity across stock groups within the Yukon River.

Table 1. Northern Bering Sea (NBS) juvenile Chinook salmon abundance index, coefficient of variation (cv) of the juvenile index, mixed layer depth (MLD) correction, Canadian-origin stock proportions, coefficient of variation (cv) of Canadian-origin stock proportions, and the Canadian-origin juvenile Chinook salmon index from surface trawl surveys conducted in the northern Bering Sea (2003-2011).

Juvenile Year	NBS Juvenile Index (1,000s)	NBS Juvenile Index CV	MLD correction	Canadian-Origin Stock Proportion	Canadian-Origin Stock Proportion CV	Canadian-Origin Juvenile Index (1,000s)
2003	4,728	0.13	0.14	0.43	0.09	2,302
2004	2,064	0.16	0.12	0.52	0.10	1,189
2005	2,563	0.12	0.29	0.47[1]	--	1,556
2006	1,356	0.17	0.13	0.46	0.12	699
2007	2,748	0.31	0.16	0.48	0.08	1,523
2008						
2009	1,846	0.36	0.01	0.47	0.14	877
2010	1,558	0.21	0.05	0.42	0.14	691
2011	3,057	0.35	0.12	0.44	0.10	1,523

[1]Stock proportion based on 2003-2007 average.

Table 2. Canadian-origin juvenile Chinook salmon abundance index, escapement, returns, juvenile survival, juveniles per spawner, and returns per spawner from surface trawl surveys conducted in the northern Bering Sea (2003-2011).

Juvenile Year	Canadian-Origin Juvenile Index (1,000s)	Canadian-Origin Escapement (1,000s)	Canadian-Origin Return (1,000s)	Juvenile Survival Index	Juveniles per Spawner	Returns per Spawner
2003	2,302	53	107	0.05	44	2.03
2004	1,189	42	52	0.04	28	1.23
2005	1,556	81	98	0.06	19	1.21
2006	699	48	56	0.08	14	1.15
2007	1,523	68	78	0.05	22	1.15
2008		63	59			0.95
2009	877	35	45	0.05	25	1.29
2010	691	34			20	
2011	1,523	65			23	
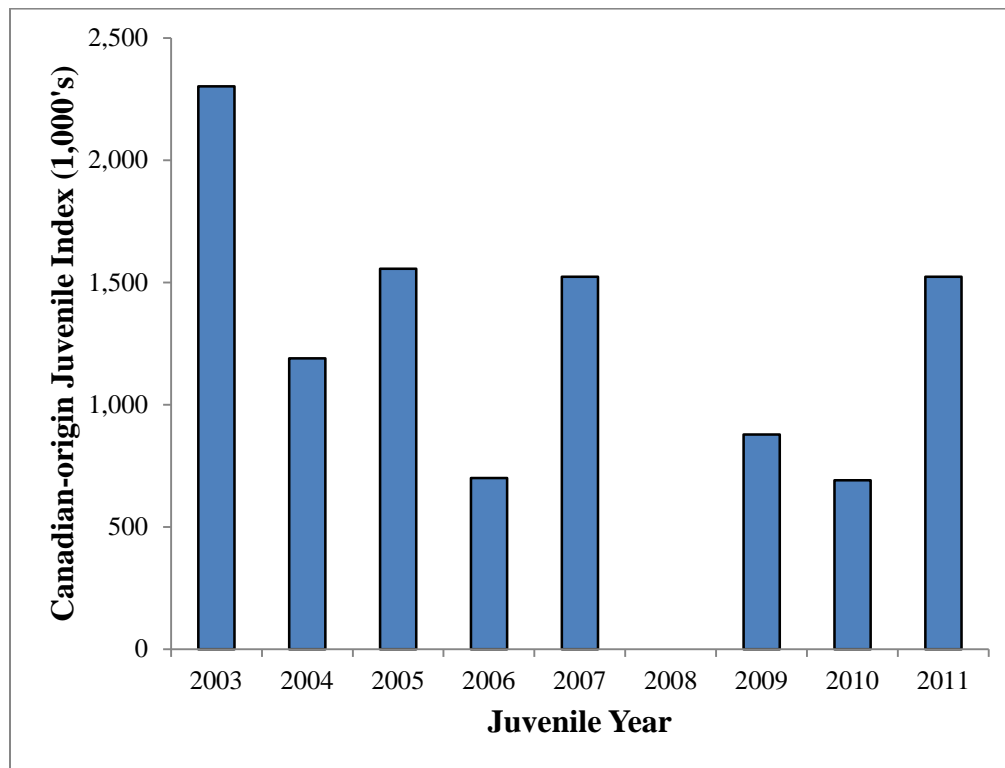
Figure 17. Canadian-origin juvenile Chinook salmon abundance index from surface trawl surveys in the northern Bering Sea (2003-2011).
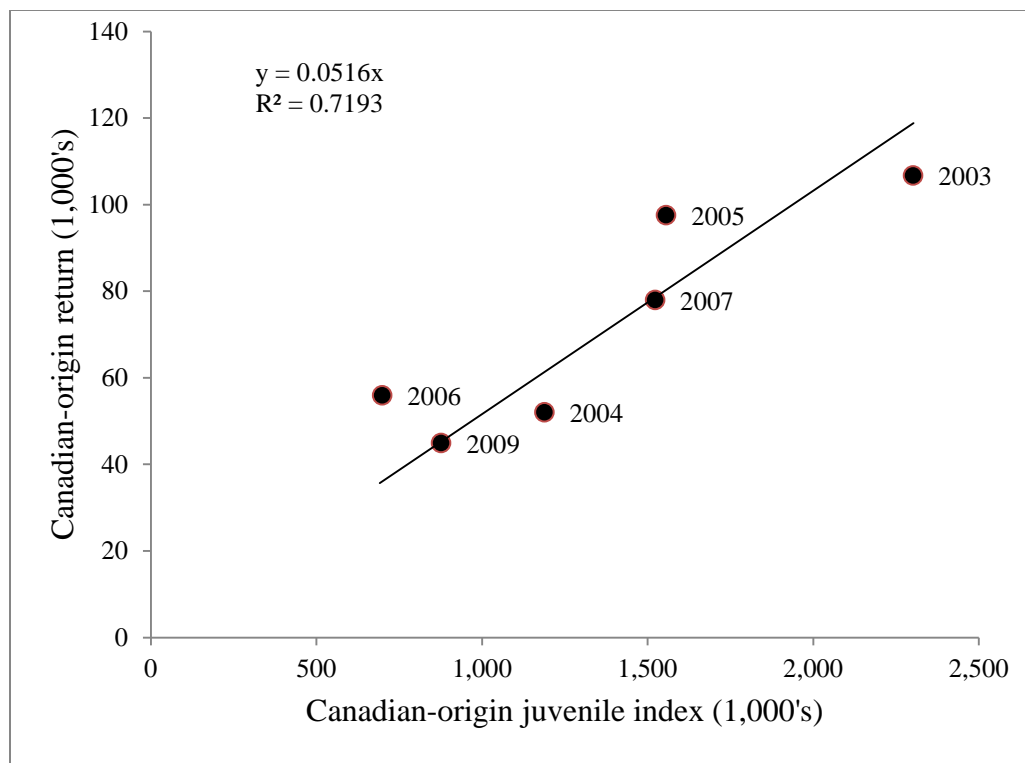
Figure 18. The relationship between juvenile and adult abundance for Canadian-origin Chinook salmon from the Yukon River. Adult abundance is based on the number of returning adults by juvenile year and the juvenile abundance index is based on surface trawl surveys in the northern Bering Sea. Years associated with each data point indicate the juvenile year.

Juvenile Distribution and Temperature

Prediction surfaces (shaded contours) and individual CPUE data (circles) are shown in Figure 19 for warm and cold survey years. Temperature conditions for each year were defined by average temperature within the mixed layer depth during surface trawl surveys. Juvenile Chinook salmon distribution during warm sampling years (2002-2007) (Fig. 19a) is similar to the distribution shown in (Murphy et al. 2009). However, a slightly different contour interval was used and CPUE was scaled to average effort, which resulted in a slightly different distribution pattern for juvenile Chinook salmon than shown in (Murphy et al. 2009).

Juvenile Chinook were caught in both the northern and southern Bering Sea during the 2002-2007 sample years; however juvenile Chinook salmon have only been caught in the northern Bering Sea since 2007. The loss of juvenile Chinook from the southern Bering Sea survey may reflect a significant change in the distribution or abundance of juvenile Chinook; however, it is not

possible to distinguish between changes in distribution and abundance from survey data alone. It is possible that the timing of Chinook salmon dispersal from nearshore habitats is later in cold years and they are simply no longer available to the location and times sampled by the southern Bering Sea survey. However, survey design changes in the southern Bering Sea survey could also be contributing to the fewer number of Chinook present in the survey. Minimum station depths increased in the southern Bering Sea after 2007 to accommodate the larger survey vessel, the NOAA Ship Oscar Dyson, and increase focus on offshore habitats to address recruitment dynamics of federally managed groundfish species such as Walleye Pollock. Minimum station depths in the southern Bering Sea ranged from 19-24m in 2002-2007 and 27-30m in 2009-2011, whereas minimum station depths remained the same during warm and cold periods in the northern Bering Sea (17-21m in 2002-2007 and 16-21m in 2009-2011). The overlap of juvenile Chinook salmon distributions with the survey is believe to be an important component of juvenile catch data in the southern Bering Sea, making it difficult to make inferences on changes in juvenile abundance.

Large difference in the distribution of juvenile Chinook in the northern Bering Sea occurred between the warm and cold years and reflects changes in the migratory trajectory of juveniles originating from drainages in the northern Bering Sea juveniles. Limited mixing of Chinook salmon from the northern and southern Bering Sea occurs during their first summer at sea (Figure 20); therefore changes in the distribution of juvenile Chinook salmon in the northern Bering Sea is believed to reflect changes in the migratory trajectories of Chinook salmon originating from northern Bering Sea drainages (principally the Yukon River drainage). Large-scale changes in the migratory pattern of juveniles have the potential to alter marine survival, the apparent relationship between the number of juveniles and returns per spawner, and marine distribution patterns during their later marine life-history stages.

Temperature limitations introduce important constraints on juvenile migration in the northern Bering Sea. Juveniles are unlikely to survive in the northern Bering Sea once sea ice forms, and quite possibly prior to the formation of sea ice. Sea ice begins to form in coastal habitats utilized by juvenile Chinook in early November and the entire northern shelf is ice covered by early January. Sea water freezes at approximately -1.7 °C in the northern Bering Sea as its salinity is in the range of 30-31PSU (practical salinity unit). Due to shallow water depths in the northern Bering Sea and the presence of the Bering Sea cold pool (Danielson et al. 2011, Sigler et

al. 2011), the water column drops to subzero temperatures as sea ice forms (Figure 7, under ice temperatures reported in Danielson et al. 2006). Salmon lose metabolic function and cannot survive in temperatures near zero for any length of time (Brett and Alderdice 1958). The southern Bering Sea is believed to be the closest suitable overwinter habitat for Yukon River Chinook salmon. Southward migration of juveniles is more consistent with the historic migration pattern observed for Yukon River Chinook salmon (Hartt and Dell 1986, Farley 2005) and juvenile distribution patterns observed in 2002-2007 (Murphy et al. 2009) may have been the result of non-typical migratory patterns associated with unusually warm conditions in the Bering Sea (Stabeno et al. 2012). Based on t-test comparisons of juvenile abundance, size, latitude position of juveniles between warm and cold periods in the northern Bering Sea, juvenile distribution appears to be more related to broad-scale temperature fields of the northern Bering Sea than abundance and size (Table 3, Figure 21a). This may reflect a greater influence of freshwater and estuarine processes on juvenile survival and growth rates that are not linked to the broad-scale temperature patterns of the eastern Bering Sea. The relatively high correlation between winter sea ice extent and mixed layer depth temperatures in the northern Bering Sea (Figure 21b) ($r=-0.809$, $p=0.015$, $R^2=0.654$) indicates that sea ice is an important feature in the broad-scale temperature fields in the northern Bering Sea and is most likely linked to the size of the cold pool (Table 3) and its impact on large-scale temperature patterns in the northern Bering Sea (Sigler et al. In Press).

Although survival estimate of juveniles are related to latitude position, the correlation between latitude position and survival is not significant (Murphy et al. 2013) (Appendix 1). Multiple factors could be contributing to the lack of significance. The number of years available to describe the connection between migration and survival is limited; additional years will be required to clarify the relationship between migration and survival. The presence of measurement error in juvenile abundance and multiple factors impacting survival confounds our ability to evaluate the influence of any single processes on survival. Finally, it is likely that the underlying process linking migration and survival is much more complex than simple correlations between average latitude and survival. Although we believe juvenile migration is an important feature of their early marine life-history stage; additional analysis will be required to link migratory patterns to survival.
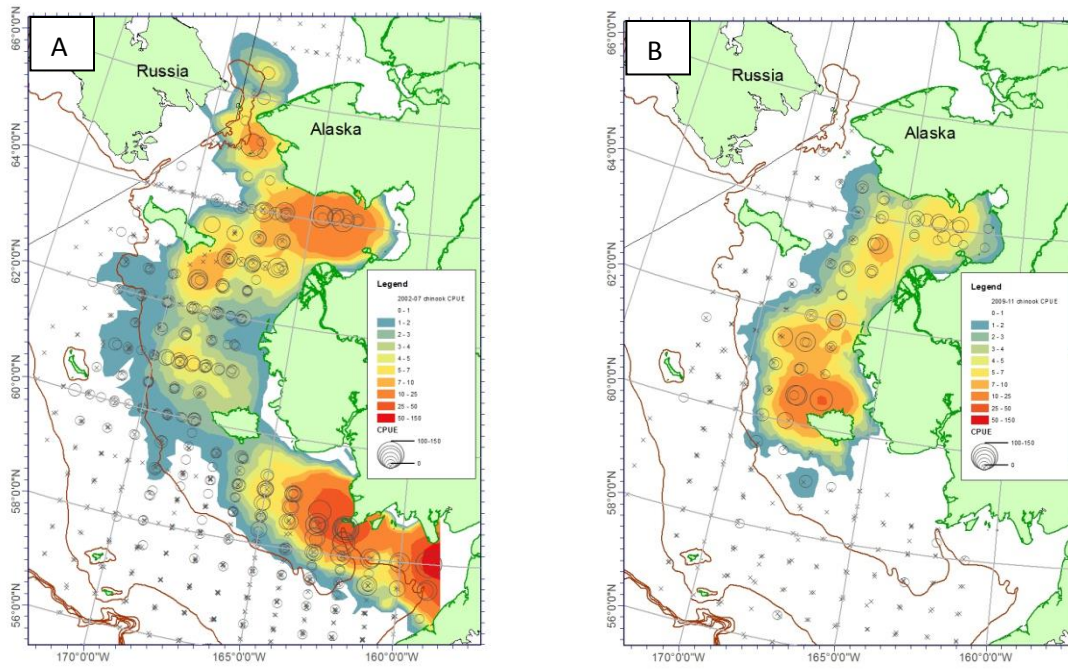
Figure 19. Kriging prediction surfaces (shaded contours) and individual catch per unit of effort (CPUE) values (circles) of juvenile Chinook captured during surface trawl surveys in the eastern Bering Sea in warm (A; 2002-07) and cold (B; 2009-11) years. Average mixed layer depth temperature during surface trawl surveys were used separate catch data into warm and cold years.
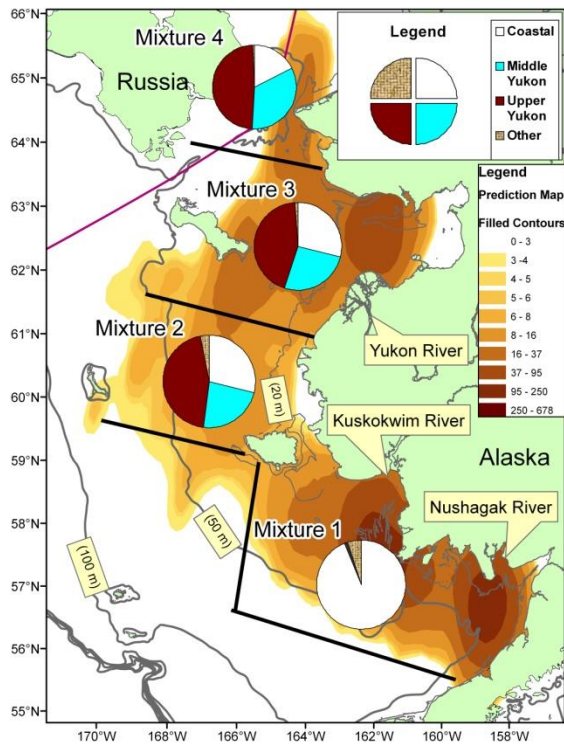
Figure 20. Stock-structured distribution of juvenile Chinook salmon (Coastal Western Alaska: white, Middle Yukon: blue, Upper Yukon: black, and other western Alaska stock groups) captured during surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Mixtures are overlaid on a map of juvenile Chinook salmon distribution and black bars identify the spatial extent of samples used for each mixture. Stock mixtures are adapted from (Murphy et al. 2009) with the inclusion of Bering Strait mixtures (data provided by Bill Templin ADFG, personal communication).

Table 3. Canadian-origin juvenile abundance index, average length, weight, latitude, and mixed layer depth (MLD) temperature from surface trawl surveys in the northern Bering Sea (2003-2011), winter sea ice extent, and the cold pool area index for the eastern Bering Sea shelf. Winter sea ice extent is based on the average number of day of >15% ice cover at the M2, M4, and M5 oceanographic moorings on the eastern Bering Sea shelf (data provided by Sigrid Salo PMEL/NOAA, personal communication). The Eastern Bering Sea (EBS) cold pool area index (km^2) is based on bottom trawl survey area with bottom temperatures less than 0°C (data provided by Bob Lauth AFSC/NOAA, personal communication). T-test probabilities of significant differences in abundance, length, weight, latitude, temperature, winter sea ice, and cold pool area between warm (2003-2007) and cold (2009-2011) years in the northern Bering Sea are included.

| Juvenile Year	Canadian-origin Juvenile Index (1,000s)	Average Length (mm)	Average Weight (g)	Average Latitude (°)	MLD Temp. (°C)	Winter Ice Extent (days)	EBS Cold Pool Index (km^2)
2003	2,302	201	102	63.18	10.15	21.67	5.19
2004	1,189	218	130	62.93	10.88	29.00	16.54
2005	1,556	217	125	62.33	9.37	23.00	30.58
2006	608	194	87	62.52	9.16	61.67	101.05
2007	1,523	231	155	63.17	8.96	61.67	91.40
2008							100.34
2009	842	223	136	61.95	8.03	90.67	141.48
2010	702	206	108	61.96	8.34	99.00	131.24
2011	1,701	195	89	62.02	7.90	65.67	39.71
2003-2007	1,436	212	120	62.83	9.70	39.40	48.95
2009-2011	1,082	208	111	61.98	8.09	85.11	104.14
p(T<=t, alpha =.05)	0.43	0.66	0.56	**<0.01**	**<0.01**	**0.02**	0.22
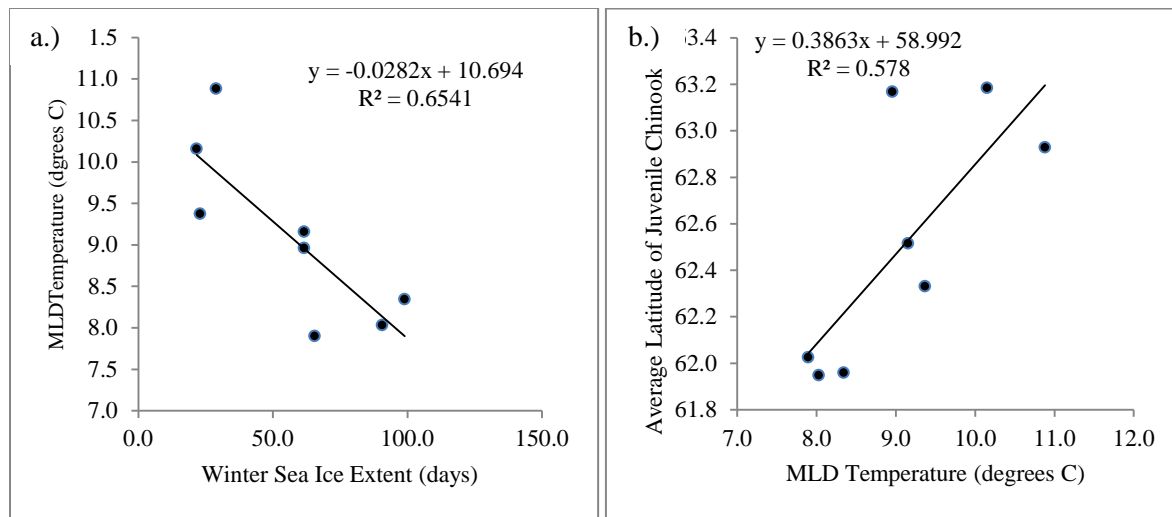
Figure 21.　Relationships between winter sea ice extent and mixed layer depth (MLD) temperature (a.), and between MLD temperature and average latitude position of juvenile Chinook salmon in the northern Bering Sea.　Winter sea ice extent is the average number of days of >15% ice cover at the M2, M4, and M5 oceanographic moorings on the eastern Bering Sea shelf (data provided by Sigrid Salo PMEL/NOAA, personal communication).

Size-Selective Mortality and Energy Density

Phenotypic responses such as growth and energy density in salmon are ultimately under the control of both genetic and environmental forcing (Conover et al. 2009); recognizing and understanding the importance of both are needed to adequately understand constraints on survival and recruitment processes of juveniles (Post and Parkinson 2001, Hurst and Conover 2003).　Size and energy density will covary based on the underlying energy allocation pattern between energy storage and growth.　Increased energetic demand for overwinter survival is expected in high latitude stocks of salmon and is evident in the contrast between energy density and weight of juvenile Chinook salmon in the northern Bering Sea and Gulf of Alaska (Figure 22).　There is a closer relationship between weight and energy density of juvenile Chinook in the northern Bering Sea, and the rate of energy allocation to storage is higher in the northern Bering Sea than the Gulf of Alaska.　Differences in the relationship between energy density and weight in the northern Bering Sea and Gulf of Alaska are believed to reflect counter-gradient variation in juvenile energy allocation (Conover et al. 2009).　Counter gradient variation occurs when genetic and environmental influences oppose one another and diminish the change in phenotypic traits across environmental gradients.　The importance of energy density to overwinter survival may increase the genetic influence on energy allocation patterns of juvenile Chinook salmon in northern Bering

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Sea. An increased genetic influence on energy allocation may explain the relatively close relationship between energy density and weight near the end of their summer growing season (Figure 23). Size-selective mortality models were subsequently developed based on juvenile weight as this is believed to provide a reasonable approximation to the overall condition of juvenile Chinook salmon in the northern Bering Sea.

Size-selective mortality is evident in size distribution differences between juveniles and survivor reconstruction from adult scales (Table 4, Figure. 24). Juveniles had a lower average weight (141 g) and minimum weight (18 g) than survivors (average weight of 169 g and minimum weight of 62 g) from 2003 to 2007. The mortality model for Yukon River Chinook salmon indicates that mortality is very high for the smallest juveniles (these are primarily late out-migrating freshwater age-0 Chinook salmon, but rapidly declines to the point of neutral selection (mortality probability of 0.5) at approximately 138 g (Figure 25). Size-selective mortality is believed to introduce important constraints on juvenile life-history through selection against late out-migration of freshwater age-0 juveniles in Yukon River Chinook salmon. Due to the presence of size-selective mortality, faster growth rates and larger juvenile sizes will improve survival.

The advantage of a size-selective mortality model is that it can be applied to juvenile forecast models without the need to rely on correlations between size and return or size and survival, which will be confounded by other sources of mortality and measurement error in abundance (Table 5). Mortality corrections were based on average juvenile weight standardized to the average date of capture (Sep-15) by an assumed growth rate of approximately 1.2% body weight per day (Walker et al. 2013). Mortality corrections based on average juvenile weight ranged from -0.21 in 2011 to 0.12 in 2007, indicating that size-selective mortality can alter subsequent juvenile survival by as much as 33%; therefore, corrections for size-selective mortality are needed in juvenile abundance-based forecast models of adult returns.

Non-linearity in mortality or survival probability with size is a key element of critical size thresholds required for juvenile survival (Beamish and Mahnken 2001). Without non-linearity in the relationship between size and survival, natural selection will simply serve to drive juveniles to the maximum habitat growth potential. With significant non-linearity, natural selection will only

provide support for juveniles to reach a critical threshold as there is less advantage to survival once juvenile size exceeds this critical threshold. Non-linearity is present in the mortality probability model (Figure 25), although it does not appear to be highly non-linear. However, it is possible that sampling error of reconstructed size of juveniles and/or the effect of combining multiple juvenile years into a single probability model is blurring the true underlying mortality curve. It is reasonable to assume the true relationship has a higher level of non-linearity than we can estimate with this model. The presence of non-linearity in the relationship between size and survival is important when attempting to reconstruct juvenile size distributions from survivors as it will reduce the variation in size of survivors relative to the true size of juveniles (Figure 26) and subsequently between low and high growth periods. Caution is needed when attempting to reconstruct body size and growth rates from scale growth reconstructions during life stages with size-dependent survival.
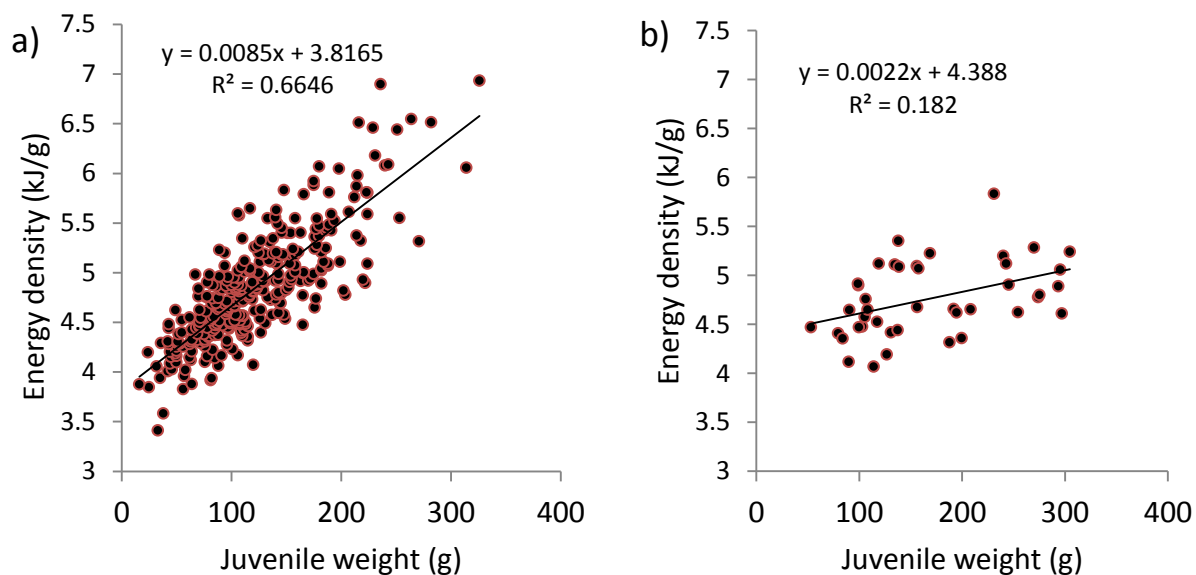
Figure 22. Relationship between weight (g) and energy density (Kj/g) for juvenile Chinook captured during surface trawl surveys in (a.) the northern Bering Sea (2005-2011) and (b.) the Gulf of Alaska (2010-2011).

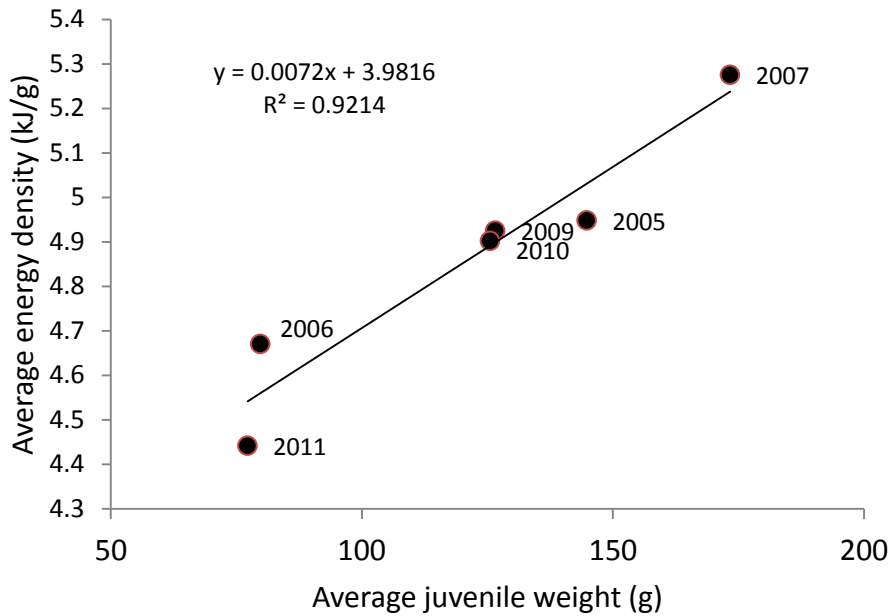Figure 23. Relationship between average weight and average energy density of juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea (2005-2011).
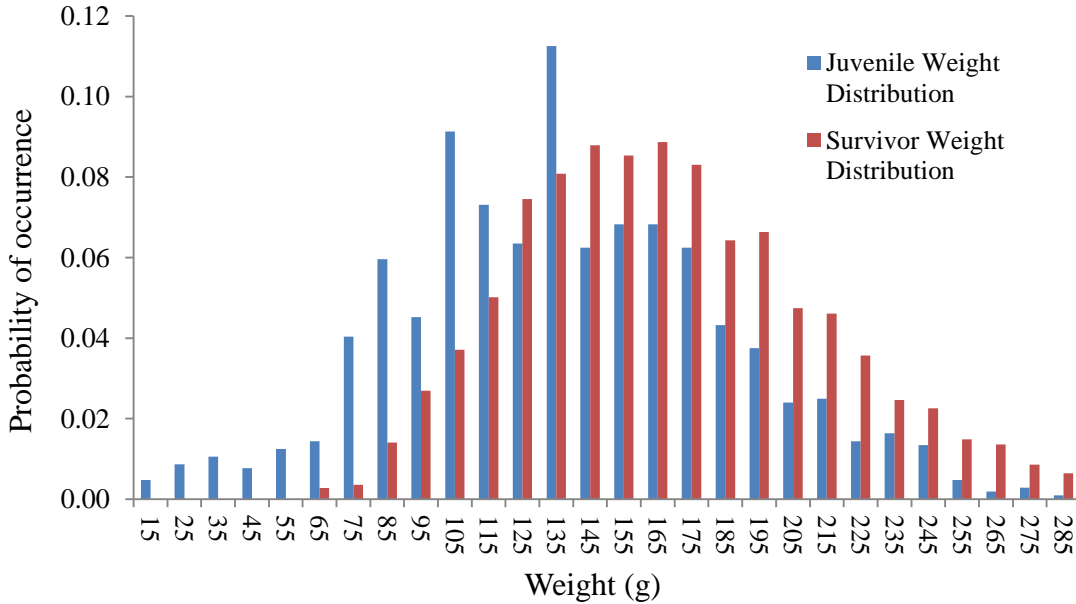
Figure 24. Distribution of juvenile Chinook salmon weight (g) during surface trawl surveys in the northern Bering Sea (2003-2007) and the distribution of surviving juvenile weight (g) based on scale growth measurements of returning adults.

Table 4. Observed juvenile weight distribution, reconstructed weight distribution of surviving juveniles, mortality odds, and size-selective mortality probability for juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea 2003-2007. Reconstructed weight distribution of surviving juveniles was estimated from adult scales collected at Pilot Station, Yukon River.

Weight Bin (g)	Juvenile Weight Distribution	Survivor Weight Distribution	Size-Selective Mortality Odds	Size-Selective Mortality probability
10-20	<0.01	0.00	NA	1.00
20-30	0.01	0.00	NA	1.00
30-40	0.01	0.00	NA	1.00
40-50	0.01	0.00	NA	1.00
50-60	0.01	0.00	NA	1.00
60-70	0.01	<0.01	5.11	0.84
70-80	0.04	<0.01	11.24	0.92
80-90	0.06	0.01	4.22	0.81
90-100	0.05	0.03	1.68	0.63
100-110	0.09	0.04	2.46	0.71
110-120	0.07	0.05	1.46	0.59
120-130	0.06	0.07	0.85	0.46
103-140	0.11	0.08	1.39	0.58
140-150	0.06	0.09	0.71	0.42
150-160	0.07	0.09	0.80	0.44
160-170	0.07	0.09	0.77	0.44
170-180	0.06	0.08	0.75	0.43
180-190	0.04	0.06	0.67	0.40
190-200	0.04	0.07	0.57	0.36
200-210	0.02	0.05	0.51	0.34
210-220	0.03	0.05	0.54	0.35
220-230	0.01	0.04	0.40	0.29
230-240	0.02	0.02	0.66	0.40
240-250	0.01	0.02	0.60	0.37
250-260	0.00	0.01	0.32	0.24
260-270	0.00	0.01	0.14	0.12
270-280	0.00	0.01	0.34	0.25
280-290	0.00	0.01	0.15	0.13

Table 5. Average weight, date of capture, assumed growth rate, date corrected weights, size-selective mortality probability, and mortality corrections by year for juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea (2003-2011). Mortality corrections are based on annual mortality probabilities relative to the 2003-2007 average (years with adult return data and used to calculate average survival).

Year	Weight (g)	Date	Date Difference (Days)	Growth Rate (g/g/day)	Date Corrected Weight (g)	Size-Selective Mortality Probability	Size-Selective Mortality Correction
2003	102	14-Sep	1.80	0.015	104	0.67	-0.11
2004	136	15-Sep	0.80	0.015	137	0.51	0.05
2005	142	23-Sep	-7.20	0.015	130	0.54	0.02
2006	80	8-Sep	7.80	0.015	88	0.76	-0.20
2007	169	19-Sep	-3.20	0.015	163	0.44	0.12
2009	121	5-Sep	10.80	0.015	136	0.52	0.04
2010	118	19-Sep	-3.20	0.015	113	0.62	-0.06
2011	75	4-Sep	11.80	0.015	86	0.77	-0.21
Average (03-07)	126	15-Sep	0.00		126	0.56	
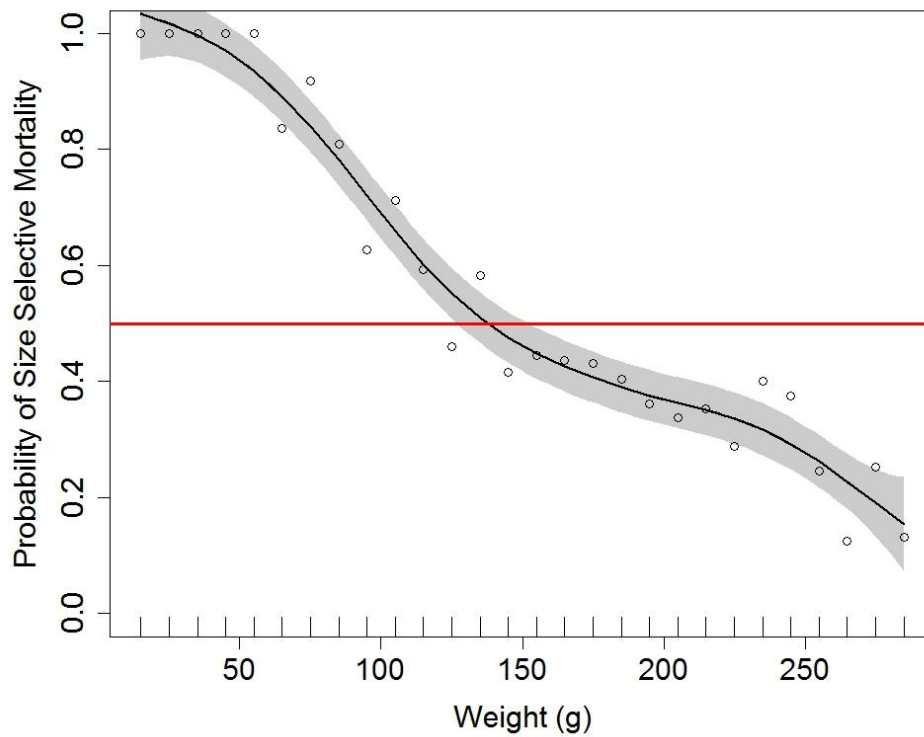
Figure 25. General additive model fit to size selective mortality probabilities of juvenile Yukon River Chinook salmon based on differences between actual juvenile weights and reconstructed weights of surviving juveniles. The 0.5 probability line identifies the reference point of neutral selection; selection is against weights smaller than this point, selection is for weights larger than this point.

Figure 26. Interannual variation in juvenile Chinook salmon fork length (mm) captured during surface trawl surveys in the northern Bering Sea, 2002-2011.
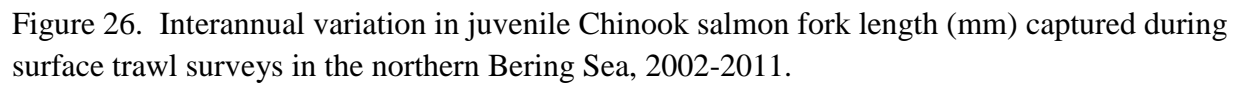
Juvenile Diet, Prey, and Thiamine

Information on juvenile Chinook salmon diet in the northern Bering Sea has been published in two earlier manuscripts (Farley et al. 2009, Cook and Sturdevant 2013) (Appendix 3). Murphy et al. (2012) (Appendix 4) provided a review of the marine ecology of juvenile Chinook salmon in the northern Bering and this review also included information on juvenile diet.

Diet composition by weight of each prey species was estimated by year for juvenile Chinook salmon in the northern Bering Sea and averaged for warm (2004-2007) and cold (2009-2011) years based on mixed layer depth temperature (Figure 27, Table 6). Based on the analysis of stomach contents, juvenile Chinook salmon in the northern Bering Sea predominately feed on larval or age0 life-history stages of fish near the end of their first summer at sea and therefore are largely piscivorous by this stage. Maximum fish prey size consumed by juvenile Chinook salmon was under 90 mm and generally limited to the larval or age0 life-history stage of fish. Biomass estimates of key forage species of juvenile Chinook in the northern Bering Sea were estimated by expanding average surface trawl catch rates to the survey area (Figure 28, Table 7). Distribution of key forage fish species, Pacific Herring (*Clupea pallasii*) and Capelin (*Mallotus villosus*) on the eastern Bering Sea shelf are shown in Figure 29 and Figure 30; however, climate conditions are based on the entire eastern Bering Sea, not the northern Bering Sea, therefore warm and cold years are classified differently (Andrews et al. In Review).

Although Pacific Herring are the largest fish biomass present in surface trawl surveys in the northern Bering Sea, they were minimally present in the diet of juvenile Chinook salmon (6% in warm years and 3% in cold years). Biomass levels in Figure 28 and Table 7 do not reflect the forage biomass available to juvenile Chinook as it includes all life-history stages of fish (except for age-0 Pollock biomass). Juvenile Chinook are only able to feed on the smaller age-0 life-history stage of fish. A closer look at interannual diet and size structure of Pacific Herring, indicates that the occurrence of herring in juvenile Chinook diets is likely a combination of age-0 Pacific Herring abundance and the ability of age-0 herring to outgrow the prey size spectrum of juvenile Chinook salmon by September. The only year that Pacific Herring contributed significantly to the diet of juvenile Chinook salmon was during 2004 (20% of juvenile Chinook diet, Table 6). Although the biomass of herring was not the highest in 2004, most of the herring were within the age-0 size class (Figure 31). However, even with large numbers of age-0 herring in 2004, other species like Pacific sandlance (34% of the diet in 2004) contributed more to the

diet of juvenile Chinook than Pacific Herring. The occurrence of age-0 herring in the diet of juvenile Chinook appears to follow interannual variability in their abundance, but most of the age-0 herring exceed the prey size window observed for juvenile Chinook salmon in the Northern Bering Sea during September.

Capelin were an important prey item in both warm and cold years, but comprised the majority (57%) of the diet during cold years. The increase in capelin in the diet of juvenile Chinook is consistent with the increase in Capelin biomass in the northern Bering Sea during cold years (Figure 28). Biomass estimates are of all ages and sizes of Capelin not just the age0 life-history stage that juvenile Chinook salmon utilize for forage so it is not possible to make direct correlations between trawl catch biomass and prey availability. However, increased biomass of Capelin implies improved recruitment and therefore will, in general, reflect greater availability of the age-0 life-history stage of Capelin. The smallest size mode of capelin in surface trawl catches (50 mm; Figure 32) is consistent with the typical fish size observed in stomach contents of juvenile Chinook salmon (typically 40-80 mm). Age0 capelin abundance peaks in September and October in the Gulf of Alaska bongo net tows (Doyle et al. 2002) and their size distribution is consistent with the smallest size mode of capelin in the northern Bering Sea and age0 capelin sizes observed during October in Prince William Sound (Brown 2002). Trawl catchability for age0 capelin is believed to be very low; therefore the occurrence of this size mode only indicates presence, not abundance.

Sandlance (*Ammodytes hexapterus*) was the second most important diet item and comprised a similar proportion of juvenile Chinook salmon diets in both warm and cold year (21% in warm years and 20% in cold years). Interestingly, sandlance are only minimally present in the catch biomass (Table 7) and may reflect low trawl catchability for adult sandlance or a feeding preference of Chinook salmon on sandlance.

Age0 pollock (*Theragra chalcogramma*) were only present in the diet of juvenile Chinook salmon during warm years and is consistent with increase catch of age-0 pollock in the northern Bering Sea (Table 7). Increased biomass and northward dispersal of age-0 pollock from the southern Bering Sea has been observed in warm years in the eastern Bering Sea (Hollowed et al. 2012). Other fish species included in juvenile Chinook diets included rainbow smelt (*Omerus mordax*) and Greenland halibut (*Reinhardtius hippoglossoides)* larvae; other diet items include invertebrate species such as small Pandalid shrimp (*Pandalus borealis).*

Size-spectrum of prey species is believed to be important feature in the foraging ecology of juvenile Chinook salmon and increases their dependency on recruitment success and spawn timing of key forage fish populations like Capelin and herring. The small size of Capelin could be the principal reason why capelin are the dominate prey of juvenile Chinook in September. If the absence of age0 herring in the diet of Chinook is primarily due to their ability to outgrow the prey size window for juvenile Chinook, it is unlikely that this will be true earlier in the summer and herring could be an important prey species for juvenile Chinook earlier in the summer. Prey species that juvenile Chinook utilize during their initial marine life-history stage may be very important to their survival, therefore it is essential to have diet information earlier in their growing season to provide a clearer picture of marine ecosystem dependencies of juvenile Chinook salmon.

Figure 27. Proportion of different prey species present in stomach contents of juvenile Chinook salmon captured during surface trawl surveys in the northern Bering Sea during warm years (2004-2007) and cold years (2009-2011). Proportions are based on a catch weighted stomach content index. Average mixed layer temperatures during surface trawl surveys in the northern Bering Sea were used to separate diet data into warm and cold periods.
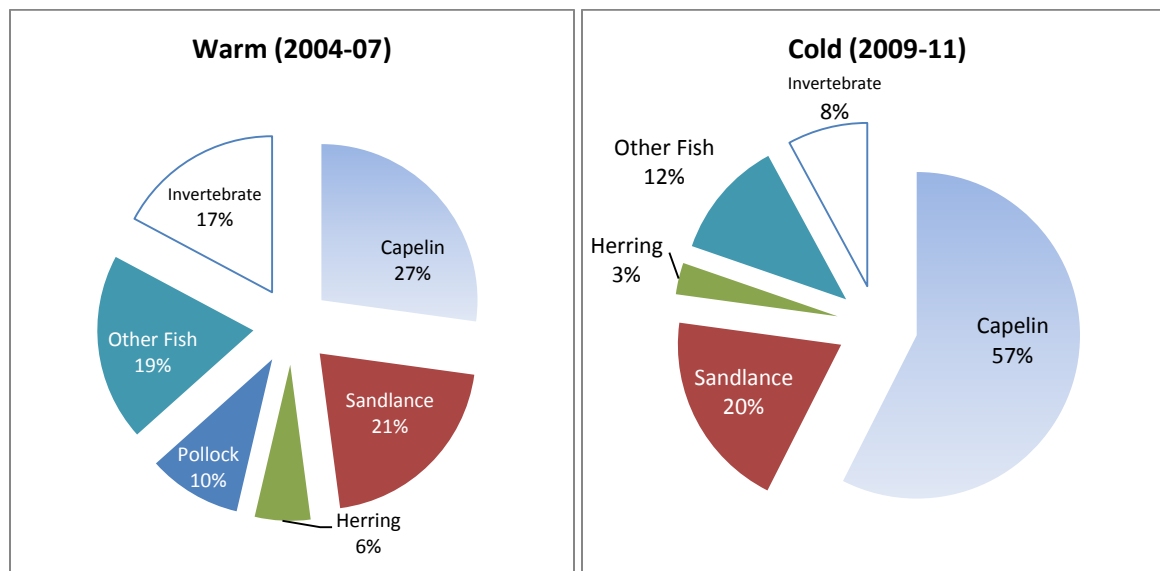
Table 6. Proportion of fish and invertebrate prey species present in the diet of juvenile Chinook salmon captured during surface trawl surveys in the Northern Bering (2004-2011).

Year	Capelin	Pacific Sandlance	Pacific Herring	Walleye Pollock	Other Fish	Invertebrate
2004	0.15	0.34	0.20	0.12	0.01	0.18
2005	0.39	0.02	0.03	0.17	0.09	0.30
2006	0.23	0.30	0.00	0.08	0.29	0.11
2007	0.32	0.17	0.00	0.03	0.39	0.10
2009	0.66	0.21	0.00	0.00	0.00	0.13
2010	0.71	0.05	0.02	0.00	0.15	0.07
2011	0.36	0.33	0.07	0.00	0.20	0.04
Warm (2004-07)	0.27	0.21	0.06	0.10	0.19	0.17
Cold (2009-11)	0.57	0.20	0.03	0.00	0.12	0.08
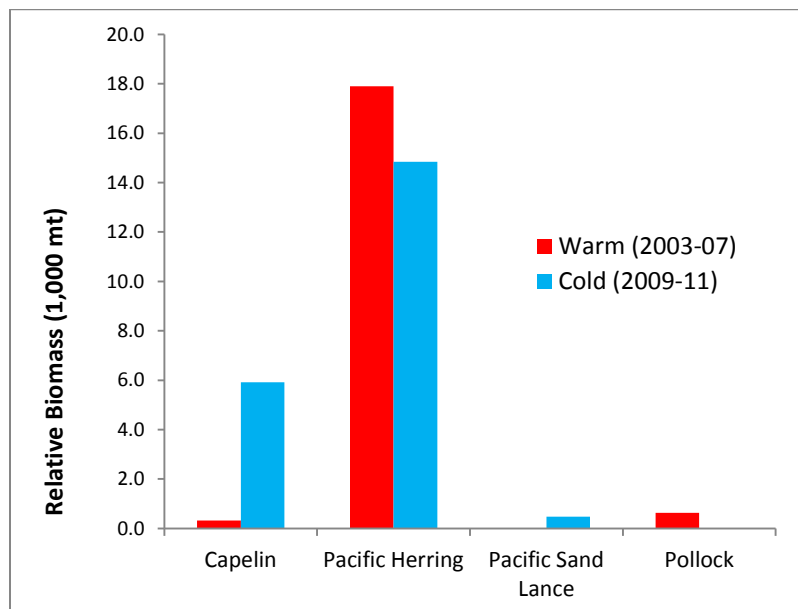
Figure 28. Relative biomass for all ages and sizes of forage fish prey species (except Pollock) observed in juvenile Chinook salmon diet during surface trawl surveys in the northern Bering Sea (2004-2011). Biomass estimates of Pollock are for just the age0 life-history stage. Mixed layer depth temperatures during surface trawl surveys in the northern Bering Sea were used to separate biomass data into warm and cold periods.

Table 7. Relative biomass estimates (mt) of Capelin, Pacific Herring, Pacific Sandlance, and Walleye Pollock from surface trawl surveys in the northern Bering Sea (2003-2011). Average mixed layer depth temperature was used to separate years between warm and cold periods.

Year	Capelin	Pacific Herring	Pacific Sandlance	Walleye Pollock
2003	35	11,347	45	242
2004	90	24,654	0	1,166
2005	823	9,541	1	1,738
2006	89	28,562	1	3
2007	573	15,411	0	17
2009	786	5,005	34	0
2010	14,358	10,209	1,199	5
2011	2,622	29,325	180	0
Warm (2003-07)	322	17,903	9	633
Cold (2009-11)	5,922	14,846	471	2

Figure 29. Capelin biomass (kg/km^2) and abundance (num/km^2) plots of Warm (2003-2005) and Cold (2006-2011) climate periods (Andrews et al. In Review). Colored layers were created using local polynomial interpolation. Circles represent haul effort and magnitude of biomass or abundance.

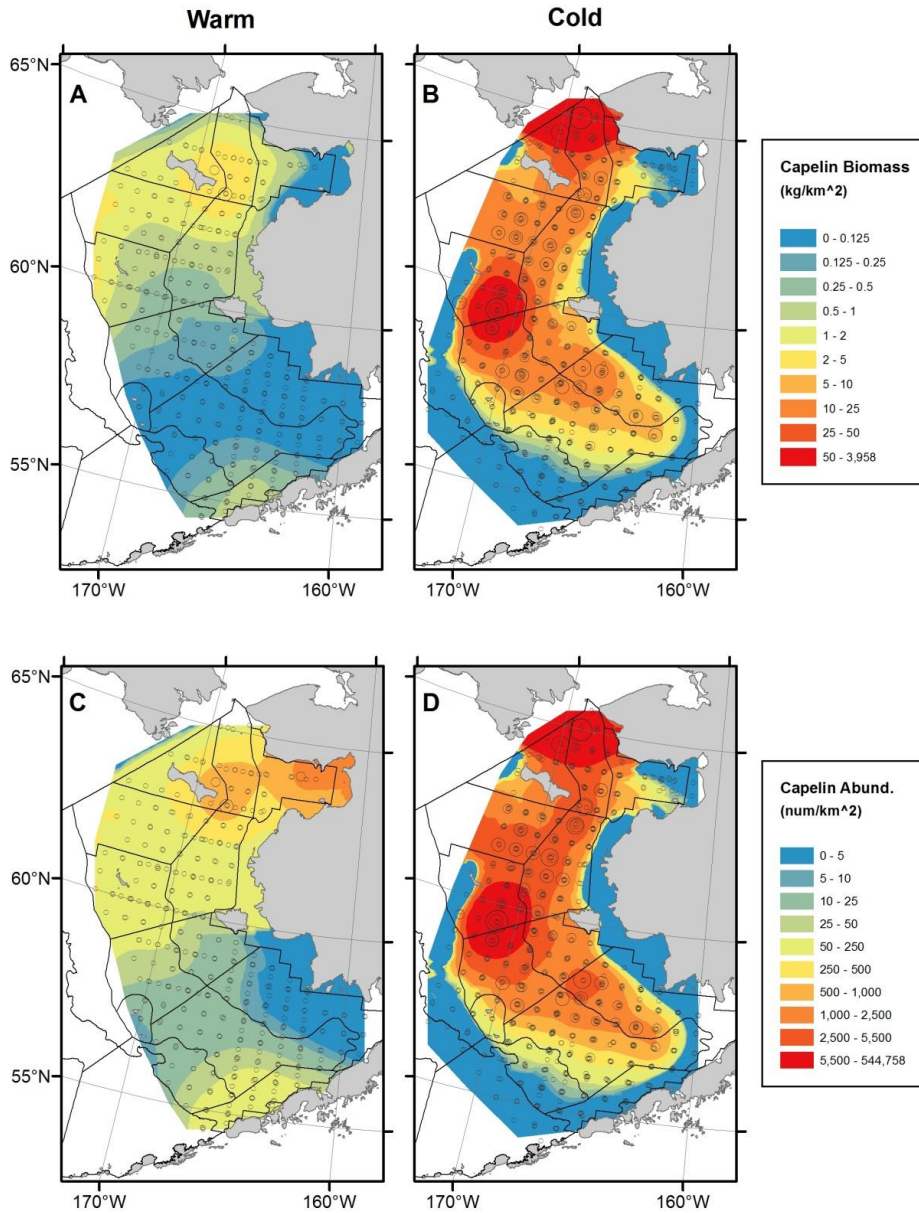Figure 30. Herring biomass (kg/km^2) and abundance (num/km^2) plots of Warm (2003-2005) and Cold (2006-2011) climate periods (Andrews et al. In Review). Colored layers were created using local polynomial interpolation. Circles represent haul effort and magnitude of biomass or abundance.
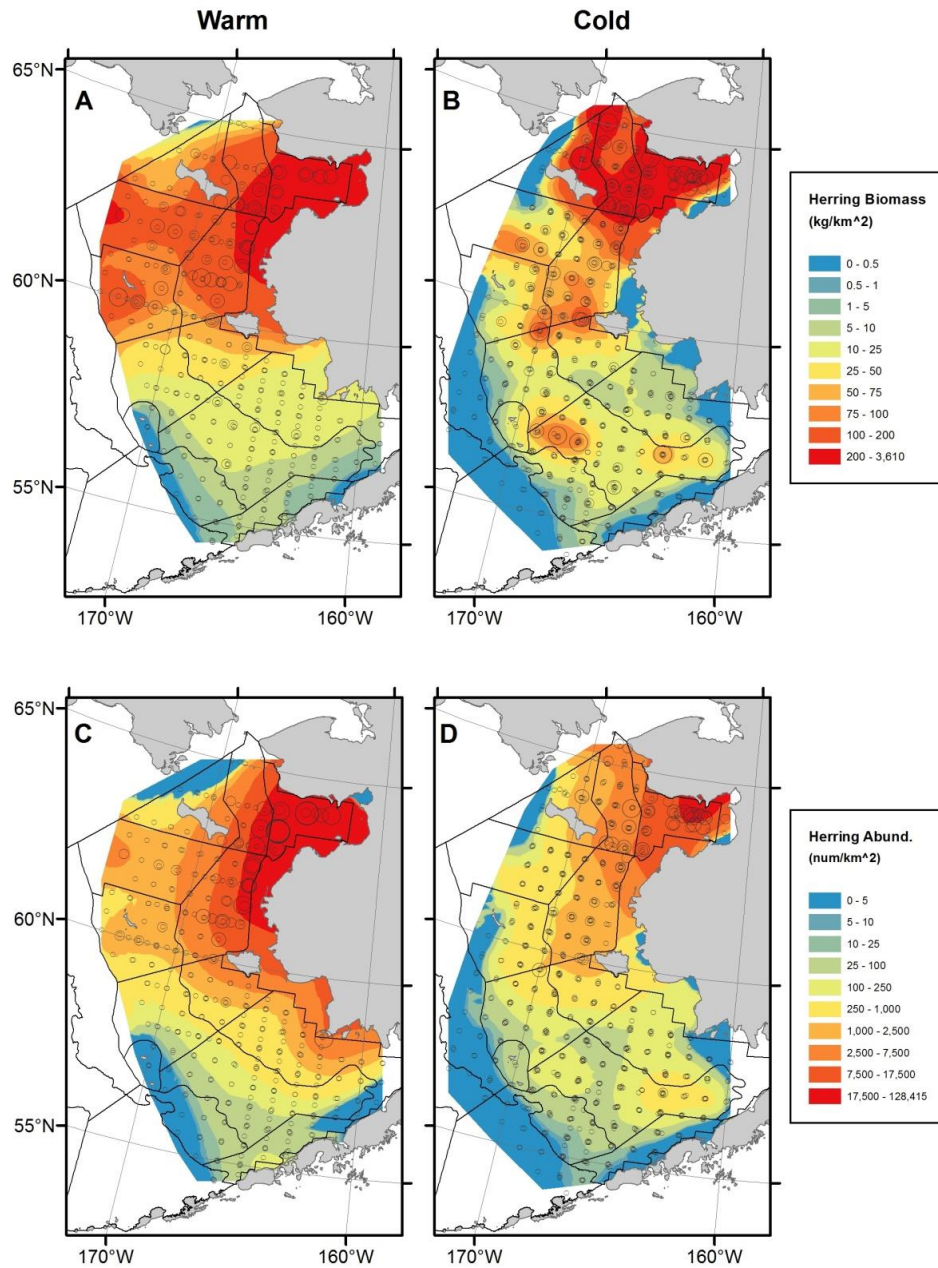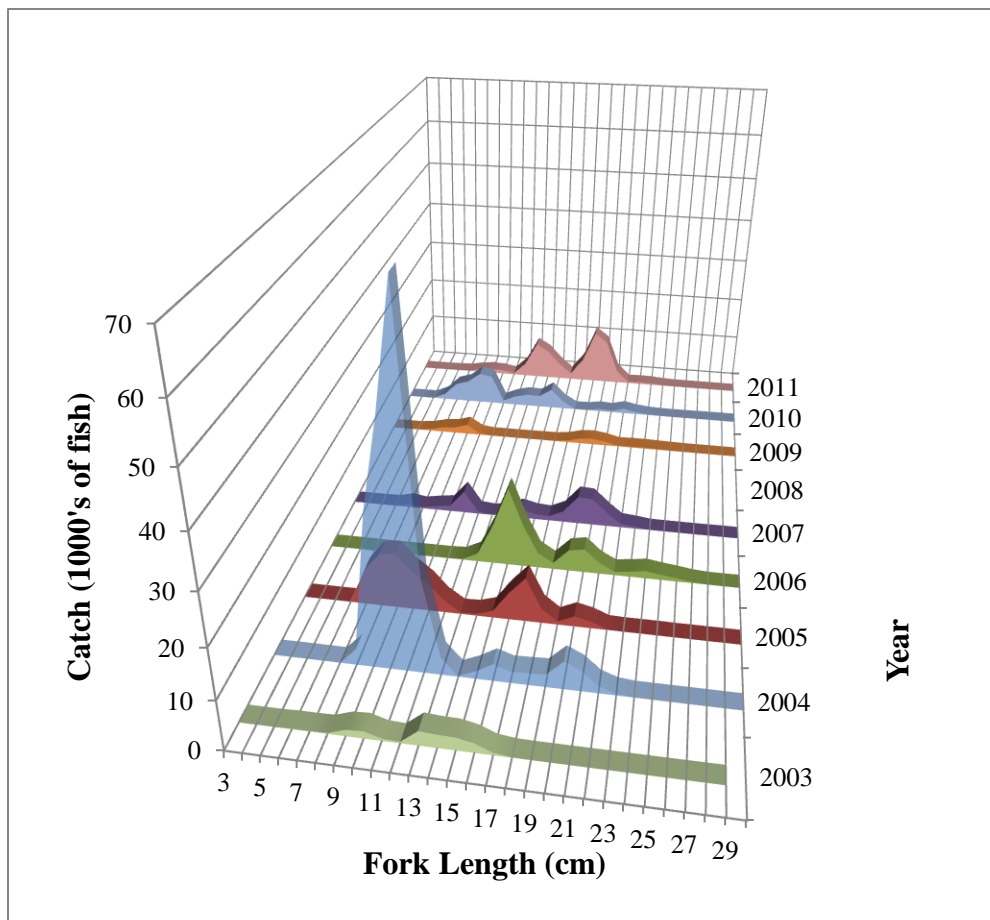
Figure 31. Length distributions of herring captured during surface trawl surveys in the northern Bering Sea (2003-2011).
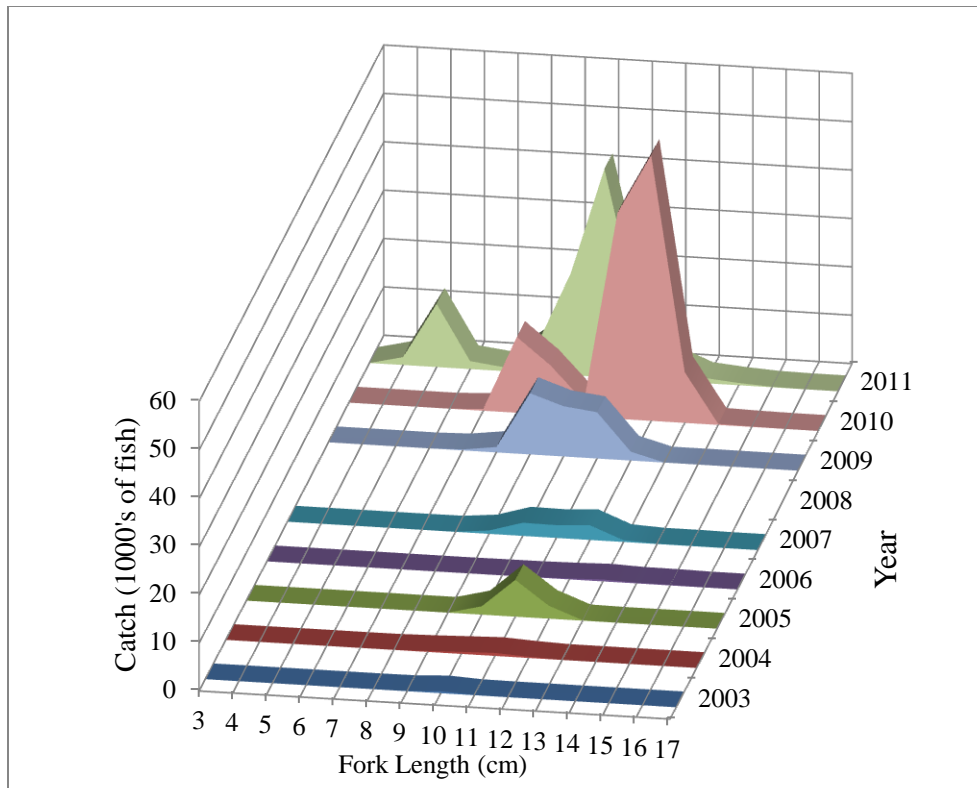
Figure 32. Length distributions of Capelin captured during surface trawl surveys in the northern Bering Sea (2003-2011).

Dietary sources of thiamine and thiaminase are known to result in important nutritional deficiencies in fish populations (Honeyfield et al. 2005). Egg samples collected from Yukon River Chinook salmon in 2012 were compared with egg samples collected in 2001 to explore the potential for thiamine deficiency as a contributing factor in recent production declines in Yukon River Chinook salmon (Honeyfield et al. In Prep) (Appendix 5). Most of the female Chinook salmon sampled from the Yukon River (79%, 30 of 38 egg samples) in 2012 showed evidence of thiamine deficiency in egg thiamine levels (<8.0 nmol/g total thiamine); however only one female (3%) contained egg thiamine levels low enough to result in overt fry mortality (<1.5 nmol/g total thiamine). Egg thiamine concentrations decreased with migratory distance, reflecting the utilization of thiamine during upstream migration of adults, similar to the pattern observed in coho salmon and Rainbow trout (Fitzsimons et al. 2005, Ketola et al. 2005). Thiamine deficiency was not present in egg thiamine in 2001 (> 8 nmol/g total thiamine); however, egg thiamine levels were lower in the Upper Yukon collection (9.6 nmol/g total thiamine) than the Kuskokwim River (11.7 nmol/g total thiamine), consistent with migratory depletion of thiamine. The 2001 Upper

Yukon egg samples were collected at a different location (Rampart Rapids) than the 2012 collections (Whitehorse Hatchery), which may also be contributing to differences in thiamine concentrations between the two time periods. The 2001 brood year of the Upper Yukon stock group was more productive (returns per spawner = 2.03) than recent returns to the Yukon River (returns per spawner < 1.25) (JTC 2013); fully replete egg thiamine levels may have contributed to the higher productivity of Upper Yukon Chinook salmon in 2001. Additional analysis of egg thiamine will be required to adequately assess and understand thiamine status of Yukon River Chinook salmon as well as the role of thiamine depletion during upstream migration; however, results from this exploratory analysis indicate that a closer look at thiamine deficiency in Yukon River Chinook is warranted.

Total thiamine levels in muscle and liver tissue of juvenile salmon were above critical levels and varied with the dietary intake of thiaminase positive prey (Honeyfield et al. In Prep) (Appendix 5). Thiaminase is an enzyme found in the gut cavity of certain fish prey and is the primary cause of thiamine deficiency in fish. Thiamine concentrations (nmol/g total thiamine) in juvenile Chinook (muscle=3.8, liver=16.4) and Coho (4.2, 18.3) salmon were lower than juvenile Chum (8.9, 23.9) and Pink (9.6, 22.2) salmon. Chinook salmon diets consisted of 73% thiaminase positive prey (primarily Capelin *Mallotus villosus*) and more than half of the Coho salmon diet (54%) consisted of thiaminase positive prey. In contrast, Chum and Pink salmon diets contained only 4% and 11% thiaminase positive prey, respectively. Dietary sources of thiamine and thiaminase are the primary factors determining thiamine deficiency in fish populations; therefore, improved understanding of the feeding ecology of Chinook salmon in marine ecosystems will improve our understanding of how changes in marine prey could be contributing to thiamine deficiency in Yukon River Chinook salmon.

SUMMARY

Juvenile abundance (2003-2007) is significantly related to adult abundance for Canadian-origin Yukon River Chinook salmon. This indicates that early life-history stages (freshwater and estuarine) have contributed more to the survival and production of Canadian-origin Chinook salmon in recent years than the later marine life-history stages (highseas). Assuming this pattern in production continues in the future, juvenile abundance can be used as a meaningful indicator of future returns to assist pre-season fishery management decision.

Migratory patterns of juvenile Chinook salmon in the northern Bering Sea are dynamic and juvenile Chinook tend to be distributed further north during warm years. Northward dispersal of juvenile Chinook from the Yukon River is expected to displace juveniles from their closest suitable overwinter habitats in the southern Bering Sea. Some evidence exists that migratory patterns may be impacting juvenile survival, but additional analysis of juvenile migration is needed before it can be applied to survival.

The importance of energy density to overwinter survival in juvenile Chinook salmon in northern Bering Sea is believed to result in stronger genetic control over energy allocation to storage. This effect is believed to allow juvenile weight to be used as a reasonable approximation to the overall condition of juvenile Chinook. Size-selective mortality models, based on juvenile weight, indicate that mortality is very high for the smallest juveniles present in the juvenile population but rapidly declines to the point of neutral selection at approximately 138 g. Size-selective mortality is believed to introduce important constraints on juvenile life-history through selection against late out-migration of freshwater age-0 juveniles in Yukon River Chinook salmon. Changes in juvenile size over time introduce important variation in survival and corrections for size-selective mortality are needed in return forecast models based on juvenile abundance.

Juvenile Chinook salmon in the northern Bering Sea are largely piscivorous near the end of their first summer at sea (September). Age-0 Capelin were the primary prey species in the diet of juvenile Chinook salmon and their importance varied with abundance. Age-0 Pacific Herring were present in the diet of juvenile Chinook, but their overall importance was much less than smaller prey species like age-0 Capelin and Sandlance. Although prey biomass is an important feature in juvenile Chinook salmon diets; size-spectrum of prey species is believed to be particularly important in Chinook salmon diets during their first summer at sea. Due to their high level of piscivory, Chinook salmon are particularly susceptible to adverse effects of thiamine deficiency through the ingestion of thiaminase. Thiamine deficiency is believed to be present in Yukon River Chinook salmon and additional research on thiamine deficiency is needed to understand its effect on survival.

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Appendix 1. Murphy, J., K. Howard, L. Eisner, A. Andrews, W. Templin, C. Guthrie, K. Cox, and E. Farley. 2013. Linking abundance, distribution, and size of juvenile Yukon River Chinook salmon to survival in the northern Bering Sea. North Pacific Anad. Fish. Comm. Tech. Rep. 9:25-30.

Linking Abundance, Distribution, and Size of Juvenile Yukon River Chinook Salmon to Survival in the Northern Bering Sea

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Significant harvest restrictions, including the closure of commercial fisheries and reductions in subsistence fisheries, have been implemented in response to declining production levels of Yukon River Chinook salmon stocks. Causes of their production decline are unclear; however concurrent declines throughout the Yukon River drainage (JTC 2013), production declines in other regions of Alaska (ADFG 2012), declines in marine survival in southeast Alaska Chinook salmon stocks (Guyon et al. 2013), and the presence of bycatch in marine fisheries (Stram and Ianelli 2009) emphasize the importance of ocean conditions and the marine life-history stage of Chinook salmon.

Yukon River Chinook salmon utilize marine habitats adjacent to or on the eastern Bering Sea shelf throughout most of their marine life-history stage (Myers, et al. 2009). Sea ice and its impact on ecosystem level processes on the shelf is an important feature in the marine ecology of western Alaska salmon populations (Farley and Trudel 2009; Moss et al. 2009). Although the principal change in Arctic sea ice has occurred during the summer melt season through the loss of multi-year ice levels, sea ice primarily impacts the Bering Sea through winter/spring ice extent and seasonal ice levels. Winter/spring ice extent has not declined in a manner similar to summer ice and has actually increased in recent years, resulting in recent cooling of the Bering Sea (Stabeno et al. 2012). We review information on juvenile abundance, distribution, and size in relation to survival of Yukon River Chinook salmon and describe how they are connected to sea ice and broad-scale temperature changes in the eastern Bering Sea.

A Canadian-origin juvenile abundance index constructed from surface trawl catch, stock composition, and mixed layer depth data was used to describe juvenile abundance. Juvenile data were provided by the Alaska Fisheries Science Center as part of the US Bering-Aleutian Salmon International Survey (NPAFC 2001) and similar ecosystem-based projects in the northern Bering Sea. Surface trawl operations are described in Murphy et al. (2003) and Farley et al. (2009).

Average juvenile Chinook salmon CPUE (catch/km²) was expanded to an abundance index by the survey area, sampling grid area, and number of stations. The northern Bering Sea was divided into four spatial strata: 60°-62°N, 62°-64°N, Norton Sound, and Bering Strait, and corrections were used to adjust for inconsistent survey effort in the Norton Sound and Bering Strait strata over time. A single nucleotide polymorphism (SNP) genetic baseline (Templin et al. 2011b) was used to estimate stock mixtures of juvenile Chinook salmon through genetic mixed stock analysis (Pella and Masuda 2001). Canadian-origin stock proportions in the northern Bering Sea were reported in Murphy et al. (2009), Templin et al. (2011a), and Guthrie et al. (2013).

Mixed layer depth (MLD) corrections were applied to juvenile catch data to adjust for variation in trawl depth and vertical distribution of juvenile Chinook salmon by assuming a uniform distribution of juvenile Chinook salmon within the surface mixed layer. The MLD was defined as the depth where seawater density increased by 0.10 kg/m³ relative to the surface (Danielson et al. 2011). The MLD correction to trawl catch, θy, was estimated as:

$$\theta_y = \sum_j \frac{MLD_{j,y}}{TD_{j,y}} C_{j,y}.$$

where $MLD_{j,y}$, $TD_{j,y}$, and $C_{j,y}$ are the mixed layer depth, trawl depth, and catch, respectively, at stations, j, where trawl depth is above the mixed layer, and year, y. MLD trawl catchability correction, q_y, was estimated by:

$$q_y = \frac{\theta_y}{\Sigma_i C_{i,y}}.$$

where $C_{i,y}$, is the catch at the ith station in year, y.

Brood year returns of Canadian-origin Chinook salmon to the Yukon River (JTC 2013) and the Canadian-origin juvenile index were used to define the relationship between juvenile and adult abundance. Brood year returns were rescaled to juvenile year based on the assumption that all juveniles were freshwater age-1. Although freshwater age-0 and age-2 Chinook salmon are present in the juvenile population, their numbers are low relative to the number of freshwater age-1 juveniles.

Juvenile scales and body size in the northern Bering Sea (2002-2007), and age structure and scales of adult Chinook salmon returning to the Yukon River (2004-2011) were used to model size-selective mortality. A subsample of 150 scales from Pilot Station in the lower Yukon River was digitized for each juvenile year proportional to age structure. The average (22) and standard deviation (1.98) of juvenile scale circuli counts after the last freshwater annulus were used as the sampling distribution of adult scale circuli. Adult scale measurements were converted to juvenile length (mm) from the juvenile scale radius (mm) model (length = 149.98*radius+49.367) and reconstructed juvenile lengths (mm) were converted to weight (g) with the length-weight relationship for juvenile Chinook (ln(weight) = 3.0816*ln(weight)-11.735). Weight models were used to describe size-selective mortality as size-selective mortality at this life-history stage is believed to be primarily a function of energy storage (Beamish and Mahnken 2001). Due to the underlying energy allocation patterns of juvenile Chinook salmon in the northern Bering Sea, energy density is primarily a function of size and is linear with juvenile weight (Fig. 1). Size selective mortality probabilities, ρ_i, were estimated from the proportion of juvenile, j_i, and surviving adults, a_i, within each weight interval, i, as:

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

Generalized additive models (Chambers and Hastie 1992) were fit to mortality probabilities and used to describe size-selective mortality in juvenile Chinook salmon.
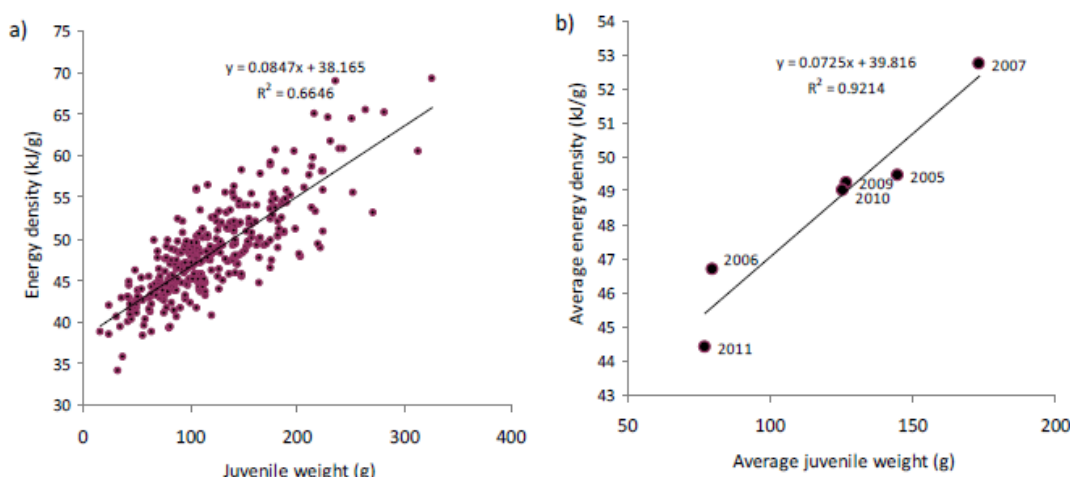
Fig. 1. The relationship between weight (g) and energy density (kJ per gram) of juvenile Chinook salmon in the northern Bering Sea for individual fish (a) and by year (b).

Average seawater temperature within the mixed layer from the BASIS surface trawl surveys were used to define inter-annual variability in seawater temperature of the northern Bering Sea shelf. Significant differences in juvenile abundance, distribution, and size between warm (2003-2007) and cold (2009-2011) years were evaluated with a Student's t-test.

Juvenile abundance of the Canadian-origin stock group was positively correlated with adult returns (r = 0.89, p = 0.04 r² = 0.62 n = 5; Fig. 2) indicating that juvenile abundance explains a significant (p < 0.05) amount of the variability present in recent adult returns. This emphasizes the importance of freshwater and estuarine (early marine) life history stages to inter-annual variability in adult returns. However, the average juvenile survival index is low (0.06; Table 1) and, therefore, mortality after the juvenile stage is important to their overall production; ecosystem and fishery effects on survival after the juvenile stage are needed to adequately address production dynamics of Yukon River Chinook salmon.

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Fig. 2. The relationship between the Canadian-origin juvenile Chinook salmon abundance index and adult returns by juvenile year (2003-2007). Juvenile year is added to each data point.

Temperature limitations in the northern Bering introduce important constraints on juvenile migration. Juveniles are unlikely to survive in the northern Bering Sea o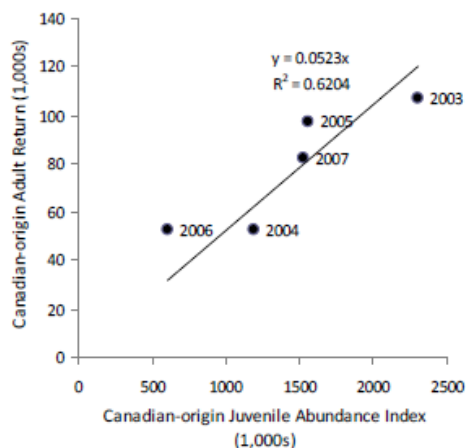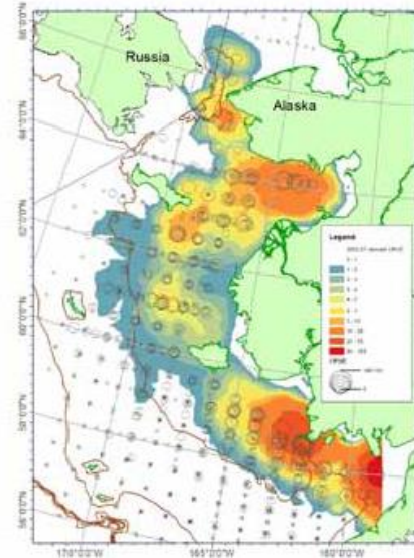nce sea ice forms, and quite possibly prior to the formation of sea ice. Sea ice begins to form in coastal habitats utilized by juvenile Chinook in early November and the entire northern shelf is ice covered by early January. Sea water freezes at approximately -1.7 °C in the northern Bering Sea as its salinity is in the range of 30-31 PSU (practical salinity unit). Due to shallow water depths in the northern Bering Sea, the entire water column drops below zero as sea ice forms (under ice temperatures reported in Danielson et al. 2006). Salmon lose metabolic function and cannot survive in temperatures near zero for any length of time (Brett and Alderdice 1958). The southern Bering Sea is believed to be the closest suitable overwinter habitat for Yukon River Chinook salmon. Northward dispersal/migration of juveniles through increased current speeds or northward migration behavior will displace juveniles away from winter habitats and may impact their survival (Fig. 3). Average latitude position of juveniles was negatively correlated with survival (r = -0.68, n = 5, $p = 0.21$; Table 1), and provides support (but not significant ($p < 0.05$) support) for the linkage between juvenile migration and survival.

Table 1. Juvenile abundance index, mixed layer depth (MLD) corrections, Canadian-origin stock proportions in northern Bering Sea juveniles, adult returns, and survival index for Canadian-origin Yukon River Chinook salmon from surface trawl surveys in the northern Bering Sea (2003-2011). Average length, weight, and latitude position of juvenile Chinook in the northern Bering Sea, and average seawater temperatures above the mixed layer depth from surface trawl surveys in the Bering Sea. T-test probabilities of significant differences in abundance, length, weight, latitude, and temperature between warm (2003-2007) and cold (2009-2011) years.

Juvenile Year	Juvenile Index (1,000s)	MLD correction	Canadian Stock Proportion	Canadian Juvenile Index (1,000s)	Canadian Return (1,000s)	Survival Index	Length (mm)	Weight (g)	Latitude (°)	MLD Temp. (°C)
2003	4,728	0.14	0.43	2,302	107	0.05	201	102	63.18	10.15
2004	2,064	0.12	0.52	1,189	53	0.04	218	130	62.93	10.88
2005	2,563	0.29	0.47	1,556	97	0.06	217	125	62.33	9.37
2006	1,179	0.13	0.46	608	53	0.09	194	87	62.52	9.16
2007	2,748	0.16	0.48	1,523	82	0.05	231	155	63.17	8.96
2008										
2009	1,846	0.01	0.45	842			223	136	61.95	8.03
2010	1,558	0.05	0.43	702			206	108	61.96	8.34
2011	3,209	0.16	0.46	1,701			195	89	62.02	7.90
2003-2007	2,656	0.17	0.47	1,436			212	120	62.83	9.70
2009-2011	2,204	0.07	0.45	1,082			208	111	61.98	8.09
p(T <= t, alpha =.05)				0.43			0.66	0.56	<0.01	<0.01

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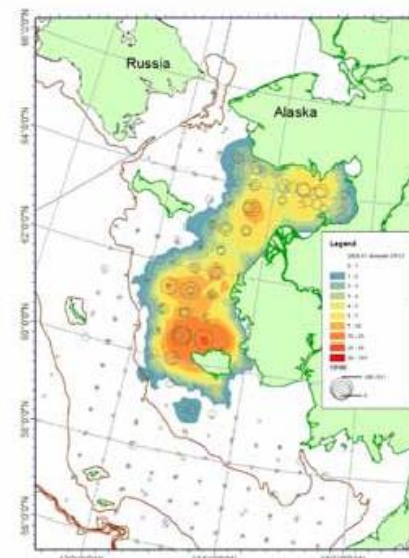a) 2002-2007   b) 2009-2011

Fig. 3. Distribution of juvenile Chinook salmon catch-per-unit-effort (CPUE, catch/km²) from surface trawl surveys on the eastern Bering Sea Shelf, August-September (2002-2011). Circles are CPUE data at each sample location and average CPUE is shaded from low to high with hues from blue to red. Distributions are shown for two time periods (a) 2002-2007 and (b) 2009-2011. Bering Sea temperatures were warmer during 2002-2007 than 2009-2011.

Size-selective mortality is evident in size distribution differences between juveniles and survivor reconstruction from adult scales (Fig. 4). Juveniles had a lower average weight (141 g) and minimum weight (18 g) than survivors (average weight of 169 g and minimum weight of 62 g). The mortality model for Yukon River Chinook salmon indicates that mortality is very high for the smallest juveniles (these are primarily late out-migrating freshwater age-0 Chinook salmon, distinguishable from age-1 Chinook by the presence of freshwater parr marks), but rapidly declines to the point of neutral selection (mortality probability of 0.5) at approximately 138 g (Fig. 5). Size-selective mortality is believed to introduce important constraints on juvenile life-history through selection against late out-migration of freshwater age-0 juveniles in Yukon River Chinook salmon. Due to the presence of size-selective mortality, faster growth rates and larger juvenile sizes will improve survival.
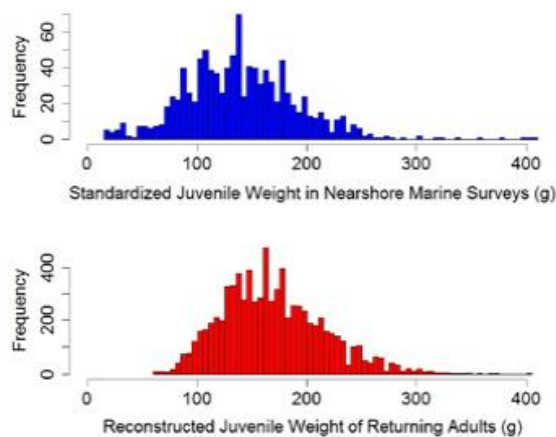
Fig. 4. Distribution of juvenile Chinook salmon weights (g) during September (2002-2007) in the northern Bering Sea and survivor weights reconstructed from adult scales collected at Pilot Station in the lower Yukon River.
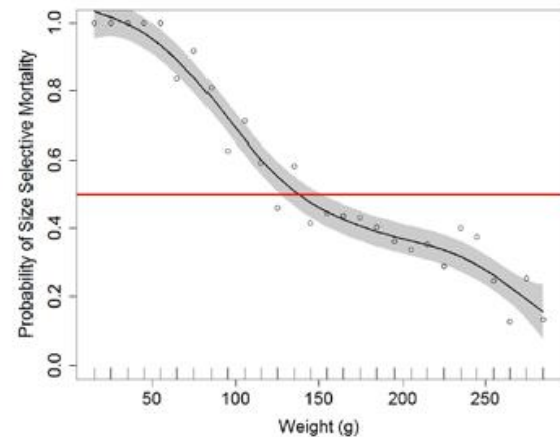
Fig. 5. A generalized additive model fit to size-selective mortality probability of juveniles collected during September (2002-2007) in the northern Bering Sea.

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Although juvenile abundance and size were lower in colder years, juvenile distribution (average latitude) was the only feature of the juvenile population that differed significantly (Student's t-test $p = 0.01$, alpha = 0.05) between warm and cold years (Table 1). The absence of significance may reflect a greater dependency of juvenile abundance and size on freshwater and estuarine (local) processes not linked to broad-scale temperature patterns of the eastern Bering Sea. Marine distribution patterns of juveniles appear to have a closer linkage to broad-scale ecosystem patterns of the Bering Sea ecosystem and emphasize the potential negative impact that the loss of sea ice and warming of the Bering Sea could have on juvenile migration and survival. Although adult returns appear to be primarily a function of juvenile abundance and not juvenile survival, juvenile survival impacts the ability to use juvenile abundance as a leading indicator of future returns to the Yukon River

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Appendix 2. Gann, J. C., L. B. Eisner, and S. Danielson. 2013. How do oceanographic characteristics of the northern Bering Sea relate to juvenile salmon biomass? North Pacific Anad. Fish. Comm. Tech. Rep. 9:83-89.

How do Oceanographic Characteristics in the Northern Bering Sea Relate to Juvenile Salmon Biomass?

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Keywords: oceanography, North Bering Sea, juvenile salmon, temperature, salinity, zooplankton abundance

The oceanography and shelf dynamics of the southern East Bering Sea (EBS) have been well-studied, while less attention has been given to the northern EBS, although commercially important fisheries are present in both the south and the north. Sea ice extent and duration, and freshwater inputs from the Yukon River are substantially higher in the north compared to the south, resulting in large variations in oceanography between the northern and southern EBS and between regions within the northern EBS. Our goal is to describe spatial and inter-annual variations in oceanographic characteristics (currents, salinity, temperature, and zooplankton abundance) for pre-defined regions (Ortiz et al. in press), and compare these characteristics to juvenile salmon biomass (all species combined) in the northern EBS. Initial findings indicate that, depending on region, juvenile salmon biomass varies with small and large zooplankton abundance, bottom temperature, and salinity.
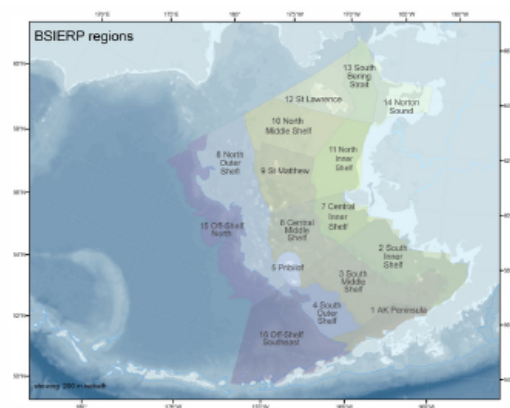
Fig. 1. Bering Sea Integrated Ecosystem Research Program (BSIERP) regions of the northern and southern East Bering Sea (from Ortiz, et al. in press).

Sampling was conducted on a station grid using a CTD (SBE 19, 25 or 9-11) equipped with a Wet Labs fluorometer and beam transmissometer. The survey grid (60 km station spacing) encompassed areas between 60°N and 65°N latitude over the EBS shelf. Sampling occured from August to October 2002-2011. Data were also collected from multiple University of Alaska Fairbanks (UAF) moorings outfitted with an Acoustic Doppler Current Profiler (ADCP) for velocity measurements and an assortment of temperature (T), T/conductivity (C), and T/C/pressure (P) data loggers. Data from the World Ocean Database (WOD) was used to extend the model area output. Zooplankton was collected over the water column: large taxa with oblique bongo-net tows (505 μm) and small taxa with a vertical Juday-net tow (168 μm). Samples were preserved in 5% formalin and enumerated at shore-based facilities. Juvenile salmon were caught with a surface rope trawl (Can trawl model 400-580; spread 60 m [width] by 15 m [depth]) towed for 30 min at 3.5 to 5 kts. Salmon weights were measured for each species (chum, pink, Chinook, coho, sockeye), and the multispecies biomass catch per unit effort (CPUE) was estimated for all species combined. Bering Sea Integrated Ecosystem Research Program (BSIERP) region delineations were drawn by consensus across researchers based on observed oceanography, bathymetry, benthic fauna, fish, seabird and marine mammal distribution (Ortiz et al. in press). Data were stratified by BSIERP region (Fig. 1) and year and analyzed graphically. Data from moorings (currents, temperature, and salinity) were modeled using MATLAB.

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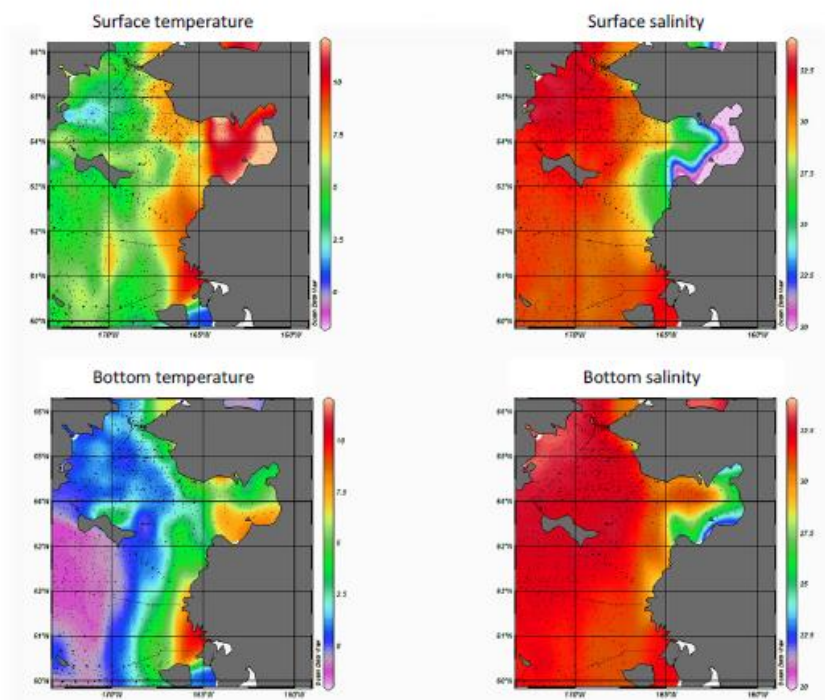**Fig. 2.** Northern Bering Sea shelf surface and bottom temperature (left panels) and salinity (right panels) for May-July, 1975-present.
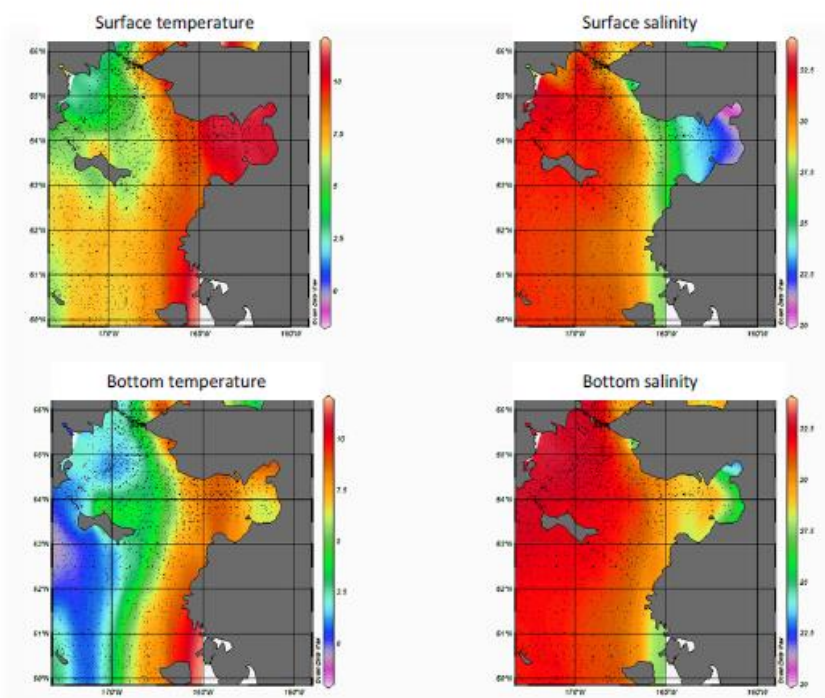

Fig. 3. Northern Bering Sea shelf surface and bottom temperature (left panels) and salinity (right panels) for August-October, 1975-present.
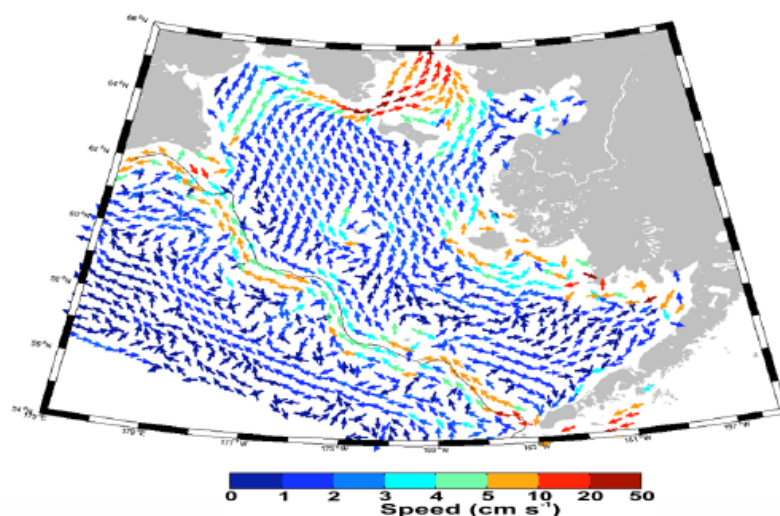
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Fig. 4. Mean value for Bering Sea surface currents, 1987-2007.

Salinity increases and temperature decreases from east to west across the northern Bering Sea shelf (Figs. 2 and 3). Low bottom temperatures observed southwards of St. Lawrence Island show the cold pool location (water temperature < 2°C that is formed during previous winter freezing). Temperature varies between domains with distinctly cooler surface temperatures over the St. Lawrence and South Bering Strait domains. Temperatures are considerably higher for both surface and bottom waters in August-October than in May-July. Currents are generally northward, moving at about 2-3 cm·s^{-1} near St. Lawrence Island, and increase through the Bering Strait (Fig. 4). Norton Sound stands out as a distinct region characterized by high surface and bottom water temperatures and low surface and bottom salinities (Figs. 2 and 3; Table 1) due to ice breakup and high fresh water run-off. Beam (light) transmission is lower than average due to high particulate suspension (Table 1). There is no predominant current direction in Norton Sound and speeds vary from < 1 to > 3 cm·s^{-1} (Fig. 4). The South Bering Strait and North Inner regions are areas of high juvenile salmon biomass, as well as high numbers of large zooplankton (South Bering Strait) and high numbers of small zooplankton (North Inner; Table 1). Highest light transmission values are observed with high bottom and surface salinity in the St. Lawrence region, and low transmission values are found with low bottom and surface salinity in Norton Sound (Table1).

Table 1. Oceanographic parameters, large and small zooplankton abundance, and juvenile salmon biomass stratified by BSIERP region. Red indicates high/maximum values and blue indicates minimum values.

BSIERP region	Temp Top (°C)	Temp Bottom (°C)	Salinity Top	Salinity Bottom	Transmission (% light trans)	Large zoo abund. (# m-3)	Small zoo abund. (# m-3)	Juvenile salmon biomass (kg km-2)
North Inner	8.25	6.53	30.63	30.92	82	84	104127	3706
North Middle	7.83	1.26	31.15	31.57	83	90	54969	819
Norton Sound	9.70	8.92	27.00	28.29	65	41	13037	575
South Bering Strait	7.51	5.15	31.11	31.59	82	2418	10399	2287
St. Lawrence	7.65	2.97	31.80	32.20	89	183	13108	194
St. Matthews	7.61	1.33	31.32	31.74	84	67	5941	930

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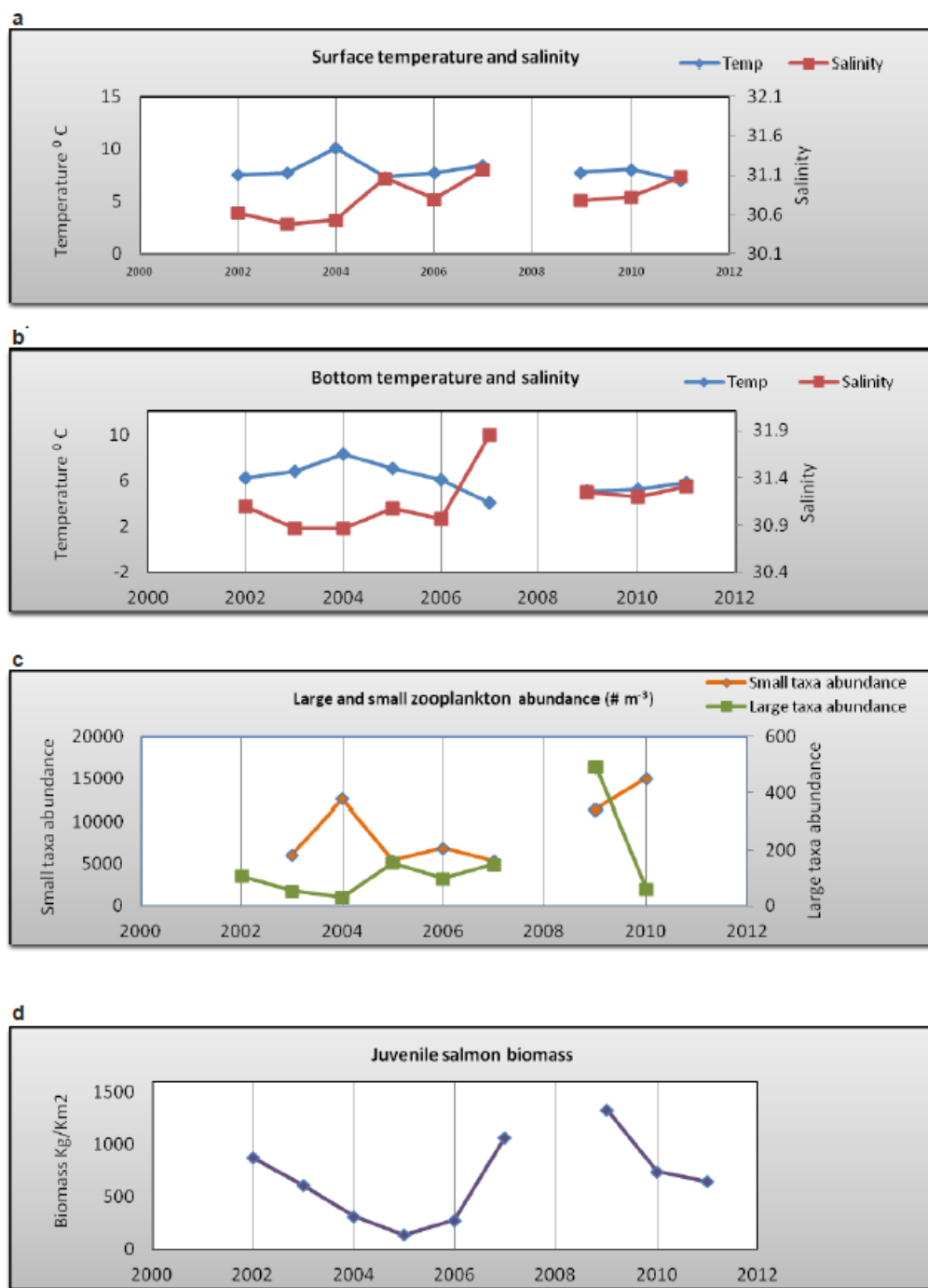
Fig. 5. Temperature and salinity (a, b), large and small zooplankton abundance (c) and juvenile salmon biomass (d) for combined BSIERP regions, 2002-2011. Regions: North Inner and South Bering Strait (NI-SBS).
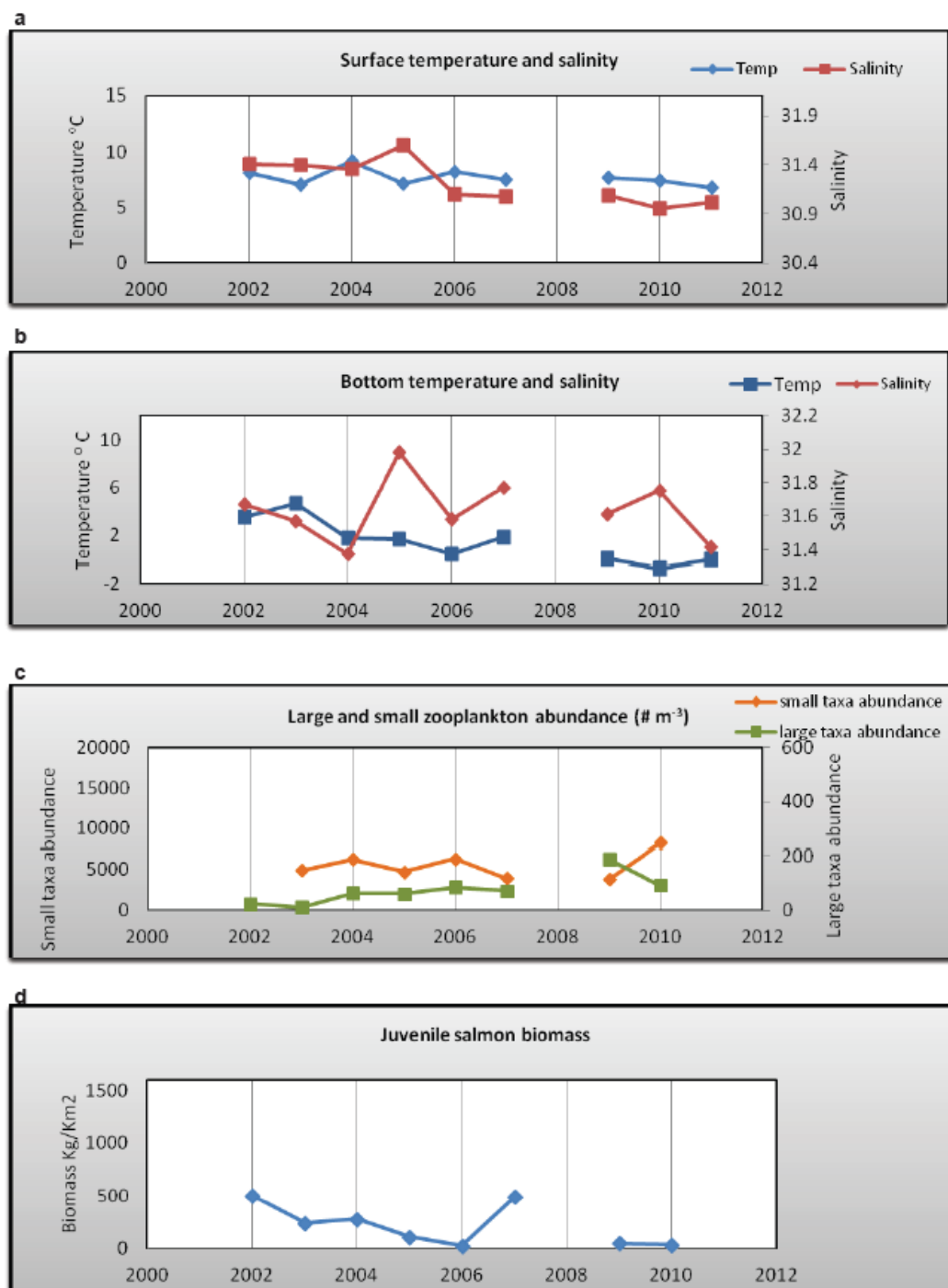
Fig. 6. Temperature and salinity (a, b), large and small zooplankton abundance (c) and juvenile salmon biomass (d) for combined BSIERP regions, 2002-2011. Regions: North Middle and St. Matthews regions (NM-SM).

Fig. 7. Matrix plot for of surface (Top) and bottom (Bottom) temperature (T) and salinity (S), large (Large zoo) and small zooplankton (Small zoo) abundance, and juvenile salmon biomass for North Middle and St. Matthews (NM-SM) combined BSIERP regions.
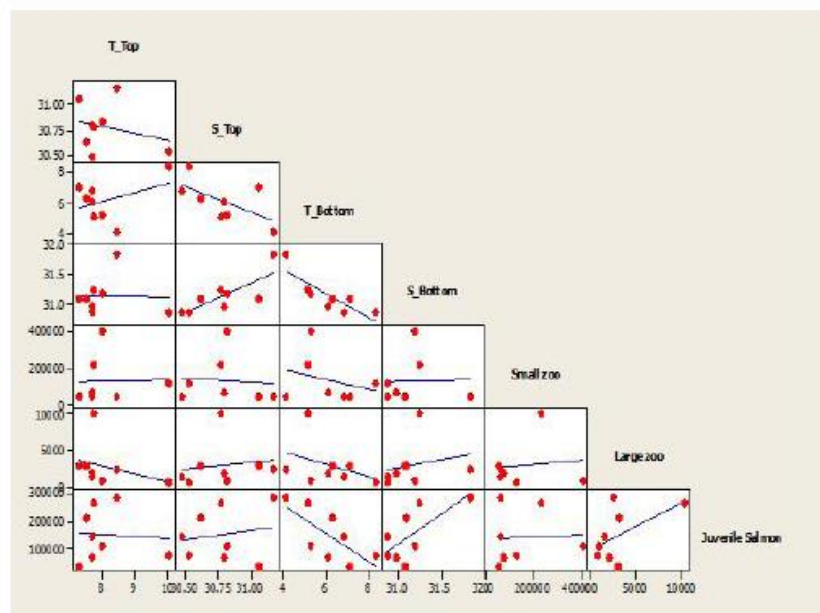
Fig. 8. Matrix plot for of surface (Top) and bottom (Bottom) temperature (T) and salinity (S), large (Large zoo) and small (Small zoo) zooplankton abundance, and juvenile salmon biomass for North Inner and South Bering Strait (NI-SBS) combined BSIERP regions.

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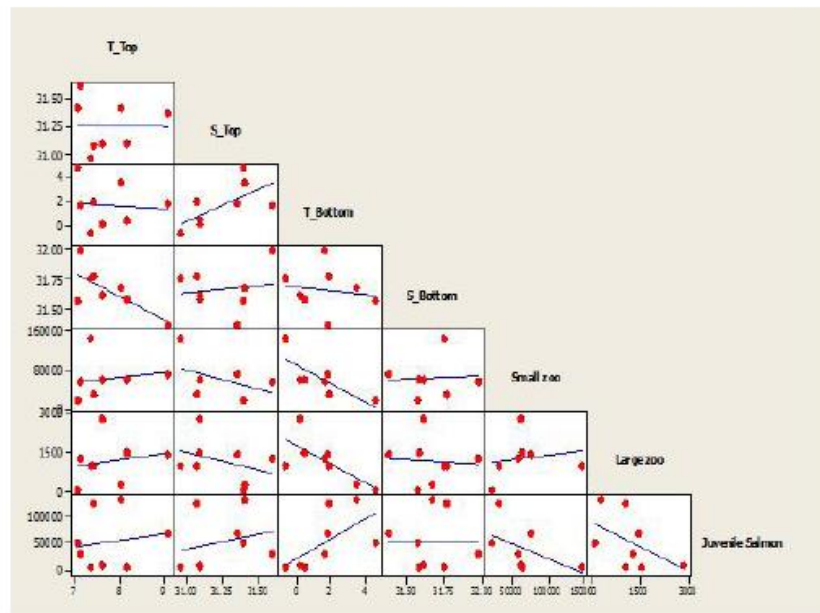BSIERP regions were combined to investigate temporal trends (2002-2011) in parameters (salinity, temperature, large and small zooplankton abundance, and juvenile salmon biomass) by combining North Inner and South Bering Strait regions (NI-SBS; Fig. 5a-d), and North Middle and St. Mathews regions (NM-SM; Fig. 6a-d). Analysis of yearly trends revealed a positive relationship between surface salinity and large zooplankton abundance (NI-SBS) until 2009-2010 (Fig. 5a and c). There is a negative relationship between large and small zooplankton in NI-SBS, and a positive relationship is seen in NM-SM (Figs. 5c and 6c). Juvenile salmon biomass in NI-SBS increased in years with colder, saltier bottom waters (Fig. 5d). In contrast, salmon biomass in NM-SM increased in years with warmer bottom temperatures (Fig. 6d). A matrix plot confirmed the relationships described above (Figs. 7 and 8).

Initial findings reveal connections between juvenile salmon and bottom temperature, bottom salinity, and large and small zooplankton, depending on the region. Surface temperature and salinity changes over the northern EBS can change considerably from season to season and from nearshore to offshore. Norton Sound is a distinct area oceanographically, with relatively low juvenile salmon biomass during late summer/early fall, and the highest juvenile salmon biomass is found in South Bering Strait and North Inner regions. Because the highest abundances of large and small zooplankton were seen in the South Bering Strait and North Inner regions, respectively, large zooplankton could be important prey for juvenile salmon in the South Bering Strait region, and small zooplankton could be important prey for juvenile salmon in the North Inner region. Future analysis will focus on individual salmon species by investigating salmon spatial and temporal relationships with oceanographic parameters.

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Appendix 3. Cook, M., E., A., and M. V. Sturdevant. 2013. Diet composition and feeding behavior of juvenile salmonids collected in the northern Bering Sea from August to October, 2009-2011. North Pacific Anad. Fish. Comm. Tech. Rep. 9:118-126.

Diet Composition and Feeding Behavior of Juvenile Salmonids Collected in the Northern Bering Sea from August to October, 2009–2011

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Keywords: juvenile Chinook salmon, pink salmon, chum salmon, coho salmon, sockeye salmon, diel feeding, diet overlap, prey composition, northern Bering Sea

An understanding of the feeding habits and prey composition of juvenile Pacific salmon species in the northern Bering Sea is essential for assessing the growth and stock productivity of salmonids confronted with a short growing season, population changes, and changing oceanic conditions (Farley et al. 2007; Irvine and Fukuwaka 2011). Juvenile salmon food habits were examined from samples collected during BASIS (Bering-Aleutian Salmon International Survey) surface trawl operations in the northern Bering Sea in August-October, 2009-2011 (Farley et al. 2005; Moss et al. 2009). This study describes juvenile salmon diet composition, identifies important salmon prey taxa, and relates feeding patterns and behavior to diel periodicity for juvenile Chinook, pink, chum, coho, and sockeye salmon in the northern Bering Sea.
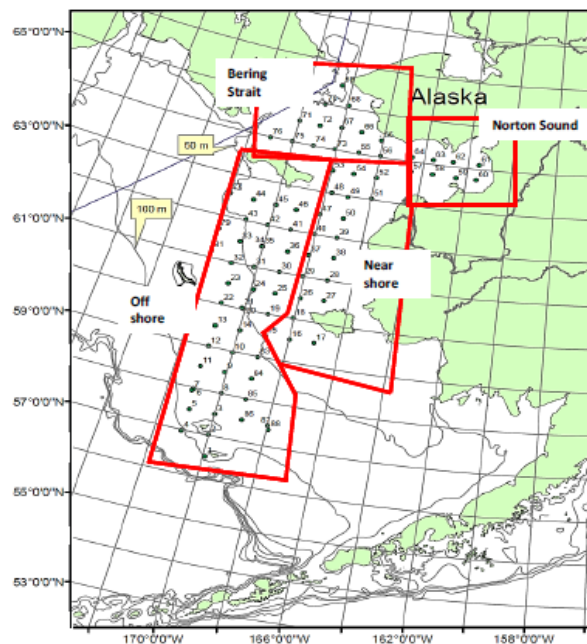
Fig. 1. Regions of the Bering Sea sampled by the BASIS (Bering-Aleutian Salmon International Survey) Program for juvenile salmon diet analysis in August-October, 2009-2011. Regions of the sampling grid are identified by the areas indicated by red lines.

Diets of 1,145 juvenile salmon were examined on board the research vessel from samples collected from four regions of the northern Bering Sea (near shore, Norton Sound, Bering Strait, and off shore; Fig. 1) in August to October, 2009-2011. Feeding intensity was assessed by both volume and weight of prey. The volumetric fullness index (% volume) was determined by visually ranking the total volume of food consumed relative to stomach size based on a scale of 1-4

(where 1 = empty, 2 = less than 25%, 3 = 50-75%, and 4 = 100% full to distended stomachs). Diet composition was then determined by sorting, enumerating, and identifying prey to the lowest possible taxonomic category. Individual prey were pooled and weighed by category, or assigned a percentage of total contents when weights could not be obtained. General diet composition was characterized as the percentage of total prey weight comprising seven prey categories (Fig. 2). Prey encountered infrequently (chaetognaths, insects, ctenophores, and pteropods) were grouped and categorized as "other." The index of fullness (percent body weight: %BW) for i = 1 to n prey taxa was computed as follows:

$$\%BW = [\sum(x_i)*(w_i)/(BW - \sum(x_i)*(w_i))]*100$$

where w_i is the weight for i = 1 to n prey taxa and BW is fish body weight. Specific diet composition by prey taxa (e.g., *Ammodytes hexapterus*) was computed as the stomach content index (SCI; Hyslop 1980; Orlova et al. 2005).

$$SCI = (w_i/BW * 10^4)$$

The SCI values sum to the total stomach fullness index (SFI; Starovoytov 2007a). Diet similarity between species pairs was calculated as the percent similarity index (PSI; Hurlbert 1978) based on percent weight, and diel feeding periodicity was calculated as percent of stomach volume for 3-hour increments.
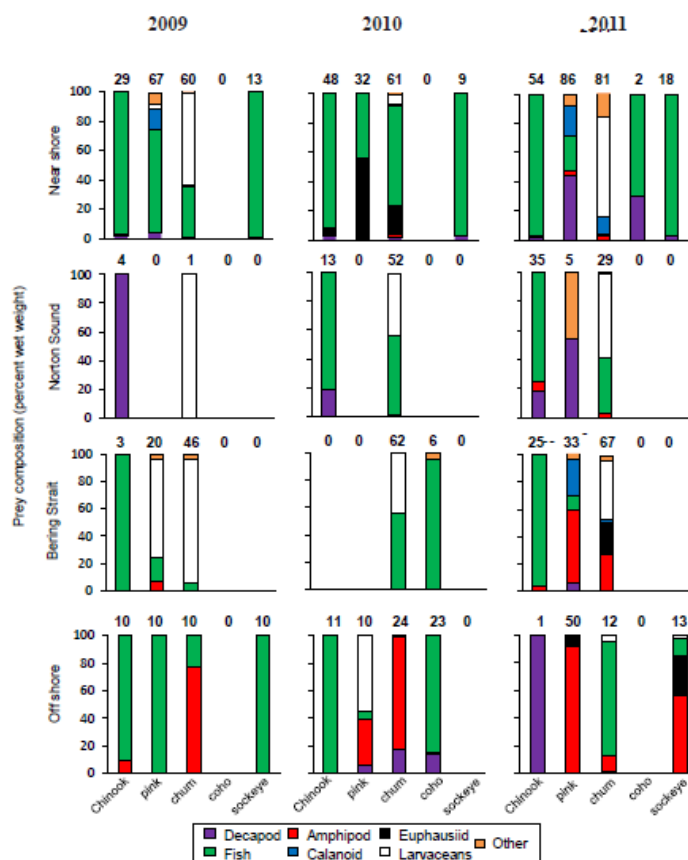
Fig. 2. Prey composition (percent wet weight) of juvenile Chinook, pink, chum coho, and sockeye salmon stomach contents collected in August-October in four regions of the northern Bering Sea, 2009-2011. Fish sample size is indicated above the bars.

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Juvenile salmon diets were summarized by region, year, and diel feeding period to assess potential prey differences and feeding patterns among the species. Most salmon species were sampled in the nearshore, strait, and offshore regions (Fig. 1). Catches in the Norton Sound region were limited and catches of coho salmon were mainly in the nearshore region (Murphy et al. 2009). Diets differed among the regions and years and included both fish and plankton (Landingham 1998; Boldt and Haldorson 2003; Davis et al. 2009). Prey was diverse for piscivorous Chinook and coho salmon and for planktivorous pink, chum, and sockeye salmon (Brodeur et al. 2007). Fish were the primary prey in the nearshore region each year, especially for Chinook and coho salmon (Fig. 2). The larger body size of these salmon requires larger high-energy prey for growth (Schabetsberger et al. 2003), although intensive feeding on alternative, lower-quality prey can also enhance survival (Weitkamp and Sturdevant 2008). The most common fish prey included sand lance *(A. hexapterus;* 40-50 mm) and capelin *(Mallotus villosus;* 60-80 mm), taxa rich in lipids necessary for growth and development (Litzow et al. 2006). Chum and pink salmon diets varied in odd- and even-numbered years, a strategy that may reduce competition (Wilson et al. 2006) and be related to the lower lipid content of chum salmon observed in years when pink salmon are abundant (Kaga et al. 2013). Chum salmon consumed more larvaceans *(Oikopleura* spp.) in samples collected in odd-numbered years and switched to consuming more fish in 2010, whereas pink salmon consumed more crustaceans in odd-numbered years as compared to consumption of more euphausiids and fish in 2010 (Fig. 2). Sockeye salmon diets included fish and brachyuran megalopae in samples collected near shore as compared to diets including hyperiid amphipods and euphausiids *(Thysanoessa* spp.) in offshore samples.

Fig. 3. Stomach content indices (SCI) of juvenile Chinook, pink, chum coho, and sockeye salmon collected in the northern Bering Sea in August-October, 2009-2011. The SCI values are based upon individual prey types.
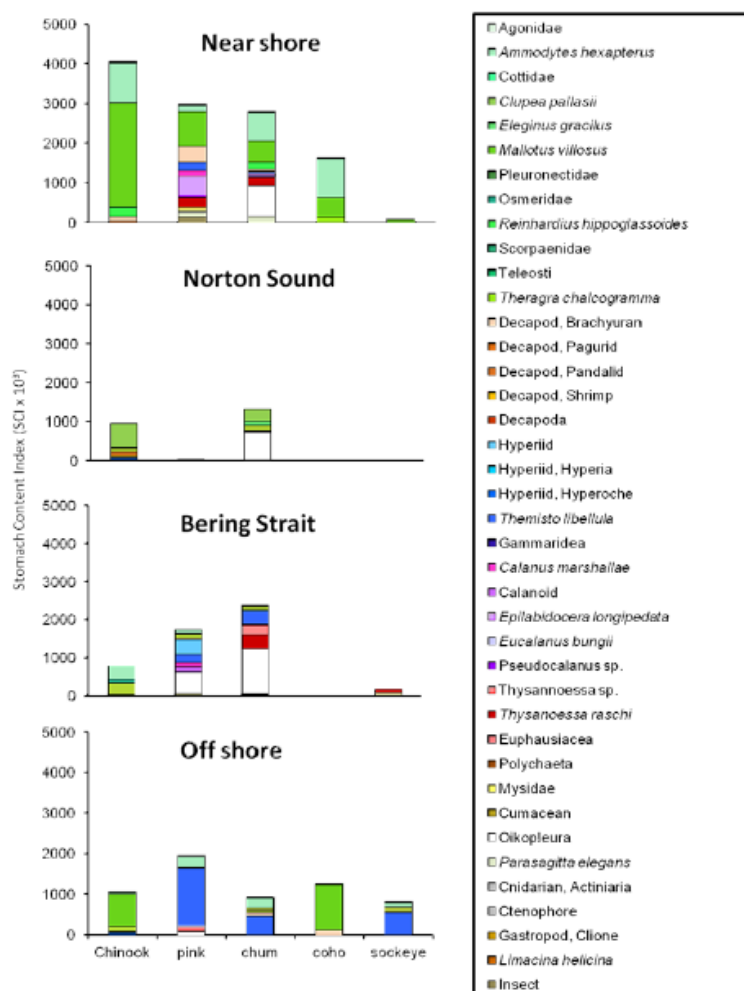
In the Norton Sound region, Pacific herring (*Clupea pallasi*; 30-40 mm) were the primary foods of juvenile Chinook and chum salmon. Local populations of herring over-winter north of the sound and can be an important prey for piscivorous juvenile salmon (Funk 2001; Tojo 2007). Larvaceans and hyperiid amphipods (*Hyperoche* sp. and *Themisto libellula*) were consumed by juvenile chum salmon (Fig. 2). Juvenile chum salmon preference for rapidly-digested gelatinous prey (Boldt and Haldorson 2003) has been described throughout its range (Brodeur et al. 2007; Karpenko and Koval 2012). Reports of pink salmon feeding on larvaceans are also common (Purcell et al. 2005), however, insects and brachyuran megalopae were the common pink salmon prey in this study (Fig. 2).

Catches of juvenile salmon other than chum salmon were patchy in the Bering Strait. In contrast to samples from Norton Sound, fish prey from the strait region included rainbow smelt (*Osmerus mordax*), Pleuronectidae, and sand lance consumed by Chinook salmon, Pleuronectidae consumed by pink salmon, and Pleuronectidae and Cottidae consumed by chum salmon (Fig. 3). In 2011, pink and chum salmon diets principally comprised of the amphipod *T. libellula*. Chum salmon also consumed euphausiids and larvaceans, while pink salmon consumed more of the large calanoid copepod *Calanus marshallae* (Fig. 2). Since *C. marshallae* is also important in the diet of *T. libellula* (Auel and Werner 2003; Pinchuk et al. 2013), the carrying capacity of the Bering Strait could be affected by interactions between juvenile salmon and carnivorous macrozooplankton if climate change impacts the availability of these prey (Coyle et al. 2011). These amphipods and calanoids are substantial sources of fatty acids that juvenile salmon require during cold periods (Scott et al. 2002; Persson and Vrede 2006).

In the offshore region, hyperiid amphipods, *Themisto* spp., were important prey and contributed a high percentage of the diets of juvenile salmon diets in 2010 and 2011 (Starovoytov 2007b; Temnykh et al. 2010). Fish, such as sand lance (35-45 mm), capelin (60-80mm), Cottidae (16-20 mm), Scorpaenidae (15-25 mm), and Agonidae (20-27mm), were also a high percentage of the diet. The SCI values indicated that hyperiid amphipods were important prey to all species except coho and Chinook salmon (Fig. 3), which consumed large percentages of capelin in this region. Capelin located along the continental shelf provide substantial food to migrating salmon (Vilhjalmsson et al. 2005). Larvaceans contributed a substantial percentage to the diets of pink salmon in 2010 (Fig. 2), but overall SCI values for hyperiid amphipods were higher for pink salmon caught off shore in all three years (Fig. 3).
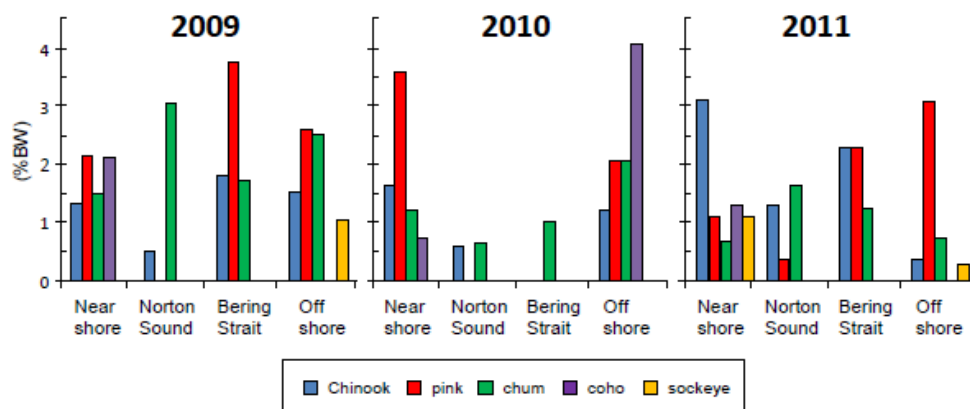
Fig. 4. Percent of salmon body weight (% BW) comprising prey and observed in salmon stomach contents of juvenile Chinook, pink, chum coho, and sockeye salmon collected in four regions of the northern Bering Sea in August-October, 2009-2011.

The amount of prey as a percentage of salmon body weight is a size-related index of feeding intensity and prey availability (Graeb and Dettmers 2004). The percent body weight of prey in stomach contents of Chinook salmon was highest (> 1%) in samples from the nearshore and strait regions, whereas coho salmon fed most intensively in the offshore region (> 4 %BW; Fig. 4). The percentage of Chinook salmon body weight represented by prey in samples collected near shore was unusually high in 2011, despite similar sizes across years in this region (Fig. 5). Pink salmon tended to have the highest percent body weight comprising prey among the salmon species, but their annual body size varied in both the near-shore and off-shore regions where it was often highest. Percent body weight of prey observed in Chinook and chum salmon stomach contents collected off shore decreased over the study period, and pink salmon values increased overall. Small sample sizes and differences in salmon distributions (Sturdevant et al. 2012) may have contributed to some of the feeding differences observed.

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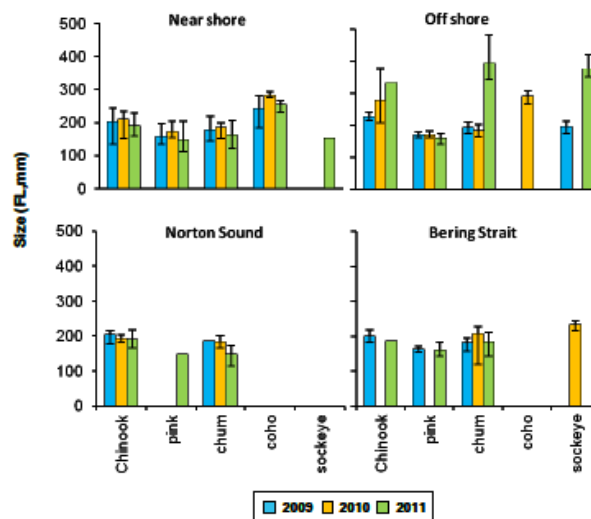
Fig. 5. Average fork length (FL, mm) of juvenile Chinook, pink, chum coho, and sockeye salmon collected in four regions of the northern Bering Sea and pooled over the three-year period, 2009-2011.

Diet overlap (PSI) was calculated for 44 co-occurring species-pairs collected from nearshore and offshore regions (Table 1), but samples were limited to 12 species-pairs in the Norton Sound and Bering Strait regions. Diet overlap of coho and Chinook salmon was consistently > 95% PSI in nearshore regions each year and was based on consumption of fish prey, whereas overlap between other species-pairs varied from year-to-year and was usually low (< 60%; Brodeur et al. 2007). Differential annual movement patterns of juvenile salmon to offshore regions affect their spatial overlap and therefore could affect diet similarity measures (Farley et al. 2007). By contrast, the PSI was significant (81%) only for pink and chum salmon in 2009 in samples collected from the Bering Strait (Table 1; Fig. 2). Diet overlap between piscivorous Chinook and coho salmon is commonly reported (Bollens et al. 2010), but can be overestimated if fish prey taxa differ (Rindorf and Lewy 2004). In this study, both species consumed capelin and sand lance, however, coho fed on pollock (*Theragra chalcogramma*) more than the other salmon species, perhaps alleviating competition for food (Bollens et al. 2010) or indicating different habitat utilization patterns (Weitkamp and Sturdevant 2008).

Table 1. Diet overlap (percent similarity index: PSI) by region and year based on examination of juvenile Chinook, pink, chum, coho and sockeye salmon stomach samples collected in the northern Bering Sea in August-October, 2009-2011.

	2009			2010			2011		
				Near shore					
	Chinook	pink	chum	Chinook	pink	chum	Chinook	pink	chum
pink	72.5	-		49.3	-		27.4	-	
chum	100	41.5	-	74.1	64.6	-	2.6	24.1	-
coho	100	70.8	35.0	95.2	44.7	69.6	98.6	26.9	1.2
sockeye							72.2	53.8	1.2
				Norton Sound					
	Chinook			Chinook			Chinook	pink	
pink	-			-			17.8	-	
chum	-			55.8			46.0	1.0	
				Bering Strait					
	Chinook	pink		chum			Chinook	pink	
pink	17.2	-		-			14.5	-	
chum	5.7	81.6		-			5.0	35.7	
sockeye	-	-		0.8					
				Off shore					
	Chinook	pink	chum	Chinook	pink	chum	Chinook	pink	chum
pink	90.5	-		5.6	-		0.2	-	
chum	32.3	22.8	-	0.0	39.7	-	2.2	11.3	-
coho	-	-	-	85.8	11.8	14.2	-	-	-
sockeye	90.5	100	22.8	-	-	-	1.5	64.4	26.2

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Variation in capelin biomass has been linked to climatic changes and abundance of other pelagic species such as herring and pollock (Benson and Trites 2002; Vilhjalmsson et al. 2005). Similarly, changes in oceanic conditions can limit production of some prey and lead to shifts in planktivorous feeding (Aydin and Mueter 2007; Andrews et al. 2009). Diets of highly piscivorous juvenile salmon species overlapped with planktivorous juvenile salmon species only when the latter ate fish. Thus, diet overlap based on preferred prey is expected to be low when alternate prey is available, but diet quality may differ as a result (Davis et al 2005; Karpenko et al. 2007; Weitkamp and Sturdevant 2008).

A diel feeding rhythm was observed for all juvenile salmon in the northern Bering Sea (Fig. 6). Morning was the period observed with the highest percentage of stomachs that were empty or contained only trace amounts of food. Stomach fullness increased between 09:00 and mid-day hours, dipped in early afternoon, and then remained high until the final sampling period at 21:00 (Temnykh et al. 2010). The afternoon decrease in feeding we observed was similar to sockeye and chum salmon feeding rhythms reported for samples collected in the Bering Sea in summer (Azuma 1992), but rhythms differed with those of pink and chum collected in Southeast Alaska (Sturdevant et al. 2004). Feeding behavior, feeding intensity, and diel prey composition of salmon could be influenced by latitudinal differences in light cycles that affect visual feeding (Schabetsberger et al. 2003; Bieber 2005).
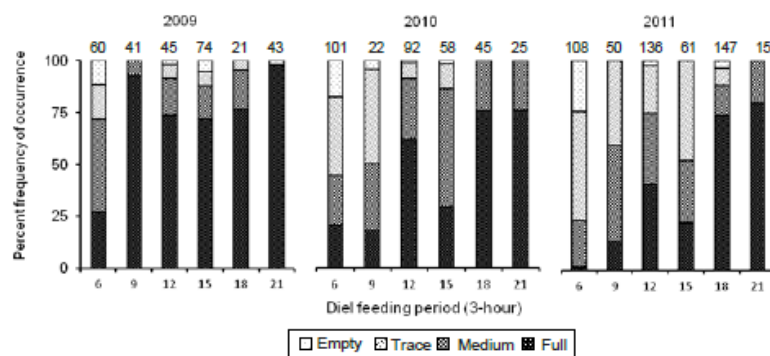
Fig. 6. Juvenile salmon diel feeding rhythm per three-hour period measured as the percent frequency of occurrence of empty, trace, medium, and full stomach volume. Data are grouped for juvenile Chinook, pink, chum, coho, and sockeye salmon collected in all regions of the northern Bering Sea in August-October, 2009-2011. Fish sample size is indicated above the bars.

We examined multivariate trophic relationships among the species and regions using the SCI prey data. Values were square root-transformed and Bray-Curtis similarity matrices were derived. The nonmetric multi-dimensional scaling procedure (nMDS) was used to produce a 2-dimensional ordination plot (PRIMER-E; Plymouth Routines in Multivariate Ecological Research, v6; Clarke and Warwick 2001). The stress value of 0.13 indicates moderately strong relationships among the groups, with species gradients evident in each region except Norton Sound (Fig. 7). The trophic position of sockeye salmon was shown to be distinct from the other species.
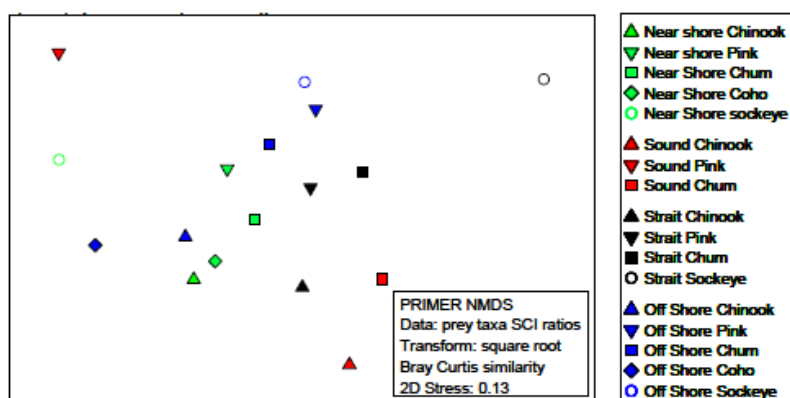
Fig. 7. Multivariate trophic relationships among juvenile Chinook, pink, chum coho, and sockeye collected in the four regions in the northern Bering Sea in August-October, 2009-2011. Diet data are stomach content indices for 40 prey taxa averaged across the three years. Symbol shape represents species; symbol color represents region.

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We documented regional and inter-annual differences in juvenile salmon diets for the northern Bering Sea and corroborated previous reports of trophic niches for Chinook, pink, chum, coho, and sockeye salmon and high overlap in the diets of piscivorous Chinook and coho salmon.

As prey fish and invertebrate populations adapt to climate change in the Bering Sea (Overland and Stabeno 2004; Coyle et al. 2011), availability of important pelagic salmon prey resources that can fill the nutritional requirements of juvenile salmon is a concern (Miller et al. 2013), particularly in the face of salmon stock collapses (Orsi et al. 2013). The feeding patterns of migrating juvenile salmon in the Bering Sea suggest that flexibility in feeding on a diverse spectrum of prey types alleviates competition for preferred food types among co-occurring species (Benson and Trites 2002). In the current period of climate and cyclic changes (Andrews et al. 2009; Chittenden et al. 2009; Coyle et al. 2011), information from this and other diet studies contributes to a clearer understanding of the trophic patterns important to the early marine survival of juvenile Pacific salmon in the northern Bering Sea.

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Synopsis

Poor returns of western Alaska Chinook during the late 1990s triggered restrictions to commercial harvest and the Alaska Board of Fisheries listed the Yukon River stock as a stock of yield concern in 2000. Despite adequate salmon escapement to the spawning grounds returns have not recovered to historic levels. Returns-per-spawner are currently near replacement and harvest restrictions by all user groups have been necessary to ensure escapement goals are met. Reasons for the decline in productivity are unknown and similar production declines are occurring in other western Alaska Chinook salmon stocks, implicating macro-scale factors and marine conditions as the potential contributors to production declines in western Alaska Chinook salmon stocks.

Research surveys in the eastern Bering Sea shelf have been conducted by NOAA fisheries in the northern Bering Sea annually since 2002 as part of the Bering-Aleutian Salmon International Survey (BASIS). These surveys collect a wide range of ecological, oceanographic and biological data, including information on juvenile salmon (after their first summer at sea), and offer what is currently the only data specific to this life stage for western Alaskan salmon. Canadian-origin Yukon Chinook salmon stocks have been genetically identified in these collections and are used here to provide stock-specific juvenile abundance estimates to evaluate stock productivity of the Canadian-origin stock group.

Low numbers of juveniles-per-spawner follow the declining trend observed in return-per-spawner and supports the interpretation that production declines are primarily occurring in the early life-history stages of Chinook (freshwater and early marine). Although juvenile marine survival varies over time (making it difficult to accurately forecast returns from juvenile abundance alone), variation in marine survival estimates is less correlated with production than juveniles-per-spawner. Uncertainty in juvenile abundance estimates is large and limits the ability to identify the true variation in marine survival over time.

A large-scale change in the migratory pattern of juvenile Chinook salmon has been observed in BASIS survey. Juvenile Chinook salmon were distributed north of the Yukon River in warm years (2002-2007), and south of the Yukon River in recent cold years (2009-2011). Although it will be several years before we can evaluate how migratory patterns of juveniles alter marine survival;

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southward migration is believed to be a more favorable migratory trajectory as it will bring Chinook salmon closer to suitable winter habitats.

Prey biomass and size-spectrum of prey species are important features of Chinook diets. Juvenile Chinook have primarily a piscivorous diet and feed on larval or age0 life-history stages of fish during their first summer at sea. Capelin (*Mallotus villosus*) are the dominate prey species in juvenile Chinook diet and their importance increased during cold years with increased capelin biomass in the northern Bering Sea. Although herring (*Clupea pallasii*) are the most abundant pelagic fish species in the northern Bering Sea, they are minimally present in juvenile Chinook salmon diets. Absence of herring in juvenile Chinook diets is thought to be the result of the ability of herring to outgrow the prey size spectrum of juvenile Chinook salmon by September. Even without herring, juvenile Chinook were able to maintain adequate energy levels, primarily by utilizing capelin as forage on capelin. If juvenile Chinook salmon are able to feed on herring during the early marine period (initial marine entry), they should have a significant prey base to feed on. If not, critical forage dependencies could be present during initial marine entry.

Chinook salmon endure long periods of low forage during winter and must rely on stored energy for routine and active metabolism. Energetic allocations into growth and energy are necessary processes for juvenile Chinook salmon to survive winter. Rapid growth occurs in the estuary systems where warmer water temperatures, diverse prey, and low salinities aid growth processes. Energy storage occurs once the fish move offshore where larger prey, colder temperatures and vertical diel movements bolster storage allocations. Energetic status of collected juvenile Chinook salmon does not seem to be limiting populations, but energetic information on pre-smolt and late fall/early winter is lacking and may provide important information prior to and after our collections.

Conclusion

Production declines in the early life-history stages of Chinook salmon is believed to be an important factor contributing to the overall production decline of AYK-region Chinook salmon. The number of Canadian-origin juveniles per spawner has declined concurrently with the number of returns per spawner. Although juvenile abundance estimates in the southern Bering Sea is complicated by changes to trawl survey design, catch data suggest juvenile abundance has also declined in the southern Bering Sea. Research is recommended to: 1) reduce uncertainty in juvenile abundance estimates, 2) improve understanding of marine migration, and 3) improve understanding of ocean entry timing of Chinook salmon in relation to initial marine diet, prey availability, and condition.

Introduction

Chinook salmon is the largest salmon species in the Yukon River and is culturally and economically valuable throughout the drainage. Chinook salmon have been documented to spawn from the Archuelinguk River (approximately 80 miles upstream from the river mouth) to nearly 2,000 miles upstream in the Canadian headwaters. Approximately 50% of the total Yukon River Chinook salmon run originates in Canada, and the Tanana River is the largest Chinook salmon producing tributary in the Alaskan portion of the drainage (JTC 2012). Chinook salmon enter the mouth of the Yukon River after ice breakup during late May or early June and continue to migrate into the river through mid-July.

The Division of Commercial Fisheries of the Alaska Department of Fish and Game (ADF&G) is responsible for the management of state subsistence, personal use, and commercial fisheries in the Alaskan portion of the Yukon River. ADF&G uses an adaptive management strategy that evaluates run strength in-season to determine a harvestable surplus above escapement requirements.   In-season run assessment includes abundance indices from test fisheries, passage estimates from various sonar projects, and spawning escapement and harvest data. Managers adjust the level of commercial, subsistence, and personal use harvests using time and area openings and closures. Excluding the greater Fairbanks area (approximately 97,580 residents), there are approximately 21,900 rural residents in the Alaskan portion of the drainage, the majority of whom reside in 43 small communities scattered along the coast, mainstem, and major tributaries (Estensen et al. 2011). A majority of the people in this region are dependent on fish and game resources for their livelihood. In addition to ADF&G, the Canadian Department of Fisheries and Oceans (DFO)oversees aboriginal, commercial, sport, and domestic salmon fisheries in the Canadian portion of the Yukon River drainage.   The Yukon River Salmon Agreement (Chapter 8 of the Pacific Salmon Treaty) guides management of Canadian-origin stocks on both sides of the border, and identifies processes related to development of escapement objectives and harvest sharing agreements between Canada and the US.

Tremendous efforts is employed annually to collect data on western Alaska Chinook salmon in their respective rivers to assist in management,. Dozens of projects throughout the region collect data on escapements, age, sex, length, genetic identity, in-river migration patterns, migration timing, spawning locations, and spawning habitat. In contrast, there is a paucity of data for all other life stages. The marine life of these fish is poorly understood, in part, because of less effort and poor genetic resolution for determining stock of origin. At this time, coastal western Alaskan stocks cannot be differentiated and fall within one reporting group: this includes Chinook salmon from Norton Sound, lower Yukon and lower Kuskokwim areas. Only

stocks in the mid to upper Yukon and upper Kuskokwim rivers are identifiable, and only Canadian-origin Yukon Chinook salmon stocks are prevalent enough for consistent detection in mixed stock mixtures.

Harvests are managed to ensure adequate escapement of fish to the spawning grounds in both the United States and Canada and both countries utilize fisheries data to fulfill their management goals. The average Chinook salmon utilization in Alaska and Canada from 1982-1999 is approximately 177,000 fish, and the average run size estimate for this time period is 296,000. Poor run abundance beginning in the late 1990s triggered restrictions to commercial harvest during the early to mid-2000s; for 2000–2006 the average utilization is 89,000 fish, and run size estimates average 208,000 for this time frame. In the most recent time period, 2007-2011, further harvest restrictions were incurred by all user groups as run abundance became even poorer; average utilization is 58,000 fish, and run size estimates average 148,000 fish (JTC 2012). Recent declines in abundance have occurred despite achieving adequate salmon escapement to the spawning grounds. Historically, returns-per-spawner have averaged around 2.5 to 3; however, returns-per-spawner have hovered near replacement in recent brood years (JTC 2012). The cause of this productivity decline is unknown and similar declines have occurred throughout western Alaska, implicating macro-scale factors as potential contributors.

Research surveys in the eastern Bering Sea shelf have been conducted by NOAA fisheries in 2000-2007 and 2009-2011. These surveys collect a variety of ecological, oceanographic and biological data, including information on juvenile salmon (after their first summer at sea), and offer what is currently the only data specific to this life stage for western Alaskan salmon. Canadian-origin Yukon Chinook salmon stocks have been genetically identified in these collections and some stock-specific information is available on the early marine life of these fish. Since early marine life appears to be a critical time in the life of a salmon (Beamish and Mahnken 2001, Hartt 1980, Moss et al. 2005), research of this life stage may illuminate whether critical influences on productivity occur in either freshwater rearing stages or in later marine life. Emphasis is on data collected from Canadian-origin Yukon Chinook salmon as this stock can be identified in mixed stock distribution of Chinook salmon and is of particular management concern.

Methods

Survey

The Bering-Aleutian Salmon International Survey (BASIS) is a cooperative research program by member nations of the North Pacific Anadromous Fisheries Commission (NPAFC). The BASIS program was created to address critical information gaps for the marine phase of Pacific salmon (*Oncorhynchus* spp.) through seasonal pelagic trawl research surveys. Phase 1 of BASIS was implemented in 2002-2006 (NPAFC, 2001), the 2nd phase of BASIS was implemented in 2009 and

will continue until 2013 (NPAFC, 2009). Pelagic trawl operations were conducted throughout out the eastern Bering Sea shelf using a systematic spatial sampling design during US BASIS surveys (Figure 1). During the 2nd phase of the BASIS program, separate survey plans were developed for the northern (north of 60N) and southern Bering Sea in an effort to focus research effort on regional research objectives. One of the principal objectives of the northern Bering Sea has been to collected information on the juvenile life-history stage of Yukon River salmon.

Trawl operations in the northern Bering Sea were conducted aboard chartered fishing vessels with Cantrawl midwater rope trawls (Cantrawl Pacific Ltd., Richmond, B.C.) and towed for a duration of 30 minutes at each station with the headrope at the surface. The 2002 northern Bering Sea survey used a model 300 Cantrawl midwater trawl (Farley, 2005), model 400 Cantrawl midwater trawls (Murphy et al. 2003) were used in all subsequent years. The Cantrawl 400 has hexagonal mesh in the wings and body, is 198 m in length, has a headrope length of 120 m, and has a 12-mm mesh liner in the codend. The trawl was configured with three 60-m bridle legs connecting the trawl to the steel alloy 5-m^2 trawl doors manufactured by Noreastern Trawl. An additional 91-kg steel plate was added to the shoe of each door to increase door stability when towing at the surface. Three polyform floats (one 80-cm and two 60-cm) were attached to the headrope on both wingtips, and two ployform F-4 buoys were attached to the net sonar kite to help keep the headrope at the surface. Main warp was set at to 250-350 m, and target towing speeds was 3.5–4.5 knots.

Shipboard processing included sorting the catch by species and measuring total catch weight by species. A subsample of 50 juvenile Chinook salmon was selected at each station for biological data and the remaining juvenile Chinook were counted to obtain total catch.
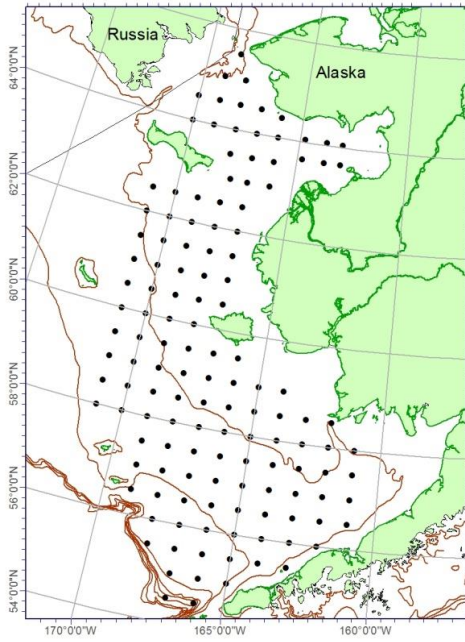
Figure 1. Typical sample survey coverage design for the United States Bering Aleutian Salmon International Survey.

Juvenile Abundance

Relative abundance (numbers) of juvenile Chinook salmon and confidence intervals (80% CI) were estimated for juvenile Chinook abundance using a bootstrap (Effron and Tibshirani, 1993) resample distribution (1,000 bootstrap samples) of average CPUE. This is accomplished by estimating the mean CPUE from n random draws of CPUE with replacement from n values of CPUE. This step is repeated 1,000 times to generate a distribution of mean CPUE. From this distribution, the overall mean and confidence intervals can be estimated. Bootstrap distributions of mean CPUE were estimated for spatial strata by year and expanded to abundance based on area. Abundance and confidence intervals by year is the sum of each spatial strata. Area was calculated by:

$$A_{y,s} = \frac{G_{y,s}}{S_{y,s}} * n_{y,s},$$

where $A_{y,s}$ is the survey area in year y and strata s, $G_{y,s}$ is the average sample grid area (km^2), $S_{y,s}$ is the average area swept (km^2), and $n_{y,s}$ is the number of stations. The survey design is based on a latitude and longitude coordinate grid, therefore the y-grid dimension (km) of the sample grid is a simple conversion of nautical miles to km and the the x-grid dimension (km) of

the sample grid is based on average latitude and is computed from the geographical coordinates as:

$$x = \cos^{-1}(\sin(lat)^2 + \cos(lat)^2 \cos(\Delta lon)) * 6371,$$

where lat (radians) is the average station latitude, Δlon (radians) is the longitude grid dimension, and 6371 is the earth's radius in km. The northern Bering Sea was divided into four spatial strata: 60-62N, 62-64N, Norton Sound, and Bering Strait. Adjustments were made to the Norton Sound and Bering Strait strata for inconsistent survey coverage over time.

Genetic stock mixtures of juvenile Chinook were used to estimate Upper Yukon River (Canadian origin) juvenile Chinook salmon from Northern Bering Sea abundance estimates. The genetic stock proportions used to scale Upper Yukon River Chinook salmon to Northern Bering Sea abundance are reported in Templin et al. (2011a) and the genetic baseline and methodology used to estimate stock proportions are reported in Templin et al. (2011b). Stock proportions for 2009-2011 sample years (2007-2009 brood years) are in progress and a provisional estimate of the average historic proportion (0.47) is used until actual estimates are available.

Spawner abundance is scaled to juvenile year based on the assumption that all juveniles are freshwater age1. Freshwater age0 and age2 Chinook salmon are present in the juvenile population; however, the age1 assumption provides a reasonable estimate as the number of age0 and age2 juveniles are low relative to the abundance of age1. The high rate of scale loss of juveniles during trawl capture results in limited information on age structure from scale collections. Work is in progress to develop age estimates from otolith collections.

In-river assessment projects by the Alaska Department of Fish and Game and the Department of Fisheries and Oceans provide information on spawner abundance and total return of Upper Yukon Chinook salmon (JTC, 2012). Spawner abundance (escapement) is estimated from boarder passage (Eagle river sonar) less Canadian harvest, returns are based on run reconstructions from US harvest and boarder passage. Age composition of the returning adults is used to scale returns to brood year.

Juvenile per spawner is the ratio of the juveniles to spawners and is relative to the survey catchability for juvenile Upper Yukon Chinook salmon. Juvenile survival is the ratio of adult returns to juvenile abundance and is also relative to survey catchability for juvenile Upper Yukon Chinook salmon.

Juvenile Distribution and Migration

Catch per unit of effort (CPUE) data are used to map juvenile Chinook densities over space using the start latitude and longitude position of each trawl sample location (station). Densities are pooled by year into the warm years (2002-2007, the original BASIS project years), and cold years (2009-2011). CPUE at each station is defined as:

$$CPUE \ = \frac{Catch}{Effort} * \overline{Effort} \ .$$

Catch is the number of juvenile Chinook captured at each station. Effort is the area swept in km^2 (distance trawled multiplied by the horizontal spread of the trawl). CPUE is multiplied by the average effort to ensure zero catches are correctly scaled to CPUE. Zero catch boundary conditions were added to land masses, and the prediction surface and distribution maps were constructed in ESRI ArcMap software.

The prediction surface was constructed from a combination of the spatial trend generated by an exponential kernel function and a kriging model fit to spatial residuals (ESRI, 2001). Local kriging models were used to estimate the kriging surface with and a neighborhood search radius including a minimum of 8 and a maximum of 20 datapoints within the covariogram sill range. Cross-validation statistics were used to optimize the spatial trend and kriging model parameters to the data.

Juvenile Diet and Prey Biomass

Juvenile diets were estimated from onboard stomach content analysis. Up to ten stomachs of juvenile Chinook salmon were sampled and contents were pooled and weighed at each station. Species composition was estimated by volume or weight. Prey composition was estimated for each year by a catch weighted stomach content index (SCI). SCI values were estimated for each prey species as the ratio of prey weight to predator weight.

Relative biomass (mt) of forage fish species (herring, capelin, sandlance, and age0 pollock) were estimated from trawl catch, effort, and the systematic spatial survey design grid as follows:

$$B_y = \frac{G_y}{S_y} * \sum_i C_{y,i}$$

Where N_y is the relative biomass in year y, G_y is the average sample grid area (km^2), S_y is the average area swept (km^2), and $C_{y,i}$ is the trawl catch (numbers or biomass) at station i in year y. Sample grid area was calculated using the same approach for juvenile Chinook salmon abundance estimates.

Energy

Energy density was measured on a subset of Chinook salmon captured at each station (generally 2 fish per haul). Additional fish were selected for energy density in 2011 to increase sample size and to provide additional size contrast in energy measurements. Energy density data were analyzed at Auke Bay laboratories (Juneau, AK) following standard bomb calorimetry procedures.   Predictive models of energy density from fish length were constructed by year and region and length distributions were used to generate estimates of juvenile energy density. Whole body energy density estimates were only available for juveniles after 2005, pooled-year prediction models for the northern Bering Sea were used to estimate juvenile energy density prior to 2005.

Results

Juvenile Abundance

Juvenile abundance, stock mixtures, and relationships to spawners and returns are given in Table 1. Relative number of Upper Yukon juvenile Chinook per spawner ranged from a high of 44 for the 2002 juvenile year to a low of 11 for the 2006 juvenile year. Relative survival ranged from 5% to 10%, with the highest survival occurring in 2006 (the year with the lowest juvenile per spawner). Figure 2 shows the variation in Upper Yukon juvenile Chinook abundance over time and Figure 3 shows the relationship between juvenile and returns per spawner. Although juvenile per spawner is not independent from return per spawner, both follow a similar trajectory over time; coherence in the trends of juvenile and returns to spawner supports the interpretation that variation in production primarily occurs prior to the time juveniles are sampled in the northern Bering Sea. This would include the early marine and freshwater life-history stages of Upper Yukon River Chinook salmon. Figure 4 shows the variation in juvenile survival and returns per spawner over time. Although marine survival estimates vary over time, variability in marine survival does not follow the pattern observed in production. Uncertainty in juvenile abundance and survival limit the ability to identify the true variability in survival and make inferences on causes of juvenile mortality subject to random error.

Additional uncertainty is present in the 2002 juvenile abundance estimate as a different trawl design was used in the northern Bering Sea shelf during the first year of the BASIS survey (a smaller Cantrawl model 300 was used in 2002, a Cantrawl model 400 was used in subsequent years). A 40% correction is applied to the 2002 abundance estimate to adjust for differences in vertical spread of the two trawl models, but true differences in trawl catchability of the two trawl designs is unknown. Due to the added uncertainty in juvenile abundance in 2002 and the high statistical leverage of the 2000 brood year productivity, Figures 5 and 6 show the relationship between juvenile, spawner, and return without the 2002 juvenile year. Removal of the 2002 juvenile year reduces the uncertainty in the relationship between juvenile and return

per spawner (Figure 5). Additional information on the trawl catchability of the two different trawls used during the BASIS survey is needed before including the 2002 juvenile year as this year could be adding more error than information.

Table 1. Relative abundance of juvenile Chinook salmon in the northern Bering Sea (juvenile abundance is relative to survey catchability), genetic stock composition estimates of Upper Yukon (Canadian origin) Chinook salmon, relative abundance of Upper Yukon juvenile Chinook in the northern Bering Sea, Upper Yukon spawner abundance, relative number of Upper Yukon juveniles per spawner, Upper Yukon return per spawner, and the relative proportion of Upper Yukon juveniles returning as adults (survival).

Juvenile Year	NBS Juvenile Abundance	Upper Yukon Proportion	Upper Yukon Abundance	Spawner[1]	Juvenile per Spawner	Return	Return per Spawner	Upper Yukon Survival
2002	2,439,123[2]	0.47	1,146,388	25,870	44.31	108,198	4.18	0.09
2003	4,728,250	0.43	2,014,235	52,564	38.32	107,264	2.04	0.05
2004	2,063,918	0.52	1,063,950	42,359	25.12	52,594	1.24	0.05
2005	2,563,069	0.47	1,204,643	80,594	14.95	97,171	1.21	0.08
2006	1,179,321	0.46	538,949	48,469	11.12	52,717	1.09	0.10
2007	2,747,988	0.48	1,314,912	68,551	19.18	82,229	1.20	0.06
2008								
2009	1,846,059	0.47[3]	866,724	34,903	24.83			
2010	1,558,059	0.47[3]	731,509	34,008	21.51			
2011	3,208,607[4]	0.47[3]	1,508,045	68,500	22.02			

1- Spawner abundance is scaled to juvenile year based on the assumption that all juveniles are freshwater age1.
2- A 40% effort correction was assumed for the different trawl design in 2002.
3- Stock composition of Upper Yukon Chinook salmon is not yet available estimates are based on the average proportion.
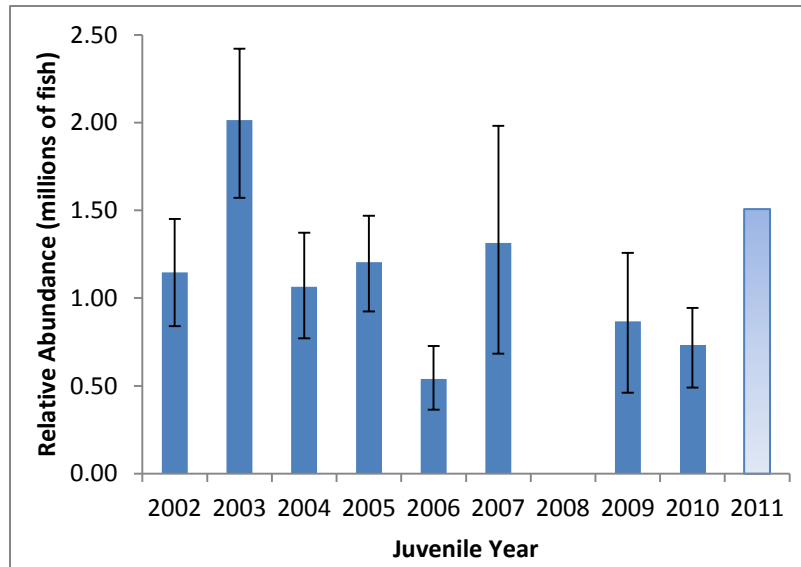
Figure 2. Relative abundance of Upper Yukon juvenile Chinook salmon in the Northern Bering Sea shelf from pelagic trawl surveys in the Northern Bering Sea shelf. Confidence intervals (80%) for abundance estimates are included. The 2011 juvenile year abundance estimate is preliminary.
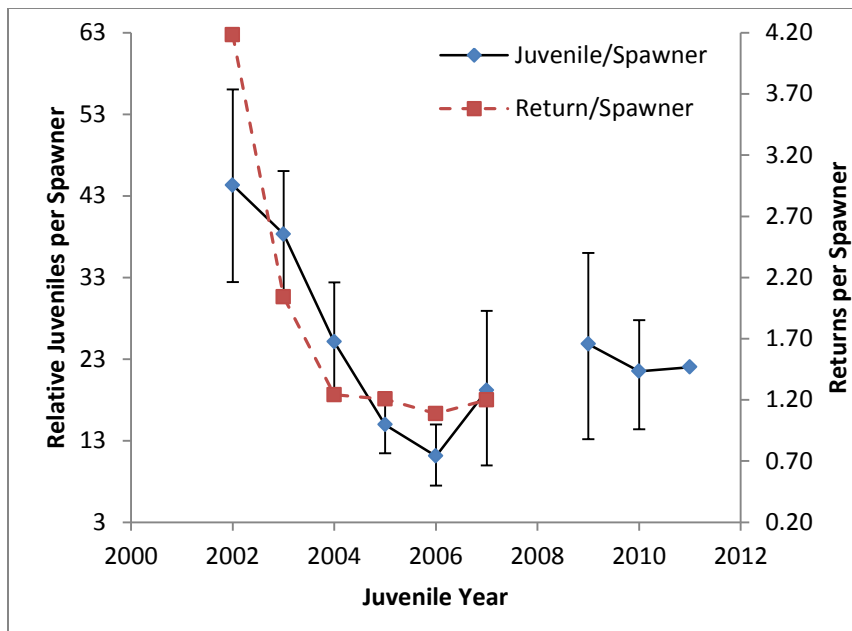
Figure 3. Relative number of Upper Yukon juvenile Chinook salmon per spawner (juvenile numbers are relative to survey catchability) with 80% confidence intervals (2002-2011 juvenile years). The number of returns per spawner (red boxes) is overlaid onto juveniles per spawner.
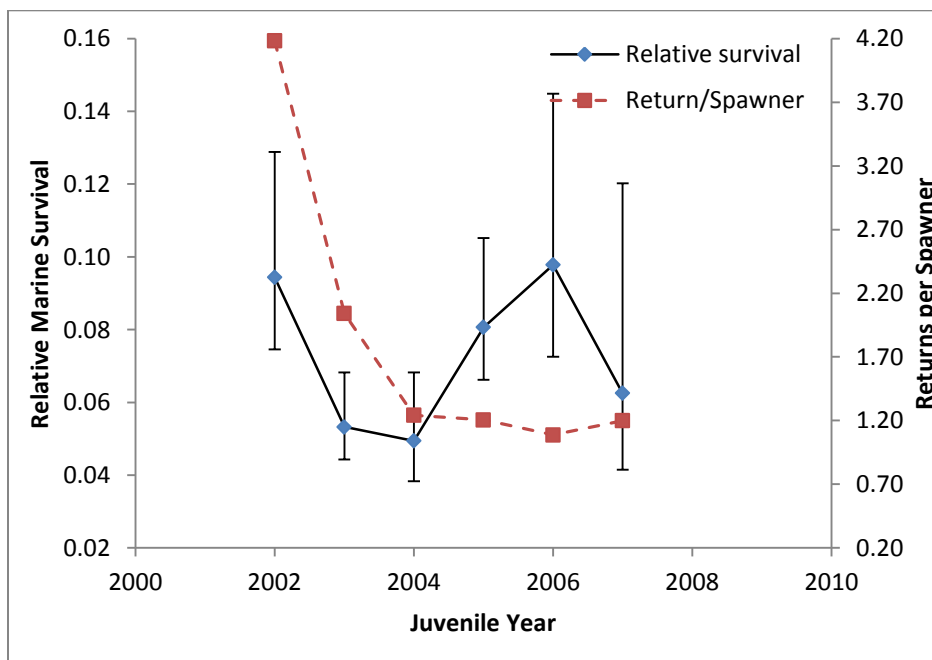
Figure 4. Relative marine survival of Upper Yukon juvenile Chinook salmon (juvenile numbers are relative to survey catchability) with 80% confidence intervals (2002-2007 juvenile years). The number of returns per spawner (red boxes) is overlaid onto marine survival.
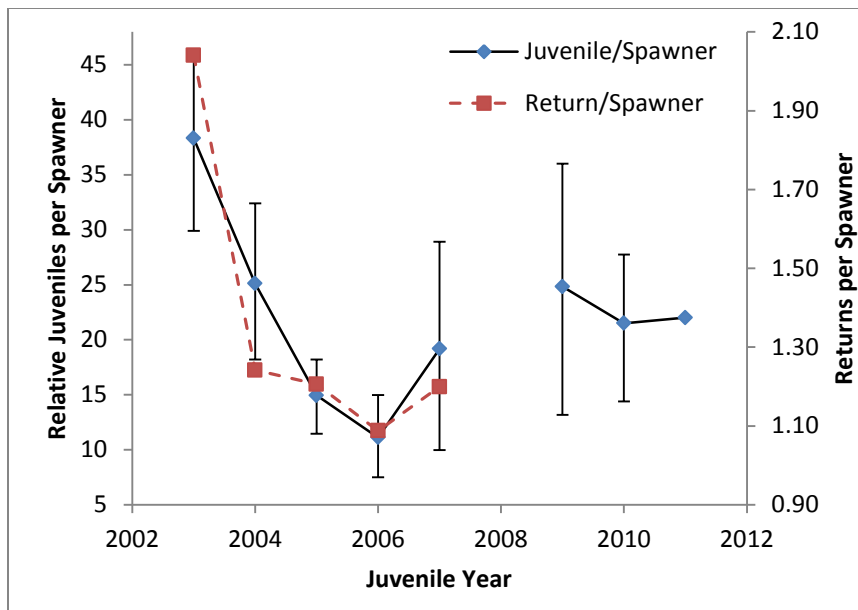
Figure 5. Relative number of Upper Yukon juvenile Chinook salmon per spawner (juvenile numbers are relative to survey catchability) with 80% confidence intervals (2003-2011 juvenile years). The number of returns per spawner(red boxes) is overlaid onto juveniles per spawner.
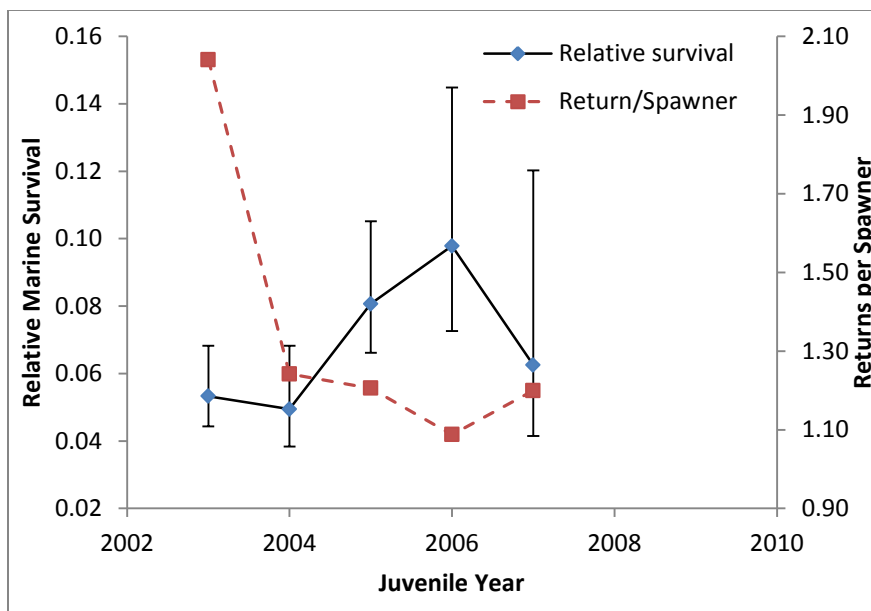
Figure 6. Relative marine survival of Upper Yukon juvenile Chinook salmon (juvenile numbers are relative to survey catchability) with 80% confidence intervals (2003-2007 juvenile years). The number of returns per spawner (red boxes) is overlaid onto marine survival.

Distribution and Migration

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Prediction surfaces (shaded contours) and individual CPUE data (circles) are shown in Figure 7 for warm and cold survey years. Temperature conditions for each year were defined by temperature anomalies of the M2 mooring on the eastern Bering Sea Shelf (Stabeno, 2007; www.beringclimate.noaa.gov). Juvenile Chinook salmon distribution during cold sampling years (2002-2007) (Fig. 5a) is similar to the distribution shown in Murphy et al. (2009). However, a slightly different contour interval was used and CPUE was scaled to average effort, which resulted in a slightly different distribution pattern for juvenile Chinook salmon than shown in Murphy et al. (2009).

Juvenile Chinook were caught in both the northern and southern Bering Sea during the 2002-2007 sample years; however juvenile Chinook salmon have only been caught in the northern Bering Sea since 2007. The loss of juvenile Chinook from the southern Bering Sea survey, may reflect a significant change in the distribution or abundance of juvenile Chinook; however, it is not possible to distinguish between distribution and abundance from survey data alone. It is possible that Chinook salmon delay their dispersal from nearshore habitats during the colder years and are simply not available to the southern Bering Sea survey area. Minimum station depths increased in the southern Bering Sea to accommodate the larger survey vessel, the NOAA Ship Oscar Dyson, and could be contributing to the loss of Chinook from the southern survey. Minimum station depths ranged from 19-24m in 2002-2007 and 27-30m in 2009-2011. Minimum station depths ranged from 17-21m in 2002-2007 and 16-21m in 2009-2011 in the northern Bering Sea.

Large difference in the distribution of juvenile Chinook in the northern Bering Sea occurred between the warm and cold years and reflects changes in the migratory trajectory of juveniles originating from drainages in the northern Bering Sea juveniles. Limited mixing of Chinook salmon from the northern and southern Bering Sea occurs during their first summer at sea (Figure 8); therefore distribution shifts are believed to reflect changes in the migratory trajectories of Chinook salmon originating from northern Bering Sea drainages (principally the Yukon River drainage). Large-scale changes in the migratory pattern of juveniles have the potential to alter marine survival, the apparent relationship between the number of juveniles and returns per spawner, and marine distribution patterns during their later marine life-history stages.

If migratory patterns of Chinook salmon impact future marine survival, the effect is more likely to improve survival than to reduce marine survival as southward migration should bring Chinook salmon closer to suitable winter habitats. Without glycoproteins to prevent freezing, juvenile Chinook are not able to survive in temperatures below freezing (Fletcher et al, 1988). Water column temperatures are believed to drop below freezing throughout most of the northern Bering Sea shelf in the winter (Irvine, et al. 2009) and in shallow habitats (<60m) of the southern Bering Sea shelf (U.S. Navy 1958). In addition, the Bering Sea cold pool (water temperatures below freezing) forms as the result of winter sea ice and typically persists year-round at bottom

depths between 50-100m in the northern Bering (Sigler, 2011). It is expected that the water column would also rapidly refreeze over the cold pool once winter ice returns; therefore water column temperatures should drop below freezing out to at least 100 m in the northern Bering, which is over 600 km offshore from the mouth of the Yukon River and is the majority of the northern Bering Sea shelf habitat. Southward migration of juveniles is more consistent with the historic migration pattern observed for Yukon River Chinook salmon (Farley et al. 2005, Hartt and Dell, 1986). Distribution patterns observed in 2002-2007 (Murphy, 2009) may have been the result of non-typical migratory patterns associated with unusually warm conditions in the Bering Sea (Stabeno, et al. 2007).
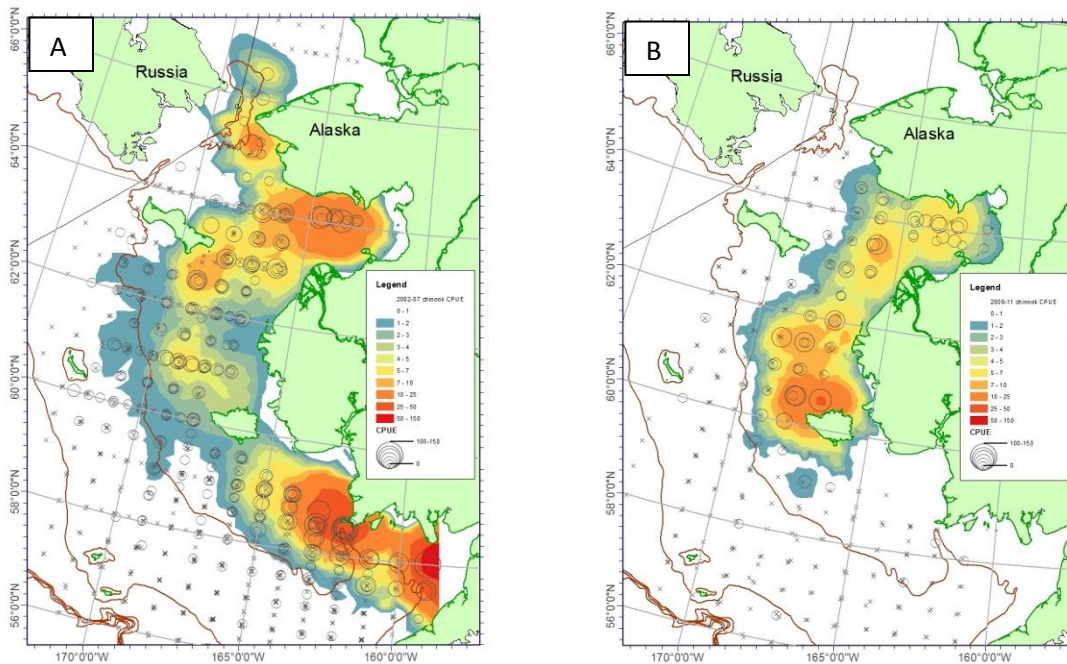
Figure 7. Kriging prediction surfaces (shaded contours) and individual catch per unit of effort (CPUE) values (circles) for juvenile Chinook during Bering Aleutian Salmon International Surveys (BASIS) from warm (A; 2002-07) and cold (B; 2009-11) years. Temperature anomalies of the M2 mooring on the eastern Bering Sea Shelf were used to split diet data into warm and cold years (Stabeno, 2007).
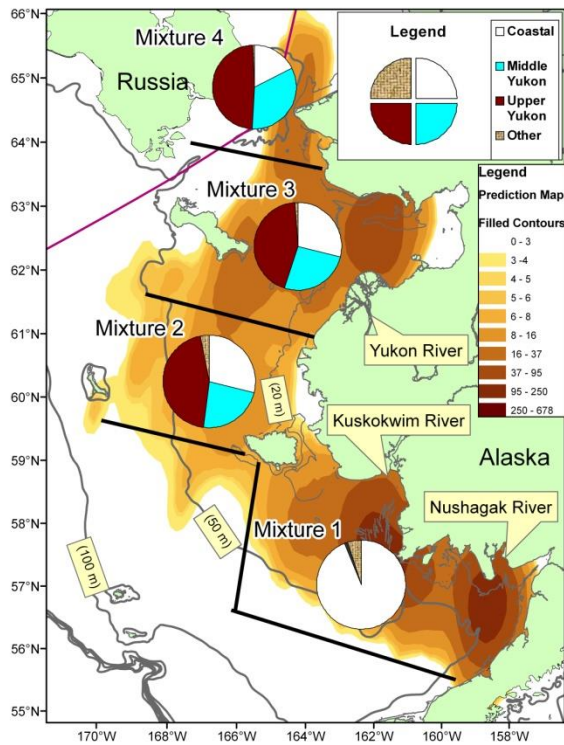
Figure 8. Stock-structured distribution of juvenile Chinook salmon (Coastal Western Alaska: white, Middle Yukon: blue, Upper Yukon: black, and other western Alaska stock groups) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Mixtures are overlaid on a map of juvenile Chinook salmon distribution and black bars identify the spatial extent of samples used for each mixture. Stock mixtures are adapted from Murphy et al. (2009) with the inclusion of 2007 mixtures (Bill Templin, personal communication).

Diet and Prey Dynamics

Diet composition by weight of each prey species was estimated by year for juvenile Chinook salmon in the northern Bering Sea and averaged for warm (2004-2007) and cold (2009-2011) years (Figure 9). Temperature conditions for each year were defined by temperature anomalies of the M2 mooring on the eastern Bering Sea Shelf (Stabeno, 2007; www.BeringClimate.noaa.gov). Capelin (*Mallotus villosus*) were an important prey item in both warm and cold years, but comprised the majority (57%) of the diet during cold years. The increase in capelin in the diet of juvenile Chinook is consistent with the increase in capelin biomass in the northern Bering Sea during cold year (Figure 10). Sandlance (*Ammodytes hexapterus*) was the second most important diet item and comprised a similar proportion of juvenile Chinook salmon diets in both warm and cold year (21% in warm years and 20% in cold years). Age0 pollock (*Theragra chalcogramma*) were only present in the diet of juvenile Chinook

salmon in warm years and is also consistent with their abundance in the northern Bering Sea. Herring (*Clupea pallasii*) were only a minor component of the diet of juvenile Chinook salmon (6% in warm years and 3% in cold years), yet were the dominate biomass present in pelagic trawl surveys of the northern Bering Sea (Figure 10). Biomass levels in Figure 8 do not reflect the available forage biomass as it includes all life-history stages of fish except for Pollock, which only includes the biomass of the age0 life-history stage. Other fish species include rainbow smelt (*Omerus mordax*) and Greenland halibut (*Reinhardtius hippoglossoides)* larvae. Other diet items include invertebrate species such as small Pandalid shrimp (*Pandalus borealis)*.

Juvenile Chinook have primarily a piscivorous diet and feed on larval or age0 life-history stages of fish during their first summer at sea (Figure 9). Based on prey size of juvenile Chinook diet, maximum prey size is under 90 mm which is generally limited to the larval or age0 life-history stage of fish. Although herring are the dominate pelagic fish biomass in the Northern Bering Sea, they are minimally present in juvenile Chinook salmon diets. Length frequency distributions of capelin and herring captured during the trawl survey indicate that few herring are within the size range that Chinook can utilize as forage (Figure 11). The general absence of herring in juvenile Chinook diets may simply be the result of herring outgrowing the prey size spectrum of juvenile Chinook salmon by September.

The smallest size mode of capelin in surface trawl catches (50 mm; Figure 12) is consistent with the size of fish observed in stomach contents of juvenile Chinook salmon (40-80 mm). Age0 capelin abundance peaks in September and October in the Gulf of Alaska bongo net tows (Doyle et al. 2002) and their size distribution is consistent with the smallest size mode of capelin in the northern Bering Sea and age0 capelin sizes observed during October in Prince William Sound (Brown, 2002). Trawl catchability for age0 capelin is believed to be very low; therefore the presence of this size mode only indicates presence, not abundance. The small size of age0 capelin may be the principal reason why capelin are the dominate prey of juvenile Chinook in September. Capelin typically spawn later than herring in Norton Sound, (Charlie Lean, personal communication) and capelin may have lower growth rates than other forage species like herring; both may be contributing to their small size in September. Although prey biomass (Figure 10) is a key feature of juvenile Chinook salmon diets, the size-spectrum of prey species is believe to be an equally important feature in the foraging ecology of juvenile Chinook salmon.

Even without herring, juvenile Chinook were able to maintain adequate energy levels (see energy section below), presumably by utilizing capelin as forage on capelin. If juvenile Chinook salmon are able to feed on herring earlier in their marine life-history period (initial marine entry), they should have a significant prey base to feed on. If not, critical forage dependencies could be present during initial ocean entry.
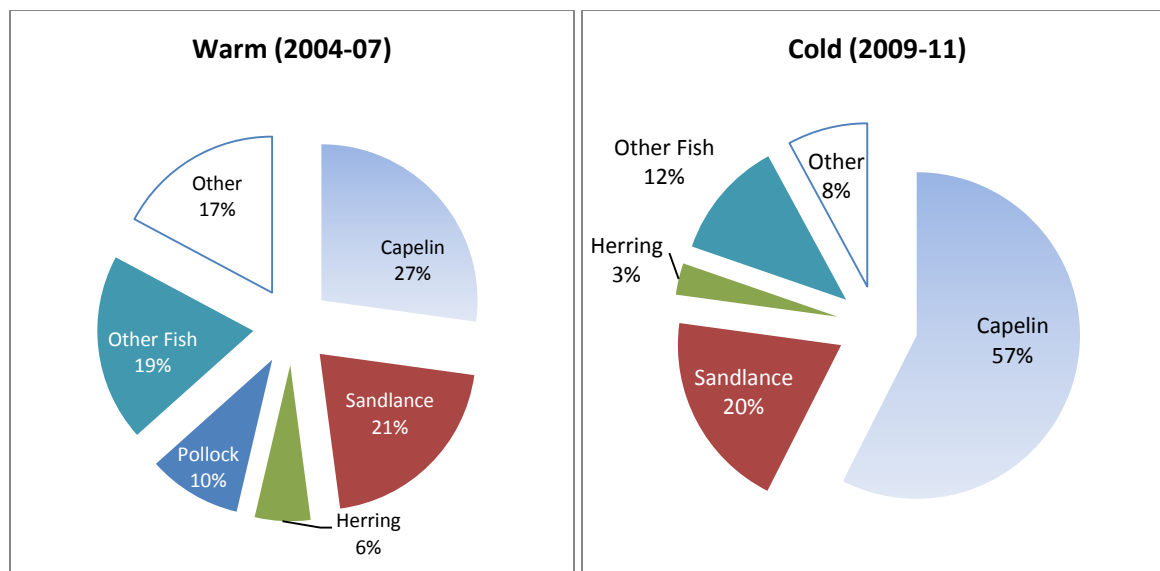
Figure 9. Proportion of different prey species present in stomach contents of juvenile Chinook salmon in the northern Bering Sea in warm years (2004-2007) and cold years (2009-2011). Proportions are based on a catch weighted stomach content index. Temperature anomalies of the M2 mooring on the eastern Bering Sea Shelf were used to split diet data into warm and cold years (Stabeno, 2007).
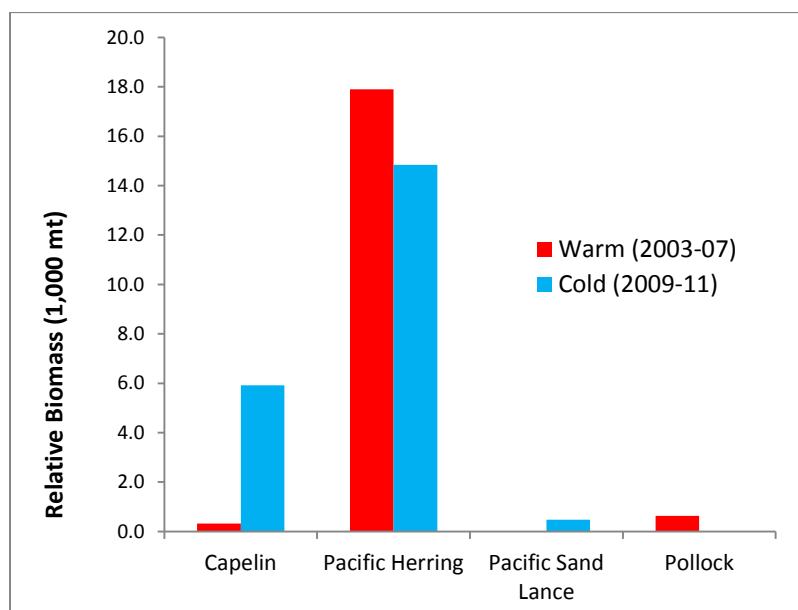

Figure 10. Relative biomass estimates of different forage fish prey species in the northern Bering Sea observed in juvenile Chinook salmon diets. Temperature anomalies of the M2 mooring on the eastern Bering Sea Shelf were used to split diet data into warm and cold years (Stabeno, 2007).
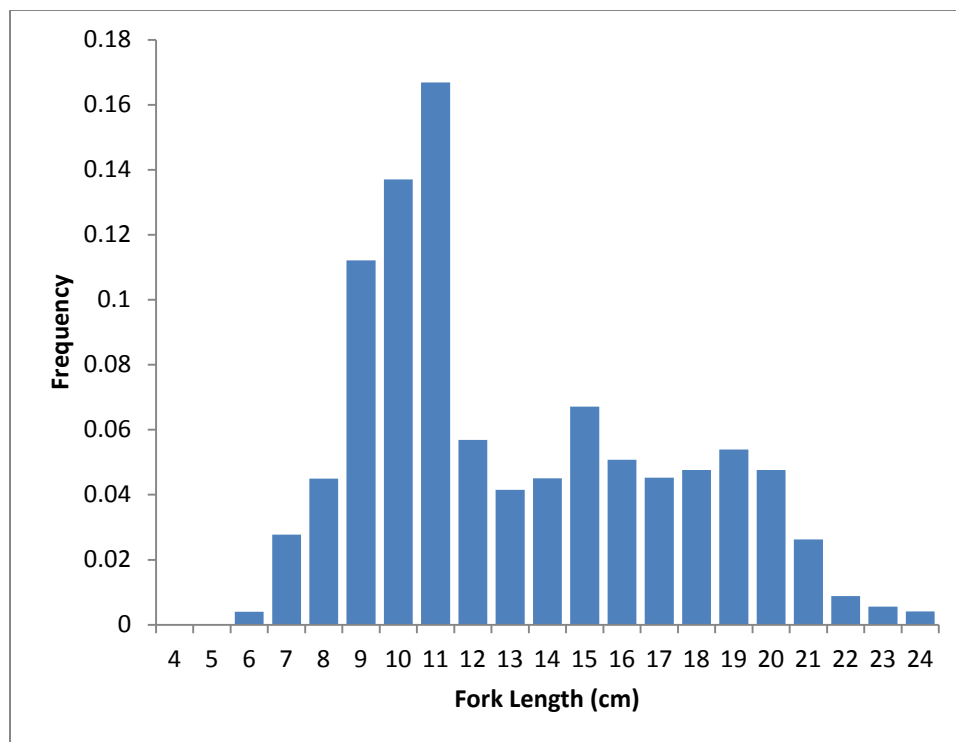
Figure 11. Length frequency distribution of herring in the northern Bering Sea (2002-2011).
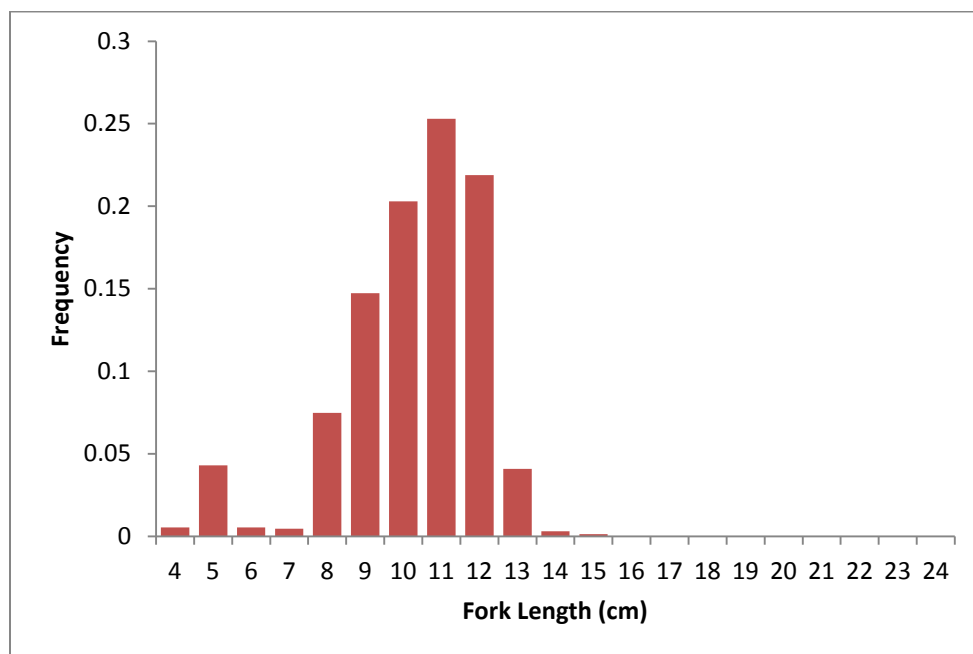
Figure 12. Length frequency distribution of capelin in the northern Bering Sea (2002-2011).

Energy

Energy density increases with size were linear in juvenile Chinook salmon. Both weight and length were correlated with energy density, $F_{(1,316)} = 587.7$, $p<0.001$, $F_{(1,316)} = 480$, $p<0.001$, respectively (Figure 13). Energy density became more variable with increases in weight and length. Predictions of energy density were made with length after lengths of fish were normalized to September 1 assuming a growth rate of 1 mm/day (Figure 14). The minimum predicted energy density was 0.76 kCal/g wet weight in 2003 and the maximum was 1.38 kCal/g wet weight in 2007. The average mean across years was 1.11 kCal/g wet weight. The range in values was greatest in 2002 (s.d.=0.11) and smallest in 3006 (s.d.=0.05). All mean energy density values at all years were above the lower critical threshold (0.9 kCal/g wet weight) observed by (Fergusson et al. 2010). In their study, juvenile chum salmon (*O. keta*) energy densities were below 0.9 kCal/g wet weight after 2 weeks of starvation. It is presumed that Chinook salmon will continue to shift energy allocations from growth into storage as winter approaches and foodstuffs become more depauperate
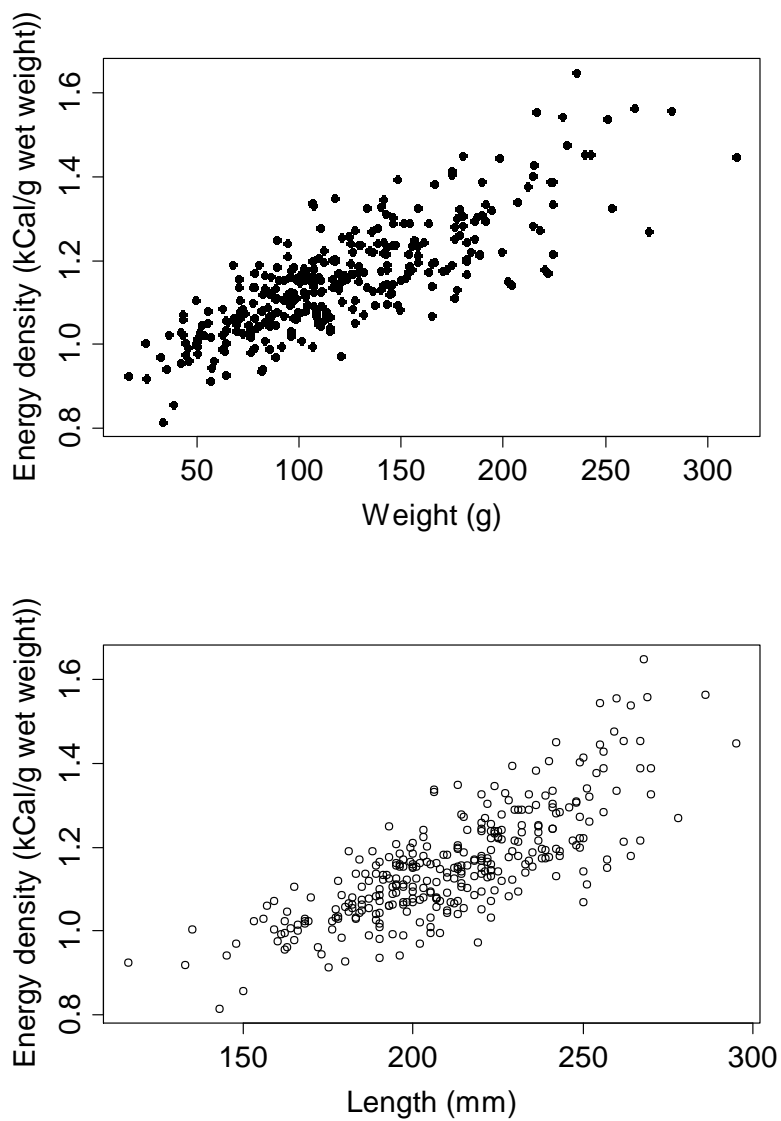
Figure 13. Regressions of length and weight with energy density (kCal/g wet weight) for Chinook salmon (*Oncorhynchus tshawytscha*) caught in the North Bering sea (north of 59˚ latitude) in years 2005-2007 and 2009-2011.
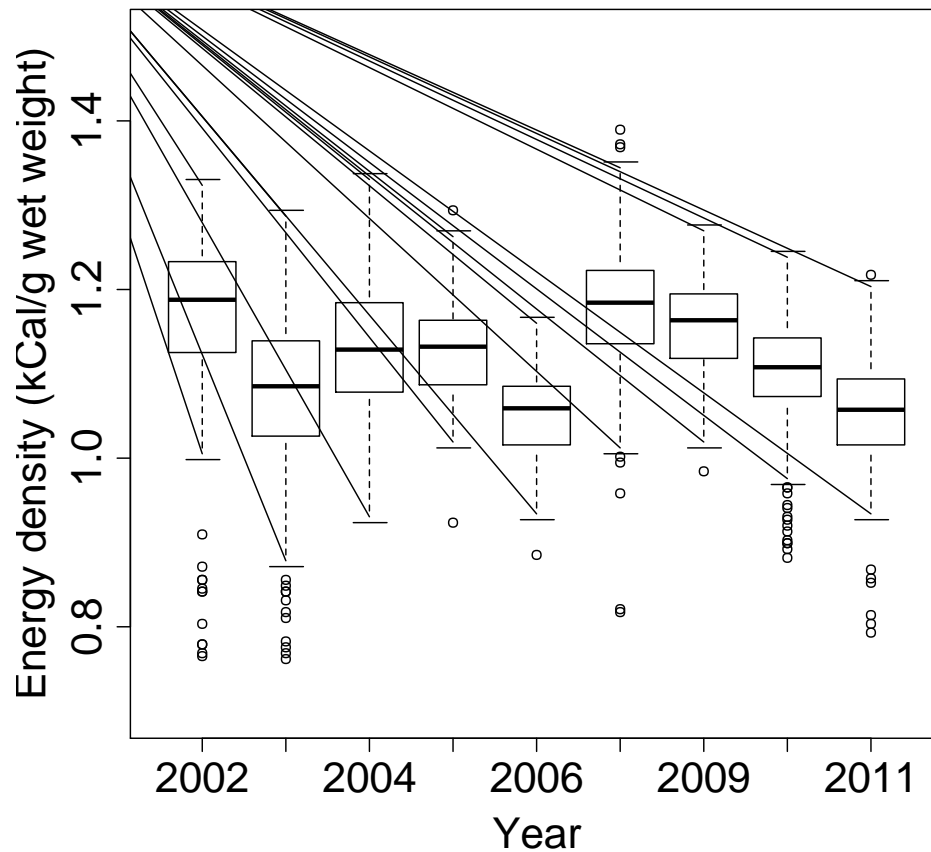
Figure 14. Predicted energy densities (kCal/g wet weight) from length measures for for Chinook salmon (*Oncorhynchus tshawytscha*) caught in the North Bering sea (north of 59˚ latitude) from 2002-2007 and 2009-2011.

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Appendix 5. Honeyfield, D.C., J. M. Murphy, K. G. Howard, W. W. Strasburger, and A. Matz. In Prep. An exploratory assessment of thiamine status in Yukon River Chinook salmon (*Onchorhynchus tshawytscha*).

ABSTRACT

Thiamine (vitamin B_1) status in Yukon River Chinook salmon *Oncorhynchus tshawytscha* was examined through egg thiamine concentration from returning females and in juvenile muscle and liver tissues from the northern Bering Sea. Only three percent of the returning females had egg thiamine concentrations low enough to produce overt fry mortality (< 1.5 nmol/g); however, 74% of the females had egg thiamine concentrations associated with secondary effects of thiamine deficiency ($1.5 - 8.0$ nmol/g), and only 23 % of the females were thiamine replete (> 8.0 nmol/g). Thiamine concentrations in juvenile muscle tissue were above critical levels (> 3 nmol/g) and varied with dietary intake of thiaminase, an enzyme present in thiaminase positive species that breaks down thiamine. Total thiamine concentrations (nmol/g) in juvenile Chinook salmon muscle (3.8) were similar to Coho *Oncorhynchus kisutch* (4.15), but lower than Chum *Oncorhynchus keta* (8.9) and Pink salmon *Oncorhynchus gorbuscha* (9.6). Thiaminase positive prey species were present in Chinook (73%) and Coho salmon (54%) diets, and were lower in diets of Chum (4%) and Pink (11%) salmon. These results provide evidence that thiamine deficiency could be contributing to the poor production levels observed in Yukon River Chinook salmon, and identifies the importance of dietary intake of thiaminase to thiamine levels in salmon.

Keywords: Thiamine deficiency, thiaminase, Yukon River, Chinook salmon, survival

INTRODUCTION

Chinook salmon returns to western Alaska have markedly declined since the late 1990s. Most notably, Yukon River Chinook salmon runs have declined by approximately half of their historical size since 2007 (ADF&G 2013). In a broader geographic scope, productivity has synchronously declined in stocks across Alaska, beginning with those cohorts spawned in 2001 (ADF&G 2013). Poor returns have occurred despite adequate numbers of salmon escaping fisheries to spawn in previous generations. These poor returns have resulted in management actions dramatically restricting subsistence harvests, and closing or severely restricting commercial and sport fisheries. Such restrictions significantly impact Alaskan fishermen and communities that depend on Chinook salmon for subsistence needs and economic opportunities. Causes of reduced productivity and poor returns are unknown, and have led to several initiatives to improve assessment and understanding of the mechanisms driving these declines (ADF&G, 2013; Schindler, et al. 2013).

Because of the significant role thiamine plays in bodily functions and evidence of thiamine-deficiency structuring survival and productivity patterns in other systems, investigating the role of this essential nutrient is an avenue of research that may provide insight into the poor returns of western Alaska Chinook salmon. Thiamine is an essential dietary nutrient required within the Krebs cycle for the production of ATP (Agyei-Owusu & Leeper 2009). Thiamine is typically found in three forms: thiamine pyrophosphate (TPP) is the active form of thiamine (coenzyme) required in enzymatic reactions in cells throughout the body; free or unphosphorylated thiamine (T) is the primary form of thiamine found in fish eggs; the metabolic importance of thiamine monophosphate (TP) is less well defined (Gubler, 1991).

Thiamine deficiency has been shown to cause adverse neuromuscular signs and mortality in reared fish consuming diets lacking thiamine, or containing high amounts of thiaminase, an enzyme that breaks down thiamine (Halver, 1989; NRC 2011). Thiamine deficiency was first linked to reproductive failure in wild fish in the mid-1990s (Fitzsimons 1995; Fisher et al. 1996). Honeyfield et al. (2005) demonstrated that Lake trout *Salvelinus namaycush* reared on a diet containing bacterial thiaminase, or Alewife *Alosa pseudoharengus* (a species known to harbor thiaminase), produced low egg thiamine resulting insignificant fry mortality. The clinical signs of

the experimental Lake trout fry were similar to those observed in wild Coho salmon
Oncorhynchus kisutch, Chinook salmon *Oncorhynchus tshawytscha*, Steelhead trout
Oncorhynchus mykiss, Brown trout *Salmo trutta*, and Atlantic salmon *Salmo salar* with high
mortality rates in the Laurentian Great Lakes, New York Finger Lakes and the Baltic Sea (Fisher
et al. 1996; Marcquenski and Brown 1997; Norrgren et al. 1998).

In addition to overt fry mortality, secondary effects of thiamine deficiency include: decreased
growth, vision, predator avoidance, prey capture and immune function, as well as limited
spawning migration and adult mortality (Brown et al. 2005a; Fitzsimons et al. 2005; Ketola et al.
2005), all of which can reduce or prevent recruitment into the population (Brown et al. 2005b;
Carvalho et al. 2009; Fitzsimons et al. 2009; Ottinger et al. 2012). Thus, thiamine deficiency
affects multiple life stages, and even non-lethal levels have the potential to negatively impact
population productivity and recruitment.

This report provides an exploratory assessment of thiamine levels in Yukon River Chinook
salmon and is the first report of the thiamine status of Alaskan salmon. The objectives of this
study were to: assess the potential for early life mortality and secondary effects of thiamine
deficiency on fry, based on egg thiamine concentrations of Yukon River Chinook salmon, and to
examine the role of diet to muscle and liver thiamine concentrations in Yukon River Chinook
salmon from juvenile collections in the Northern Bering Sea..

METHODS

Sample collection

Thiamine concentrations were examined in Chinook salmon eggs collected from the Upper,
Middle, and Lower Yukon stock groups during 2012, and from Rampart Rapids and Kuskokwim
River in 2001 (Fig. 1, Table 1). Upper Yukon egg samples were collected at the Whitehorse
Rapids Fish Hatchery and Fish Ladder during 2012 and from Rampart Rapids in 2001. Eggs were
collected from opportunistic collections during weir and carcass surveys from the Middle Yukon
rivers: Chena, Salcha, and Goodpaster, and the Lower Yukon river: Andreafsky during 2012, and
from opportunistic collections at Bethel on the Kuskokwim River during 2001. Eggs were only

collected from recently spawned females during carcass surveys and all egg samples were kept on ice or dry ice until samples could be frozen.

Thiamine concentrations in muscle and liver tissue of juvenile salmon collected during surface trawl surveys in the northern Bering Sea as part of the 2012 Arctic Ecosystem Integrated Survey (Arctic EIS 2013) (Table 2). Although several river drainages contribute to juvenile Chinook salmon stocks in the northern Bering Sea,, the Yukon River is the primary source of juvenile Chinook salmon (in the expected range of 90% of the juveniles) (Murphy et al. 2009). Species other than Chinook salmon were included in this analysis to provide a species level contrast in the relationship between thiamine levels and diet of juvenile salmon. Whole juveniles were frozen at -20 C onboard the vessel and shipped to Wellsboro, PA and stored at -80 C until analysis.

Food habits of juvenile salmon were summarized from diet information collected in the northern Bering Sea during similar surveys in 2009-2011 (Cook and Sturdevant 2013). Diet data from 2010-2011 were used in this analysis as the diet information from the 2012 survey is not yet available. Proportional prey weight (Stomach Content Index, SCI) by species and survey station was scaled by juvenile body weight and subsequently weighted by the species specific juvenile salmon catch at each station as:

$$SCIw_i = \sum_j \frac{Prey_{i,j}}{Pred_j} C_j$$

where $Prey_{i,j}$ is the total prey weight of the ith species for all stomachs examined at station j, $Pred_j$ is the total predator weight for all stomachs examined at station j, and C_j is the total predator catch at station j. $SCIw_i$ values were converted to proportions by dividing by the total $SCIw_i$ over all species within a year, and diet composition was estimated by the average the annual $SCIw_i$ expressed as a proportion.

Thiamine measurement and analysis

Thiamine concentrations were measured for egg, muscle and liver tissue by high pressure liquid chromatography following the methods of Brown et al. (1998). This method reports thiamine pyrophosphate (TPP), thiamine monophosphate (TP) and free thiamine (T). Total thiamine is the

sum of the three forms. All samples were run in duplicate. Samples were evaluated for degradation visually and by data QA/QC. Samples with evidence of degradation (increase in TP, decrease in TPP and loss of Total concentrations due to improper sample collection or handling such as refreezing thawed samples) were discarded.

Total thiamine levels were evaluated in four ways: (1) Yukon River Chinook salmon eggs and Northern Bering shelf juvenile salmon muscle thiamine concentrations were compared to reference critical levels for salmonine eggs and muscle tissues; (2) 2012 Yukon River Chinook salmon egg thiamine concentrations were compared to 2001 Chinook salmon egg collections from Yukon and Kuskokwim rivers (A. Matz, USFWS); (3) Chinook salmon egg thiamine levels from Upper, Middle and Lower Yukon stocks were compared to each other; and (4) prevalence of known thiaminase-positive prey species (Capelin *Mallotus villosus*, Rainbow smelt *Osmerus mordax,* and Pacific herring *Clupea pallasii*) was compared among the diets of juvenile salmon predator species and related to average muscle thiamine levels detected in each species of juvenile salmon.

To estimate the potential impact tissue concentration of thiamine may pose on the Yukon River Chinook, threshold or critical thiamine concentrations of egg and muscle were drawn from other studies listed in Table 3. Eggs containing less than 1.5 nmol/g of thiamine were considered to be levels consistent with high likelihood of overt fry mortality. Egg thiamine concentrations above 1.5 and below 8.0 nmol/g have been linked to secondary effects of low thiamine such as poor growth, reduced predator avoidance, reduced prey capture and immune dysfunction. These secondary effects of thiamine deficiency increase probability of mortality. Eggs with concentrations above 8.0 nmol/g total thiamine were considered replete. Thresholds levels for muscle tissue thiamine concentration are less well defined in the literature than threshold for eggs. Thiamine deficient mortality in lake trout, Atlantic salmon, Coho salmon and Rainbow trout occur when muscle tissue is below 1.0 nmol/g (Brown et al. 2005a). Although, in one study Chinook salmon with ≤ 0.5 nmol/g total muscle thiamine showed no behavioral signs of thiamine deficiency (Honeyfield et al. 2008a). For purposes of identifying potential risk from thiamine

deficiency in this report, we used 1 nmol thiamine per gram of muscle as the threshold for mortality.

RESULTS

Egg thiamine concentrations

  Average total thiamine concentrations in the majority of Chinook salmon eggs were above the concentration known to cause overt fry mortality (Table 3). Overall, three percent of females sampled had egg thiamine concentrations low enough to result in overt fry mortality; however, 74% of females sampled had egg thiamine concentrations with a potential to develop secondary effects of thiamine deficiency (1.5 – 8.0 nmol/g). Only a quarter of the egg lots were fully thiamine replete (Fig 2, 3; Table 3). Average egg thiamine concentration decreased with increasing migratory distance of adults (Lower, 9.2; Middle 7.5; and Upper Yukon River drainage 6.2 nmol/g). The predominant form of thiamine present in egg samples was unphosphorylated or free thiamine (92%) (Table 1).   Samples from 2012 exhibited much lower egg thiamine concentrations than those obtained in 2001 in an unrelated contaminants study conducted by the USFWS (Table 1; A Matz).   Average total thiamine in 2001 Chinook salmon eggs collected at Rampart Rapids (Upper Yukon) (9.6 nmol/g) were lower than Chinook salmon eggs (11.7 nmol/g) from Bethel, Kuskokwin River. Furthermore 2001 Chinook salmon egg thiamine from Bethel, Kuskowim River was similar to concentration observed in Chum salmon eggs collected from the same location in the same year (12.0 nmol/g).

The Whitehorse Hatchery (Fig. 2a; Table 1) was the only location with sufficient number of egg samples to support a site specific summary. Low sample numbers at other sampling sites were due to the opportunistic and exploratory nature of the collections (Fig. 2b; Table 1). None of the females sampled at the Whitehorse hatchery had egg thiamine concentrations low enough to cause overt fry mortality (Table 3). However, thiamine concentration in 25 of 28 (89%) egg lots was in the range associated with the deleterious secondary effects of thiamine deficiency. Only 3 of 28 (11%) egg samples at the Whitehorse hatchery were fully thiamine replete.   At the Chena River site (Fig. 2) 1 of 4 females sampled (25%) had egg thiamine concentrations sufficiently low to produce overt fry mortality; however sample size is very low for a good population estimate. Six of the 11 females sampled (55%) at Yukon River sites other than the Whitehorse hatchery had

fully replete egg thiamine levels, and 4 of 11 females (36%) contained egg thiamine levels in the range where secondary effects of thiamine deficiency are known to occur in salmonids.

Juvenile thiamine concentrations and diet

Concentrations of total thiamine (nmol/g) in muscle and liver of juvenile Chinook (3.8 and 16.4) and Coho (4.2 and 18.3) salmon were lower than that found in juvenile Chum (8.9 and 23.9) and Pink (9.6 and 22.2) salmon. Total muscle and liver thiamine from juvenile salmon (Table 2) tended to reflect the proportion of thiaminase positive forage fish consumed (Table 4).

The diet composition of the four juvenile salmon species obtained from Cook and Sturdevant (2013) consisted of seven invertebrate and eight vertebrate (Teleostei) prey items (Table 4). Invertebrate prey items were the main component of juvenile Chum and Pink salmon diet at 87% and 71%, respectively; while Chinook and Coho salmon juveniles consumed almost entirely teleosts (97%). Chinook salmon diets consisted of 73% thiaminase positive species (Pacific herring *Clupea pallasii*, Capelin *Mallotus villosus* and Rainbow smelt *Osmerus mordax*); primarily Capelin. More than half of the Coho salmon diet consisted of one thiaminase positive species, Capelin. In contrast Chum and Pink salmon diets contained few (4-11%) thiaminase positive species.

DISCUSSION

Thiamine deficiency has been linked to recruitment failure and poor productivity in a wide range of species in both marine and freshwater habitats. A compelling example of the connection between thiamine and fish recruitment is present in Lake Michigan Lake trout. Complete recruitment failures in Lake Michigan Lake trout have occurred with egg thiamine levels less than 4 nmol/g. Recent recruitment successes in Lake trout coincided with increased egg thiamine concentrations (egg thiamine levels exceeded 4 nmol/g at most sampling locations) (Hanson et al. 2013). Although there is some recruitment success in Lake Michigan Lake trout, normal population recruitment will require egg thiamine levels in excess of 8 nmol/g (cite, xxxx).

Patterns in egg thiamine levels are consistent with productivity patterns of Upper Yukon River Chinook Salmon. Upper Yukon River Chinook salmon productivity levels in 2001 were more than twice that observed in the past 6-7 years (JTC 2013). Similarly, mean egg thiamine levels in 2001 (9.6-11.7 nmol/g) were nearly twice as high as that in the observed levels in 2012 (Table 1). Mean thiamine levels in 2001 Chinook salmon eggs were fully thiamine replete and contained thiamine levels similar to Chum salmon, which are known to consume less thiaminase-positive prey (Table 4; Davis et al. 2005). Taken together, thiamine concentrations in 2001 samples and higher productivity observed as compared to 2012 egg thiamine and poor productivity in recent years is suggestive that decline in egg thiamine is a potential factor that warrants more consideration in explaining the lower productivity observed in Yukon Chinook.

Average Yukon River Chinook salmon egg thiamine concentrations decreased with migratory distance of females in 2012. Moreover, 2001 Chinook salmon from Rampart Rapids, Yukon River (Upper Yukon) were lower than 2001 samples from Bethel, Kuskokwim River, a much smaller, neighboring river drainage with a migratory distance more similar to Lower Yukon stocks. Though limited in data, the 2001 trend appears to support the egg thiamine concentration and migratory distance relationship observed in 2012. Our confidence in the data depends on the stock. The number of egg samples from Whitehorse Hatchery had sufficient replication for us to have confidence in this stock's egg thiamine status. The mean at Whitehorse Hatchery was the lowest of the three river sections. One mid Yukon River site, Chena River, had 1 of 4 eggs lots with thiamine concentrations known to cause fry mortality. Additional sampling will be required to determine true status of the Chena stock and the thiamine status of the other respective stocks investigated in this study. Patterns of reduced thiamine status related to migratory distance have also been reported in the upstream migration of Coho salmon (Fitzsimons et al. 2005) and Rainbow trout (Ketola et al. 2005). No studies have been conducted to estimate the amount of thiamine used during migration but it more likely the thiamine status is related to thiamine status established in the marine environment.

Muscle and liver thiamine concentrations (Table 2) measured in four juvenile salmon species (50-200 g body weight) from the northern Bering Sea are well above the critical or lethal levels known to exist for salmon (Table 3). Caution should be used in assuming that no adverse effect of thiamine deficiency is present as it is unclear what the requirements are for juvenile Chinook

salmon in the northern Bering Sea. Simultaneous measurement of both muscle and liver thiamine provide a better assessment of a fish's true thiamine status. In low thiamine status, muscle thiamine can be < 1.0 and the fish not in eminent danger of death if liver stores have not been fully exhausted. With the exception of the study on immune function which documented two levels of thiamine (Ottinger et al. 2012), there are no other data to describe secondary effects over a range of thiamine concentrations in sub-adult or young adult salmon. Also there are no previous studies on salmon stocks residing in the northern Bering Sea or the Gulf of Alaska for comparison.

There appears to be a clear relationship between juvenile salmon diet, specifically the prevalence of thiaminase positive prey, and thiamine status. Juvenile Chinook and Coho salmon had lower muscle and liver total thiamine concentrations than measured in Chum or Pink salmon. Juvenile Chinook and Coho salmon had the highest proportion of thiaminase positive dietary prey items (73%) followed by Coho salmon (54%; Table 4), yet muscle and liver total thiamine were similar. Juvenile Chinook salmon are known to be highly piscivorous and are much more selective for fish as prey than other species of salmon (Brodeur et al. 2007, Daly et al. 2010, Weitkamp & Sturdevant 2010). Although diet and thiamine data were not available for the same years, minimal variation is present in broad prey classes (e.g. teleost versus invertebrate prey) over time (Brodeur et al 2007; Cook & Sturdevant 2013).   Results reported here only compare diet to muscle and liver thiamine concentration in the juvenile life stage. Information from other life stages, particularly returning adults, would greatly improve our understanding of how marine food web dynamics and foraging ecology of salmon in the Bering Sea contributes to thiamine deficiency.

Oceanographic features of the northern Bering Sea are an important component of juvenile Yukon River Chinook salmon diets. The northern Bering Sea is a unique habitat for juvenile Chinook salmon (Murphy et al. 2013). During colder years, a cold pool extends through the middle of the northern Bering Sea (Stabeno et al. 2012), which represents a thermal barrier to juvenile Chinook salmon. This barrier seems to shape the near-shore distribution of juvenile Chinook salmon (Murphy et al. 2013), and may also significantly affect their diet. Forage fish species in the northern Bering share this near-shore distribution; this spatial overlap may be a contributing

factor in the high levels of thiaminase positive prey items in northern Bering Shelf juvenile Chinook salmon diet. Over 80% of the juvenile Chinook salmon diets from this area were comprised of small forage fish, primarily age-0 Capelin (Cook and Sturdevant 2013). While many other studies have described juvenile Chinook diets from other regions (Schabetsberger et al. 2003, Brodeur et al. 2007, Daly et al. 2009, Daly et al. 2010), only one other mentions Capelin as a consistent prey item (Weitkamp & Sturdevant 2010). The latter was also an Alaskan study, but in the southeastern panhandle. Typically, the dietary composition of juvenile Chinook in other regions (California Coastal Current, WA, OR, BC, and Columbia River plume) tend to be predominantly piscivorous, but focused on different taxonomic groups (e.g. *Sebastes* spp., *Hexagrammidae,* and *Engraulis mordax*).

Thiaminase activity has been shown to play an equally important role in thiaminase induced thiamine deficiency as the presence or absence of thiaminase in fish diet. Changes in dietary thiaminase can be due to diet shifts that include higher percentage of thiaminase positive prey, different thiaminase positive prey species, or no change in diet composition but a change in the thiaminase activity in the prey species consumed. Previously studies have found that thiaminase activity in species such as Alewife, Rainbow smelt, and Atlantic herring can be highly variable (Wistbacka et al. 2002; Tillitt et al. 2005; Honeyfield et al. 2012). More importantly, Wistbacka and Bylund (2008) suggested that Baltic salmon with high incidence of M74 may be more selective for Atlantic herring with higher thiaminase activity. The variability in thiaminase concentration in Alaskan prey items, such as Capelin (Ceh et al. 1964), has not been reported and it is not known if variable thiaminase contributed to the difference in thiamine concentrations in Chinook or Coho salmon. Furthermore there can be diet switching from one thiaminase positive prey to another thiaminase positive species. Diet switching among thiaminase positive fish can result in thiaminase having either a greater or lesser biological impact on thiamine status. For example thiaminase activity from Rainbow smelt has less of an effect on salmonid thiamine status than thiaminase from alewife because the optimal pH for thiaminase activity in Rainbow smelt differs from intestinal tract pH of salmonids (Zajicek et al. 2009). Therefore knowledge of thiamine and thiaminase activity of potential prey items is important information, not only for these salmon species in question but for other predators as well (Balk et al. 2009).

Thiamine deficiency directly impacts metabolic function in top predators and appears to be an indicator of ecosystem dysfunction, as has been observed in the Great Lakes basin, Baltic Sea and in the Florida lakes (Hill and Nellbring 1999; Blazer and Brown 2005; Honeyfield et al. 2008c). In each of these ecosystems, abnormal food web dynamics produced thiamine deficient mortality in top level predators. Non-native Alewife, which contain thiaminase, became the dominant salmonid prey item in the Great Lakes basin as native coregonid prey species, which do not contain thiaminase, declined or disappeared. Thiamine deficiency in Baltic Sea salmon, a phenomenon referred to as M74, resulted from marine ecosystem shifts in Baltic cod *Gadus morhua*, Sprat *Sprattus sprattus* and Atlantic herring *Clupea harengus* populations (Hill and Nellbring 1999), such that salmon with a high incidence of M74 were selectively feeding on those herring containing the highest thiaminase levels (Wistbacka and Bylund 2008). In a third case, increased predation on American gizzard shad *Dorosoma cepedianum* by adult alligator *Alligator mississippiensis* contributed to their thiamine deficiency mortality as shad populations increased as a result of changes in freshwater quality and quantity in Lake Griffin, Florida (Rice et al. 2007, Ross et al. 2009). In these examples elevated dietary thiaminase from prey species and dysfunctional ecosystem seem to go hand in hand when thiamine deficiency has been found to adversely affect aquatic top predators.

Thiamine deficiency is associated with dysfunctional immune system response and therefore could be a contributing factor in epizootic disease outbreaks. Ottinger et al. (2012) reported that juvenile Lake trout (~350 g body weight) with low thiamine had dysfunctional T-cell activity. T-cell function is an important part of the immune response to intra-cellular pathogens such as but not limited to bacterial kidney disease (BKD) and *Ichthyophonus hoferi*. Alaskan Chinook salmon are known to be affected by both BKD and *Ichthyophonus*. Kocan et al. (2009) reported that stress from elevated water temperature and exhaustive swimming increased the severity of *Ichthyophonus* in experimentally infected Rainbow trout. These authors further suggested that heart tissue damage from the infection reduced swimming performance, but concluded that something other than *Ichthyophonus* may explain the poor swimming ability. Honeyfield (unpublished data) has found that the critical swimming performance (*Ucrit*) of American eel *Anguilla rostrata* was 50 cm/s in thiamine replete eels and reduced to 29 cm/s in eels with low thiamine concentrations. Thiamine status of migrating Alaskan Chinook salmon with or without *Ichthyophonus* has not been reported. The insidious nature of low thiamine (the secondary

effects) has not been readily recognized and may have far reaching population affects, including serving as a catalyst or co-stressor in epizootic disease outbreaks.

The research reported here provides an exploratory assessment of the thiamine status of Yukon River Chinook salmon stocks. Although the data found no overwhelming evidence for acute thiamine deficiency, there is evidence for secondary effects of low thiamine that could affect these stocks. Additional research will be necessary to fully evaluate the role of thiamine status for Yukon River Chinook salmon stocks. A higher number of egg samples are needed per site to adequately estimate thiamine status, especially at sites where thiamine deficient eggs were found in this preliminary study. Additional research is warranted to understand secondary effects of thiamine deficiency on survival, including immune response and migratory ability of adults. Finally, ecosystem research is needed to improve our understanding of how changes in marine prey contribute to thiamine deficiency in salmon, including dietary sources of thiamine and thiaminase.

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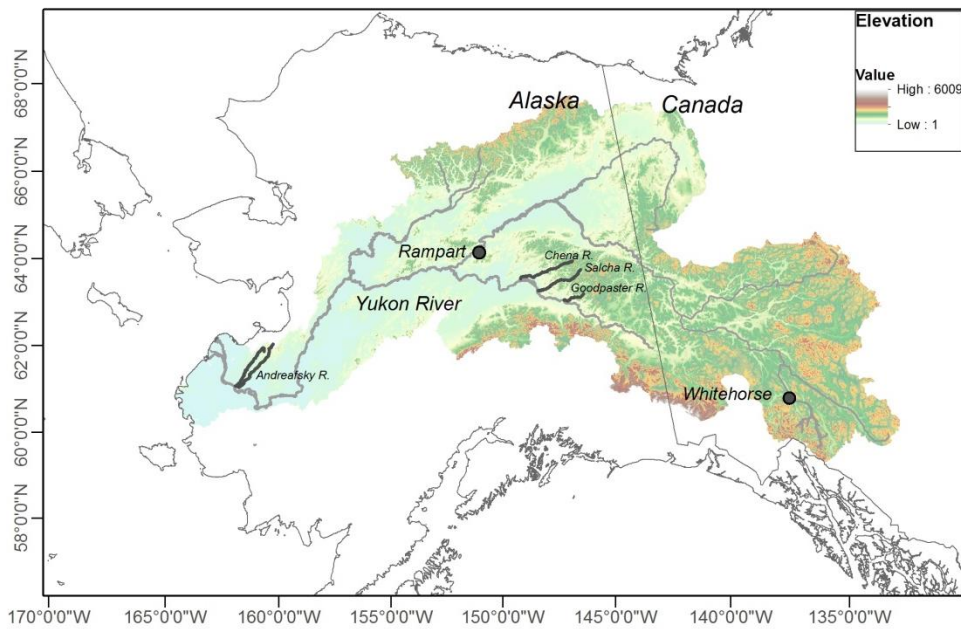
Figure 1. Egg samples were opportunistically collected from Chinook salmon stock groups from the upper (Rampart Rapids and Whitehorse Rapids Fish Hatchery), middle (Chena, Salcha, and Goodpaster rivers) and lower (Andreafsky River) sections of the Yukon River for thiamine analysis.

Eggs from upper Yukon River stock
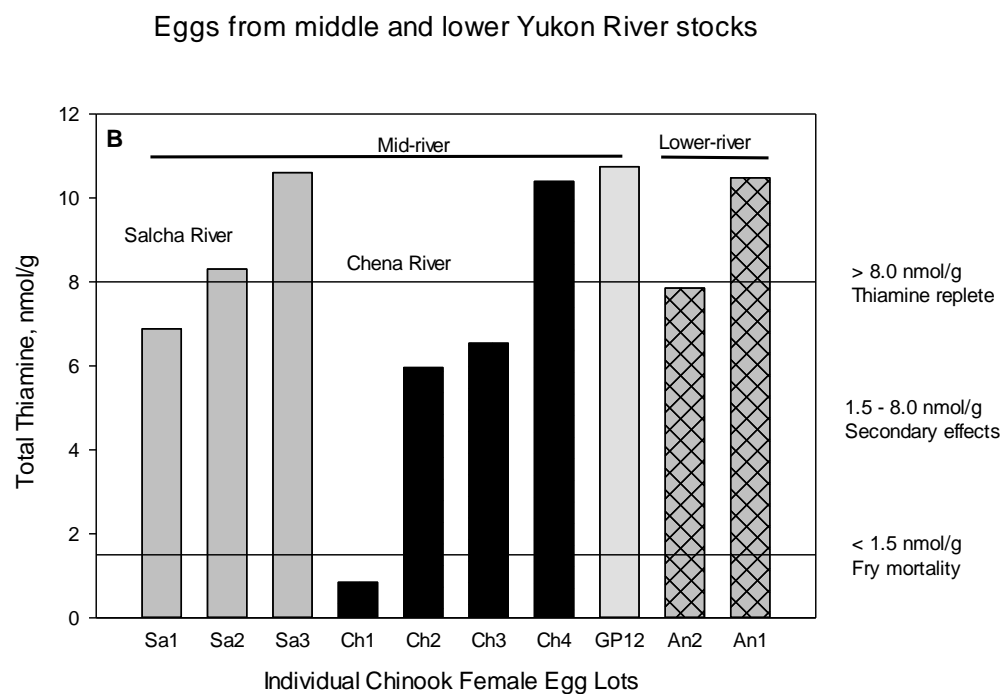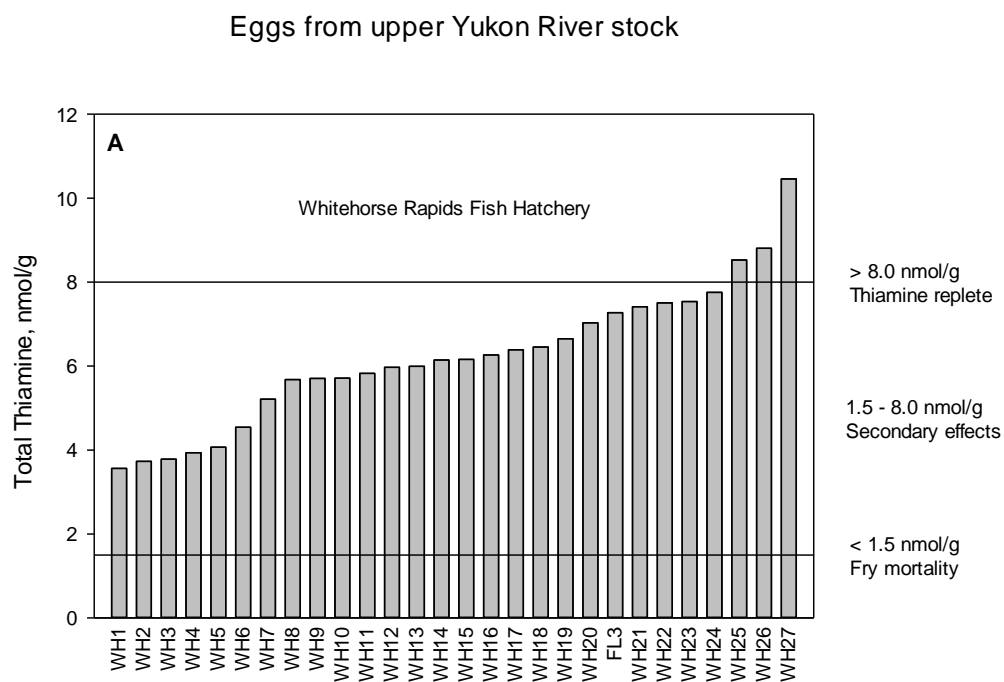

Eggs from middle and lower Yukon River stocks

Figure 2. Total thiamine (nmol/g) concentration distribution in Chinook eggs collected in the upper Yukon River (panel A), the middle and lower Yukon River sections (panel B) at Salcha, (Sa), Chena (Ch), Goodpaster (GP) and Andreafsky (An) Rivers.

Table 1. Spawning stock mean (SD) thiamine concentrations (nmol/g) in egg samples collected in Upper Yukon River drainage (Whitehorse Hatchery) and opportunistically within the Middle river drainage (Salcha, Chena and Goodpaster Rivers) and in the Lower river drainage (Andreafsky River) during carcass surveys and broodstock collections, in 2012. Thiamine concentrations are reported as thiamine pyrophosphate (TPP), thiamine monophosphate (TP), free or unphosphorylated thiamine (T) and total thiamine (sum of TPP, TP, and T).

Location	Species	Year	N	TPP	TP	T	Total
Upper Yukon	Chinook	2012	28	0.2 (0.0)	0.5(0.0)	5.6 (0.3)	6.2 (0.3)
Middle Yukon	Chinook	2012	8	0.2 (0.1)	0.4 (0.1)	7.0 (3.1)	7.5 (3.3)
Lower Yukon	Chinook	2012	2	0.2 (0.0)	0.5 (0.2)	8.5 (1.1)	9.2 (1.3)
Upper Yukon	Chinook	2001	5	0.7 (0.0)	1.0 (0.0)	10.1 (0.2)	9.6 (0.2)
Kuskokwim	Chinook	2001	5	0.7 (0.0)	1.0 (1.0)	10.1 (0.2)	11.7 (0.2)
Kuskokwim	Chum	2001	31	1.3 (0.3)	1.0 (0.2)	9.7 (1.0)	12.0 (1.3)

Table 2. Mean (SD) length, weight and thiamine concentrations (nmol/g) in muscle and liver tissue of juvenile Chinook, Coho, Chum, and Pink salmon species in the northern Bering Sea (2012). Thiamine concentrations are reported as thiamine pyrophosphate (TPP), thiamine monophosphate (TP), free or unphosphorylated thiamine (T) and total thiamine (sum of TPP, TP, and T)

Species	N	Length (mm)	Weight (g)	Muscle TPP	TP	T	Total
Chinook	13	207 (15)	107(29)	1.34 (0.49)	1.91 (0.33)	0.56 (0.24)	3.82 (0.68)
Coho	9	260 (14)	210 (37)	2.37 (0.40)	1.32 (0.30)	0.46 (0.20)	4.15 (0.62)
Chum	15	167 (16)	47 (13)	2.83 (1.28)	4.36 (1.38)	1.7 (0.69)	8.89 (2.51)
Pink	10	152 (11)	29 (6)	5.79 (1.43)	2.5 (0.98)	1.34 (0.89)	9.63 (2.94)
				Liver			
Chinook	12	--	--	1.07 (0.48)	2.96 (1.19)	12.36 (4.78)	16.39 (5.28)
Coho	8	--	--	3.15 (1.85)	4.2 (1.66)	10.98 (3.10)	18.33 (4.33)
Chum	15	--	--	0.92 (0.18)	1.5 (0.69)	21.52 (4.94)	23.94 (4.96)
Pink	10	--	--	2.68 (0.90)	3.7 (1.89)	15.78 (3.85)	22.15 (3.98)

Table 3. Reference values for egg thiamine.

Tissue	Critical Level of Total Thiamine		
	Overt Mortality	Secondary Effects	Replete
Egg	≤ 1.5 nmol/g (Honeyfield et al. 2005, Fitzsimons et al. 2007, Fisher et al. 1996)	1.5−8 nmol/g (Honeyfield et al. 2005, 2008b, Fitzsimons et al. 2009, Cavalho et al. 2009, Ottinger et al. 2012,)	> 8 nmol/g (Fitzsimons et al. 2009)
Muscle	< 1 nmol/g (Brown et al. 2005a; Honeyfield et al. 2008a)	Unknown	> 3 nmol/g (Honeyfield et al. 1998a, 1998b, Honeyfield unpublished Chinook data)

Table 4. Percent mean (SD) catch weighted diet composition of Chinook, Coho, Chum, and Pink salmon in the northern Bering Sea (2010-2011).

	X = positive Thiaminase	Chinook	Coho	Chum	Pink
Invertebrate					
Amphipod		1 (1)			1 (1)
Appendicularia				66 (19)	3 (2)
Chaetognath				10 (14)	17 (13)
Copepod				6 (13)	12 (16)
Decapod		0 (1)	2 (5)		2 (2)
Euphausiid		1 (3)		5 (7)	34 (29)
Mysid					
Polychaeta					
Pteropod				1 (1)	3 (2)
Teleost					
Capelin	X	67 (22)	54 (29)	3 (4)	11 (3)
Flatfish		5 (9)	3 (4)		
Herring	X	6 (7)		1 (0)	
Rainbow smelt	X	1 (1)			
Saffron cod				1 (1)	
Sandlance		19 (26)	39 (32)	5 (7)	10 (1)
Sculpin					5 (1)
Unkn Fish				2 (2)	2 (0)
Total diet	% thiaminase	73 (31)	54 (29)	4 (5)	11 (3)