Seasonal Bioenergetics of Pollock, Cod and Arrowtooth Flounder in the Bering Sea

NPRB Project B54 Final Report

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Abstract:

The NPRB funded Bering Sea Integrated Ecosystem Research Program (BSIERP) and NSF funded Bering Ecosystem Study (BEST) provided an unparalleled opportunity to understand how the Bering Sea ecosystem supports the production of commercially valuable species. The seasonal bioenergetics component evaluated the condition of juvenile fish at different ontogenetic stages in an effort to understand the effect of environmental variability on the health of fish populations. The intent was to increase our understanding of the mechanisms underlying recruitment variability in the southeastern Bering Sea so that fishery managers could gain the ability to understand how climate and fishing influence the variability in harvestable biomass. Specifically, the dry mass, lipid, energy density and growth of juvenile gadids and arrowtooth flounder were measured on specimens collected on a series of surveys conducted between May of 2008 and October of 2010. Over 3500 separate analyses were conducted on larvae, young-of-the-year, age-1 juveniles and their zooplankton prey. The results of these analyses were integrated into other findings from the BEST/BSIERP Program to evaluate the health of fish populations under different environmental conditions during different developmental stages.

The principle findings of the work are:

1. Walleye pollock have a relatively short time window for provisioning themselves with lipid prior to winter after they complete larval development.
2. Climatic conditions mediate their ability to provision themselves by influencing the spatial match between young-of-the-year pollock and their prey and the quality of those prey.
3. Fish that surpass a critical energy content during this period have the highest probability of surviving winter. This critical level depends on acquiring both a large size and high energy density.
4. A mechanistic connection between climate and recruitment has been identified that indicates that under so-called cool conditions in the Bering Sea, high-lipid prey are available to juvenile pollock in fall in sufficient abundance to support rapid growth and energy storage. When these conditions do not exist, recruitment can be expected to be below average.
5. Similar results have been found for Pacific cod
Key Words:
- pollock, Pacific cod, arrowtooth flounder, juvenile, larvae, energy, lipid, condition, recruitment

Citation:
Chapter 4 - Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea

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Study Chronology:

The Seasonal Bioenergetics Project depended on samples collected during NOAA, BEST and BSIERP surveys beginning in May of 2008 through October of 2010. Samples of larvae, young-of-the-year and age-1+ arrowtooth flounder, pollock, Pacific cod, Kamchatka flounder and various zooplankton species were collected and processed to determine their RNA/DNA energy or lipid content. Sample collection began with the first survey in spring 2008 conducted as part of the North Pacific Climate Regime and Ecosystem Productivity (NPCREP) Program at NOAA’s Alaska Fishery Science Center. It continued with the BEST/BSIERP surveys conducted in 2008, 2009 and 2010, the 2010 NPCREP survey and the Bering Aleutian Salmon International Surveys (BASIS) conducted in 2008, 2009 and 2010. Sample processing began shortly after the first survey and continued until June of 2011. Updates were provided to NPRB on a semi-annual basis beginning on September 28, 2008 through April 19, 2013. This is the final report.

Introduction

The work conducted under the Seasonal Bioenergetics Project (B54) was aimed at understanding how juvenile pollock, Pacific cod, and arrowtooth flounder use energy over their first year of life and how that use relates to climatic conditions in the southeastern Bering Sea (SEBS). Juvenile fish at high latitudes need to allocate energy between the conflicting demands of growth and storage during their first year of life. Understanding how they resolve those demands, by measuring their lipid and energy content, provides an index into the relative importance of growth in the near term and starvation in the long term as factors determining their survival. At the start of this project we had relatively little information of this sort for these species, particularly in the SEBS.

The basis for this work was a hypothesis (1b), developed as part of the overall framework for the Bering Sea Integrated Ecosystem Research Program. The hypothesis
Proposed that decreased storm frequency and intensity in the southeastern Bering Sea would produce a series of oceanographic effects leading to a decreased food supply for juvenile fish, which would consequently reduce their nutritional condition and productivity. The measure of nutritional condition invoked was the energy density or energy content per unit mass. Conditions thought to reduce nutritional condition included a shallowing of the stratified layer leading to nutrient depletion throughout the water column and a resulting attenuation of the fall plankton bloom. Limited primary production in fall would constrain the production of prey available for juvenile fish. Consequently, juveniles would be less able to allocate energy to storage lipids in fall, manifesting reduced energy levels in their tissues.

Juvenile fish need to meet a variety conflicting life history demands as they develop from newly hatched larvae to newly recruited adults. Early larvae need to develop muscle mass and a digestive apparatus in order to move volitionally through the water and process food into energy and tissue. Late stage larvae are more mobile but still need to complete organ development while increasing in mass and length. Growth for late stage larvae is important because it improves their locomotion, reduces their availability to predators and increases the diversity of their prey field. Post-metamorphic juveniles, commonly referred to as young-of-the-year (Y0Y) are able to move at will in the water but are still undergoing developmental processes. In addition, they need to start allocating energy to storage to forestall starvation in winter when food supplies will be reduced. Thus we hypothesized that there is a critical period in which juvenile fish must shift from an energy allocation strategy favoring growth to one favoring energy storage and that this period would commence in late summer and early fall after fish have metamorphosed. We also hypothesized that annual changes in energy density during this critical would result from the conditions specified in hypothesis 1b.

**Overall Objectives:**

The goal of this project was to determine how constraints on energy supplies influence the way in which Pacific cod, pollock and arrowtooth flounder allocate energy to protein (structure) and lipid (storage) and how these allocations relate to each species’ life
history. These data were collected to examine hypotheses relating to hypothesis 1b, which relates climatic conditions to the nutritional status of juvenile pollock, Pacific cod and arrowtooth flounder. In order to meet this goal we proposed the following objectives:

Objective 1: Characterize seasonal changes in the energy and lipid content of juvenile pollock

For this objective pollock were collected on multiple surveys and analyzed to determine their lipid and energy content. Samples included pre-flexion and post-flexion larvae collected on NPCREP (2008, 2010) and BEST surveys (2008, 2009 and 2010). Age-0 and Age-1+ juveniles were collected on BASIS surveys in 2008-2010 and AFSC beam trawl surveys (2008 and 2010). Additional age-1+ juveniles were collected on MACE acoustic surveys (2008, 2009 and 2010). Fish were returned to the laboratory, processed to determine lengths, wet weights, RNA/DNA, moisture contents, energy density and lipid content. Data collected from these analyses and those from previous years were used to write reports describing seasonal changes in the energy allocation strategy of walleye pollock (Siddon et al. 2013), annual variation in the energy content of walleye pollock (Heintz et al. 2013), and growth potential of pollock in warm and cool conditions (Siddon et al. 2014). In addition, data collected from the samples were contributed to a re-evaluation of the Oscillating control hypothesis (Hunt et al. 2011). Finally the findings and conclusions of this project were included in a review of the first year of life for walleye pollock (Duffy Anderson et al. Submitted) and a synthesis of pointing to the importance of winter in the Bering Sea (Sigler et al. Submitted). These data are reported in Chapters 2, 3 and 4.

Objective 2: Characterize seasonal changes in the energy and lipid content of juvenile Pacific cod

For this objective Pacific cod were collected on multiple surveys and analyzed to determine their lipid and energy content. Samples included pre-flexion and post-flexion larvae, and age 0+ juveniles collected on the same surveys as previously listed for walleye pollock. Much fewer fish were collected, but they were also analyzed to determine their lengths, wet weights, RNA/DNA, moisture contents, energy density and lipid content. Data collected from these analyses were used to write a report describing interannual changes in the size, condition and diet of Pacific cod (Farley et al. Submitted). This report focuses on age-0 juveniles because too few larvae were collected for a meaningful analysis. These data are reported in Chapter 5.
Objective 3: Characterize seasonal changes in the energy and lipid content of juvenile arrowtooth flounder.

Fish from the genus *Atherestes* were collected on the same surveys described for Pacific cod and pollock and returned to the laboratory. Samples included pre-flexion and post-flexion larvae, and age 0+ juveniles. Relatively few fish were collected and they were believed to represent either arrowtooth flounder (ATF) or Kamchatka flounder (KF). The fish were genetically identified to species through collaboration with the ichthyoplankton project. They were also analyzed to determine their lengths, wet weights, RNA/DNA, moisture contents, energy density and lipid content. Data collected from these analyses were used to write a report describing the distribution and seasonal energy allocation of ATF and KF (DeForest et al. Submitted). These data are reported in Chapter 6.

Objective 4: Develop an understanding of how temperature affects the development of juvenile gadids and timing of metamorphosis.

Funds awarded for this objective were used to supplement existing studies of Pacific cod (NPRB Project R0605) and ultimately published in a series of papers. In those studies the effects of temperature on growth of Pacific cod were examined in different stages of development and under food limited conditions. As part of these growth studies we examined and related the observed values of growth to observations of nucleotides in pollock and cod tissues. This work formed a chapter in a PhD thesis (Sreenivasan 2011). That work demonstrated that the cost of growth in gadid larvae is reduced at higher temperatures due to increased efficiency of translating DNA into protein. At low temperatures gadids make up for the decreased efficiency of DNA translation by increasing translational capacity, hence RNA/DNA increases at low temperatures. RNA synthesis is metabolically expensive; consequently growth is reduced at low temperatures. Finally, withholding food as one of the feeding treatments in the study provided a lower limit to RNA/DNA that could be used to identify starving fish in the field. These data are reported in Chapter 1.
Chapter 1 - The Effect of Temperature and Nutrition on RNA/DNA Ratio and Growth of Pacific Cod (*Gadus macrocephalus*) and Walleye Pollock (*Theragra chalcogramma*) Larvae

1.1 Abstract:
Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*) are among the most economically and ecologically important groundfish species in the North Pacific Ocean. In spite of their importance, little is known about many aspects of their physiology, specifically about larval growth strategies in these fish. Since larval fish growth may determine future growth patterns, which could affect recruitment success, assessments of larval growth strategies might improve predictive growth models. In this study, nucleic acids (RNA and DNA) were used to index early growth in yolk-sac Pacific cod and walleye pollock larvae cultured at two temperatures (5°C and 8°C) and in yolk-sac Pacific cod cultured in two nutritional states (fed and starved). Growth corresponded to changes in RNA/DNA. Growth responses in Pacific cod and walleye pollock larvae were affected by small differences in temperature. Exposure to the lower temperature resulted in higher RNA/DNA in both Pacific cod and walleye pollock larvae. Based on nucleic acid patterns during larval development, it was possible to identify distinct growth stanzas in Pacific cod larvae.
1.2 Introduction

Pacific cod (Gadus macrocephalus) and walleye pollock (Theragra chalcogramma) are among the most numerous (Mecklenburg et al. 2002) and commercially important groundfish species in the North Pacific Ocean (Jewett 1978, Grant et al. 1987, Stepanenko 1995, Beamish et al. 2004, Bacheler et al. 2010, Hiatt et al. 2010). Distributed from southern California north to the Bering Sea, the Aleutian Islands, the Gulf of Anadyr and the Kurile Islands, the Okhotsk Sea, the Yellow Sea, and the Sea of Japan (Ketchen 1961, Bakkala 1984, Bakkala et al. 1984), Pacific cod are an important upper-trophic level species in subarctic ecosystems (Sakurai and Hattori 1996). Walleye pollock also are broadly distributed from the Bering Sea and the Gulf of Alaska to Japan (Bacheler et al. 2010).

Assessments of early larval growth and development are, however, limited for both species. Estimating larval growth can be important since growth during this stage could determine future growth (Jonsson et al. 2005, Koedijk et al. 2010 a, b). Fish larvae are especially sensitive to minor changes in ecological factors, including temperature and nutrition (Takatsu et al. 1995), which affect growth. Most growth and recruitment assessments in nature have been feasible only after fish have reached the juvenile or adult stages. Applying most growth indices to individual larvae is not feasible because they lack adequate tissue mass. These limitations are intensified by the fragility of
larvae, which makes capture of viable samples difficult, and by associated problems of sample storage and tissue shrinkage.

The early development, behavior, and physiology of larval Pacific cod and walleye pollock have been examined in a few studies (Alderdice and Forrester 1971, Sogard and Olla 1996, Theilacker et al. 1996, Laurel et al. 2008, Hurst et al. 2010, Laurel et al. 2010, Laurel et al. 2011). These studies have highlighted the complexities of larval behavior and physiology, especially in the early post-hatch period. Diel migratory behavior in larval Pacific cod can be determined by a combination of factors, including development stage, temperature, and photoperiod (Hurst et al. 2009). Growth in turn can be affected by interacting factors, including prey availability, temperature, and development stage (Laurel et al. 2011).

In light of the studies carried out so far, a physiological index of larval growth coupled with energetic assessments in predictive growth models can improve our understanding of natural variation of larval survival and of recruitment. This laboratory study investigated whole-body nucleic acid concentrations as an index of growth in yolk-sac Pacific cod and walleye pollock larvae, assessing the responses of growth and nucleic acids to different temperatures and nutritional states.

Leatherland 2008, Janhunen et al. 2010, Teletchea and Fontaine 2010). Protein synthesis underlying larval growth is dependent on RNA concentration (translational capacity) and RNA-specific protein synthesis rate (translational efficiency; McMillan and Houlihan 1988, Fraser and Rogers 2007), and the latter is affected by temperature. A change in the relationship between translational efficiency/capacity and growth can affect energy budgets, an important consequence for larvae since they lack energetic reserves (Theilacker et al. 1996).

Even though assessing larval growth can be problematic, nucleic acid (R/D) ratios can be used as a sensitive growth index in fish larvae (Buckley 1979, 1984, Robinson and Ware 1988, McLaughlin et al. 1995, Buckley et al. 1999, Weber et al. 2003, Caldarone 2005, Stierhoff et al. 2009). While DNA concentrations remain stable (Buckley 1984, McLaughlin et al. 1995), cellular RNA concentrations increase or decrease along with protein synthesis, indicating growth and nutritional condition (Weber et al. 2003). However, temperature affects RNA translational efficiency (Lewis and Driedzic 2007) changing the ratio-growth relationship. This prevents direct R/D comparisons between fish observed at temperature differences >2°C (Buckley et al. 1999), and requires calibration of nucleic acid concentrations with growth rates over a temperature range, that is R/D-Growth-Temperature calibrated models (Buckley 1984). Nucleic acid ratios could also be developed as indicators of catabolic stages in larvae approaching terminal starvation, i.e. a “baseline” ratio.
We used R/D ratios to observe the effects of temperature on growth in Pacific
cod and walleye pollock larvae, and to measure the effects of different nutritional states
(fed and starved) on growth in Pacific cod larvae. The aim of measuring R/D ratios was
to estimate larval energetic and growth parameters and incorporate those parameters
in a predictive growth model. Our objectives were to a) examine nucleic acid and early
growth responses in Pacific cod and walleye pollock larvae at different temperatures, b)
examine nucleic acid and growth responses in Pacific cod larvae at different nutritional
states, and c) build a predictive larval Pacific cod growth model based on nucleic acids
measured over a range of temperatures and different nutritional states.

1.3 Materials and Methods
This study included two temperature treatment experiments and a starvation
experiment. In the temperature treatment experiments, Pacific cod and walleye pollock
larvae were fed and cultured at two temperatures; in the starvation experiment, groups
of Pacific cod larvae were either fed or starved at a single temperature.

Pacific cod larvae used in both experiments were hatched and cultured in the
National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science
Center (AFSC) Laboratory, Newport, Oregon in April 2008 and May 2009. Eggs were
obtained from adults at their spawning grounds in Chiniak Bay, Kodiak Island, Alaska. All
mixed gametes were held in incubation trays at 4°C, after which fertilized eggs (24 hours
post-fertilization) were shipped in insulated containers to the AFSC. Eggs were held in
flow-through plastic trays (~4 liter capacity) and maintained at 4°C until hatch, approximately 19-22 days post-fertilization.

Walleye pollock eggs were collected from mature pollock broodstock maintained by the AFSC at the Hatfield Marine Science Center. Eggs were collected using nylon mesh collectors placed on the outflow of broodstock tanks. Larvae hatched in April 2008.

1.3.1 Pacific Cod Temperature Experiment

After hatching, larvae (n = 120) were immediately sampled to measure initial condition. Larvae were then randomly assigned to two temperature treatments: cool (5°C) and warm (8°C). Larvae at 0 days post hatch (dph) were in the size range ~4.4-5 mm total length. In each treatment, larvae were held in three tanks (100 liter capacity; 400 larvae each), with a total of six tanks. All tanks had a flow rate of ~250 mL minute⁻¹ seawater and were initially held at 4°C, after which water temperatures were adjusted to experimental conditions over 48 hours. Larvae were held at a 12:12 hour light:dark photoperiod regime (Hurst et al. 2010).

Larvae in both treatments were fed on a combined diet of rotifers (Brachionus plicatilis; twice daily) and microparticulate dry food (Otohime A, Marubeni Nisshin Feed Co., Tokyo; two-three times daily). After the initial sampling after hatch, larvae were sampled (10 larvae/tank/treatment) at 23 and 36 dph. At each sampling period, larvae
were removed from tanks using droppers, placed in individual 1500 µL microcentrifuge vials on ice, and then stored at -80°C until analysis. All sampled larvae were individually photographed before being placed in vials, to measure total length post-sampling using imaging software. Larval fish lengths were measured to the nearest 0.005mm using NIS Elements D, Nikon Instruments, Melville, NY.

Growth rates (length-GR) were calculated for larvae in both treatments from each sampling date (t_2) to the hatch date (t_1) using the formula:

$$GR_L = \frac{\ln l_{t_2} - \ln l_{t_1}}{t_2 - t_1}$$

where \(l\) = mean length (mm) and ln = natural logarithm.

1.3.2 Pacific Cod Starvation Experiment

Larvae were initially held at 6.5°C in two common tanks (100 liter capacity) with a flow rate of ~250 mL minute\(^{-1}\) seawater, before transfer to fed and starved treatment tanks (two tanks/treatment; 40 liter capacity) held at 6.5°C. All larvae at 0 dph were in the size range ~5-6.5 mm total length. The feeding regimen was similar to the temperature experiment.

During May to June 2009 larvae were sampled across three sampling periods initiated at 0, 9, and 20 dph. The sampling protocol was similar to the temperature experiment. At the start of each sampling, larvae were sampled from the common tanks (10 larvae/tank), and randomly assigned to the fed or starved treatment tanks (60
larvae/tank). Larvae in the starved treatment tanks were sampled (10 larvae /tank)
when the population in the tanks reached 10% mortality and 50% mortality, with
 corresponding sampling in the fed treatment. Individual larvae were photographed to
measure total length post-sampling using imaging software. The experiment was
terminated at 25 dph.

Larval fish lengths were measured to the nearest 0.005mm using Image-Pro
Plus, Media Cybernetics, Bethesda, MD. Growth rates (length-\( GR_L \)) were calculated
similar to the temperature experiment.

1.3.3 Walleye Pollock Temperature Experiment
Larvae were cultured in duplicate tanks (n = 200 larvae/tank) at a cool (5°C) and
warm (8°C) temperature treatment. All larvae were in the size range ~6-8 mm length
and were fed for the duration of the experiment. All experimental conditions and
sampling protocols were identical to the Pacific cod temperature experiment, except for
the time of sampling (0, 19, and 40 dph). At 0 dph, larvae were sampled from each tank
(15 larvae/tank/treatment), followed by sampling at 19 and 40 dph (10
larvae/tank/treatment). Growth rates (length-\( GR_L \)) were calculated similar to the Pacific
cod temperature experiment.

1.3.4 Biochemical Analyses
Nucleic acid ratios in both Pacific cod experiments and in the walleye pollock
experiment were measured under a one dye-one enzyme (RNase) fluorometric protocol
modified from Caldarone et al. (2001). Whole larvae were processed directly in their individual storage vials thus avoiding any tissue loss. Initially, 150 µL 1% sarcosil Tris-EDTA buffer was added to each sample vial. All sample vials were then vortexed for 60 minutes. Samples were further diluted with 1350 µL Tris-EDTA buffer, and centrifuged for 15 minutes at 14000g in a Sorvall Legend Micro 21 R refrigerated centrifuge (Thermo Scientific). Supernatants were then treated with 75µL ethidium bromide (5µg ml⁻¹) according to the protocol outlined by Caldarone et al. (2001). Total fluorescence was measured in a Wallac 1420 microplate spectrophotometer (Perkin Elmer, Waltham, MA) at excitation and emission wavelengths of 355nm and 600nm respectively. Samples were treated with RNase, and the resulting reduced fluorescence measured to obtain DNA fluorescence; RNA fluorescence was obtained through subtraction of DNA fluorescence from the total fluorescence. Calibration curves were constructed using serial dilutions of 18s-28s rRNA (Sigma R-0889) and calf thymus DNA (Sigma D-4764) standards. Supernatants for R/D were read on Corning NBS 96-well black flat-bottom microplates (75µL samples). Every R/D sample was run in three individual wells. Fluorescence values for all three wells were read four times, and the coefficient of variation associated with four reads was examined. When the variation was higher than 10%, the individual well fluorescence values were examined, and the data point causing the high coefficient of variation was excluded from the analysis.

1.3.5 Statistical Analyses:
In all analyses, differences between groups were considered significant if $p \leq 0.05$

### 1.3.5.1 Pacific Cod Temperature Experiment

Growth was compared between larvae at 5°C and 8°C. A General Linear Model (GLM) with Tukey’s posthoc test was used to compare length in larvae between treatments over 0-36 dph, with length as the dependent variable, and temperature treatment and sampling day as independent variables. A GLM was used to compare instantaneous growth rates (IGR) in larvae between treatments, with IGR as the dependent variable, and temperature treatment and sampling day as independent variables. A GLM with Tukey’s test was used to compare R/D of larvae between treatments, with R/D as the dependent variable, and temperature treatment and sampling day as independent variables. All statistical analyses were made with Minitab v. 14 (Minitab Inc., State College, Pennsylvania).

### 1.3.5.2 Pacific Cod Starvation Experiment

Growth was compared between larvae in fed and starved treatments. A GLM was used to compare IGR of fed and starved larvae, with growth rates as the dependent variable, and treatment as well as sampling day as predictor variables. A GLM with Tukey’s test was used to compare R/D of fed and starved larvae over 0-25 dph, with R/D
as the dependent variable, and sampling day and treatment as the independent variables.

The R/D of starved larvae between 10% and 50% mortality was compared within each sampling period using two sample T-tests. The R/D of starved larvae at both 10% and 50% mortality was compared between the last two sampling periods with a two sample T-test.

A GLM was used to compare individual nucleic acids of fed and starved larvae over 0-25 dph, with RNA or DNA as the dependent variable, and sampling day and treatment as independent variables. All statistical analyses were made with Minitab v. 14 (Minitab Inc., State College, Pennsylvania).

### 1.3.5.3 Pacific Cod Growth Model

Calibrated growth models were generated through multiple linear regression, describing the relationship between instantaneous growth rates (IGR) and variables including R/D, RNA, DNA, and temperature. A second-order Akaike's information criterion (AICc) was used to select the best fit model from the model data set (Wagenmakers and Farrell 2004). Estimated growth rates were compared with observed growth rates for all temperature treatments using a two-sample T-test. The regression models were generated by Minitab v. 14 (Minitab Inc., State College, Pennsylvania).
Depending on the model, R/D ratios or RNA and DNA from both Pacific cod experiments were combined for the individual growth models in the model data set. Mean tank values for each sampling day (R/D, RNA, DNA) were log-transformed. The growth model only included data from larvae 23 and 36 dph in the temperature experiment and from 9 dph onward (fed fish only) in the terminal starvation experiment. This was due to lack of a correlation between R/D and growth in the early larval stages, possibly due to presence of pre-existing yolk protein.

1.3.5.4 Walleye Pollock Temperature Experiment

Growth was compared between larvae at 5°C and 8°C. All statistical analyses were identical to the Pacific cod temperature experiment and were made with Minitab v. 14 (Minitab Inc., State College, Pennsylvania).

1.4 Results

1.4.1 Pacific Cod Temperature Experiment

Larvae at 8°C were longer than larvae at 5°C at the end of the experiment ($p < 0.001$; Fig 2.1a) with a difference in length between treatments at 23 dph and 36 dph ($p < 0.001$; Table 2.1). Larvae at 8°C grew faster than larvae at 5°C and had significantly higher instantaneous growth rates over the sampling period ($p < 0.001$; Table 2.1). Larvae at 5°C had higher R/D than larvae at 8°C at the end of the experiment (Fig. 2.1b), with a difference between temperature treatments at 36 dph ($p < 0.001$; Table 2.1).
1.4.2 Pacific Cod Starvation Experiment

Fed larvae had significantly higher instantaneous growth rates ($p < 0.001$) over 5-25 dph relative to starved larvae (Fig. 2.2a; Table 2.2). Nucleic acid ratios were higher in fed larvae relative to starved larvae over 0-25 dph ($p < 0.001$; Fig. 2.2b); there were differences in nucleic acid ratios between fed and starved larvae at 5 dph ($p = 0.0061$), 11 dph ($p = 0.0101$), 15 dph ($p = 0.0003$), 23 dph ($p = 0.0180$), and 25 dph ($p = 0.0458$; Table 2.2).

A comparison of R/D between 10% and 50% mortality in starved larvae showed differences over 11-15 dph ($p = 0.034$) but not over 2-5 dph ($p = 0.134$) or 23-25 dph ($p = 0.798$). Comparison of R/D at 10% mortality between the second and third sampling periods (11 and 23 dph) showed no difference ($p = 0.071$). However, R/D differed at 50% mortality ($p = 0.006$) between second and third sampling periods (15 and 25 dph).

The RNA and DNA concentrations were higher in fed larvae relative to starved larvae over 0-25 dph ($p < 0.001$). The RNA concentrations in the fed larvae remained steady until 9 dph, increasing slightly by 11 dph (Fig. 2.3b). From 11-20 dph RNA concentrations remained steady, and increased after 20 dph. In contrast, DNA concentrations in both fed and starved larvae increased until 11 dph (Fig. 2.3c). From 11-20 dph, DNA concentrations in fed larvae remained steady, and increased after 20 dph.
1.4.3 Pacific Cod Growth Model Synthesis

A significant positive relationship was found between IGR, log RNA, log DNA, and treatment temperature ($p < 0.001$; Table 2.3). This growth model was chosen from the model data set based on a comparison of AICc values (AICc = -122; Table 2.4), and incorporated IGR, log RNA, log DNA, and treatment temperature in a multiple linear regression. The response variable was IGR; log RNA, log DNA, and treatment temperature were predictor variables. Estimated and observed growth rates did not differ for fish at 5°C ($p = 0.0180$), 6.5°C ($p = 0.479$), and 8°C ($p = 0.259$).

1.4.4 Walleye Pollock Temperature Experiment

Larvae at 8°C were longer than larvae at 5°C at the end of the experiment ($p < 0.001$; Fig. 2.4a), with a difference between treatments at 40 dph ($p < 0.001$; Table 2.5). Larvae at 8°C grew faster than larvae at 5°C and had significantly higher instantaneous growth rates over the sampling period ($p < 0.001$; Table 2.5). Larvae at 5°C had higher R/D than larvae at 8°C at the end of the experiment ($p < 0.001$; Fig 2.4b), with a difference between treatments at 0 dph ($p = 0.0050$) and 40 dph ($p < 0.001$; Table 2.5).

1.5 Discussion

Lower R/D coupled with higher growth in larvae at 8°C indicated that translational efficiency defines early growth in Pacific cod and walleye pollock. Early larval fish growth is predominantly due to protein synthesis and deposition (Tong et al. 2010), determined by RNA-specific protein synthesis rate (translational efficiency) and RNA concentration (translational capacity; Smith and Ottema 2006, Fraser and Rogers
The relative effects of translational efficiency and capacity on growth can be influenced by temperature (Foster et al. 1992, Treberg et al. 2005). Translational efficiency also defines early larval growth in Atlantic herring (*Clupea harengus*; Houlihan et al. 1995), African catfish (*Clarias gariepinus*; Smith and Ottema 2006), and rainbow trout (*Oncorhynchus mykiss*; Peragon et al. 2001).

Growth in larval Pacific cod and walleye pollock is affected by small differences in temperature. Exposure to lower temperature reduced translational efficiency in both gadids, resulting in growth driven predominantly by translational capacity. This was suggested by a lack of correspondence between R/D and growth rates. As expected, larvae at 8°C had higher growth rates and were longer than larvae at 5°C. This higher growth, coupled with lower R/D relative to larvae at 5°C, suggested heightened translational efficiency. The higher R/D at 5°C suggests a compensatory mechanism to maintain protein synthesis, i.e., heightened translational capacity in lieu of reduced translational efficiency. But with the high costs of RNA and protein synthesis (Bocharova et al. 1992, Houlihan et al. 1995, Smith and Ottema 2006), regardless of cost mitigation strategies (Houlihan et al. 1988, Wieser 1995, Smith et al. 2000, Smith and Ottema 2006), higher translational efficiency is energetically advantageous. The effect of this trade-off between translational efficiency/capacity could be significant as larvae grow and increase in size. Another potential reason for higher R/D at 5°C could be mismatched RNA degradation and synthesis rates, due to a temperature effect on enzymes essential to these processes. In this case, higher R/D would not be an active
compensatory measure corresponding to heightened protein synthesis. While protein
synthesis rates were not measured in this experiment, Atlantic cod exposed to colder
temperatures showed heightened translational capacity active in maintaining protein
synthesis (Foster et al. 1992, Treberg et al. 2005), suggesting that the higher R/D in this
experiment was a compensatory strategy.

The trade-off between translational efficiency/capacity can be examined in
terms of the R/D divergence between larvae. The timing of the divergence suggested
heightened energetic demands as larvae aged, possibly due to growth and increased
protein synthesis, as larvae increased in size and structural complexity. Crucially, the
consistently lower growth at 5°C suggested lower translational efficiency prior to the
divergence in R/D ratios. However, the lack of an immediate compensatory response
could be due to energetic costs involved in heightened translational capacity as well as
lower larval energy requirements. As larvae grow, energetic constraints could lead to
heightened translational capacity. However, this could be energetically expensive,
potentially affecting long-term growth as in Atlantic cod larvae (Koedijk et al. 2010a, b).

This experiment highlighted early larval Pacific cod and walleye pollock growth
strategies in terms of translational efficiency and capacity. Pacific cod and walleye
pollock larvae appear to have physiological compensatory mechanisms to maintain
growth trajectories, which could be energetically expensive. Cellular growth indices
such as R/D can highlight physiological growth strategies, a prerequisite to further
studying any associated metabolic costs which should be accounted for in growth assessments.

The terminal fasting experiment examined the growth and R/D relationship in Pacific cod larvae (0-25 dph) based on nutritional state. In contrast to other vertebrates, where post-natal growth is hypertrophic (an increase in muscle fiber size; Smith et al. 2000) teleost growth is a combination of hypertrophy and hyperplasia (formation of new muscle fibers). Early teleost development involves hyperplasic organogenesis (Tanaka et al. 1996, Zouiten et al. 2008, Tong et al. 2010) followed by somatic growth which is both hyperplasic and hypertrophic (Westerman and Holt 1994, Tong et al. 2010). These development patterns are common across species, shown by a steady decrease in R/D ratios over the immediate post-hatch period (Clemmeson 1987, Puvanendran and Brown 1999, Caldarone et al. 2003).

In common with other fish species, R/D in Pacific cod larvae decreased over the initial post-hatch period, and then stabilized. The initial decrease was due to increasing DNA in fed and starved larvae (0-11 dph) coupled with stable (fed group) or reduced (starved group) RNA. The increased DNA content with stable or reduced RNA could correspond to hyperplasic organogenesis. Both RNA and DNA in fed larvae stabilized over 11-20 dph, potentially the transition phase after yolk absorption to complete reliance on exogenous food. Stable R/D in fed larvae implied a lack of growth during the transition to external food, evidenced by a corresponding decrease in growth rate. A
similar trend was observed in larval Turbot (*Scophthalmus maximus*) after yolk depletion (Tong et al. 2010). Laurel et al. (2008) found that Pacific cod larvae had no growth immediately after yolk absorption, while fed Atlantic cod larvae also had the lowest growth and R/D coinciding with yolk absorption (Caldarone et al. 2003). Atlantic cod larvae have also shown closely corresponding transition periods (Yin and Blaxter 1986, Hunt von Herbing et al. 1996, Caldarone et al. 2003) at similar temperatures. While the rate of yolk absorption can be temperature dependent (Laurel et al. 2008), the timing of the transition phase (11-20 dph) integrates the initial increase in DNA (0-11 dph) with yolk absorption.

The timing of the transition phase suggested yolk absorption over the preceding 0-11 dph, coinciding with the increase in DNA potentially indicating organogenesis. Since organogenesis can utilize lipid and protein components of yolk (Cejas et al. 2004), yolk in Pacific cod larvae appears primarily utilized in organogenesis. While yolk is the most cost-effective source of protein, the energetic cost of protein absorption remains substantial (Smith and Ottema 2006). However, with even higher costs of protein synthesis (Hawkins 1991, Smith and Houlihan 1995), efficient larval growth strategies emphasize absorption of preexisting yolk protein into tissues (Wieser et al. 1988). Similar growth strategies have been observed in larval African catfish (*Clarias gariepinus*; Smith and Ottema 2006), Atlantic herring (*Clupea harengus*; Houlihan et al. 1995), and nase (*Chondrostoma nasus*; Houlihan et al. 1992). Yolk absorption coinciding with organogenesis was observed in both starved and fed treatments. This suggested
the relative importance of organogenesis, as starved larvae did not divert any yolk towards somatic growth, and had relatively lower growth rates, R/D, and RNA.

In conjunction with increases in R/D and RNA after the transition period (20 dph), the growth rate in fed larvae increased. This indicated the channeling of resources to somatic growth after organogenesis. In larval Pacific cod, increased growth after the transition phase also coincided with the start of diel vertical migrations (Hurst et al. 2009) and heightened responses to prey (Colton and Hurst 2010). In common with other fish species, this growth phase, characterized by increasing RNA, DNA, R/D, and growth rate, is probably a combination of hypertrophy and hyperplasia (Tong et al. 2010).

Nucleic acid ratios of starved larvae could potentially be used as indicators of terminal starvation, i.e., a “baseline” ratio. Averages of ratios from larvae sampled at 10% and 50% starvation over the 2nd and 3rd sampling periods, while preliminary and approximate (~2.5), have promise as a starvation index, but require further validation studies.

The Pacific cod growth model incorporated nucleic acids (RNA and DNA) and temperature as variables in predicting growth rate. This model estimated 65.5% of the observed variation in growth rate. Based on both adjusted $r^2$ and AICc values, individual nucleic acids appear to predict early larval growth in Pacific cod better than a model based on R/D ratios. With the lack of correlation between growth and R/D in early stage
yolk-sac larvae (Caldarone et al. 2003), this growth model did not include data from 0 dph larvae (temperature experiment) or from 0-5 dph larvae (terminal starvation experiment). The ready availability of protein (yolk) in early larval stages could cause the lack of correlation between nucleic acids and growth. This growth model relates nucleic acids to growth and condition of individual larvae and can have applications in management, since growth and condition estimates are required in recruitment and stock assessments. This model is useful in estimating growth in Pacific cod at an early life-stage. Additionally, it enables growth estimation in field-sampled larvae using a single measure, a requirement since it is not realistically possible to periodically sample the same fish in the field to estimate growth.

1.6 Conclusion
Nucleic acid ratios have potential as a growth index in larval Pacific cod and walleye pollock; this index was sensitive enough to bring out differences in early larval growth responses and physiological strategies. Larval Pacific cod and walleye pollock growth strategies are affected by small differences in temperature, while nutritional state also affected early growth in Pacific cod. Exposure to a lower temperature resulted in higher R/D in both cod and pollock larvae, potentially a compensatory strategy. This could be due to increased energetic demands as larvae increase in size and complexity. These higher ratios were only manifested after a period of consistently lower growth, suggesting costs associated with this strategy.
Fed Pacific cod larvae as expected had higher growth relative to starved larvae, shown by R/D and growth rates. Changes in R/D, RNA, and DNA could be used to identify distinct stanzas in early growth of Pacific cod larvae, possibly yolk absorption and organogenesis, exogenous feeding (transition phase), and post-transition growth. Similar growth stages are seen in larvae of other fish species. Yolk appears predominantly utilized towards organogenesis, even in starved fish. While R/D reduced in both treatments over the yolk absorption phase, the R/D in the starved treatment remained lower, indicating that exogenous food supply may be added to energy reserves available to growth despite the presence of yolk. The Pacific cod growth model was able to estimate 65.5% of observed variation in growth rate. This model could have applications in management, since growth and condition estimates are required for recruitment and stock assessments.

1.7 Acknowledgements
We thank Elaine Caldarone, who was extremely generous with her time in helping to adapt her R/D protocol to this research, as well as Dr. Franz Mueter, University of Alaska Fairbanks, and Dr. Chris Hay-Jahans, University of Alaska Southeast, for their advice on statistical methods. We also thank Dr. Sherry Tamone, University of Alaska Southeast, the Rasmuson Fisheries Foundation for fellowship support awarded to AS, and NOAA, who supported this research.

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1.9 Figures and Tables

**Figure 1.1a, b**: *Gadus macrocephalus*. Length and RNA/DNA in larvae at 5°C and 8°C. Comparison of length (1a) and RNA/DNA (R/D) ratios (1b) between Pacific cod larvae cultured at 5°C (open symbols) and 8°C (closed symbols). Symbol bars represent standard error. Significant differences ($p \leq 0.05$) between treatments represented by
Figures 1.2a,b: Gadus macrocephalus. Growth rate and RNA/DNA in fed and starved larvae. Comparison of instantaneous growth rates (I.G.R) (2a) and RNA/DNA (R/D) ratios (2b) between fed (closed symbols) and starved (open symbols) Pacific cod larvae. Symbol bars represent standard error. Significant differences ($p \leq 0.05$) between fed and fasted treatments represented by
Figure 1.3a,b,c: Gadus macrocephalus. Nucleic acid trends in fed and starved larvae. Comparison of RNA/DNA (R/D) ratios (2.3a), nucleic acids (RNA and DNA) (2.3b), and DNA (2.3c) between fed (closed symbols) and starved (open symbols) Pacific cod larvae from 0-25 days post hatch. Significant differences ($p \leq 0.05$) between fed and starved groups shown by
Figure 1.4a,b: Theragra chalcogramma. Length and RNA/DNA in larvae at 5°C and 8°C.
Comparison of length (2.4a) and RNA/DNA (R/D) ratios (2.4b) between walleye pollock larvae cultured at 5°C (open symbols) and 8°C (closed symbols). Symbol bars represent standard error. Significant differences ($p \leq 0.05$) between treatments represented by
Table 1.1: *Gadus macrocephalus*. Growth in larvae at 5°C and 8°C. Statistical comparison of total length, instantaneous growth rate (I.G.R.), and RNA/DNA between Pacific cod larvae cultured at two temperature treatments (5°C, 8°C) over 0-36 days post hatch (dph). *P*-values ≤ 0.05 are statistically significant.

<table>
<thead>
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<tr>
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<tr>
<td>RNA/DNA</td>
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Table 1.2: *Gadus macrocephalus*. Growth in fed and starved larvae at 6.5°C. Statistical comparison of instantaneous growth rate (I.G.R.), and RNA/DNA (R/D) between larval Pacific cod cultured at two nutritional states (fed and starved) at 6.5°C over 0-25 days post hatch (dph). *P*-values ≤ 0.05 are statistically significant.

<table>
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<th>Between treatment comparison over 0-25 dph</th>
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<td></td>
<td>0 dph    2 dph    5 dph    9 dph    11 dph   15 dph   20 dph   23 dph   25 dph</td>
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<tr>
<td>I.G.R.</td>
<td>&lt; 0.001</td>
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<tr>
<td>R/D</td>
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</table>
Table 1.3: *Gadus macrocephalus*. Growth model regression. Multiple linear regression coefficients describing the relationship between instantaneous growth rates (I.G.R.), log RNA-\(a_1\), log DNA-\(b_1\), and temperature-\(c_1\) for Pacific cod larvae. Equation is of the form I.G.R. = \(a_1+b_1+c_1+C\), where C is a constant. The regression was significant (\(p < 0.001\)). SE is standard error.

<table>
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<th>Coefficients (+/- SE)</th>
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<th>(b_1)</th>
<th>(c_1)</th>
<th>C</th>
<th>Adjusted (r^2)</th>
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<td>0.0002160 (0.0004581)</td>
<td>0.004515 (0.006022)</td>
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Table 1.4: *Gadus macrocephalus*. AIC<sub>c</sub> comparison. Model selection by second-order Akaike Information Criterion (AIC<sub>c</sub>) values. Coefficients (± SE) in alternative regression models of growth in larval Pacific cod. In all models, \( p < 0.001 \). Log R/D = Log RNA/DNA ratio, T = treatment temperature, K = number of model parameters (including intercept), \( \Delta \text{AIC} \) = difference in AIC with respect to the best fit model.

<table>
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<th>Model Parameters</th>
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<th>RNA</th>
<th>Log RNA</th>
<th>DNA</th>
<th>Log DNA</th>
<th>Log R/D</th>
<th>T</th>
<th>Intercept</th>
<th>Adjusted ( r^2 )</th>
<th>K</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
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Table 1.5: *Theragra chalcogramma*. Growth in larvae at 5°C and 8°C. Statistical comparison of total length, instantaneous growth rate, and RNA/DNA between walleye pollock larvae cultured at two temperature treatments (5°C, 8°C) over 0-40 days post hatch (dph). *P*-values ≤ 0.05 are statistically significant.

<table>
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<td>I.G.R.</td>
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<tr>
<td>R/D</td>
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<td>0.0050</td>
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</table>
Chapter 2 - Conceptual model of energy allocation in walleye pollock (*Theragra chalcogramma*) from larvae to age-1 in the southeastern Bering Sea

Elizabeth C. Siddon*, Ron Heintzb, Franz J. Muetera

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2.1 Abstract
Walleye pollock (*Theragra chalcogramma*) support the largest commercial fishery in the United States and are an ecologically important component of the eastern Bering Sea (EBS) pelagic ecosystem. Alternating climate states influence the recruitment success of walleye pollock through bottom-up control of zooplankton communities. Relating the seasonal progression of energy content and allocation to the distribution and abundance of walleye pollock allows for detection of spatial and temporal trends in fish condition. This provides critical information for predicting overwinter survival and recruitment to age-1 because age-0 walleye pollock rely on energy reserves to survive their first winter. Larval, age-0, and age-1 walleye pollock were collected in the EBS from May to September 2008-2010. Fish condition was determined through quantification of energy density (kJ/g) and proximate composition (% lipid, protein, ash, moisture) with variation in energy density primarily driven by variability in % lipid. Energy densities remained relatively low during the larval phase in early summer, indicating energy allocation to growth and development. Lipid acquisition rates increased rapidly after transformation to the juvenile form, with energy allocation to lipid storage leading to higher energy densities in fall. We propose that this physiologically and ecologically important shift, occurring after the end of larval development (25-40 mm), represents a
short critical period for determining fall condition and overwinter survival of juvenile walleye pollock.

2.2 Keywords:
Walleye pollock (*Theragra chalcogramma*), Larval fish, Bering Sea,

2.3 Introduction
Multiple factors during the early life stages of fishes result in variable recruitment success, including prey availability and environmental conditions (Cushing 1982). Variability in the spatial and temporal overlap of predator and prey (match/mismatch hypothesis; Cushing 1969; 1990), as well as differences in prey quality (Sogard and Olla, 2000; Litzow et al., 2006), affect fish growth and energy storage, which may directly affect differences in year-class success of many marine fish species, such as walleye pollock, *Theragra chalcogramma* (Hunt et al., 2011). In addition, cold water temperatures generally delay ontogenetic development of walleye pollock (Blood 2002; Smart et al., in prep) while also lowering routine metabolic demands (Ciannelli et al., 1998). Such trade-offs affect larval fishes’ ability to achieve sufficient size and energy reserves prior to their first winter (Sogard and Olla, 2000; Heintz and Vollenweider, 2010).

In high latitude systems, winter is a period of low light, cold temperatures, and reduced prey availability, and is therefore a significant source of mortality and determinant of recruitment success of marine fishes (Hurst 2007). Overwintering survival is likely size-dependent because most sources of mortality tend to select against the smallest individuals (Houde 1987; Bailey and Houde, 1989; Paul and Paul, 1999). Hence, depletion of lipid reserves may be preferred over tissue loss in an effort to maintain
overall body size, which is supported by examples of increased survival for larger fish (Schultz and Conover, 1999; Heintz and Vollenweider, 2010). These ideas are encapsulated in the ‘critical size and period hypothesis’, which emphasizes the importance of increased growth in late summer and fall as indicative of winter survival (Beamish and Mahnken, 2001). Lab studies have experimentally corroborated the importance of size on rates of energy depletion (Schultz et al., 1998), which is proportionally greater in smaller fish (Schultz and Conover, 1999; Kooka et al., 2007). Given the shorter growing season in high latitudes, marine fishes may have adapted to grow particularly fast in response to size-selective winter mortality (Conover 1990).

Understanding variability during the early life stages of commercially important species is pivotal to fisheries management in predicting year-class success (Megrey et al., 1996) and subsequent recruitment to the fishery. Numerous studies have established empirical links between recruitment and environmental variability (see Beamish and McFarland, 1989), but incorporating the impacts of climate variability on survival into stock assessments requires knowledge of the mechanistic responses to alternate climate states (Hollowed et al., 2009). Fish condition in fall is increasingly recognized as a predictor of overwintering success for walleye pollock in the eastern Bering Sea (Heintz et al., 2013 and provides a potential early metric of recruitment success to age-1.

The Oscillating Control Hypothesis (Hunt et al., 2002; revised in Hunt et al., 2011) provides a theoretical framework within which to predict ecosystem responses to warm and cold regimes in the southeastern Bering Sea (SEBS). In warm regimes with early ice retreat, stratified waters maintain production within the pelagic system (Walsh and McRoy, 1986), which was predicted to result in enhanced survival of species such as
Walleye pollock (Hunt and Stabeno, 2002; Mueter et al., 2006; Moss et al., 2009).

However, recent data indicate that changes in prey composition and abundance during a warm regime may be detrimental to walleye pollock survival. Specifically, larger zooplankton taxa (e.g., large calanoid copepods and euphausiids) were less abundant during recent warm years, which resulted in reduced growth rates and lipid reserves of young-of-year (YOY) walleye pollock and may have increased their predation risk and decreased their overwinter survival (Coyle et al., 2011). In contrast, higher abundances of larger, lipid-rich zooplankton taxa during cold years, combined with lower metabolic demands, allows YOY walleye pollock to acquire greater lipid reserves by fall, resulting in increased overwinter survival (Hunt et al., 2011).

Walleye pollock support the largest commercial fishery in the U.S. and are an important component of the eastern Bering Sea pelagic ecosystem. Walleye pollock are major consumers of zooplankton (Aydin et al., 2007) with pronounced changes in prey preference throughout their early life (Ciannelli et al., 2004; WW Strasburger, unpubl. data). The transition to diel vertical migration and nocturnal feeding, which occurs at approximately 50 mm standard length (SL; Brodeur et al., 2000), coincides with increased gape size and shifts to larger prey (i.e., euphausiids), affecting fish condition (Ciannelli et al., 1998). Walleye pollock are also an important forage species for other predators, including arrowtooth flounder, *Atheresthes stomias*, Pacific cod, *Gadus macrocephalus*, skates, flathead sole, *Hippoglossoides elassodon*, Pacific halibut, *Hippoglossus stenolepis*, sea birds, and marine mammals (Aydin and Mueter, 2007).
addition, older age classes exhibit strong cannibalism on YOY walleye pollock (Wespestad and Quinn, 1996), especially in warmer climate regimes (Hunt et al., 2011). Despite the important role of walleye pollock in the Bering Sea, and the relationship between age-0 fall condition and overwinter survival, the seasonal energetic patterns from age-0 to age-1 remain poorly understood. This paper examines the link between larval and juvenile strategies for growth and energy storage in walleye pollock. By maximizing growth and transitioning the larval period rapidly, larvae minimize exposure to increased mortality during this stage (i.e., match/mismatch hypothesis; Cushing 1990). In contrast, overwinter survival is higher in fish that are both larger and have increased lipid reserves, indicating that energy allocation during the age-0 juvenile stage will favor lipid storage while also increasing fish size (i.e., critical size and period hypothesis; Beamish and Mahnken, 2001; Heintz and Vollenweider, 2010). We hypothesize that energy allocation strategies will differ seasonally among life stages and we tested this by contrasting body compositions of larval, age-0, and age-1 fish. The goals of this study were to (1) describe cohort-specific patterns in fish condition for walleye pollock from age-0 to age-1, (2) describe seasonal patterns in energy allocation during larval and juvenile (age-0) development leading to condition estimates prior to their first winter, and (3) develop a conceptual model of energy allocation with implications for overwinter survival and recruitment to age-1.

2.3.1 Study region
The SEBS is characterized by a broad continental shelf (> 500 km) with an average depth of about 70 m and supports a highly productive ecosystem owing to on-shelf flow of
nutrient-rich waters. Alternating climate states have resulted in periods of both warm and cold conditions in recent years. The most extensive ice cover and coldest water column temperatures since the early 1970s were observed beginning in 2006 and continued through at least the winter of 2010/11.

Current trajectories over the shelf are generally northwestward with the Bering Slope Current flowing along the shelf break and Alaska Coastal Current waters following either the 50 m or 100 m isobaths (Stabeno et al., 2001). The onset and location of fronts affect current trajectories (Kachel et al., 2002) and, therefore, transport pathways of larvae (Duffy-Anderson et al., 2006). The main spawning areas for walleye pollock in the SEBS include the waters off Bogoslof Island, north of Unimak Island and along the Alaska Peninsula, and around the Pribilof Islands (Bacheler et al., 2010); isolated spawning of deeper water aggregations also occurs along the shelf break. Larvae are generally advected northward over the shelf with slope-spawned larvae advected onto the shelf via the Bering Slope Current.

2.4 Materials and methods
2.4.1 Biological sampling
Age-0 and age-1 walleye pollock were collected opportunistically from 13 research cruises conducted in the southeastern Bering Sea between May and September 2008-2010 (Table 1; Fig. 1). The geographic coverage varied across cruises. Sampling for age-0 fish approximately reflected the actual distributions, while age-1 fish were predominantly sampled from the shelf break (Fig.1). Gear type, mesh size, and sampling depth also varied across cruises to target the life stages occurring at the time of
sampling (Table 1). Vertically integrated oblique bongo tows were made to a maximum depth of 300 m (or to within 10 m of the substratum). Walleye pollock were also sampled from the drogue net of the MOCNESS, which was open during deployment, thereby providing vertically integrated samples to a maximum depth of 100 m (or to within 10 m of the substratum). The ship speed was monitored and adjusted (1.5-2.5 knots) throughout all bongo and MOCNESS tows to maintain a wire angle of 45°. Surface (midwater) trawls were conducted above (below) the pycnocline, as determined by water column profiles of temperature and salinity. In addition, near-bottom fishes were sampled with a beam trawl. Our samples are believed to be broadly representative of age-0 and age-1 walleye pollock in the SEBS during the year of sampling.

Bongo and MOCNESS sampling occurred 24 hours a day; vertically integrated tows were conducted to a water depth of 100 m, therefore it was assumed that they were not affected by diel vertical migrations by larval and age-0 juvenile walleye pollock. Sampling occurred in daytime only during BASIS surveys in fall of 2008-2010 (Table 1) using either surface or mid-water rope trawls at depths consistent with observed layers from a hydro-acoustics survey (i.e., above or below the pycnocline, respectively). Fish were predominantly observed and collected from surface waters in fall 2008 and from the surface and mid-water in 2009; in 2010, only walleye pollock collected from surface trawls were used in the analyses in order to facilitate interannual comparisons across 2008-2010. This study does not address vertical differences in energy content.

After retrieval of the gear, all walleye pollock collected were flash frozen (-80 °C) for later chemical analysis at the Alaska Fisheries Science Center, NOAA (National
Oceanic and Atmospheric Administration) in Juneau, Alaska, USA. Pre-flexion larvae were measured to the nearest 0.01 mm length (standard, fork, or total) and post-flexion larvae were measured to the nearest mm fork length (FL). All lengths were converted to SL using established conversions for walleye pollock preserved by freezing (Buchheister and Wilson, 2005). Fish were classified as either age-0 (<110 mm SL) or age-1 (>120 mm SL and <215 mm SL) based on length-frequency distributions constructed for each cruise. Stomach contents of fish >8 mm SL were removed prior to chemical analysis so as not to affect estimates of fish condition.

2.4.2. Chemical Analysis

2.4.2.1. Energy content

Energy density (ED; kJ/g dry mass) was estimated directly using bomb calorimetry or indirectly from estimates of % lipid (see below). Larvae (<30 mm SL) were dried in a drying oven (60°C) and all data are presented on a dry mass basis. Homogenized tissue was pressed into a pellet form and a Parr Instrument 6725 Semimicro Calorimeter with 6772 Precision Thermometer and 1109A Oxygen Bomb was used to measure the energy released from combustion of the sample pellets. The minimum pellet weight was set at 0.025 g of dry material; samples were composited across stations as needed to attain sufficient dry masses for the pre-flexion larvae collected in 2008-2010. Age-0 and age-1 fish (>30 mm SL) were dried to a constant weight at 135°C using a LECO Thermogravimetric Analyzer (TGA) 601 or 701 which provided % moisture values. The dried tissue was homogenized and processed using the bomb calorimeter as described above. Moisture analyses were replicated when sufficient tissue masses were available.
to ensure the coefficient of variation was less than 1 standard deviation (SD). When sufficient mass was not available, we relied on the coefficient of variation for a reference material (dried adult walleye pollock homogenate) for duplicate estimates of moisture or energy density processed with each batch ($n=15$ for moisture; $n=17$ for energy density) of fish.

Quality assurance (QA) samples for the bomb calorimeter included (1) replicate tissue samples to evaluate precision and (2) replicate reference material (benzoic acid standard) to evaluate precision and accuracy. Pre-determined limits for variation observed in QA samples were set, where precision estimates from replicate tissue and reference samples must not vary by more than 1.5 SD or 15% coefficient of variation (CV) and reference samples must not vary by more than 15% CV for accuracy. QA samples did not exceed these limits for any batch of samples used in this study.

2.4.2.2. **Proximate composition**

For larvae (<30 mm SL), a Sulfo-phospho-vanillin (SPV) colorimetric analysis (Van Handel 1985) was performed to determine % lipid composition. Dried material was sonicated in 2:1 (by volume) chloroform:methanol solvent in glass centrifuge tubes for 60 minutes. Washes of 0.88% KCl and 1:1 (by volume) methanol:water were performed on the extracts as in the modified Folch extraction method (Vollenweider et al., 2011). Resulting chloroform extracts were evaporated in a LabConco RapidVap for 30 minutes at 40°C and 250 mbar until reduced to approximately 1 ml in volume. Extracts were evaporated to dryness in 12 mm test tubes on a heating block at 75°C and then allowed to cool. Concentrated sulfuric acid was added to the tubes prior to incubation at 100°C
for 10 minutes with subsequent cooling. SPV reagent (1.2 mg/ml vanillin in 80% phosphoric acid) was added to each tube and allowed to develop for 10 minutes. Absorption was measured on an Agilent 8453 Spectrophotometer at 490nm and extrapolated from species-specific calibration curves determined prior to analysis; % lipid is presented on a dry mass basis. For age-0 and age-1 fish (>30 mm SL), proximate composition analysis was performed as previously described (Vollenweider et al., 2011), with lipid extractions utilizing a Dionex ASE (Accelerated Solvent Extractor) 200 and a modified Folch extraction procedure using a 2:1 (by volume) chloroform:methanol solvent mixture. Analysis was conducted using wet material and estimates of % moisture (see above) were used to convert observations to a dry mass basis presented here.

QA samples for the SPV samples included two blank runs to estimate background absorption, two method blank samples containing all analysis reagents but no lipid extract to evaluate contamination and reagent absorption, and two reference samples (adult walleye pollock homogenate) to examine precision and accuracy for each batch of 15 samples. Mean background absorbance was subtracted from sample absorbance values. Method blank samples had to be < 10 mg of lipid and walleye pollock reference samples had to vary by < 1 SD and be accurate within 15% of the established lipid value. ASE samples used similar QA criteria except that the method blank samples were allowed to be as high as 0.1 mg of lipid (due to much higher analyzed lipid masses).

To compare energy densities of walleye pollock from age-0 to age-1 for the cohort analysis, a linear regression was used to predict energy density estimates from %
lipid values for age-1 fish collected during two cruises (BASIS 2009 and MACE 2009; Table 1). All age-1 fish processed for both energy density and % lipid (n=83) were used to develop a regression relationship, ED = 20.1 + 0.76*% lipid (r^2 = 0.79), that was used to predict energy density. The size of the fish used in the regression ranged from 109 - 194 mm SL. Direct estimates of energy density from the bomb calorimeter were used when available.

2.4.3. Statistical analysis
Cohort-specific patterns in energy density from age-0 to age-1 were examined to determine the extent of interannual variation in the seasonal pattern of fish condition using two complete cohorts. The 2008 cohort was sampled as age-0 fish in summer (July) and fall (September) 2008, and as age-1 fish in summer (July) and fall (September) 2009. The 2009 cohort was sampled as age-0 fish in summer (June) and fall (September) 2009, and as age-1 fish in summer (July) 2010. Fish condition was compared between cohorts within each season (age-0 and age-1 in summer, age-0 in fall) using separate one-way ANOVAs (analysis of variance).

Seasonal patterns in energy allocation during larval and early juvenile development (age-0) were analyzed using generalized additive mixed models (GAMM) to identify the seasonal timing and size at which walleye pollock shift energy allocation strategies from growth to lipid storage. These models do not specify a fixed functional form, but rather quantify the relationship between a set of predictors and available estimates of fish condition through non-parametric smooth functions of the predictor.
variables. The optimum amount of smoothing was chosen by generalized cross-validation as implemented in the R package ‘mgcv’ (Wood 2006).

The sampling area differed among cruises as did the number of fish processed per location, therefore modeling approaches that accounted for spatial patterns and/or included a random station effect were compared using Akaike’s Information Criterion (AIC) (Akaike 1973; Burnham and Anderson, 2002). Fish for which measurements of standard length were not available were removed from models of energy density or % lipid ($n=5$ and 6, respectively). Based on residual diagnostics, estimates of energy density and % lipid identified as outliers ($n=5$ and 8, respectively) were removed from further analyses resulting in a total of 247 estimates of energy density and 271 estimates of % lipid.

Variability in energy density and % lipid over the first summer were modeled as a function of sampling date (Day of year, DOY) to estimate seasonal trends in energy density (% lipid) and as a function of standard length (SL) to estimate changes in energy allocation with fish size. The models also included a spatial smooth term to account for differences in the mean across stations within years to address autocorrelation, as well as a year term to account for possible differences in the average energy density (% lipid) between years. The full model also included station as a random effect to account for variability among stations ($a_i$), in addition to within-station residual variability ($\varepsilon_{ik}$). The best model for energy density included both a spatial smooth term and a random station effect to account for autocorrelation (see below) while the random station effect was not significant for % lipid and therefore dropped from the best model (Table 2).
Energy density = $\alpha + f_1(\text{DOY}) + f_2(\text{SL}) + f_3(\text{latitude, longitude})_k + Y_k + a_i + \varepsilon_{ik}$ \hspace{1cm} (Eq. 1)

$a_i \sim N(0, \sigma_a^2)$

$\varepsilon_{ik} \sim N(0, \sigma_e^2)$

where $f_1$, $f_2$, and $f_3$ are smooth functions, $Y_k$ is the year-specific intercept for year $k$, $a_i$ is the station-specific, random intercept for station $i$, and $\varepsilon_{ik}$ is the residual. The random effects $a_i$ and residuals $\varepsilon_{ik}$ are assumed to be independent and normally distributed.

Residuals and random effects from the models were examined for normality, homoscedasticity, and independence by plotting them against all relevant covariates and by examining spatial patterns in the random station effects by year.

Patterns in fish length (mm SL) were also modeled as a function of sampling date (DOY) to estimate seasonal trends in fish growth; the model included a spatial smooth term to account for differences in the mean across stations within years to address autocorrelation and a year term to account for possible differences in the average length between years. The best model also included station as a random effect (Table 2).

$\text{SL} = \alpha + f_1(\text{DOY}) + f_2(\text{latitude, longitude})_k + Y_k + a_i + \varepsilon_{ik}$ \hspace{1cm} (Eq. 2)

$a_i \sim N(0, \sigma_a^2)$

$\varepsilon_{ik} \sim N(0, \sigma_e^2)$

where $f_1$ and $f_2$ are smooth functions, $Y_k$ is the year-specific intercept for year $k$, $a_i$ is the station-specific, random intercept for station $i$, and $\varepsilon_{ik}$ is the residual.
2.5. Results

2.5.1. Biological sampling
A total of 1501 walleye pollock larvae, age-0, and age-1 fish collected from 13 cruises over the 3-year sampling period were measured for standard length with 341 resulting estimates of energy density (kJ/g) from bomb calorimetry \( n=257 \) age-0 including 13 composite samples, \( n=84 \) age-1) and 423 estimates of % lipid \( n=285 \) age-0 including 41 composite samples, \( n=135 \) age-1) (Table 1). The overall mean energy density (± SE) of age-0 and age-1 walleye pollock was 22.43 ± 0.11 and 23.67 ± 0.12 (kJ/g dry mass), respectively, and overall mean % lipid (± SE) for age-0 and age-1 fish was 10.58 ± 0.40 and 20.53 ± 0.49 (on dry mass basis), respectively.

2.5.2. Cohort-specific patterns from age-0 to age-1
Age-0 fish from the 2008 and 2009 cohorts had relatively low mean energy densities in early summer with no significant difference between cohorts (1-way ANOVA: \( F_{(1,9)}=1.07, P=0.33 \) (Table 1, Fig. 2, Fig. 3a). Corresponding low values for % lipid in 2008 and 2009 (Table 1, Fig. 4a) indicate energy allocation to growth and/or development rather than energy storage during the early larval period. There was a short period from early-July to mid-September (DOY: 184-261) during which energy density rapidly increased to higher values in fall 2008 and 2009 (Table 1, Fig. 2). Energy density during NOAA/BASIS 2008 was significantly higher than NOAA/EcoFOCI 2008 (1-way ANOVA: \( F_{(2,120)}=7.04, P<0.01 \), with NOAA/BASIS 2009 having an intermediate energy density.

Energy densities are presumed to decrease over winter when water column temperatures, prey availability, and feeding rates decrease. By the fall of the second year, age-1 juveniles of both the 2008 and 2009 cohorts had regained energy densities.
similar to those of age-0 fish the previous fall (Table 1, Fig. 2). However, the 2009 cohort
had significantly greater energy density at age-1 than the 2008 cohort (1-way ANOVA:
$F_{(2,85)}=13.68, P<0.001$; Fig. 2).

2.5.3. Seasonal patterns in energy allocation of age-0 fish
Energy density and % lipid both varied non-linearly with fish length and season (Fig. 3, a and b; Fig. 4, a
and b, respectively) with significant differences between years. Energy density was highest in
2008, lowest in 2009, and intermediate in 2010 (Fig. 3c) while % lipid showed a decrease from
2008 through 2010 (Fig. 4c). The effect of size is difficult to separate from the seasonal pattern
because SL is strongly correlated with sampling date for both energy density ($r=0.56$) and % lipid
($r=0.91$), although largely uncorrelated for fish larger than 30 mm SL (energy density $r=0.086$; %
lipid $r=-0.35$). Therefore, for fish >30 mm SL, we can statistically separate the apparent effects of
size and seasonal pattern on fish condition. Residual diagnostics for all models showed no
unusual trends and no evidence of remaining spatial autocorrelation.

Few estimates of energy density for preflexion larvae (<30 mm SL) were possible
because samples had to be composited to acquire sufficient dry mass for analytical
processing. Therefore, patterns in energy density for preflexion larvae are uncertain
(i.e., Fig. 3b). Preflexion larvae had negative energy density anomalies indicating below-
average condition; a period of rapidly increasing energy density occurred between
approximately 20-60 mm SL until reaching an asymptote at approximately 70 mm SL
(Fig. 3a). The seasonal trend in energy density shows little effect of sampling date,
indicating that changes in energy density are primarily driven by changes in fish size as
opposed to seasonal timing. Energy density reaches a minimum in early fall
(approximately DOY 250; September 6, Fig. 3b).
Percent lipid in fish <30 mm SL showed a decrease with increasing length that may correspond with the transition to exogenous feeding after hatching, which occurs at 3-4 mm SL.

In fish >40 mm SL, % lipid increases linearly with increasing size (Fig. 4a). The seasonal trend in % lipid varied non-linearly, although variability in these estimates was high (Fig. 4b). The effect of fish size on patterns of % lipid was greater than the seasonal effect, as indicated by the range in % lipid anomalies between Figures 4a and 4b.

2.5.4. Seasonal patterns in length of age-0 fish
Walleye pollock length increased slowly during the pre-flexion stage (<30 mm SL), but rapidly after DOY 200 (July 19). Fish lengths reached an asymptote between approximately DOY 235 (August 23) and DOY 250 (September 6) before increasing again over the remaining sampling period (Fig. 5). Fish lengths were more variable in fall than in spring and early summer. The asymptote in fish length corresponds to the minimum observed in energy density (Fig. 3b).

2.6 Discussion
This study provides estimates of fish condition for larval, age-0, and age-1 walleye pollock and suggests how YOY fish allocate resources to growth and energy storage. Patterns in energy allocation differed among larval and juvenile fish. Constraints of the match/mismatch hypothesis (Cushing 1969; 1990), which would favor energy allocation to growth and development in order to escape size-dependent predation, appear limited to larval development. In contrast, age-0 juvenile fish adopt an allocation strategy consistent with the constraints suggested by the critical period hypothesis (Beamish and Mahnken, 2001). Our results suggest a period of rapid growth associated with an increase in energy allocation to storage during late summer. Presumably, differences in prey availability and quality (Coyle et al., 2011) during this period are reflected in differences in energy density (Heintz et al., 2013). This allocation strategy has potentially important consequences for overwinter survival because fish
condition at the end of summer directly relates to observed differences in year-class strength between alternating climate states in the SEBS (Hunt et al., 2011; Heintz et al., 2013). One possible explanation for the apparent link between energy density and recruitment is size-dependent mortality, which contributes to differential overwinter survival (Schultz et al., 1998; Heintz and Vollenweider, 2010). Therefore, we propose that late summer represents a critical period for energy storage in YOY walleye pollock and their subsequent recruitment success.

In the recent cold years of 2006-2010, the zooplankton community over the Bering Sea shelf has been dominated by large copepods (i.e., *Calanus marshallae*) and euphausiids (i.e., *Thysanoessa raschii*), providing walleye pollock with a lipid-rich diet and sufficient energy reserves for increased overwinter survival. Under warmer conditions (2002-2005), smaller zooplankton taxa were dominant (i.e., *Pseudocalanus* spp., *Acartia* spp., Coyle et al., 2011) and the lack of larger prey appeared to have limited growth and energy storage, leading to poor condition and reduced year-class recruitment. The limited availability of large zooplankton coincided with increased rates of cannibalism by older age-classes of walleye pollock, further reducing age-0 survival in warm years (Coyle et al., 2011). Hence, prey quality may be as important as the thermal regime for determining overwinter survival (Hurst 2007), although prey availability and prey quality are closely linked to temperature conditions (Coyle et al., 2011).

The 2008 and 2009 cohorts showed similar seasonal patterns of energy allocation for age-0 fish, likely reflecting similar oceanographic conditions and prey resources. The differences observed for age-0 fish during early fall likely reflect the difference in sampling time between cruises and highlight early fall as a period of rapidly increasing energy density in walleye pollock. The 2009 cohort had higher energy
densities by age-1, which could be due to differential overwinter survival, reduced
winter energy loss for the 2009 cohort leading to less of an energy deficit in spring 2010,
and/or differences in prey availability for age-1 fish during their second summer. The
2009 cohort likely experienced greater prey availability and less intra-species
competition as the 2009 year-class estimate remains well below the 2008 estimate
(Ianelli et al., 2011).

Low lipid and energy density levels in spring and early summer indicate larvae
preferentially allocate energy to development (i.e., protein synthesis) with little increase in
overall fish growth (i.e., tissue accretion) during the preflexion stage (<30 mm SL) until the
transformation to the juvenile form. The decrease in lipid content with size as larvae increase
from ~5 – 15 mm (Fig. 4a) most likely reflects the transition to exogenous feeding with
decreasing energy stores as larvae learn to capture prey. This study was conducted during three
cold years in the SEBS (Stabeno et al., in press), therefore delayed development times likely
resulted in smaller fish sizes relative to warmer years (Smart et al., in prep). Although the
average lipid content of YOY walleye pollock decreased significantly from 2008 to 2010 (Fig. 4c),
we did not see a consistent decrease in average energy density over the same time period.
However, we do not have estimates of % lipid for all sampling periods (spring, summer, and fall)
in all years of the study, therefore we cannot fully address interannual differences in % lipid.
During summer, walleye pollock appear to be growing in size while also increasing lipid
stores, although patterns in energy allocation are poorly defined due to lack of samples during
this period. That said, late July – August seems to be a period when energetic demands are
highest. The length at transformation from larval to juvenile form occurs at 25-40 mm SL (Brown
et al., 2001) and marks a threshold after which lipid acquisition rates increased, leading to
higher energy density in fall as energy was allocated to storage for overwinter survival. Our
samples fall on either side of this size range, supporting the inference that fish below this length range are allocating energy to development and fish above this length range are allocating energy to storage.

Early juvenile (age-0) walleye pollock reach an asymptotic length concurrent with a minimum energy density in early fall which may indicate a shift in prey preferences with increasing gape size (i.e., switch to euphausiids) and associated foraging capability. A similar energy minimum was observed in walleye pollock (46 mm SL) near the Pribilof Islands and was attributed to changes in feeding habits (Ciannelli et al., 2002). The energy density of walleye pollock near the Pribilof Islands during 1994-1996 and 1999 showed an asymptote when fish reached 80 mm SL (Ciannelli et al., 2002); the asymptotic size observed in fall 2008-2010 was approximately 60 mm SL. Cold water temperatures observed during the study period likely delayed and/or limited fish growth and development (Smart et al., in prep).

While our study focused on seasonal patterns in energy allocation, spatial patterns in the distribution of larvae relative to prey may be equally important in determining recruitment success. Age-0 walleye pollock in the Gulf of Alaska during fall experience spatially variable habitat conditions for growth due to differences in water temperature and prey (Mazur et al., 2007). Because of such differences, both the horizontal and vertical distribution of larvae affects their growth and condition.

Hydrography affects larval drift trajectories (Duffy-Anderson et al., 2006) as well as prey resources, which can be concentrated at frontal structures (Ciannelli et al., 2004). Once larvae are capable of diel vertical migration, the vertical position in the water column (i.e., above or below the pycnocline) affects temperature-dependent metabolic rates, as well as trade-offs in feeding rates versus predation risk (Sogard and Olla, 1996). Juvenile
walleye pollock are capable of selecting habitat based on temperature, prey availability, and predator abundance (Kooka et al., 2007). Consequently, we plan to incorporate both local-scale environmental conditions and estimates of prey availability into a bioenergetics model to quantify fine-scale spatial variability in fish condition and growth potential and to support the development of predictive models for recruitment success of walleye pollock in the SEBS.

The current study provides a conceptual model of how energy allocation strategies shift in walleye pollock during the larval and juvenile phases. This shift represents adaptations to survival constraints associated with distinct ontogenetic stages. Our results suggest that after a period of enhanced somatic growth until metamorphosis, early juvenile (age-0) fish favor energy storage in late summer/fall. This supports the critical period concept and the hypothesis that overwinter survival is dependent on sufficient storage in the previous growing season and may be an important determinant of recruitment success.

2.7 Acknowledgements
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is contribution EcoFOCI-XXX to NOAA's Fisheries-Oceanography Coordinated Investigations, NPRB XXXX, and BEST-BSIERP XXXX.

2.8 References


Megrey BA, Hollowed AB, Hare SR, Macklin SA, Stabeno PJ (1996) Contribution of FOCI research to forecast of year class strength of walleye pollock in the Shelikof Strait, Alaska. Fish Oceanogr 5 (S1): 189-203.


### 2.9 Table legends

Table 1. Cruise name, year, dates of sampling, and gear used to collect walleye pollock (*Theragra chalcogramma*). The mean (± SE, *n*) energy density, % lipid, and standard length (mm) are shown for each cruise by age class. Energy density values in *italics* were
predicted from % lipid values based on the regression relationship (ED = 20.1 + 0.76*% lipid).

Table 2. Summary of generalized additive mixed model (GAMM) fits for energy density, % lipid, and standard length showing terms, coefficient estimates, standard error (S.E.) for fixed coefficients, degrees of freedom (d.f.; number of parameters for each term in the model, estimated for smooth terms), and P-values. P-values for parametric terms (intercept, year coefficients) based on t-test of the null hypothesis that the coefficient is equal to zero; for smooth terms ($f_i$) based on an approximate F-test (Wood 2006); for random effects term ($\sigma_a$) based on likelihood ratio test. The intercept ($\alpha$) corresponds to the 2008 means and the subsequent year effects correspond to the difference between that year's mean and the intercept.

2.10 Figure legends
Figure 1. Map of the southeastern Bering Sea showing the location of sample collections by age-class and year. Distribution of collections approximates the actual distribution of age-0 and age-1 fish at the time of sampling. Depth contours are shown for the 50m, 100m, and 200m isobaths.

Figure 2. Plot of energy density (kJ/g dry mass) for the 2008 and 2009 cohorts of walleye pollock (Theragra chalcogramma). Errors bars are plotted as ±1 standard deviation (SD) to show the variability in energy density estimates for each sampling interval. Different
letters indicate significant differences in energy density within season. Note x-axis is consecutive days across the first two years of walleye pollock life.

Figure 3. Results from generalized additive mixed model (GAMM) regression analyses showing the relationship between energy density (kJ/g dry mass) and (a) standard length (mm), (b) Day of year, and (c) year for age-0 walleye pollock (*Theragra chalcogramma*). Dashed lines denote 95% confidence intervals.

Figure 4. Results from generalized additive mixed model (GAMM) regression analyses showing the relationship between % lipid (on a dry mass basis) and (a) standard length (mm), (b) Day of year, and (c) year for age-0 walleye pollock (*Theragra chalcogramma*). Dashed lines denote 95% confidence intervals.

Figure 5. Results from generalized additive mixed model (GAMM) regression analyses showing the relationship between standard length (mm) and Day of year for age-0 walleye pollock (*Theragra chalcogramma*). Dashed lines denote 95% confidence intervals.
1 Table 1.

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Figure 1.
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Figure 5.
Chapter 3 - Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions

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3.1 Abstract

Fishery managers require an understanding of how climate influences recruitment if they are to separate the effects of fishing and climate on production. The southeastern Bering Sea offers opportunities to understand climate effects on recruitment because inter-annual oscillations in ice coverage set up warm or cold conditions for juvenile fish production. Depth-averaged temperature anomalies in the Bering Sea indicate the last nine years have included 3 warm (2003-2005), an average (2006), and 5 cold (2007-2011) years. We examined how these climatic states influenced the diet quality and condition (size, energy density and total energy) of young-of-the-year (YOY) pollock (*Theragra chalcogramma*) in fall. The implications of fall condition were further examined by relating condition prior to winter to the number of age-1 recruits-per-
spawner the following summer (R/S). The percentage of lipid in pollock diets was
threefold higher in cold years compared with warm years, but stomach fullness did not
vary. Consequently, fish energy densities were 33% higher in cold years ($P < 0.001$) than
in warm years. In contrast, neither fish size ($P = 0.666$), nor total energy ($P = 0.197$)
varied with climatic condition. However, total energy was significantly ($P = 0.007$) and
positively correlated with R/S ($R^2 = 0.736$). We conclude that recruitment to age-1 in the
southeastern Bering Sea is improved under environmental conditions that produce
large, energy dense YOY pollock in fall.

3.2 Keywords:
pollock, Bering Sea, recruitment, climate change, winter, prey quality
3.3 Introduction

Fishery managers are limited in their ability to predict the number of young fish recruiting into fisheries because recruitment is the product of a linked series of complex and non-linear processes (e.g. Bailey et al. 2005). Most recruitment models rely on the number and fecundity of spawning females to project the future number of recruits. However, offspring must negotiate larval and prolonged juvenile stages prior to recruitment, so there is often little or no correlation between the number of spawners and subsequent recruits (e.g. Zheng, 1996). The problem of predicting recruitment may be exacerbated in the future because climate change will unpredictably alter the present interactions between the biotic and abiotic drivers. Consequently it is important that fishery managers develop a quantifiable and mechanistic understanding of how recruitment processes function under different climate conditions (Hollowed et al., 2009).

The southeastern Bering Sea can be viewed as a natural laboratory for understanding climate effects on fisheries recruitment. It occupies a broad, flat continental shelf north of the Aleutian Islands on the western coast of Alaska. In spring, summer, and fall oceanographic fronts bound distinct hydrographic areas known as the inner, middle and outer domains. The southern extent of ice coverage in this area varies annually in response to atmospheric forcing. The sea ice undergoes periods of relatively little coverage (warm years) followed by periods of almost complete coverage (cold years). This oscillation influences the development of oceanographic fronts with a profound
influence on the ecological processes within each domain. These effects of winter ice
cover have been incorporated into the Oscillating Control Hypothesis (OCH) (Hunt et al.,
2002), which predicts how warming temperatures will affect recruitment of walleye
pollock (*Theragra chalcogramma*) in the southeastern Bering Sea. The pollock harvest
there constitutes the largest fishery (by weight) in the United States. Consequently,
pollock recruitment in the southeastern Bering Sea is the object of intense interest.

A recent revision of the OCH focuses on the relationship between the eastern Bering Sea
zooplankton community and the timing of ice retreat in spring (Hunt et al., 2011). Early
ice retreat in warm years results in an absence of large crustacean zooplankton over the
middle shelf domain and favors communities comprised of small copepods such as
*Pseudocalanus, Acartia, Oithona* and *Centropages*. Conversely, the zooplankton biomass
over the middle shelf is dominated by medium-sized calanoids and euphausiids in cold
years (Coyle et al., 2011, Hunt et al., 2011, Ressler et al., 2012, Stabeno et al., 2012). The
species composition in cold years has been theorized to supply zooplanktivorous fishes
with improved access to lipid and subsequently increased recruitment success (Moss et
al., 2009).

Improved access to lipid-rich prey is important because young-of-the-year (YOY) pollock
face severe energy deficits as they enter winter (e.g. Sogard and Olla, 2000). These
energetic deficiencies are believed to account for winter mortality (Hurst 2007), which
can significantly reduce year class strength (Farley et al. 2007). High latitude fish need to
satisfy those energy deficits with endogenous energy (Post and Parkinson 2001) stored
as lipid. The time window during which pollock can provision themselves with lipid occurs between the completion of metamorphosis in early August and the onset of oceanographic winter (Willson et al., 2011, Siddon et al. 2013). This highlights the importance accessing lipid rich prey in late summer and early fall. Those individuals that can consume high lipid prey during this critical period should survive winter better than individuals consuming leaner prey.

The size of fish prior to winter is also an important determinant of winter survival. Observations of size-dependent mortality during winter for many freshwater and marine species have led to the so-called critical size hypothesis (Farley et al. 2007; Hurst 2007). Empirical evidence suggests that mortality among high latitude fish in winter depends on size, with larger individuals having the greater chance of survival. Size-dependent mortality during winter has been described for silversides (Menidia menidia) (Conover 1984), Pacific herring (Clupea pallasi) (Norcross et al. 2001), pollock (Sogard and Olla 2000; Heintz and Vollenweider, 2010), pink (Oncorhynchus gorbuscha) (Moss et al. 2005) and sockeye (O. nerka) (Farley et al. 2011) salmon. Larger fish are thought to survive winter better than small fish because they have a greater capacity to store energy (Schultz and Conover 1999). These data indicate that foraging conditions during the critical pre-winter period should be an important determinant to recruitment success because those conditions that allow fish to grow and store lipid will maximize winter survival. Yet, none of these studies has considered food quality as a factor contributing to winter survival.
We examine the hypothesis that YOY pollock are better prepared to survive winter in the eastern Bering Sea when they are able to forage on lipid-rich zooplankton communities characteristic of cold years. The objectives of this study were to understand how climatic conditions in the eastern Bering Sea influence the pre-winter condition of YOY pollock, and how that condition influences their winter survival. We compared the nutritional condition (size, energy density, total energy) of walleye pollock collected from warm and cold years to the percent lipid in their diets. Finally, the importance of fall condition is examined by correlating the pre-winter condition of YOY pollock with their winter survival, expressed as the number of age-1 recruits-per-spawner the following summer.

3.4 Materials and methods

3.4.1 Pollock collection and processing

Pollock were sampled during the Bering Aleutian Salmon International Survey (BASIS) conducted by the National Marine Fisheries Service each year between 2003 and 2011. Years were classified as warm (20003-2005), average (2006) or cold (2007-2011) based on ice coverage in March/April and the depth averaged temperature anomaly between April and October at mooring M2 following Stabeno et al. (2012). BASIS is a fisheries oceanographic survey of the eastern Bering Sea that takes place between mid August and the end of September. Fish were collected by surface trawl during the day in a gridded series of 81 fixed stations (Figure 1; Farley and Moss, 2009). Over the course of the study period the actual number of stations surveyed has varied due to weather and other constraints. However, the core areas where YOY pollock were historically caught
have been sampled in all years. In this report we only consider fish sampled from surface trawls deployed south of 60° north latitude to maintain consistency between years.

YOY pollock <100 mm total length, as delineated by Moss et al. (2009), were processed from each station. The total number caught was counted or estimated from subsamples of the total mass. The average weight of the YOY pollock at each station was recorded by dividing the total mass of YOY by the number of YOY in that mass. A subsample of up to 10 fish was retained to estimate diet composition. Another subsample of up to 15 fish was retained and frozen for calorimetry.

Fish collected for diet analysis were processed immediately on the vessel to estimate the average diet composition for each station. The stomach contents were removed from each fish, pooled into a common sample and weighed to estimate the average bulk mass of the stomach contents. The average stomach fullness at each station was recorded as the bulk stomach content mass divided by the total fish mass and multiplied by 100. The taxa comprising the bulk were identified to the lowest practical level and weighed. The percentage contribution of each taxon to the bulk weight was recorded. Diet compositions in warm and cold years have been described elsewhere (Moss et al., 2009; Coyle et al., 2011) and are only briefly reviewed here.

The energy density (kJ/g wet mass) of the YOY pollock from each cruise (2003-2011) was measured by bomb calorimetry. Samples for bomb calorimetry from a given station were stratified by length. They were dried, pulverized and combusted using a Parr 6725
semi-micro bomb calorimeter. Pulverized homogenates were pressed into pellets weighing at least 25 mg prior to combustion. Calorimetric data collected after 2007 were supplemented with energy densities calculated from proximate compositions. Conversions to energy density from proximate composition relied on linear regressions relating percent lipid to energy density in samples for which both analyses had been performed. Details for the calorimetry and proximate analysis along with quality assurance protocols can be found in Siddon et al. (2013).

3.4.2 Collection and processing of zooplankton

The percent lipid of pollock prey items was estimated from zooplankton samples collected in a warm (2004) and cold (2009) year. Estimates of zooplankton percent lipid for the warm year come from samples collected between 26 July and 19 August on a survey centered near the Pribilof Islands. That survey also included a transect over the shelf break and a grid of stations centered on a mooring (M2) on the continental shelf (56.8° N 164° W) (Hunt et al., 2008, Figure 1). During this survey, zooplankton samples were collected at night using the drogue net (150 µm mesh) of a MOCNESS with a nonfiltering cod end. The MOCNESS was fished obliquely from the surface to near bottom and prey species were sorted under a dissecting microscope on ice and then frozen and transported to the lab in liquid nitrogen. Estimates of zooplankton percent lipid for the cold year (2009) come from samples obtained during the BASIS survey between 30 August and 28 September. During this survey, zooplankton samples were collected using bongo nets (505 µm mesh) (Coyle et al., 2011) fished vertically from at most 100 m depth to the surface during the day. Zooplankton were sorted immediately
after collection and representative individuals of each species were frozen in separate air tight vials and held at < -75° C until they were processed in the laboratory.

Prey quality was measured in the laboratory as the percent lipid in the zooplankton wet mass. Zooplankton were gently blotted to remove liquid and weighed to the nearest 10 µg. When individuals were too small to weigh individually, the average wet mass was estimated from compositied samples; weighed in bulk. Average mass was estimated by dividing the bulk weight by the number of individuals in the composite. Lipid was extracted from each sample using a modified Folch method. The minimum sample size for extraction was 25 mg (wet mass), which often required compositing 3 to 35 individuals. Samples were extracted using a solvent mixture of 2:1 chloroform:methanol in a Dionex Accelerated Solvent Extractor (ASE). See Siddon et al. (2013) for details on the extraction protocol and quality assurance procedures. Samples from 2004 that were < 25 mg were extracted in the same solvent mix using hand maceration. The extract was passed over a micro-column of sodium sulfate as a drying agent to remove tissue material. The same quality assurance methods and reference materials were used as those extracted using the ASE to ensure comparability.

3.4.3 Data analysis

3.4.3.1 Climate effects on prey quality

Climate effects on prey quality were examined by comparing the percent lipid of prey sampled from eastern Bering Sea in 2004 and 2009. The percent lipid of five species was measured in both years, *Theragra chalcogramma*, *Neocalanus cristatus*, *Calanus* spp,
Thysanoessa inermis and Thysanoessa raschii. We compared their percent lipid between years using a two-way ANOVA with year, species and their interaction as fixed factors. Assumptions regarding normality (Anderson Darling) and homogeneity of variance (F-test) of the response variables relative to climatic state were tested prior to the analysis.

3.4.3.2 Climate effects on pollock diet

The diet compositions obtained in each survey year were combined with the percent lipid (wet mass basis) of the prey to estimate the average percent lipid of diets in warm, cold and average years. Percent fullness and dietary lipid of fish collected from the BASIS surveys in warm, cold and average years was compared using a one-way ANOVA. The average percent lipid of the diet \( l_{st} \) observed at each station \( s \) in a given year \( t \), expressed as the percent of ingested wet mass was calculated as:

\[
l_{st} = \sum_{i} p_{ist} L_{ic}
\]

where \( p_{ist} \) is the proportional contribution of prey type \( i \) at station \( s \) to the total mass ingested and \( L_{ic} \) is the percent lipid of prey type \( i \) under climate condition \( c \). When only one lipid value was available it was used for both the warm and cold year diets. When diet could only be identified to taxon (i.e. genus, family or order), the overall average lipid value for that taxon was applied. We calculated the average dietary percent lipid
for each year, \( \bar{I}_t \), by weighting \( I \), by the catch at each station in year \( t \) (\( C_{ts} \)) to account for the highly variable number of fish caught at each station.

\[
\bar{I}_t = \frac{\sum C_{ts} I_s}{\sum C_{ts}}
\]

Estimates of fullness were also weighted by catch prior to analysis.

3.4.3.3 **Climate effects on pre-winter condition**

Climate effects on fish condition were examined by comparing the catch-weighted averages across years. Climate responses were examined using a one-way ANOVA. Climate classification was considered a fixed variable. The response variables included catch-weighted average weight, energy density and total energy. The latter response (i.e. kJ per fish) was estimated as the product of the catch-weighted average weight and catch-weighted average energy density for a given year. We used total energy based on the assumption that winter survival is optimized when fish can simultaneously accrete tissue mass and allocate energy to depot lipids. Assumptions regarding normality (Anderson Darling) and homogeneity of variance (F-test) of the response variables relative to climatic state were tested prior to the analysis.

2.3.4 **Influence of pre-winter condition on survival**

We used regression analysis to evaluate the strength of the relationship of YOY condition in fall and subsequent survival to age-1. Survival of year class \( t \) (\( S_t \)) was indexed as the number of age-1 recruits (\( R_{t+1} \)) per female spawner (\( F_t \)) calculated as
using data provided in the Bering Sea Pollock Stock Assessment (Ianelli et al., 2011). The number of recruits-per-spawner (hereafter referred to as survival) was regressed against three indices of condition: catch-weighted average fish mass, catch-weighted energy density and total energy.

3.5 Results

3.5.1 Climate effects on prey quality

We estimated the percent lipid in 22 zooplankton taxa between our 2004 and 2009 collections, five of those taxa were sampled in both years (Figure 2). The average percent lipid of zooplankton differed significantly between years ($F_{1,80} = 12.59$, $p < 0.001$), and there was no interaction between species and year ($F_{1,80} = 0.12$, $p = 0.890$). Prey species had higher percent lipid in the cold year compared with the warm year. This was true for the euphausiids, *Thysanoessa raschii* and *Thysanoessa inermis*, as well as teleosts such as pollock, which all increased in percent lipid by at least 21%. *Calanus* spp. increased in percent lipid by 37% between the warm and cold year and *Neocalanus cristatus* increased by 50%.

3.5.2 Climate effects on pollock diets

YOY pollock consumed a more diverse diet in warm years, but tended to have lower average fullness than in cold years. The diets of the fish sampled in 2004-2007 were previously reported by Moss et al. (2009), while those from 2003-2009 were reported by
Coyle et al. (2011). The diets observed in 2010 and 2011 conformed to the previously described patterns. In general, diets were most diverse in warm years (Figure 3), including many additional prey taxa not observed in cold years. The most frequent taxon in warm years was *Pseudocalanus* spp., (listed as “Small copepod” in Fig. 3), accounting for up to 60% of the ingested mass. In cold years *Pseudocalanus* spp. were also relatively frequent, but they made up a smaller proportion of the mass ingested because larger taxa were also ingested. The most frequent items in cold years were *Calanus* spp., but euphausiids accounted for the majority of the mass. Despite the compositional differences between warm and cold years, stomach fullness remained constant ($F_{2,6} = 1.52, p = 0.293$). Although, the average fullness increased from $1.7 \pm 0.1\%$ (mean $\pm 1$ s.e.) in the warm years to $2.2 \pm 0.4\%$ in the cold years.

Pollock diets had a greater amount of lipid in cold years due to the larger contributions of *Calanus* spp and euphausiids. Items typical of warm years, such as small copepods (including *Pseudocalanus* spp.), were intermediate in percent lipid (Figure 2), but can also be seen in cold year diets. In contrast, *Calanus* spp. and euphausiids have higher percent lipid (Figure 2), and were abundant in the diets of pollock sampled in cold years (Figure 3). Consequently, pollock diets had significantly more lipid in the cold years than in the warm years ($F_{2,6} = 12.84, p = 0.007$), averaging about threefold greater (Figure 4).

The taxa in our collection were sufficient to describe the percent lipid of >98% of the mass observed in pollock stomachs from cold years. We had to supplement our collection of percent lipid with published values (Figure 2) to account for the more
diverse diets observed in warm years. Inclusion of published values allowed us to account for a median of >90% of the mass observed in those stomachs.

3.5.3 Climate effects on pre-winter condition

Neither the size nor the total energy content of pollock were influenced by climate, but there was an effect of climate on energy density. Pollock were slightly lighter in mass during the warm years averaging 1.97 ± 0.25 g compared with 2.35 ± 0.28 g in the cold years, but these differences were not statistically significant (F2,5 > 0.43 p > 0.666) (Figure 5). In contrast, the catch-weighted average energy density was highly correlated with climatic condition (F2,6 = 35.38, p < 0.001; Figure 5b). Energy density in the cold years (4.90 ± 0.11 kJ/g) was 33% greater than the warm years (3.67 ± 0.04 kJ/g). In contrast to energy density, there was no relation between climate and the total energy content of YOY pollock (F2,6 = 2.16, p = 0.197). However, there was a trend of greater total energy in cold years (11.2 ± 1.5 kJ/fish) compared to warm years (7.3 ± 0.9 kJ/fish).

3.5.4 Influence of pre-winter condition on survival

Total energy was the best predictor of survival. The product of weight and energy density expressed as total energy was significantly (F1,6 = 16.77, p = 0.006) and positively (r2 = 0.736) correlated with recruitment to age-1 (Figure 6). Weight (r2 = 0.496) and energy density (r2 = 0.677) were also positively correlated with survival (F1,6 > 5.92, p < 0.051), but accounted for less of the variation in survival over the last nine years.
3.6. Discussion

These data demonstrate that the ability of YOY pollock to provision themselves prior to winter has direct bearing on their survival to age-1. Climate effects on prey field composition (Coyle et al. 2011) led to the consumption of high lipid diets in cold years. Fish that consumed high lipid diets had higher energy densities as a result of the increased level of lipid in their tissues (Anthony et al. 2000). The effect of consuming high lipid diets on body composition is well known (e.g. Arzel et al., 1994). In larval pollock high lipid diets may also increase survival by reducing activity costs (Davis and Olla, 1992). However, consuming high lipid diets did not guarantee survival in this study, fish also needed to reach sufficient size. This indicates the critical size hypothesis should be refined to reflect both the effects of large size late in the growing season and the availability of high lipid diets. The oceanographic conditions that produce large, energy dense fish are also those conditions likely to lead to increased winter survival of YOY pollock.

3.6.1 Climate impacts on food abundance and quality

Food limitation is often cited as a mechanism restricting production and recruitment in fish populations, but the data presented here indicate food quality is also important. Zooplankton biomass in cold years was twice that of warm years in the southeastern Bering Sea (Coyle et al., 2011), but pollock catch-per-unit-effort on BASIS surveys was lower in cold years (Hunt et al., 2011). This indicates the per capita availability of prey was likely much higher in cold years. Pollock consumption rates are higher at warm temperatures (Kooka et al. 2007) suggesting lower average stomach fullness in warm
years reflected a density-dependent impact on foraging success. However, pollock in warm years would have had to ingest three times more food in warm years to ingest the same amount of lipid as fish in cold years. It is unlikely that pollock would be able to consume three times as much food in warm years if the food were available because maximum consumption rates only increase about twofold between 3 and 12 °C (Kooka et al., 2007).

The processes which led to the increased availability of high quality prey in cold years was augmented by the increased percent lipid found in specific prey taxa. Improved quality in *Calanus spp.* likely relates to mechanisms associated with their increased abundance such as improved coupling between spring blooms and metamorphosis (Baier and Napp, 2003) or reduced stratification and increased nutrient supply during summer (Coyle et al. 2011). However, it is possible that the climate related changes in food quality we observed are related to seasonal effects on lipid storage. Zooplankton sampled in 2009 were collected as much six weeks later in the year than those in 2004 and the percent lipid of the specific prey increased by 20% to 65%. However this seasonal effect, if it exists, is only of marginal importance because the majority of the warm year diets were comprised of leaner prey taxa than in cold years.

### 3.6.2 Importance of winter

Larger fish can store proportionately more energy and they use it more slowly than smaller fish. This is because the allometry for lipid storage before winter has a steeper slope than the allometry for lipid depletion during winter (Schultz and Conover, 1999). Therefore, the correlation between pollock condition and their subsequent survival to
age-1 was a product of both their size and energy density, which accounts for the relatively poor survival of the 2007 year class. Fish from the 2007 year class had high energy densities and consumed lipid-rich diets, but were relatively small in size. Consequently, their overall energy content was low at the onset of winter.

Conditions during the period in which pollock provision themselves for winter seem to have been more important in determining winter survival, than conditions earlier in summer. In warm years pollock may spawn earlier (Smart et al., 2012) and grow faster if food supplies are not limiting (Kooka et al., 2007). Warm conditions apparently led to improved larval survival and supported the production of YOY pollock as indicated by the catches-per-unit-effort during the late summer and early fall in the southeastern Bering Sea (Hunt et al., 2011). However, density dependence during the provisioning period may have ultimately limited the production of age-1 pollock. These observations suggest winter survival in the Bering Sea determines recruitment to a greater extent than larval production, a process similar to that reported for pollock in the Gulf of Alaska (Bailey, 2000; Cianelli et al., 2005).

Moderation of the severity of winters and a warming of the upper water column during winter are probable consequences of changing climate in southeastern Bering Sea. Over the past 30 – 40 years, the stormy spring-winter-fall period has decreased in length resulting in a longer summer stable period and decreased frequency of summer storms (Stabeno et al., 2012). These storms promote new production in the late summer/early fall and may prolong the period during which YOY pollock can find lipid-rich prey items.
In addition, decreased ice cover in the southeastern Bering Sea during warm periods has been associated with a later spring phytoplankton bloom (Hunt et al., 2011; Stabeno et al., 2012). Thus increased water temperatures may present a three-fold challenge to juvenile pollock: 1) low densities of lipid-rich prey in the late summer/early fall result in low lipid reserves, 2) higher temperatures result in higher basal metabolic costs, and 3) a delay in the production cycle the following winter/spring means the period without sufficient prey resources is longer.

3.7 Conclusion

These observations provide a quantitative basis for predicting recruitment as a function of environmental conditions. Estimates of total energy in fall integrate the effects of climate, diet, growth, prey abundance and quality at the end of the first growing season. The effects of climate on diet quality and condition of YOY pollock are consistent with observations of an inverse relationship between late summer sea surface temperatures and survival (Mueter et al., 2011). These data further demonstrate how fishery managers can take a significant step towards an ecosystem-based approach by linking recruitment models to the environmental and biological parameters responsible for production.

3.8 Acknowledgements

We thank all of the people involved in collecting and sorting the samples used in this study. This includes the crews of numerous vessels. In addition it includes numerous students that have helped to sort, prepare and process samples in the laboratory. Collection of summer 2004 prey samples was supported by NSF Grant OPP-0327308 (to
G.L. Hunt, Jr.) and NOAA’s North Pacific Climate Regimes and Ecosystem Productivity (NPCREP) research program. This research is contribution NPRB 414, BEST-BSIERP 93, and EcoFOCI-NXXX to NOAA’s NPCREP Program. References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA. The findings and conclusions in this paper are those of the authors and even though NOAA reviewed the work and paid our salaries the views here do not represent those of NMFS or NOAA.

3.9 References


3.10 Figures

Figure 1. Map of the eastern Bering Sea showing BASIS sampling stations (X’s).
Zooplankton were collected at stations identified with filled circles in 2009 and at
stations identified by open circles in 2004.

Figure 2. Average percent lipid (± 1 s.d.) of prey consumed by YOY pollock in 2004 and
2009. Bar colors reflect year the sample was collected, open bars show prey collected in
2004, closed bars show prey collected in 2009, gray bars show values taken from other
sources: ¹(Nomura and Davis, 2005), ²(Yamamoto et al., 2008), ³(Foy and Paul, 1999),
⁴(Lee et al., 2006) and ⁵(Peters, 2006).

Figure 3. Average percent composition (±1 s.d.) of YOY pollock diets in warm (2003-
2005) and cold (2007-2011) years. Each prey item is expressed as percent of total mass
of prey examined within a year and averaged across the appropriate years. Only those
prey items that averaged at least 1% of the mass examined are shown. Taxa have been
combined to simplify presentation. For more detailed comparisons of diets in warm and
cold years see Moss et al. (2009) and Coyle et al. (2011).

Figure 4. Catch-weighted average (± 95% confidence interval) lipid content of YOY

Figure 5. Catch-weighted average weight (± 1 s.d.) (top panel) and energy density
(bottom panel) of YOY pollock sampled from 2003 to 2011.

Figure 6. Relationship between catch-averaged weight, energy density and total energy
of YOY pollock with survival. Survival is estimated as the number of age-1 recruits per
female spawner and was not available for 2011 year class at time of publication.
Figure 1. Eastern Bering Sea showing BASIS sampling stations (X’s). Zooplankton were collected in 2009 at stations identified with filled circles. Zooplankton sampling in 2004 was conducted at locations identified by open circles.

Figure 2. Average percent lipid (± 1 s.d.) of prey consumed by YOY pollock in 2004 and 2009. Bar colors reflect year the sample was collected, open bars show prey collected in 2004 (Warm), and filled bars show prey collected in 2009 (Cold).
2004, closed bars show prey collected in 2009, gray bars show values taken from other sources: ¹ (Nomura and Davis, 2005), ² (Yamamoto et al., 2008), ³ (Foy and Paul, 1999), ⁴ (Lee et al., 2006) and ⁵ (Peters, 2006).
Figure 3. Average percent composition (±1 s.e.) of YOY pollock diets in warm (2003-2005) and cold (2007-2011) years. Each prey item is expressed as percent of total mass of prey examined within a year and averaged across the appropriate years. Only those prey items that averaged at least 1% of the mass examined are shown. Taxa have been combined to simplify presentation. For more detailed comparisons of diets in warm and cold years see Moss et al. (2009) and Coyle et al. (2011).
Figure 4. Catch-weighted average (± 95% confidence interval) lipid content of YOY pollock diets in warm (2003-2005), average (2006) and cold (2007-2011) years.
Figure 5. Catch-weighted average weight (± 1 s.d.) (top panel) and energy density (bottom panel) of YOY pollock sampled from 2003 to 2011.
Figure 6. Relationship between catch-averaged weight, energy density and total energy of YOY pollock with survival. Survival is estimated as the number of age-1 recruits per female spawner and was not available for 2011 year class at time of publication.
Chapter 4 - Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea

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4.2 Abstract

Understanding mechanisms behind variability in early life survival of marine fishes through modeling efforts can improve predictive capabilities for recruitment success under changing climate conditions. Walleye pollock (Theragra chalcogramma) support the largest single-species commercial fishery in the United States and represent an ecologically important component of the Bering Sea ecosystem. Variability in walleye pollock growth and survival is structured in part by climate-driven bottom-up control of zooplankton composition. We used two modeling approaches, informed by observations, to understand the roles of prey quality, prey composition, and water temperature on juvenile walleye pollock growth: (1) a bioenergetics model that included local predator and prey energy densities, and (2) an individual-based model that included a mechanistic feeding component dependent on larval development and behavior, local prey densities and size, and physical oceanographic conditions. Prey composition in late-summer shifted from predominantly smaller copepod species in the warmer 2005 season to larger species in the cooler 2010 season, reflecting differences in zooplankton composition between years. In 2010, the main prey of juvenile walleye pollock were more abundant, had greater biomass, and higher mean energy density, resulting in better growth conditions. Moreover, spatial patterns in prey composition and water temperature lead to areas of enhanced growth, or growth ‘hot spots’, for juvenile walleye pollock and survival may depend on the overlap between fish and these areas. This study provides evidence that a spatial mismatch between juvenile walleye pollock and growth ‘hot spots’ in 2005 contributed to poor recruitment while a higher
degree of overlap in 2010 resulted in improved recruitment. Our results indicate that climate-driven changes in prey composition and quality can impact growth of juvenile walleye pollock, potentially severely affecting recruitment variability.

4.3 Introduction
The match-mismatch hypothesis [1] proposes that predator survival is dependent on the temporal and spatial overlap with prey resources [2]. Factors affecting temporal overlap, such as climate variability through altered phenology, can lead to changes in survival at critical life stages [3,4]. Temporal variation in spatial patterns of physical or biological conditions may concurrently affect survival. For example, in temperate and sub-arctic marine ecosystems, the timing of the spring bloom varies between years, driven by physical oceanographic conditions that change due to climate variability (e.g., [5]). These conditions, such as the onset of stratification and light availability, also affect the spatial patterns of zooplankton abundance, which further influences the feeding success of planktivorous fish species. Hence, variability in the spatial overlap of predator and prey, as well as differences in prey quality [6,7], may directly affect differences in year-class success of many marine fish species [8,9].

Variability in year-class strength of gadids is often associated with changing physical conditions [10,11]. The eastern Bering Sea (EBS) has experienced multi-year periods of both warm and cold conditions since the turn of the 21st century [12], with cold years having much higher walleye pollock (Theragra chalcogramma) recruitment on average [13]. Changes in zooplankton composition between these periods have been
identified as an important driver of recruitment success for walleye pollock [9,14], but the mechanistic links remain poorly understood.

Interannual changes in ocean temperatures [12] and shifts in the spatio-temporal distribution of prey [14] make walleye pollock in the EBS an ideal case study to better understand drivers of recruitment success in sub-arctic marine fish. Larger zooplankton taxa, such as lipid-rich *Calanus* spp., were less abundant during recent warm years, possibly causing reduced growth rates and subsequent year-class strength of juvenile walleye pollock (hereafter juvenile pollock). In contrast, higher abundances of lipid-rich prey, combined with lower metabolic demands in cold years, may have allowed juvenile pollock to acquire greater lipid reserves by late summer and experience increased overwinter survival [9]. Although the energetic condition of juvenile pollock in late summer is recognized as a predictor of age-1 abundance during the following summer in the EBS [13], the causal mechanism linking differences in prey abundance and quality to walleye pollock survival remains untested.

The objectives of this study were to better understand the roles of prey quality, prey composition, and water temperature on juvenile pollock growth through (1) estimating spatial differences in maximum growth potential of juvenile pollock using a bioenergetics modeling approach, (2) comparing maximum growth potential to predicted growth from an individual-based model (IBM), and (3) quantifying the impact of temperature, prey abundance, and prey quality on spatial variability in growth potential.
4.4 Materials and methods

4.4.1 Ethics statement

Collection of physical and biological oceanographic data and fish samples during the US Bering-Aleutian Salmon International Surveys (BASIS) conducted on the EBS shelf was approved through the National Marine Fisheries Service, Scientific Research Permit numbers 2005-9 and 2010-B1. Collection of biological data in the US Exclusive Economic Zone by federal scientists to support fishery research is granted by the Magnuson - Stevens Fishery Conservation and Management Act.

4.4.2 Modeling approaches

Two alternative modeling approaches were parameterized based on samples of juvenile pollock, zooplankton, and oceanographic data collected during the BASIS surveys conducted on the EBS shelf from mid-August to October 2005 and 2010 ([15]; Figure S1). We selected 2005 (warm) and 2010 (cold) for our analyses based on data availability and the pronounced contrast in ocean conditions between these years (e.g., depth-averaged temperature anomalies over the middle shelf; [12]). Extensive spatial coverage of the surveys, combined with varying climate conditions between years, provided ample data with which to inform the models and compare differences in predicted growth between a representative warm and cold year in the EBS.

Maximum growth potential from a Wisconsin-type bioenergetics model parameterized for juvenile pollock (modified from [16]) was compared with predicted growth from a mechanistic IBM [17]. Comparing model-based predictions of growth allowed for a better understanding of the mechanisms behind temporal and spatial variability in growth patterns and an evaluation of the importance of different model
parameters. Growth (g•g⁻¹•day⁻¹; weight measures refer to wet weight throughout) was estimated for 65 mm standard length (SL; 2.5 g) juvenile pollock, corresponding to the average size of age-0 fish (<100 mm total length; TL) observed in late summer (2005: 64.1 ± 6.7 mm SL [mean ± SD] and 1.97 ± 0.93 g; 2010: 64.3 ± 9.2 mm SL and 2.39 ± 0.94 g; conversion between TL and SL followed [18]).

4.4.3 Field observations

Juvenile pollock abundance

Juvenile pollock were collected from the EBS shelf (inner domain: 0-50 m isobath, middle domain: 50-100 m isobath, and outer domain: 100-200 m isobath) using a midwater rope trawl following methods described in [19]. Catch per unit effort (CPUE; #•m⁻²) was calculated as:

\[ CPUE_i = \frac{n_i}{d_i \cdot h} \]  

where \( n_i \) is the number of fish collected in a given haul \( i \), \( d_i \) is the trawl distance (m) calculated from starting and ending ship position, and \( h \) is the horizontal spread of the trawl net (m). Only surface tows at pre-defined stations were used to compute CPUE because midwater tows specifically targeted acoustic sign of walleye pollock.

Water temperature

Vertical profiles of water temperature were collected at each station sampled for oceanography using a Sea-Bird Electronics (SBE) conductivity-temperature-depth (CTD) profiler SBE-25 (2005) or SBE-911 (2010). The average temperature in the upper 30 m of the water column was used in the bioenergetics model, assuming juvenile pollock collected from surface trawls were concentrated within the upper 30 m [15]. For the
IBM, the water column was divided into 1 m discrete depth bins. For all IBM simulations, the depth of the water column was set to the upper 100 m of all deeper stations ($n=9$ of 116 in 2005, $n=27$ of 160 in 2010) because MOCNESS data used to develop vertical profiles of zooplankton distribution (see ‘Zooplankton vertical profiles’ below) was limited to 100 m. For stations with missing temperature data ($n=1$ for 2005), data from the nearest station with similar depth was used. For stations with incomplete temperature profiles ($n=1$ for 2005), temperatures were linearly interpolated between depths.

Zooplankton data

**Determination of main prey taxa**

Juvenile pollock (<100 mm TL) collected from both surface (2005 and 2010) and midwater (2010) tows were used in the analysis to characterize diets across the EBS shelf in two contrasting years ($n=26$ stations in 2005, $n=47$ stations in 2010 [$n=16$ surface tows, $n=31$ midwater tows]). Stomach content analyses followed standard methods as described in [19]. Individual prey taxa were allocated a proportional contribution to total stomach contents, as % volume, of each prey taxon to the diet. To compute overall average diet composition, contributions were weighted by the CPUE of juvenile pollock at each station and averaged across stations. All prey taxa of juvenile pollock that cumulatively accounted for at least 90% of the diet by volume and individually accounted for at least 2% of the diet by volume were included in the bioenergetics and IBM models (Table 1). Main prey taxa from either year were included in models for both years for comparing growth across years.
Zooplankton abundance

Water-column abundances of small and large zooplankton taxa were estimated from Juday and bongo net samples, respectively, as described in [14]. Small zooplankton representing main prey taxa included *Acartia clausi*, *Acartia* spp. (2010 only), *Centropages abdominalis*, and *Pseudocalanus* sp. Large zooplankton included *Calanus marshallae*, *Eucalanus bungii*, *Limacina helicina*, *Neocalanus cristatus*, *N. plumchrus* (2005 only), *Oikopleura* sp., *Thysanoessa inermis*, *T. inspinata*, and *T. raschii*.

Zooplankton biomass

Total sample weights (g) of taxa collected from the Juday net were computed from wet weight tables [20]. Densities (g•m$^{-3}$) of taxa collected from the bongo net were measured during sample processing at the University of Alaska Fairbanks (2005; [21]) and NOAA/NMFS/Alaska Fisheries Science Center (2010). The year-specific average biomass of individuals for the main prey taxa was calculated by dividing the sum of the biomass of all specimens weighed (i.e., subsample) by the total number of specimens subsampled in a given year (Table S1).

Zooplankton energy density

Taxa-specific energy density (ED; kJ•g$^{-1}$) values obtained from available zooplankton collections from the EBS during 2004 (warm; no ED data available from 2005) and 2010 (cold) were used to estimate average ED values during warm and cold conditions for the main prey taxa. For taxa lacking sufficient information to estimate separate ED values ($n=5$), a single estimate was used in both years (Table S1). In these cases, only differences in abundance and biomass contributed to differences in average prey energy.
between years in the models. A biomass-weighted mean prey ED was calculated for each station and used as input to the bioenergetics model. At each station, the biomass of individual taxa was divided by the total prey biomass, multiplied by the taxa-specific energy density for each year, and summed across all taxa present at a given station.

Estimates of ED and % lipid were available for several copepod species (C. *marshallae*, *N. cristatus*, and *N. plumchrus/flemingeri*) from 2010 (see [22] for details on the biochemical processing). A linear regression was developed to predict species specific ED ($\omega_i$) from % lipid values for other copepod species and/or climate conditions (Table S1), such that:

$$\omega_i = \alpha + \beta L_i + \varepsilon_i, \quad \text{where} \quad \varepsilon_i \sim N(0, \sigma^2)$$

Eq. 2

where $\alpha$ and $\beta$ represent the intercept and slope of the regression, respectively, $L_i$ is the lipid composition (%) of the individual copepod sample $i$ and $\varepsilon_i$ is a residual. The residuals, $\varepsilon_i$, are assumed to be independent and normally distributed with mean 0 and variance $\sigma^2$ ($\alpha = 19.3, p = 0.02; \beta = 0.41, p = 0.07; R^2 = 0.98$).

Zooplankton vertical profiles

To account for diel vertical migrations, taxa-specific vertical profiles for day and night were developed for all main prey taxa as input for the IBM. Vertical profiles were based on summer MOCNESS surveys that provided depth-stratified abundance estimates. MOCNESS data were available for 2004 (warm) and 2009 (cold); these vertical profiles were applied to late-summer model runs for 2005 and 2010, respectively, assuming that the vertical behavior of zooplankton taxa is conserved seasonally and across years within similar oceanographic conditions. To assess the effect of this assumption, a
sensitivity analysis was conducted using constant abundances by depth (see ‘IBM
sensitivity analyses’ below).

In 2004, vertically stratified MOCNESS samples were collected at 5 daytime and
42 nighttime stations over the EBS shelf [21]. In 2009, 7 daytime and 22 nighttime
stations were sampled (A. Pinchuk, unpubl. data). Daytime extended from
approximately 07:00 (sunrise) to 23:30 (sunset) Alaska Daylight Savings Time during the
sampling periods; stations sampled during crepuscular periods were excluded from the
analysis. The depth increments of the MOCNESS varied depending on water depth;
therefore, data were binned to the finest resolution available (i.e., 5-20 m). Zooplankton
abundance was assumed to be uniform within sampling depths and averaged across all
daytime and nighttime tows within a given year to obtain four vertical profiles for each
taxon (day vs. night, 2004 vs. 2009). *Centropages abdominalis* were not collected by the
MOCNESS and a uniform distribution throughout the water column was applied for both
years because their distribution during the 2005 and 2010 BASIS surveys was
predominantly at shallow, well-mixed stations of the inner domain. *Oikopleura* sp. did
not occur in daytime tows in 2004; therefore, the 2009 daytime vertical distribution was
applied for both 2005 and 2010 model runs. *Thysanoessa inspinata* were rarely
collected by the MOCNESS (n=1 for 2005; n=3 for 2010), therefore an average vertical
profile based on all *Thysanoessa* spp. was applied.

**4.4.4 Bioenergetics model**

A bioenergetics model was used to estimate spatially explicit maximum growth
potential of juvenile pollock. We used the broadly applied Wisconsin bioenergetics
modeling approach [23,24] that has been adapted for walleye pollock including appropriate model validation ([16, 25]; Table S2). The model estimates temperature- and weight-specific maximum daily ($d$) consumption for an individual fish at station $k$ in year $t$ ($C_{\text{max},d,kt}$: $g\cdot g^{-1}\cdot d^{-1}$) as:

$$C_{\text{max},d,kt} = \alpha W_d^{-1} \cdot f(T_{d,kt})$$  \hspace{1cm} \text{Eq. 3}

where $C_{\text{max},d,kt}$ is parameterized from independent laboratory observations of consumption rates for the species, absent competitor or predator interference, and is assumed to scale exponentially with fish weight ($W$) according to $\alpha$ and $\beta$ (the allometric intercept and slope of consumption) and thermal experience according to the temperature scaling function $f(T)$ (Table S2).

Realized individual daily consumption rates ($C_{d,kt}$: $g\cdot g^{-1}\cdot d^{-1}$) based on in situ fish are typically much lower than $C_{\text{max},d,kt}$ because inter- and intra-species competition, mismatched prey phenology or distributions, and predator avoidance behaviors by prey species often limit capture and consumption rates [16,26]. The ratio of realized consumption to maximum consumption (i.e., $\bar{h} = C_{d,kt}/C_{\text{max},d,kt}$), or the mean relative foraging rate, is a measure of in situ foraging efficiency. The rate $\bar{h}$ can be estimated using field observations of growth or it can be set to a specific value and used to predict daily growth ($G_{d,kt}$) using the mass balance equation where growth is the difference between energy consumed ($C_{d,kt}$) and energy lost to metabolism and waste ($\delta |C_{d,kt},W_{d-1},T_{d,kt}$)), such that:

$$G_{d,kt} = (C_{d,kt} - \delta |C_{d,kt},W_{d-1},T_{d,kt}) \cdot \zeta_{kt}$$  \hspace{1cm} \text{Eq. 4}
where $G_{d,kt}$ is the estimated daily specific growth ($g \cdot g^{-1} \cdot d^{-1}$), $C_{d,kt}$ is realized consumption ($C_{d,kt} = \chi \cdot C_{\text{max},d,kt}$), $W_{d-1}$ is the weight of an individual fish at the start of the simulation day $d$, $T_{d,kt}$ is the water temperature on simulation day $d$, and $\eta_{kt}$ is the ratio of predator energy to prey energy density and is used to convert consumed biomass of prey into predator biomass (for more information see [26]). We used station-specific energy densities for prey ($\omega_k$) but annual mean predator energy density ($\bar{v}_t$) for year $t$ because predator information was not available at all stations.

Energy density values for the main prey taxa were used to derive mean station-specific ($k$) available prey energy density for both years ($\bar{\omega}_k$); diet composition was assumed to be proportional to the relative biomass of zooplankton prey at each station. Individual fish energy density ($v_i$) was determined using biochemical processing (see [22]). At stations where sufficient numbers of juvenile pollock were collected ($n=91$ in 2005 and $n=12$ in 2010), 2-8 fish were selected to represent the size range at each station. Station-specific mean energy density in a given year ($\bar{v}_{kt}$) was weighted by CPUE and the number of fish processed at each station to calculate the average fish energy density by year ($\bar{v}_t$).

We ran the model for a single simulation day (i.e., $d=1$) using base scenario input parameter values (Table 2; see also [16] Tables I and II) that were kept constant across stations and years (i.e., $W=2.5$ and $\bar{\eta}=1$), were constant across stations but varied by year (i.e., $\bar{v}_t$), or varied by station and year (i.e., $T_{kt}$ and $\omega_{kt}$). Because the model is size-specific, running the model for a single simulation day minimized compound errors that can accumulate over multiple simulation days when predicting growth and allowed for a
comparative index of growth across stations. Keeping fish starting weights \((W)\) constant allowed us to evaluate spatial effects of changes in the other parameters; setting \(\eta=1\) implies that growth was constrained by physiological processes, but not by prey consumption, hence we evaluated variability in maximum growth potential. Annual average fish energy density was applied across stations in each year \((\bar{\nu}_{2005}=3.92\text{ kJ}\cdot\text{g}^{-1};\)
\(\bar{\nu}_{2010}=5.29\text{ kJ}\cdot\text{g}^{-1})\).

Bioenergetics sensitivity analyses

Individual input parameters were increased and decreased by 1 standard deviation (SD) and the change in growth relative to maximum predicted growth under the base scenario was recorded. A pooled SD was calculated across stations after removing the annual means. Relative foraging rate \((\bar{\eta})\) was held at 1 for all sensitivity model runs in order to compare the relative effect of other parameters on maximum growth potential.

Station-specific parameters (i.e., \(T_{kt}\) and \(\bar{\omega}_{kt}\)) were varied to evaluate the relative effect on predicted growth and to examine resulting changes in spatially explicit growth patterns in each year. To evaluate the effect of variability in fish starting weight and energy density \((W'\) and \(\bar{\nu}',\) respectively) on estimated growth in 2005 and 2010, we used Monte Carlo simulations at a representative station (see Figure S1). A single station was used because mean fish weight and energy density input values did not vary across stations in the model due to data limitations; hence the spatial pattern in estimated growth is not affected by varying these values by a constant amount. The model was run 1000 times using parameter values drawn at random from a normal distribution with
the observed mean and SD for each parameter. The resulting distribution of predicted
maximum growth potential was examined.

**Mechanistic individual-based model**

A mechanistic, depth-stratified IBM was used to predict average growth \((g \cdot g^{-1} \cdot d^{-1})\) and
depth (m) of 100 simulated juvenile pollock by station. The details of the IBM and model
validation are described in [17,28]. The IBM was reparameterized for juvenile pollock
and forced with input data for water column temperatures and prey availability in 1 m
discrete depth bins. Prey abundance \((\# \cdot m^{-3})\) was allocated into depth bins according to
vertical profiles of zooplankton distribution and scaled to station depth.

The IBM used a mechanistic prey selection component that simulated the
feeding behavior of juvenile pollock on zooplankton. The species composition of main
prey taxa was based on observations; stage-specific length and width estimates were
based on literature values or voucher collections from the EBS (Table S1). Optimal prey
size was estimated to be 5-8% of fish length based on larval Atlantic cod research
[29,30]; juvenile pollock are predicted to have nearly 100% capture success for prey
smaller than 5% of fish length, while the probability of capture success decreases with
larger prey [17]. The simulated feeding ecology depended on juvenile pollock
development (e.g., swimming speed, gape width, eye sensitivity) and vertical migratory
behavior, prey densities and size, as well as light and physical oceanographic conditions
(for details see [17]). Gape width was calculated as a function of fish size; conversion
between length and weight followed [31]. Juvenile feeding processes were modeled
with light-dependent prey encounter rates and prey-capture success (see [29]).
Vertical migratory behavior was modeled assuming that juvenile pollock would seek deeper depths to avoid visual predation risk as long as ingestion rates would sustain metabolism and growth. If not, juvenile fish would seek the euphotic zone where light enhances feeding success, but also increases predation risk. Prey distributions switched between daytime to nighttime profiles when the light level (i.e., irradiance) reached 1 μmol•m\(^{-2}\)•s\(^{-1}\) [28]. The cost of vertical migration was included as a maximum of 10% of standard metabolic rates if the fish swims up or down at its maximum velocity, and scaled proportionally for shorter vertical displacements.

Swimming velocity was a function of juvenile fish size [32].

Gut fullness was estimated based on the amount of prey biomass that was ingested and digested per time step (1 hour) according to the feeding module. Prey biomass flowing through the alimentary system supplied growth up to a maximum growth potential (\(C_{\text{max}}\) [25]), and standard metabolic cost, egestion, excretion, and specific dynamic action [16] were subtracted. Both maximum growth and metabolic costs were functions of fish weight and water temperature.

For all base model scenarios, the starting weight of the fish was held constant across stations, while zooplankton abundance and vertical distribution varied according to observations. Fish starting weight was 2.5 g ± 30% assuming a random uniform distribution around the mean. Year-specific vertical profiles (day and night) for the main prey taxa and station-specific temperature and prey abundance profiles were applied.

The model scenarios were run for 72 hours, but only the last 24 hours of the simulations
were used for the analysis to avoid the early part of the simulations that may be unduly influenced by random initial conditions.

**IBM sensitivity analyses**

Fish starting weights and the vertical prey profiles were varied and resulting growth and average depth predictions were compared to values under the base model scenario (see [28] for sensitivity of the IBM model to variability in other parameters). To evaluate the effect of fish size separately from the effects of environmental controls, estimated growth based on fish starting weights of 2.0 g ± 30% was compared to the base scenario (2.5 g ± 30%), encompassing the mean weight of juvenile pollock from the BASIS surveys in 2005 (1.97 ± 0.93 g, mean ± SD) and 2010 (2.39 ± 0.94 g, mean ± SD). To test the effect of vertical distributions and diel migrations of prey taxa, model runs assuming a uniform distribution of prey with depth were compared to the base scenario, highlighting the effects of non-uniform zooplankton distribution and diel vertical migrations on juvenile pollock prey selection.

### 4.5 Results

#### 4.5.1 Field observations

Juvenile pollock abundance

Juvenile pollock abundance and distribution had distinct spatial patterns in the surface layer between warm and cold years, with a more northerly distribution in warm years. Specifically, during warm late-summer conditions of 2005 juvenile pollock were distributed over a broad extent of the middle and outer domain, while in the cooler late summer of 2010 fish were concentrated over small regions of the southern shelf and
outer domain (Figure 1, a and b). Abundance also varied between years with higher 
mean CPUE observed in 2005 as compared to 2010 (CPUE = 0.08 fish m\(^{-2}\) vs. 0.001 
fish m\(^{-2}\), respectively) at positive catch stations.

**Water temperature**

The average water temperature in the upper 30 m of the water column during the BASIS 
survey was 8.8ºC in 2005 and 7.6ºC in 2010 (Figure S2, a and b), while the average 
temperature below 40 m was 4.5ºC in 2005 and 2.9ºC in 2010 (Figure S2, c and d). The 
warmest surface temperatures occurred in nearshore waters, although 2005 had warm 
temperatures over much of the southern shelf. Bottom temperatures reflected the 
extent of the cold pool (waters <2ºC), which was limited to the northern portion of the 
study area in 2005 and covered much of the shelf in 2010.

**Zooplankton**

*Main prey taxa*

Diets of juvenile pollock shifted from smaller copepod species in the warmer 2005 
summer season (e.g., *Pseudocalanus* sp.) to larger species in the cooler 2010 summer 
season (e.g., *N. cristatus*). Several large zooplankton species were present in the diets 
across years, including *L. helicina*, which was the predominant prey item in both years, 
as well as *C. marshallae* and *T. raschii*. In 2010, the main prey taxa of juvenile pollock 
collected in surface tows were similar to those from midwater tows, with the exception 
of *E. bungii* accounting for 0% and 3% of surface and midwater tows, respectively. 
*Eucalanus bungii* was included in further analyses because it represented approximately 
3% of combined diets by volume (Table 1).
Changes in juvenile pollock diet composition reflect spatial and temporal variability in zooplankton species composition and availability. In 2005, the abundance of available prey was highest in the inner domain and decreased towards the outer domain and northern Bering Sea. The abundance of prey in 2010 was greater in the inner domain; in the southern region of the shelf, abundances decreased towards to the middle and outer domains (Figure 1, c and d). The lowest abundance of zooplankton occurred in areas corresponding to higher concentrations of juvenile pollock predators. The total abundance of zooplankton within the optimal prey size range for 65 mm SL juvenile pollock (species with mean length within 5-8% of fish length) was higher in the northwest region of the study area and over the southern shelf in the outer domain in 2005, with lesser overlap with juvenile pollock. In 2010, optimal prey was located across the middle and outer domains with highest abundances in the southern region, mirroring the distribution of juvenile pollock (Figure 1, c and d). Spatial patterns of zooplankton abundance accounting for all taxa <8% of fish length reflected total abundance patterns in both years, indicating that areas of highest zooplankton abundance are driven by small (<5% of fish length) zooplankton taxa.

In 2005, available prey energy was highest in the northwest region of the shelf, with low prey energy over most of the shelf south of 60 °N (Figure 1e) where juvenile pollock abundances were higher. In contrast, prey energy was very high across much of the southern shelf in 2010 (Figure 1f), particularly within the cold pool, where juvenile
pollock were more abundant. Spatial patterns in prey energy were similar to spatial
patterns of abundance for optimal prey size classes (Figure 1, c and d) because highest
energy prey taxa are within 5-8% of fish length.

4.5.2 Bioenergetics model
Differences in the spatial pattern of maximum growth potential \( (g \cdot g^{-1} \cdot d^{-1}) \) of juvenile
pollock occurred between a warm and cold year in the EBS (Figure 2, a and b). In 2005,
growth potential was highest in the northwest region of the shelf (north of 60 °N) and
lowest in the inner domain with one station having negative growth. Gradients in
growth potential, from low to high, occurred from the inner to outer domains and from
southern to northern regions of the shelf (Figure 2a). In 2010, growth was positive at all
stations with highest growth potential over the southern shelf and lower growth
predicted in the northeast region (Figure 2b).

Bioenergetics sensitivity analyses

Effect of water temperature and prey energy density
In 2005, increasing temperatures by 1 SD (Figure 2c) resulted in areas of decreased
predicted growth at shallow inner domain and southern shelf stations where water
temperatures already approached thermal thresholds. Growth could not be estimated
at one inner domain station because the increased temperature exceeded 15 °C, the
maximum temperature for consumption \( (T_{cm}) \) in the model. Decreasing water
temperatures, resulting in increased growth, had the greatest effect in the same areas
(not shown) because temperature-dependent control of growth is magnified where
temperatures are close to thermal thresholds. In 2010, the effect of increasing water
temperatures was an order of magnitude less than in 2005 (Table 3), but the spatial patterns were similar with shallow stations in the inner domain being most sensitive, as well as a small area in the outer domain (Figure 2d). Increasing available prey energy resulted in increased predicted growth rates across the region in 2005 (Figure 2e), with weaker effects in the inner domain and northwest region. In 2010, increased prey energy also resulted in elevated growth rates, but the magnitude of change was much lower than in 2005 and the spatial pattern differed; stronger effects occurred in the inner domain and southern region of the outer domain (Figure 2f).

Predicted maximum growth potential generally increases with temperature and prey energy until temperature-dependent controls limit growth (Figure 3). Predicted growth is negative when available prey energy cannot meet metabolic demands under increased temperatures. Water temperatures were warmer in 2005, therefore juvenile pollock experienced conditions at or near their metabolic threshold at some stations. Colder water temperatures and higher available prey energy in 2010 resulted in better growing conditions over the shelf.

**Effect of fish starting weight and fish energy density**

Increasing fish starting weight resulted in lower predicted growth rates in both years because larger fish have higher metabolic demands (Table 3). Increasing fish energy density had a variable effect across stations in 2005 (not shown). In general, the effect of varying fish energy is dependent on initial fish energy and the relative available prey energy at each station. In 2010, increasing fish energy density resulted in lower predicted growth rates across stations when available prey energy was held constant.
Variability in fish starting weight resulted in a broader distribution of predicted growth rates (2005: 0.002 – 0.109; 2010: 0.017 – 0.170 $g\cdot g^{-1}\cdot d^{-1}$) than variability in fish energy (2005: 0.007 – 0.013; 2010: 0.022 – 0.036 $g\cdot g^{-1}\cdot d^{-1}$) from Monte Carlo simulations, indicating that the model was more sensitive to inputs of fish weight. The simulated mean predicted growth rates, when varying fish starting weight or fish energy, were lower and less variable for 2005 (0.012 ± 0.009 [mean ± SD] for varying $W$; 0.010 ± 0.001 for varying fish energy) than for 2010 (0.029 ± 0.012 for varying $W$; 0.027 ± 0.002 for varying fish energy).

4.5.3 Mechanistic individual-based model

Predicted mean growth rates from the IBM were 30% (2005) and 46% (2010) lower than maximum growth potential from the bioenergetics model (Tables 3 and 4) as foraging rates are restricted in the IBM based on stomach fullness and the prey selection module (i.e., capture success). The reduction in growth was greater in 2010, resulting in similar predicted growth rates from the IBM in 2005 and 2010. In addition, predicted growth rates from the IBM have a narrower range than maximum growth potential from the bioenergetics model.

In 2005, growth was positive across the region with moderate growth predicted across the southern shelf. North of 60 °N, predicted growth rates decreased from the inner to outer domain (Figure 4a). The average depth (m) of juvenile pollock was 44 m (Table 4), with shallower distributions in the northeast region and deeper distributions in the southern region of the outer domain (Figure 4b). In 2010, growth was positive across the region, with highest predicted growth in the inner domain and areas of lower
growth in the middle domain (Figure 4c). The spatial patterns of average depth of juvenile pollock (Figure 4d) mirrored those of 2005 with a slightly deeper average depth of 47 m (Table 4).

IBM sensitivity analyses

The effect of smaller fish starting weights on predicted growth was positive across the region, with stronger effects in 2005 than 2010 (Table 4). Similarly, effect strengths varied spatially in both years with areas of higher predicted growth in the middle domain (Figure 4, e and g). In 2005, smaller starting fish weights resulted in shallower depth distributions across the region (mean=-2.6 m; Table 4), with much shallower depths at two stations in the middle domain (Figure 4f). The average change in depth distribution was similar in 2010 (mean=-2.4 m; Table 4), but spatially more variable than in 2005 (Figure 4h).

Applying uniform vertical distributions to prey taxa had variable effects on predicted growth rates in both years, with similarly small effect strengths (Table 4). Under uniform prey distributions, modeled fish may move vertically in response to other cues (i.e., predation risk, thermal boundaries) regardless of diel patterns. In 2005, uniform distributions resulted in increased predicted growth rates at several stations in the northern-most region of the shelf (Figure 4i). While the average depth of juvenile pollock was 2.1 m deeper across the region, fish at some of the northern-most stations had shallower depths (Figure 4j). In 2010, strongest effects on growth were observed in the middle domain of the southern shelf, with high spatial variability (Figure 4k).

Changes in the depth of fish in response to uniform prey distributions mirrored spatial
patterns in growth effects; stations showing deeper mean depths also resulted in a decrease in growth and vice versa (Figure 4l).

4.5.4 Spatial comparison of bioenergetics- and IBM-predicted growth

Predicted growth rates from the IBM were within the range of maximum growth potential from the bioenergetics model, but spatial patterns varied due to differences in input parameters of each model. In both years, the bioenergetics model predicted higher growth rates than the IBM over the middle and outer domains. The greatest difference occurred in the northwest region of the shelf in 2005 (Figure 5a) and over the southern region of the middle domain in 2010 (Figure 5b). The IBM predicted higher growth in the shallow, well-mixed inner domain in both years.

4.6 Discussion

This study demonstrates that warm and cold conditions in the EBS lead to spatial differences in zooplankton species composition, energy content, and abundance, which subsequently affect the feeding ecology and growth of juvenile pollock. Particularly, prey distribution and quality in combination with water temperatures create spatial patterns of increased growth potential (‘hot spots’) that vary with climate conditions. Spatial heterogeneity in growth conditions results from a combination of prey quality and quantity, water temperature, and metabolic costs, which may contribute to size-dependent fish survival and subsequent annual variability in recruitment. We provide evidence that a spatial mismatch between juvenile pollock and growth ‘hot spots’ in 2005 is the mechanism that contributed to poor recruitment to age-1 while a higher degree of overlap in 2010 resulted in 42% greater [33] recruitment to age-1.
In the EBS, changes in oceanographic conditions can impact larval and juvenile fish distributions through front formation [34] and subsequent changes in drift trajectories [35]. The resultant variability in fish distributions relative to their prey during late summer and fall may be particularly important because the time period after the completion of larval development and before the onset of winter has been identified as a critical period for energy storage in juvenile pollock [22]. As the spatial distribution of fish, including spawning locations of adult walleye pollock, and zooplankton vary under alternate climate conditions, so do patterns in juvenile fish growth and recruitment success (Figure 6). Here, we find support for the argument that warm years produce smaller, less energy-rich prey and that this reduced prey quality, in combination with higher metabolic demands, results in lower growth of juvenile pollock. Conversely, cold years produce larger, more energy-rich prey which, when combined with lower metabolic demands, are favorable for juvenile pollock growth and survival. Thus, mechanisms responsible for controlling growing conditions during the critical pre-winter period can be linked to variability in recruitment.

Projected declines in walleye pollock recruitment under changing climate conditions [11] do not account for adaptive behaviors or changes to phenology that could enable fish to maintain higher growth rates. The sensitivity analyses helped to identify when and where favorable growth conditions may occur under alternate climate conditions. In the bioenergetics model, varying fish size had a stronger effect on growth potential than changes in initial fish energy density. Larger fish have greater capacity for growth due to increased gape size, which allows them to take advantage of
larger, more energy rich prey resources (e.g., euphausiids) prior to winter. The sensitivity analysis of increasing water temperatures showed weaker effects in the cold year of 2010 because fish had a broader range of temperatures over which growth potential was relatively high (Figure 3), including warmer surface waters and a colder refuge in deeper waters that allows fish to conserve energy and avoid predation. In 2005, fish were near thermal limits based on temperature-dependent functions in the bioenergetics model; hence further increases in temperature are predicted to result in negative growth. Increasing available prey energy also had a stronger effect in the warm year of 2005 because metabolic demands were greater and mean prey energy density was lower than in 2010.

The relative foraging rate was held constant at $\eta=1$ across all bioenergetics model scenarios, but lower values would better reflect realistic foraging rates and could exacerbate thermal constraints on growth. To maintain positive growth rates at half of all the stations required relative foraging rates of $\eta=0.71$ in 2005 and $\eta=0.57$ in 2010. These values correspond to a 29% and 43% reduction in achieved growth relative to maximum growth potential and are similar to the mean differences between growth rates in the bioenergetics and IBM models (i.e., 30% in 2005 and 46% in 2010), providing support of model agreement. A higher relative foraging rate was required in 2005 in order to achieve positive growth at half of all stations, similar to results based on larger juvenile and adult walleye pollock [25], indicating that juvenile pollock growth was more prey limited and constrained by temperature in 2005 than in 2010. Thus, a greater reduction in both achieved growth from the IBM relative to maximum growth potential
and relative foraging rates was observed in 2010 compared to 2005. In 2010,
zooplankton abundance was lowest in areas with higher concentrations of juvenile
pollock predators, potentially indicating prey limitation. While our study was not
designed to explicitly test this question, other research demonstrates that pollock do
not have strong top-down control of euphausiid abundance in the eastern Bering Sea (P.
Ressler, pers. commun.).

The vertical behavior of modeled juvenile pollock in the IBM moderated
predicted growth rates leading to differences across domains based on stratification.
Smaller (i.e., younger) fish were predicted to move shallower in the water column to
improve prey detection, which is dependent on eye development and light availability.
Moving into the surface layer also exposed juvenile pollock to higher predation risk
because of the stronger light intensity. In the middle and outer domains, once sufficient
growth was attained, fish were predicted to move deeper to seek refuge from
predation. While the models were run at all stations in both years, observed juvenile
pollock abundances were concentrated over the middle and outer domains in 2005 and
over small regions of the southern shelf and outer domain in 2010. Few fish were
observed in the well-mixed inner domain, possibly due to reduced growth potential
based on available prey energy or lack of stratification and predation refuge in deeper
waters. Additionally, the inner front, which delineates the stratified middle domain from
the well-mixed inner domain [34], may act as a barrier to juvenile pollock distribution
[36].
Spatial patterns in juvenile pollock growth differed between models; these differences elucidate underlying mechanisms in feeding potential and ultimately the possible causes for growth ‘hot spots’ and variability in recruitment success between warm and cold climate conditions. The bioenergetics model uses biomass-weighted mean energy density of available prey, assuming fish feed proportional to what is available in the environment. The IBM is length-based and growth is dependent on available prey resources, light conditions, metabolism, development of the fish, and fish behavior. In the middle and outer domains where the water column is stratified, the bioenergetics model predicted higher growth than the IBM; the bioenergetics model allowed fish to feed at maximum consumption while the IBM indicated that fish moved deeper in the water column to conserve energy or avoid predation. In the inner domain, the IBM predicted higher growth; here juvenile pollock may opt to take advantage of available prey and warmer water temperatures to maximize growth because predator avoidance in deeper waters was not an option.

Comparing the bioenergetics model and the IBM provided insights that could not be gained by either approach alone. For example, the bioenergetics model highlights the importance of differences in prey energy, a metric not included in the IBM, in determining spatial patterns of growth. On the other hand, the mechanistic feeding behavior implemented in the IBM highlights the role of prey size composition, the vertical distribution of prey, and the tradeoff between predator avoidance and maximizing growth. In practice, data requirements may limit the applicability of the IBM, whereas the bioenergetics model can be applied when less information on prey
resources is available. Future research could benefit from including information on prey energy into IBMs to disentangle not only the importance of prey species and size composition, spatial distribution and abundance, but also prey quality.

Warm temperature conditions are predicted to result in reduced prey quality and low energy density of juvenile pollock in late summer [9,13]. Warmer water temperatures are associated with decreased growth [this study], resulting in lower overwinter survival and recruitment to age-1 [33]. The warm years of 2002-2005 had 67% lower average recruitment to age-1 relative to the cold years of 2008-2010, although variability during the cold years was very high with strong year classes in 2008 and 2010 separated by a weak 2009 cohort [33]. These findings agree with projected declines in recruitment of age-1 walleye pollock [11] under increased summer sea surface temperatures of 2°C predicted by 2050 [37]. Our results corroborate these previous studies and suggest that climate-driven increases in water temperature will have the largest effect on recruitment during anomalously warm years. This study provides evidence that climate-driven changes in prey dynamics can have ecosystem-level consequences via bottom-up control of fish populations in sub-arctic marine ecosystems. This work has improved our understanding of the mechanisms behind recruitment variability, in particular the underlying spatial patterns that drive relationships between prey availability, water temperature, growth, and survival. Our findings inform ongoing discussions of climate effects on predator-prey interactions and recruitment success of marine fishes.

4.7 Acknowledgements
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collection and database management as well as the officers and crew of the R/V *Oscar
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Anadromous Fish Commission. MOCNESS data were provided from the PROBES (2004)
and BEST-BSIERP (2009) surveys. This is NPRB publication #444 and BEST-BSIERP Bering
Sea Project publication #111. T.K. was supported by the Norwegian Research Council
project SWIM #13375.

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4.9 Figure legends

Figure 1. Log(CPUE) of juvenile walleye pollock collected in surface trawls in 2005 (a) and 2010 (b). Circle size is proportional to catch (#•m⁻²) at each station; note difference in scale between years. Stations with zero catch (×) are shown on white background. Log of total zooplankton abundance (#•m⁻³) for the main prey taxa is shown for 2005 (c) and 2010 (d). Circle size is proportional to the abundance of zooplankton within the optimal
size range for 65 mm SL juvenile pollock (5-8% of fish length); note difference in scale
between years. Biomass-weighted mean energy density (ED) of available zooplankton
prey is shown for 2005 (e) and 2010 (f).

Figure 2. Predicted growth ($g \cdot (g^{-1} \cdot d^{-1})$) of juvenile walleye pollock from the bioenergetics
model. Top panel (a and b) shows growth under the base model scenarios for 2005 and
2010 ($W=2.5 \ g$, Temp=average temperature in upper 30 m, $\bar{\omega}=1.0$, $\omega_k=$prey energy
density, $\bar{\nu}_{2005}=3.92 \ kJ \cdot g^{-1}$; $\bar{\nu}_{2010}=5.29 \ kJ \cdot g^{-1}$). Middle panel (c and d) shows changes in
predicted growth when temperature is increased by 1 standard deviation (SD).

Predicted growth could not be estimated at one station in 2005 (c) in the inner domain
under increased temperatures because the water temperature in the upper 30 m was
greater than 15 °C ($T_{cm}=15 \ °C$ in the model). Lower panel (e and f) shows changes in
predicted growth when prey energy density is increased by 1 SD. Spatial plots of
predicted growth when parameters are decreased by 1 SD are not shown, but can be
visualized by subtracting the anomalies (lower two panels) from the base scenario plots
(top panel).

Figure 3. Predicted growth ($g \cdot (g^{-1} \cdot d^{-1})$) of juvenile walleye pollock interpolated over the
range of observed temperatures and prey energy density values across both 2005 and
2010, providing a continuous scale of growth over a broad range of possible
environmental and biological scenarios. The observed fish energy density was higher in
2010 ($\nu_{2010}=5.29 \ kJ \cdot g^{-1}$; used in plot shown); therefore this interpolation demonstrates
the range of predicted growth for fish with high energy density. Temperatures included
0-16 °C to show possible range under variable climate conditions. The dashed rectangle
encompasses the range of temperatures and prey energy density values observed in
2005; solid rectangle encompasses values in 2010. Points are shown for average
temperature and prey energy density conditions in 2005 and 2010. Predicted growth
above 15 °C was not possible (black) because the bioenergetics model has a
temperature threshold of 15 °C.

Figure 4. Predicted growth (\(g \times g^{-1} \times d^{-1}\)) and average depth (m) of juvenile walleye pollock
from the IBM. Top panel shows growth (a and c) and average depth (b and d) under the
base model scenarios for 2005 and 2010 (\(W=2.5 \text{ g, zooplankton prey distributed}
\)) according to vertical profiles). Middle panel shows changes in predicted growth (e and
g) and average depth (f and h) for 2.0 g fish, highlighting the relative importance of fish
size (relative to 2.5 g) and water temperature between years. Lower panel shows
changes in predicted growth (i and k) and average depth (j and l) when uniform vertical
distributions of prey are implemented, highlighting the effect of zooplankton diel
vertical distribution and migrations on juvenile walleye pollock prey selection. Negative
changes in depth indicate a shallower distribution; positive values indicate a deeper
distribution.

Figure 5. Difference in predicted growth (\(g \times g^{-1} \times d^{-1}\)) of juvenile walleye pollock between
the bioenergetics model and the IBM for 2005 (a) and 2010 (b). Areas of positive
differences indicate where maximum growth potential from the bioenergetics model was higher than predicted growth from the IBM.

Figure 6. Conceptual figure of the spatial relationship between juvenile fish abundance (yellow) and zooplankton prey availability (blue). Where these areas overlap (green), juvenile fish are predicted to have higher growth rates and increased survival. Under warm climate conditions, there is reduced spatial overlap between juvenile fish and prey availability, resulting in lower overwinter survival and recruitment success to age-1. In colder conditions, increased spatial overlap between juvenile fish and prey availability results in increased overwinter survival and recruitment to age-1.

Figure S1. Eastern Bering Sea with locations of sampling stations at which the bioenergetics model and IBM were run in 2005 (•) and 2010 (□). The Monte Carlo Station (▲) is the representative station used for Monte Carlo simulations. Depth contours are shown for the 50 m, 100 m, and 200 m isobaths.

Figure S2. Water temperatures interpolated across all stations (•) sampled by the CTD. Top panel shows the mean temperature in the upper 30 m of the water column in 2005 (a) and 2010 (b). Bottom panel shows the mean temperature below 40 m in 2005 (c) and 2010 (d).
Table 1. Main prey taxa included in the models for 2005 and 2010. Prey items cumulatively accounting for at least 90% of the diet by % volume and individually accounting for at least 2% of the diet by % volume were included. Prey taxa common to both years are shown in **bold**.

<table>
<thead>
<tr>
<th>2005</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Taxa</strong></td>
<td><strong>Taxa</strong></td>
</tr>
<tr>
<td><strong>Individ % Vol</strong></td>
<td><strong>Cum % Vol</strong></td>
</tr>
<tr>
<td><em>Limacina helicina</em></td>
<td>26.33</td>
</tr>
<tr>
<td><em>Pseudocalanus sp.</em></td>
<td>26.04</td>
</tr>
<tr>
<td><em>Oikopleura sp.</em></td>
<td>11.86</td>
</tr>
<tr>
<td><em>Centropages abdominalis</em></td>
<td>8.98</td>
</tr>
<tr>
<td><em>Thysanoessa raschii</em></td>
<td>8.48</td>
</tr>
<tr>
<td><em>Thysanoessa sp.</em></td>
<td>4.63</td>
</tr>
<tr>
<td><em>Acartia clausi</em></td>
<td>3.40</td>
</tr>
<tr>
<td><em>Calanus marshallae</em></td>
<td>1.71</td>
</tr>
</tbody>
</table>

*Neocalanus plumchrus* was not identified in the 2010 bongo data, but did occur in the Juday data (small-mesh; not quantitative for large zooplankton taxa). Due to the absence in the bongo data, *N. plumchrus* was excluded from further analyses.
Table 2. Parameter definitions and values used in the bioenergetics model to estimate maximum growth potential ($g \cdot g^{-1} \cdot d^{-1}$) of juvenile walleye pollock. Parameters were used as inputs to the bioenergetics model described in [16].

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition (units)</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C$</td>
<td>Consumption ($g \cdot g^{-1} \cdot d^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\eta$</td>
<td>Relative foraging rate</td>
<td>0-1</td>
<td>$^{a}$</td>
</tr>
<tr>
<td>$O_2 \text{ cal}$</td>
<td>Activity multiplier; convert g O$_2$ $\rightarrow$ g prey</td>
<td>13560</td>
<td>$^{a}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Intercept of the allometric function for $C$</td>
<td>0.119</td>
<td>$^{a}$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Slope of the allometric function for $C$</td>
<td>-0.46</td>
<td>$^{a}$</td>
</tr>
<tr>
<td>$Q_c$</td>
<td>Temperature dependent coefficient</td>
<td>2.6</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$T_{co}$</td>
<td>Optimum temperature for consumption</td>
<td>10</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$T_{cm}$</td>
<td>Maximum temperature for consumption</td>
<td>15</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$R$</td>
<td>Respiration ($g \cdot O_2 \cdot g^{-1} \cdot \text{day}^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_r$</td>
<td>Intercept of the allometric function for $R$</td>
<td>0.0075</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$B_r$</td>
<td>Slope of the allometric function for $R$</td>
<td>-0.251</td>
<td>$^{b}$</td>
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<tr>
<td>$Q_r$</td>
<td>Temperature dependent coefficient</td>
<td>2.6</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$T_{ro}$</td>
<td>Optimum temperature for respiration</td>
<td>13</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$T_{rm}$</td>
<td>Maximum temperature for respiration</td>
<td>18</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$D_s$</td>
<td>Proportion of assimilated energy lost to Specific Dynamic Action</td>
<td>0.125</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$A_m$</td>
<td>Multiplier for active metabolism</td>
<td>2</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$F$</td>
<td>Egestion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_a$</td>
<td>Proportion of consumed energy</td>
<td>0.15</td>
<td>$^{b}$</td>
</tr>
<tr>
<td>$U$</td>
<td>Excretion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$U_a$</td>
<td>Proportion of assimilated energy</td>
<td>0.11</td>
<td>$^{b}$</td>
</tr>
</tbody>
</table>

$^{a}$ [25]; $^{b}$ [16]
Table 3. Summary of sensitivity analyses for the bioenergetics model in 2005 and 2010 showing the minimum (min), mean, and maximum (max) growth potential over all stations. Base values are predicted maximum growth potential ($g \cdot g^{-1} \cdot d^{-1}$) of juvenile pollock from the base model scenarios ($W = 2.5$ g, Temp=average temperature in upper 30 m, $h = 1.0$, $k = $prey energy density, $v_{2005} = 3.92$ kJ•g$^{-1}$; $v_{2010} = 5.29$ kJ•g$^{-1}$). All other values denote the change in growth rate resulting from indicated changes in inputs; therefore (-) effects indicate that varied conditions resulted in lower predicted growth and vice versa. Pooled standard deviations (SDs) for each parameter were calculated across stations after removing the annual means. $W$ and $v_t$ are constant values applied across all station, so changes (± 1 SD) act as a scalar and result in similar spatial patterns across the area. Temperature and $\omega_k$ vary across stations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>SD</th>
<th>2005 min</th>
<th>2005 mean</th>
<th>2005 max</th>
<th>2010 min</th>
<th>2010 mean</th>
<th>2010 max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base</td>
<td>-0.0056</td>
<td>0.0146</td>
<td>0.0291</td>
<td>0.0069</td>
<td>0.0172</td>
<td>0.0272</td>
<td></td>
</tr>
<tr>
<td>$W + 1$ SD</td>
<td>0.935</td>
<td>-0.0056</td>
<td>-0.0041</td>
<td>-0.0017</td>
<td>-0.0052</td>
<td>-0.0037</td>
<td>-0.0023</td>
</tr>
<tr>
<td>$W - 1$ SD</td>
<td>0.935</td>
<td>0.0034</td>
<td>0.0076</td>
<td>0.0103</td>
<td>0.0041</td>
<td>0.0068</td>
<td>0.0094</td>
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<tr>
<td>Temp + 1 SD</td>
<td>1.75</td>
<td>-0.0227</td>
<td>-0.0053</td>
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<td>-0.0071</td>
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<td>Temp - 1 SD</td>
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<td>-0.0026</td>
<td>0.0008</td>
<td>0.003</td>
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<tr>
<td>$\omega_k + 1$ SD</td>
<td>497.5</td>
<td>0.0046</td>
<td>0.0061</td>
<td>0.0065</td>
<td>0.0032</td>
<td>0.0044</td>
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<td>$\omega_k - 1 \text{ SD}$</td>
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<td>-0.0065</td>
<td>-0.0061</td>
<td>-0.0046</td>
<td>-0.0048</td>
<td>-0.0044</td>
<td>-0.0032</td>
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<tr>
<td>---------------------------</td>
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</tr>
<tr>
<td>$w_i + 1 \text{ SD}$</td>
<td>395.93</td>
<td>-0.0027</td>
<td>-0.0013</td>
<td>0.0005</td>
<td>-0.0019</td>
<td>-0.0012</td>
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<tr>
<td>$w_i - 1 \text{ SD}$</td>
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<td>0.0016</td>
<td>0.0033</td>
<td>0.0006</td>
<td>0.0014</td>
<td>0.0022</td>
</tr>
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</table>

1

2
Table 4. Summary of sensitivity analyses for the IBM model in 2005 and 2010 showing the minimum (min), mean, and maximum (max) growth potential and depth (m) over all stations. Base values are predicted growth ($g \cdot g^{-1} \cdot d^{-1}$) and depth (m) of juvenile pollock from the base model scenarios ($W=2.5$ g, zooplankton prey distributed according to vertical profiles). All other values are predicted changes in growth and depth. Negative changes in depth indicate a shallower distribution; positive values indicate a deeper distribution. Weight is a constant value applied across all station, so varying the parameter acts as a scalar and results in similar spatial patterns across the area. The effect of applying a uniform distribution of zooplankton prey with depth varies across stations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2005</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>min</td>
<td>mean</td>
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<td>-2.6</td>
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<td>Prey distribution (Uniform)</td>
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<tr>
<td>Growth</td>
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</tr>
</tbody>
</table>
Figure 1

2005

2010

Latitude (°N)

Longitude (°W)

Parameters:
- **CPUE (#/m²)**
  - 0.17
  - 0.49
  - 0.66

- **Log CPUE**
  - Values from -12 to -2

- **Log Zooplankton Abund**
  - Values from 3 to 9

- **Mean Prey ED**
  - Values from 3.5 to 5.5

MAP A

MAP B

MAP C

MAP D

MAP E

MAP F
Figure 2.
Figure 3.

![Graph showing energy density and growth rate as functions of temperature and prey density. The graph contains data points for 2005 and 2010.]
Figure 4

2005

Growth (g·g⁻¹·d⁻¹)

Depth (m)

2010

Growth (g·g⁻¹·d⁻¹)

Depth (m)
Figure 5.
Figure 6.

The diagram illustrates the distribution of fish and zooplankton prey under warm and cold conditions. The x-axis represents longitude (°W), while the y-axis represents latitude (°N). The map shows the regions where fish and zooplankton prey are likely to be found under different environmental conditions.
4.10 Supporting Information:

4.10.1 Comparison of observed and predicted prey preferences

4.10.1.1 Methods

Stomach contents of juvenile pollock (<100 mm SL) were identified from selected stations across the eastern Bering Sea shelf to compare observed diet composition, model-predicted diets, and available prey. Chesson’s prey preference index [1] was calculated for the main prey taxa in each year and compared to the individual-based model (IBM) estimates of prey preference at corresponding stations. Chesson’s index ($\alpha_i$) for a given prey taxon $i$ is the ratio between ingested prey items ($r_i$) and the frequency of their occurrence in the environment ($n_i$), standardized by the sum of the ratios over all $m$ prey types:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum_{j=1}^{m} \frac{n_j}{r_j}}$$

Eq. 1

The standardization implies that neutral selection ($\alpha_{neu}$) corresponds to $1/m$ and a specific prey item or group was actively selected if the index is $\alpha > \alpha_{neu}$, as they appear more frequently in the diet than their abundance in the environment would suggest. To calculate Chesson’s index for observed diets, % volume in the diet was used as a proxy for biomass consumed ($r_i$) relative to prey biomass in the environment ($n_i$).

Chesson’s prey preference indices for main prey taxa in each year, based on observed and predicted diets, were compared at each station for which observed diet, predicted diet, and zooplankton composition was available and where at least 90% of
the observed prey taxa (by % volume) were accounted for in the zooplankton data (n=7 in 2005; n=9 in 2010). Zooplankton samples that did not include a known prey item were not considered for this analysis because the lack of a known prey item in zooplankton samples collected at the same station suggests that the sample is not representative of prey availability due to small-scale patchiness, or indicates a spatial and/or temporal mismatch between where captured juvenile pollock were foraging and where samples were collected. To compare observed ($\alpha_{\text{obs}}$) and predicted ($\alpha_{\text{pre}}$) prey preferences, we computed differences between these prey preferences relative to neutral selection:

$$\frac{\alpha_{\text{obs}}}{\alpha_{\text{neu}}} - \frac{\alpha_{\text{pre}}}{\alpha_{\text{neu}}}$$  \hspace{1cm} \text{Eq. 2}

and averaged them across all stations within each year, as well as by domain (i.e., inner: 0-50 m isobath, middle: 50-100 m isobath, and outer: 100-200 m isobath).

4.10.1.2 Results and Discussion

Modeled diets from the IBM were comparable to observed diets from the 2005 and 2010 surveys (Fig. S1; most differences overlap zero), indicating that the model may adequately capture predator-prey dynamics. Relatively small differences between observed and predicted prey preference were consistent across domains in both years. Limacina helicina, the predominant component of diets across years, was more prevalent in observed diets (except in the inner domain south of 60°N in 2005), as was Thysanoessa raschii. Modeled diets, however, consistently overestimated consumption of Calanus marshallae and Eucalanus bungii (2010 only) across domains.
Shifts in *C. marshallae* abundance between warm and cold years in the EBS have been proposed as a major contributor to differences in juvenile pollock condition and survival [2]. However, observed diets of juvenile pollock (<100 mm SL) in 2005 and 2010 do not reflect its relative importance to growth because *C. marshallae* was less prevalent than expected. Greater prevalence of specific prey items in observed diets (e.g., *Centropages abdominalis* in 2005) indicates that the IBM model underestimates the ability of juvenile pollock to detect, capture, and ingest that prey item. Alternatively, the prey could have been more abundant in the areas where juvenile pollock were feeding than in the area sampled by the bongo and/or Juday net due to patchiness. Differences between observed and predicted diets may also be explained by prey escape behaviors or size-selectivity by juvenile pollock that is more complex than the prey selection component of the IBM [3]. Juvenile pollock collected in late-summer likely feed more heavily in surface waters during crepuscular or nighttime periods [4], moving deeper during the daytime, while observed diets for this study were sampled from daytime surface hauls. However, the spatial and temporal disconnect between where juvenile pollock feed and were collected for diet analyses likely did not affect our results as previous work has shown that proportional diet compositions do not vary between day and night [4,5] and the IBM integrates predicted diets over 24 hours, encompassing diel vertical patterns.

4.10.2 References


Table S1. Stage, sampling gear, length range, width, biomass (g, wet weight), and energy density (kJ•g\(^{-1}\), wet weight) values for the main prey items of juvenile walleye pollock in late summer 2005 and 2010. Biomass estimates were obtained during processing of the zooplankton samples from 2005 (warm) and 2010 (cold) (NA=stage was not collected); energy density values were obtained from zooplankton collected in the eastern Bering Sea during 2004 (warm) and 2010 (cold). Single estimates of energy density (shown in bold) were used when year-specific information was not available for individual taxa.

<table>
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<th>Species</th>
<th>Stage</th>
<th>Gear</th>
<th>Length range (mm TL)</th>
<th>Width (mm)</th>
<th>Warm Biomass (g WW)</th>
<th>Cold Biomass (g WW)</th>
<th>Warm Energy Density (kJ•g(^{-1}) WW)</th>
<th>Cold Energy Density (kJ•g(^{-1}) WW)</th>
<th>Comments</th>
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<td>0.22(^b)</td>
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<td>3.5 E-05</td>
<td>3.816(^c)</td>
<td>3.816(^c)</td>
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<td>Juday</td>
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<td>0.29(^b)</td>
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<td>0.16(^b)</td>
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<td>7</td>
<td>0.0026</td>
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<td>0.0137</td>
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<td>III</td>
<td>Bongo</td>
<td>3.2</td>
<td>0.85</td>
<td>8.83 E-4</td>
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<td>IV</td>
<td>Bongo</td>
<td>4.9 – 5.3</td>
<td>1.36</td>
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<td>0.0025</td>
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<td>V</td>
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<td>N. plumchrus</td>
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<td>Oikopleura sp.</td>
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<td>Bongo</td>
<td>0.1 – 0.6</td>
<td>0.35</td>
<td>1.73 E-4</td>
<td>1.7 E-4</td>
<td>4.076</td>
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<td>Pseudocalanus</td>
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<td>Juday</td>
<td>0.65 – 1.2</td>
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<td>4.44 E-05</td>
<td>3.6 E-05</td>
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<td>Length range for P. moultoni</td>
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<td>AF</td>
<td>Juday</td>
<td>1.05 – 2.27</td>
<td>0.42</td>
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<td>8.01 E-05</td>
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<td>4.13 E-5</td>
<td>5.42 E-5</td>
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<tr>
<td>I</td>
<td>Juday</td>
<td>0.5 – 0.7 s</td>
<td>0.16 b</td>
<td>NA</td>
<td>5.98 E-06</td>
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<tr>
<td>II</td>
<td>Juday</td>
<td>0.65 – 0.8 s</td>
<td>0.19 b</td>
<td>1.01 E-05</td>
<td>1.08 E-05</td>
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<tr>
<td>III</td>
<td>Juday</td>
<td>0.8 – 1 s</td>
<td>0.24 b</td>
<td>1.26 E-05</td>
<td>2.0 E-05</td>
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</tr>
<tr>
<td>I-III</td>
<td>Juday</td>
<td>0.5 – 1 s</td>
<td>0.2 b</td>
<td>NA</td>
<td>1.01 E-05</td>
<td></td>
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<td>IV</td>
<td>Juday</td>
<td>1 – 1.2 s</td>
<td>0.3 d</td>
<td>3.06 E-05</td>
<td>3.19 E-05</td>
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<td>V</td>
<td>Juday</td>
<td>1.2 – 1.5 s</td>
<td>0.37 d</td>
<td>8.89 E-05</td>
<td>4.93 E-05</td>
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<td>II-V</td>
<td>Juday</td>
<td>0.65 – 1.5 s</td>
<td>0.29 d</td>
<td>3.55 E-05</td>
<td>2.8 E-05</td>
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<tr>
<td><strong>Thysanoessa</strong></td>
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<tr>
<td><strong>inermis</strong></td>
<td>A</td>
<td>Bongo</td>
<td>10.1 – 29.2</td>
<td>2.4</td>
<td>2.4 d</td>
<td>NA</td>
<td>0.083</td>
<td><strong>4.99</strong>m</td>
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<td>AF</td>
<td>Bongo</td>
<td>10.1 – 29.2</td>
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<td>2.4</td>
<td>2.4 d</td>
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<tr>
<td>AM</td>
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<td>2.4</td>
<td>2.4 d</td>
<td>0.069</td>
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<td>J</td>
<td>Bongo</td>
<td>8.5 – 13.8</td>
<td>1.4</td>
<td>1.4</td>
<td>1.4 d</td>
<td>NA</td>
<td>0.011</td>
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<tr>
<td>J (L)</td>
<td>Bongo</td>
<td>11.1 – 13.8</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5 d</td>
<td>0.061</td>
<td>0.11</td>
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<td>J (S)</td>
<td>Bongo</td>
<td>8.5 – 11.1</td>
<td>1.2</td>
<td>1.2</td>
<td>1.2 d</td>
<td>0.011</td>
<td>0.024</td>
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<td><strong>T. inspinata</strong></td>
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<tr>
<td>J</td>
<td>Bongo</td>
<td>12 – 17</td>
<td>2.2</td>
<td>2.2</td>
<td>2.2 w</td>
<td>0.0012</td>
<td>0.0128</td>
<td><strong>4.99</strong>r</td>
<td><strong>4.99</strong>r</td>
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<td><strong>T. raschii</strong></td>
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<tr>
<td>A</td>
<td>Bongo</td>
<td>7 – 29.1</td>
<td>3.3</td>
<td>3.3</td>
<td>3.3 g</td>
<td>0.006</td>
<td>NA</td>
<td><strong>4.30</strong>g</td>
<td><strong>5.23</strong>g</td>
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<tr>
<td>AF</td>
<td>Bongo</td>
<td>7 – 29.1</td>
<td>3.3</td>
<td>3.3</td>
<td>3.3 g</td>
<td>0.077</td>
<td>0.0903</td>
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<tr>
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<td>15.3 – 20.2</td>
<td>2.7</td>
<td>2.7</td>
<td>2.7 d</td>
<td>0.046</td>
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<td>J</td>
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<td>7.4 – 8.4</td>
<td>1.45</td>
<td>1.45</td>
<td>1.45 d</td>
<td>0.005</td>
<td>0.0117</td>
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<tr>
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<td>Bongo</td>
<td>7.9 – 8.4</td>
<td>1.5</td>
<td>1.5</td>
<td>1.5 d</td>
<td>0.0476</td>
<td>0.0936</td>
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<tr>
<td>J (S)</td>
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<td>$7.4 - 7.9^2 \cdot 1.4^d$</td>
<td>$0.0089$</td>
<td>$0.0059$</td>
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Estimated width = 26.7% of length (based on *Pseudocalanus* sp. relationship); Energy density estimated from % lipid (2.25% wet weight assuming 80% moisture [2]) using the regression relationship: \( ED = (0.4098 \times \% \text{ lipid}) + 19.287 \); E. Fergusson, NOAA/AFSC, unpublished data; Estimated width = 26.6% of length (based on *C. marshallae* relationship); Energy density estimated from % lipid (10.5%; R. Heintz, NOAA/AFSC, unpublished data); E. Fergusson, NOAA/AFSC, unpublished data; Energy density estimated from % lipid (2.6% wet weight [4]); Energy density estimated from % lipid (3.55%; R. Heintz, NOAA/AFSC, unpublished data); Energy density estimated as 7.1% higher in cold years (based on copepod data; [this study]); C. Stark, UAF, unpublished data; Energy density estimated from % lipid (5.85%; R. Heintz, NOAA/AFSC, unpublished data); Energy density estimated from % lipid (6.83%; R. Heintz, NOAA/AFSC, unpublished data); Trunk length/width [5]; Energy density estimated from % lipid of Chaetognatha (2.67%; R. Heintz, NOAA/AFSC, unpublished data); Energy density estimated from % lipid of Chaetognatha (2.04%; R. Heintz, NOAA/AFSC, unpublished data); Energy density estimated from % lipid (4% wet weight [7]); Carapace width from [8]; converted to TL using equations from [9]; Length range of ‘spineless’ *T. longipes* [10]; Estimated width as 15% of length; Used energy density of *T. inermis*; Minimum size for *T. inermis* and maximum size for *T. spinifera* [8]; converted to TL using equations from [9]; Minimum size for *T. inermis* and maximum size for *T. spinifera* [11]; converted to TL using equations from [9]; Energy density estimated as 17.65% higher in cold years (R. Heintz, NOAA/AFSC, unpublished data).


Table S2. Component equations of the bioenergetics model used to estimate maximum growth potential ($g \cdot g^{-1} \cdot d^{-1}$) of juvenile walleye pollock.

<table>
<thead>
<tr>
<th>Component</th>
<th>Equation</th>
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<tbody>
<tr>
<td>Consumption</td>
<td>$C = a \times W \times f(T) \times h$</td>
</tr>
<tr>
<td></td>
<td>$f(T) = V^X \times e^{(X \times (1-V))}$</td>
</tr>
<tr>
<td></td>
<td>$V = (T_{cm} - T)/(T_{cm} - T_{co})$</td>
</tr>
<tr>
<td></td>
<td>$X = (Z^2 \times (1 + (1 + 40/Y)^{0.5})^2)/400$</td>
</tr>
<tr>
<td></td>
<td>$Z = \ln(Q_c) \times (T_{cm} - T_{co})$</td>
</tr>
<tr>
<td></td>
<td>$Y = \ln(Q_c) \times (T_{cm} - T_{co} + 2)$</td>
</tr>
<tr>
<td>Respiration</td>
<td>$R = (A_r \times W^{br} \times f(T) \times A_m \times 13560) + (D_s \times (C - F))$</td>
</tr>
<tr>
<td></td>
<td>$f(T) = V^X \times e^{(X \times (1-V))}$</td>
</tr>
<tr>
<td></td>
<td>$V = (T_{rm} - T)/(T_{rm} - T_{ro})$</td>
</tr>
<tr>
<td></td>
<td>$X = (Z^2 \times (1 + (1 + 40/Y)^{0.5})^2)/400$</td>
</tr>
<tr>
<td></td>
<td>$Z = \ln(Q_r) \times (T_{rm} - T_{ro})$</td>
</tr>
<tr>
<td></td>
<td>$Y = \ln(Q_r) \times (T_{rm} - T_{ro} + 2)$</td>
</tr>
<tr>
<td>Egestion</td>
<td>$F = F_a \times C$</td>
</tr>
<tr>
<td>Excretion</td>
<td>$U = U_a \cdot (C - F)$</td>
</tr>
</tbody>
</table>
Figure S2

2005

All Stations ($n=7$)

Southern BS Inner Domain ($n=3$)

Southern BS Outer Domain ($n=3$)

2010

All Stations ($n=9$)

Southern BS Middle Domain ($n=7$)

Southern BS Outer Domain ($n=2$)

LH PS OS CA TR TS AC CM
Figure S3

2005

2010

Temperature (°C)

Latitude (°N)

Longitude (°W)

Latitude (°N)

Longitude (°W)
Chapter 5 - Size, diet, and condition of age-0 Pacific cod (Gadus macrocephalus) during warm and cool climate states in the eastern Bering Sea

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5.1 Abstract
The revised Oscillating Control Hypothesis for the Bering Sea suggests that recruitment of groundfish is linked to climatic processes affecting seasonal sea ice that, in turn, drives the quality and quantity of prey available to young fish for growth and energy storage during their critical life history stages. We test this notion for age-0 (juvenile) Pacific cod (Gadus macrocephalus) by examining the variability in size, diet, and energetic condition during warm (2003 to 2005), average (2006), and cool (2007 to 2011) climate states in the eastern Bering
Sea. Juvenile cod stomachs contained high proportions of age-0 walleye pollock (by wet weight) during years with warm sea temperatures with a shift to euphausiids and large copepods during years with cool sea temperatures. Juvenile cod were largest during years with warm sea temperatures and smallest during years with colder sea temperatures. However, energetic status (condition) of juvenile cod was highest during years with cool sea temperatures. This result is likely linked to the shift to high quality, lipid rich prey found in greater abundance on the shelf and in the stomach contents of juvenile cod during cool years. Our examination of juvenile cod size, diet, and energetic status provided results that are coincident with juvenile pollock, suggesting that the common mechanisms regulating gadid recruitment on the eastern Bering Sea shelf are sea temperature, prey quality and quantity, and fitness of gadids prior to winter.
5.2 Introduction

The continental shelf of the eastern Bering Sea supports important fisheries for walleye pollock ($Gadus$ *chalcogrammus*), Pacific cod ($G. macrocephalus$), flatfish and crab. These populations have undergone large fluctuations due to both natural climate variability and potential anthropogenic forcing (climate warming). The potential for climate warming in the Bering Sea has heightened the need for data to better understand impacts of climate variability on ecologically and commercially important fish stocks. Probably the greatest effect of climate variability on the southeastern Bering Sea ecosystem will be the annual difference in the extent and duration of winter and spring sea ice (Stabeno et al., 2012). These characteristics are believed to affect the quality and quantity of prey resources that, in turn, impact growth, fitness, and survival of young fish (e.g. walleye pollock; Hunt et al., 2011).

Understanding how fish allocate energy for growth and lipid storage during critical life history stages is important for assessing climate impact on fish recruitment. For young fish, differential mortality occurs during two critical periods (first feeding and winter) that are related to energy allocation strategies in larval and juvenile fish (Post and Parkinson, 2001). For larval fish, somatic growth is important because smaller fish may be more susceptible to size-selective predation. For juvenile fish, large size and high energy reserves (lipid) are important because they can face severe energy deficits prior to, and during winter (Sogard and Olla, 2000; Heintz and Vollenweider, 2010; Farley et al., 2011). For instance, the energetic status of age-0 Bering Sea walleye pollock in late summer is increasingly recognized as a predictor of age-1 abundance the following summer (Heintz et al., 2013). Therefore, consumption of high quality prey should
improve the growth and nutritional condition in juvenile fish, reduce energy deficits over-
winter and lead to increased survival.

The oscillating control hypothesis (OCH) that links climate variability to Bering Sea groundfish
(e.g. walleye pollock) recruitment (Hunt et al., 2002) was revised (Hunt et al., 2011) based in
part on new findings regarding the importance of energetic status to fish survival (Heintz et al.,
2013). Originally, the OCH predicted warmer temperatures and early ice retreat on the eastern
Bering Sea shelf would lead to increased productivity in the pelagic ecosystem that would
improve the chances of successful recruitments for groundfish. However, recent data indicate
that changes in prey composition and abundance during periods of anomalously warm
temperatures and early ice retreat may have been detrimental to age-0 groundfish survival.
Specifically, larger zooplankton taxa, such as lipid-rich *Calanus* spp., were less abundant during
years with anomalously warm temperatures, when reduced lipid reserves in age-0 pollock at
the end of summer, led to increased over-winter mortality (Coyle et al., 2011). Thus, the OCH
was revised to state that, reduced overwinter mortality for age-0 pollock occurs during years
with anomalously cool temperatures because increased numbers of lipid-rich prey, combined
with lower metabolic demand, allows age-0 walleye pollock to acquire greater lipid reserves by
late summer (Hunt et al., 2011).

Pacific cod is a widespread marine species found on the continental shelves throughout the
North Pacific and Bering Sea. Pacific cod spawn demersal eggs with larvae rising to the surface
waters immediately after hatch (Doyle et al., 2009; Hurst et al., 2009). By July, age-0 cod are
known to settle to the bottom and inhabit the demersal, shallow waters of coastal Alaska
(Abookire et al., 2007; Laurel et al., 2007); however, in the Bering Sea, age-0 cod do not appear to be restricted to shallow nearshore habitats, but instead are commonly captured across the broad shelf in both demersal and pelagic trawl surveys (Hurst et al., 2012). Observational data for age-0 Pacific cod and walleye pollock during late summer suggest that their distributions overlap on the eastern Bering Sea shelf, but that pollock distribution tends to be more widespread and variable than Pacific cod (Hurst et al., 2012). While there may be some differences in distribution between age-0 walleye pollock and Pacific cod on the eastern Bering Sea shelf, their recruitment dynamics appear to be synchronous (Mueter et al., 2007), suggesting that the primary ecological drivers (e.g. OCH) of recruitment in these two species are similar in the Bering Sea.

In this paper, we describe patterns of interannual variation in size, diet, and energetic status of age-0 Pacific cod in the eastern Bering Sea based on 8 years of fishery-independent survey data. The period examined (2003 to 2011) was characterized by significant variation in thermal regime in the Bering Sea, allowing us to consider the potential effects of climate variability on the biological characteristics of cod that may impact their winter survival. These biological characteristics for cod are discussed in relation to age-0 walleye pollock and their potential for understanding recruitment processes in relation to climate variability.

5.3 Methods

5.3.1 Field sampling

The biological characteristics (size, diet, energy content) of age-0 Pacific cod (hereafter “juvenile cod”) in the eastern Bering Sea were described for 8 cohorts (2003 to 2011; 2009 was omitted due to lack of samples), based on catches from the Bering-Aleutian Salmon
International Survey (BASIS). Surveys were conducted from chartered fishing vessels (38-m FV “Sea Storm” or the 49-m FV “Northwest Explorer”) or the 64-m NOAA ship “Oscar Dyson”. The surveys were conducted during similar time periods (mid-August through late September), with sampling effort beginning in eastern Bristol Bay and moving northwest through the eastern Bering Sea (Fig. 1). Slight changes in the survey locations, sampling dates, and the number of stations sampled in a given year were due to weather conditions and other factors. A summary of annual sampling is provided in Table 1. Fish were collected with a 198-m long midwater rope trawl composed of hexagonal mesh wings and a body fitted with a 1.2-cm mesh codend liner (Farley et al., 2005). Buoys were attached to the headrope to fish near-surface depths (mouth opening of 55-m horizontal by 20-m vertical). The net was towed at speeds from 3.5 to 5.0 knots (approx 6.5 – 9.3 km per hour) for 30 min during daylight hours.

Several caveats on the use of surface trawl samples for understanding early marine ecology of juvenile cod were explained in Hurst et al. (2012). Briefly, while the survey was not designed to sample 0-group Pacific cod, they are a regular component of the catch. In addition, catch rates of juvenile cod are correlated with those of age-1 fish captured in the Bering Sea bottom trawl survey. There is also little known on when juvenile cod settle to a fully benthic distribution, but during late summer, the surface trawl is catching more juvenile cod than the bottom trawl surveys. Therefore, the assumption is that the catches in the surface trawl survey during late summer adequately represent basin-scale patterns in size, diet, and energy content of juvenile cod.
The contents of the trawl were emptied onto a sorting table on deck, and juvenile cod were sorted from other life stages and species of fish (see Hurst et al., 2012 for details). A subsample of up to 100 fish were individually measured (binned in 5 mm increments during 2003 to 2005 and to 1 mm fork length, during 2006 to 2011) to determine average length. The average weight at each station was determined by bulk weighing all measured fish or counting the number of fish in a pre-weighed subsample.

Similar to Hurst et al. (2012), we used a subset of core sampling sites that were sampled a minimum of four times between 2004 and 2011 to minimize the potential influence of interannual variation in spatial coverage of sampling effort on diet and caloric content. This resulted in the inclusion of 99 sampling sites in the core sampling area (Fig. 1; Hurst et al. (2012) found 92 core sampling stations within the same area). These core sampling sites were then divided into three domains: inner, middle, and outer based on geographic landmarks and depth contours associated with recognized hydrographic domains (Kinder and Schumacher, 1981; Overland et al., 1999). Data were also categorized into years with anomalously warm sea temperatures and low sea ice extent on the eastern Bering Sea shelf (2003 to 2005) and years with anomalously cool sea temperatures and extensive sea ice extent (2007 to 2011; Fig. 2). While spring sea temperatures were anomalously cold during 2006, sea ice extent and summer temperatures during that year appeared to represent transitional (defined as average) conditions between the two periods (Stabeno et al., 2012).

5.3.2 Size

Pacific cod size used in the analyses of size, diet, and energetic status was limited to fish less than or equal to 110 mm. In comparison, Hurst et al. (2012) included all fish <= 140 mm in the
analysis for distribution. Prey composition and energetic status are both a function of fish size, therefore we chose the lower size for this analysis to reduce the chance of biasing our analyses on energetic status and diet with fish that could be from an older year class. Analysis of variance (ANOVA, fixed effect) tests were used to examine interannual differences in length of juvenile cod. In this analysis, all juvenile cod less than 110 mm captured in the trawl were included because sample sizes were relatively small. To look for broader effects of climate regime and oceanographic domain on fish length, sizes from each domain (inner, middle, and outer) and climate condition (warm, average, and cool) were pooled across years and analyzed with a 2-way main effects ANOVA. Data were analyzed using Minitab 16 statistical software. If a significant difference \( (P < 0.05) \) occurred, Tukey’s multiple comparison test was used to calculate the 95% confidence intervals \( (\alpha = 0.05) \) for all pairwise differences between the dependent variable means.

5.3.3. Fish diet

Food habits followed methods described in Moss et al. (2009) using the standard methods developed at Tikhookeanskiy Nauchno-Issledovatelskiy Institut Rybnoho Khozyaystva I Okeanografii (TINRO; Pacific Ocean Research Institute of Fisheries and Oceanography; Volkov et al., 2007; Chuchukalo and Volkov, 1986). At each station where juvenile cod were captured, their stomach content was examined by removing and pooling the contents of the entire food bolus from up to 20 randomly selected individuals from the total catch of juvenile cod. Pooled stomach contents were weighed to the nearest 0.001 g, sorted, and identified to the lowest feasible taxonomic group. The contribution of each prey taxa to the diet was determined by dividing the volume occupied by each prey taxa by the total volume of prey contained in the
stomachs and multiplying that proportion by the total weight of the stomach contents. This resulted in 111 diet compositions each representing the average diet of fish collected at a given station among the 99 core sites for this analysis. The number of stations with diet data in a given year ranged from 3 (2004) to 46 (2006) depending on the occurrence of juvenile cod. Differences in dietary composition among climate regimes and domains were analyzed using one-way analysis of similarity (ANOSIM) using a Bray-Curtis similarity matrix constructed from the 111 diet compositions collected in 2003 -2005 (warm years) and 2007-2011 (cool years). To simplify the analysis 51 prey taxa were combined into 17 diet categories (Table 2). Similarity indices ($S_{BC}$) in the matrix were calculated as:

$$S_{BC} = \frac{\sum 2 \times \min (n_{1i}, n_{2i})}{\sum n_{1i} + \sum n_{2i}}$$

Where $n_{1i}$ is the proportion of the $i^{th}$ prey class in diet sample 1. The ANOSIM $R$ statistic indicates the magnitude of the difference in the mean rank similarity for two samples when samples are considered between groups and within groups. If the mean rank difference between two groups is the same as that within groups then $R$ will equal zero; differences are normalized so that $R$ varies between -1 and 1. In an analysis of similarity (ANOSIM) samples are randomized and a distribution of $R$ statistics is generated. The observed $R$ statistic is compared with the randomized distribution to determine if between group similarity is significantly different from the within group similarity. The nine sampling strata considered included each of the three domains (inner, middle and outer) in each of the three periods (warm, average, cool). The similarities between diets were visualized by plotting them in two dimensions following transformation by multidimensional scaling. The contributions of different prey items to the
total dissimilarity between warm and cool diets (pooled across all domains) were evaluated using a similarity percentages (SIMPER) analysis. This permitted identification of those prey items that contributed most to the difference between strata. ANOSIM and SIMPER analysis were both performed with PRIMER software (version 6).

5.3.4. Energy content
The energy density (kJ/g wet mass) of juvenile cod was determined following methods in Heintz et al. (2013). Random subsamples of 10-20 juvenile cod per station were sealed in plastic bags, frozen at sea, and transported to the Auke Bay Laboratories in Juneau, Alaska, for energy density analysis. In the laboratory, juvenile cod were thawed, and after their stomach contents were removed, they were dried and pulverized to form a homogenate. Samples were processed in the fall of 2012, so they were frozen for different amounts of time. Pulverized homogenates were pressed into pellets weighing at least 25 mg and combusted using a Parr 6725 semi-micro bomb calorimeter. Approximately 17 fish from each year were processed. Samples for processing were selected so that the mean size of a sample was similar to the mean size of fish in the catch. Juvenile cod samples were not routinely retained for calorimetry in the early years of the BASIS survey and they were often opportunistic when they were collected. Consequently, energy data were only available from a few years (2005, 2007, 2010 and 2011) and from a limited number of stations in each of those years. Samples processed from 2005 had no station information, in 2007 only two stations were sampled, in 2010 fish from 13 stations were processed and fish from 11 stations were processed in 2012.

Energy densities were compared among years by a nested ANOVA. The independent values for the ANOVA were year and stations nested within years. In addition, we regressed the energy
density for each year averaged over the stations against the average energy density of juvenile pollock sampled in the same year as reported in Heintz et al. (2013). The pollock data set has a much better sample coverage, thus the regression was intended to verify that patterns observed in the less well-covered cod data set corresponded with those reported for pollock. All statistical analyses involving cod energy densities were performed on a dry mass basis to remove potential biases from different times in frozen storage. Results of the cod and pollock regression are presented on a wet mass basis for comparability.

5.4 Results

5.4.1. Size

The mean lengths of juvenile cod were significantly ($p < 0.001$) different among years examined (Table 3; Fig. 3). Mean lengths were largest during 2004 and 2005 and smallest during 2007 and 2010. When juvenile cod lengths were pooled by domain and climate condition, lengths were significantly larger in all domains during warm years than during cool years ($p < 0.001$ Fig. 4). During the average year of 2006, lengths of juvenile cod in the inner and middle domains were similar to those observed during the cool years; lengths in the outer domain were intermediate to those observed in the warm and cool conditions. In all three climate conditions, juvenile cod were smaller in the outer domain than they were in the inner and middle domains ($p = 0.002$).

5.4.2. Diet

Juvenile cod diets differed among the climate regimes in each of the domains (Fig. 5). Juvenile cod diets in the middle and inner domains in warm years were significantly different from those observed in cool years (Table 4) ($R > 0.351; p < 0.01$). There were only a few juvenile cod diets available for analysis in the outer domain during warm years, consequently ANOSIM tests
involving the outer domain diets in warm years had few (<66) possible permutations, obscuring interpretation of the associated R statistic. Pollock and crab zoea accounted for 63% of the consumed mass in juvenile cod diets from the inner domain in warm years. In the average year, pollock were not found in juvenile cod diets in the inner domain, instead crab zoea and euphausiids accounted for 61% of the diet. In the cool years, crab zoea were replaced by large copepods, together with euphausiids they accounted for 55% of the inner domain diets. Hence, diets during the year with average sea temperatures were more similar to the years with cool sea temperatures in the inner domain (R = 0.166, p = 0.074) than during years with warm sea temperatures (R = 0.298; p = 0.057). In the middle domain, pollock and crab zoea accounted for 85% of the diet. The transition in diets from the years with warm to average sea temperatures in the middle domain was characterized by decreased consumption of pollock; euphausiids, pteropods and crab zoea accounted 87% of the diet. In cool years, juvenile cod within the middle domain primarily consumed euphausiids, hyperiid amphipods, crab zoea and large copepods, which accounted for 80% of the diet. Consequently, juvenile cod diets in the middle domain during the average year were equally different from warm (R = 0.20; p = 0.049) and cool years (R = 0.256; p = 0.001). In the outer domain euphausiids, crab zoea, and pteropods were always the most important juvenile cod prey by mass, accounting for at least 73% of the diet, regardless of climate. This meant that outer domain diets in the average year were indistinguishable from the warm (R = -0.12; p = 0.685) and the cool year diets (R= 0.009; p = 0.426).

The differences in diet between warm and cool years reflected a change from diets dominated by pollock and crab zoea in warm years to diets favoring adult euphausiids, hyperiid
amphipods, large copepods, pteropods, mysids and shrimp in cool years (Fig. 6). Analysis of the 
contributions of each prey group to the similarity among warm year diets indicated crab zoea 
and pollock dominated the warm year diets, accounting for > 90% of the average similarity 
between pairs. In contrast, euphausiids, large copepods, and hyperiid amphipods dominated 
cool year diets, accounting for >70% of the average similarity among pairs of cool year diets. 
These same five prey categories accounted for > 66% of the average dissimilarity between 
warm and cool year diets.

5.4.3. Energy content

Juvenile cod energy densities differed among years ($p < 0.001$). Even though energy densities 
were available for only one year with warm conditions, average energy density (20.29 kJ/g dry 
mass) observed in 2005, was lower than the averages observed in three cool years (21.04 – 
20.72 kJ/g). Post-hoc analysis indicated the energy densities in each of the cool years differed 
from the warm year ($p < 0.05$). The annual variation in energy densities in juvenile Pacific cod 
was correlated with values previously reported for juvenile pollock in the same four years, but 
the correlation was marginally significant ($P =0.051, R^2 = 0.901$; Fig. 7).

5.5. Discussion

Oceanographic conditions in the Bering Sea during warm years led to conditions that favored 
large size, but low nutritional condition in juvenile cod, whereas the opposite was true for cool 
years. Oceanographic conditions driving the differences in size and nutritional status of juvenile 
cod include temperature and the availability of prey. Depth-averaged water temperatures at 
mooring M2 in the southeastern Bering Sea were near 6° C in summer during the warm years 
Perhaps more importantly, ice retreat from the survey region was delayed in the cool years. Prey fields available to pelagic juveniles in cool years had a higher abundance of large copepods and adult euphausiids compared with warm years (Coyle et al., 2011). Consumption of these abundant and lipid-rich prey led to increased energy densities age-0 pollock (Heintz et al., 2013). Our examination of age-0 Pacific cod on the Bering Sea shelf indicates a similar response.

It is important to recognize that size differences among years may not necessarily reflect differences in growth rate. The effects of temperature on spawn timing could contribute significantly to the size differences. For instance, Neidetcher et al. (in press) found that cod spawning occurred earlier in warm (2005) than in cool (2007) years. Walleye pollock also spawned earlier during the years with anomalously warm sea temperatures (Smart et al., 2012). Consequently juvenile pollock appeared in trawls approximately 15 days earlier in warm years than they did in cool years. This early appearance would increase the amount of time in which fish had to grow prior to sampling in BASIS surveys. Furthermore, Farley et al. (2011) ascribed that relatively large size of juvenile Bristol Bay sockeye salmon that were distributed throughout the eastern Bering Sea during anomalously warm years was due to earlier ice break up in the freshwater lakes leading to earlier outmigration to the marine environment, providing more time for growth. Because growth rate of fish is a function of temperature and adequate prey supplies, warmer temperatures may augment these differences in size assuming adequate food supplies were available.
It is interesting that across years, larger body sizes of cod were associated with lower, not higher, energy densities. In both field and laboratory studies favorable growth conditions frequently result in positively correlated size and energy storage (Hurst and Conover, 2003; Sogard and Spencer, 2004). However, the energy density pattern observed in cod appears consistent with that observed in juveniles of at least two other Bering Sea fishes. Energy density of age-0 walleye pollock was also higher in cool years (although body sizes were more similar across climate conditions, Heintz et al., 2013). Juvenile sockeye salmon in cool years had smaller body sizes but higher energy content than in warm years as observed here for juvenile cod (Farley et al., 2011). The consistent pattern of climate effects on size and energy content in these co-occurring species could reflect an adaptation to growth opportunity to reduce predation risk in at larval and juvenile life history stages and one of lipid storage during late summer to increase overwinter survival (Siddon et al., 2013). Alternatively, the pattern could be related to the significant differences in juvenile fish diets observed across climate states in the EBS.

Increased lipid storage in juvenile cod was coincident with a shift in the quality of prey consumed during warm and cool years. In warm years, juvenile cod consumed prey that averaged between 2% and 4% lipid; whereas, the predominate prey consumed in cool years averaged 4% to 12% lipid (Heintz et al., 2013). These same factors also account for the observation that walleye pollock and juvenile salmon in the eastern Bering Sea, sampled at the same time as the juvenile cod, had higher energy densities in cool years (Heintz et al., 2013). For instance, juvenile (age-0) walleye pollock fed primarily on small zooplankton during warm years and large zooplankton during cool years (Coyle et al., 2011). Juvenile salmon diets were
dominated by age-0 walleye pollock during warm years, but their diet shifted to large zooplankton during cool years (Coyle et al., 2011; Farley and Trudel, 2009; Farley et al., 2009). Thus, evidence indicates that when abundance of large zooplankton on the eastern Bering Sea shelf is low during warm years (Coyle et al., 2011), apex predators feed on forage fish (mainly age-0 walleye pollock) that were highly abundant within the middle domain during years with anomalously warm spring and summer sea temperatures (Moss et al., 2009; Hollowed et al., 2012). This shift in diet of some larger age-0 and juvenile fish from zooplankton during years with cool sea temperatures to age 0 pollock during years with warm sea temperatures may be one explanation for increased mortality and low recruitment of these fish during years with warm sea temperatures.

We found that juvenile cod diets were more diverse during years with cool temperatures than those with warm temperatures. This result is likely a function of the shift in these prey within the eastern Bering Sea ecosystem between warm and cool periods. For instance, age-0 walleye pollock dominated juvenile cod diets during warm years in the inner and middle domain but were absent from the diets in cool years. Age-0 walleye pollock were found to be widely distributed in surface waters during warm years within middle and inner domains of the Bering Sea but declined in abundance in surface waters during cool years (Parker-Stetter et al. 2013; Hollowed et al. 2012). During cool years, hyperiid amphipods and large copepods were some of the dominant prey for juvenile cod found in the middle domain. Recent research on hyperiid amphipods suggests that they were always absent in the inner domain, but their abundance increased in the middle domain (Coyle et al., 2011; Pinchuk et al., 2013). There was a consistent increase in *C. marshallae* in both the inner and middle domains during years with
cool sea temperatures, but the increase in their abundance was much greater in the middle
domain (Coyle et al., 2011). The distribution of juvenile cod was relatively stable and did not
shift markedly in response to variation in spring and summer temperatures on the shelf (Hurst
et al., 2012), thus the significant differences in diet among domains during cool years was likely
related to shifts in prey available to juvenile cod within each domain.

Large size and high energy reserves for age-0 fish enable them to withstand severe energy
deficits prior to and during winter (Sogard and Olla, 2000; Hurst, 2007). For instance, smaller
age-0 pollock from southeast Alaska that lacked sufficient energy to meet metabolic demands
during winter had higher size-selective mortality (Heintz and Vollenweider, 2010). Smaller, leaner juvenile Bristol Bay sockeye salmon also had increased mortality during winter (Farley et
al., 2011). For age-0 pelagic fish, prey quality and quantity are important because there is a
small time window between the completion of metamorphosis and the onset of winter in which
juveniles can provision themselves (Siddon et al., 2013). Therefore, consumption of high
quality prey should improve fitness in age-0 fish, reduce their energy deficits over winter and
lead to increased survival.

Understanding the relationships between climate, ecosystem productivity, and juvenile fish
condition are important because condition of juvenile fishes prior to winter is believed to
control recruitment in the Bering Sea (e.g. walleye pollock; Heintz et al., 2013). Moreover,
models relating environmental factors to survival indicate late summer temperatures account
for more variation in recruitment than either the timing of ice retreat or a spring transition
index (Mueter et al., 2011). We found a positive correlation between juvenile cod and pollock
energy density. This result, coupled with the understanding that walleye pollock and Pacific cod recruitment appear synchronous (Mueter et al., 2007), suggests that condition of juvenile cod prior to winter may be an important predictor of overwinter survival in the Bering Sea.

5.6 Conclusion

Our results provide evidence that condition of juvenile gadids prior to winter is a function of prey quality and sea temperature regimes on the eastern Bering Sea shelf. Measures of fish condition during late summer and fall may also be a good predictor of recruitment to age-1 fish. Periods of anomalously warm sea temperatures were associated with decreased nutritional quality of available prey resulting in reduced energetic status of juvenile gadids on the Bering Sea shelf, suggesting increased risk of overwinter mortality. Our examination of juvenile cod size, diet, and energetic status, provided results that are similar to those from studies on juvenile pollock (Moss et al. 2009; Coyle et al. 2011; Hunt et al. 2011; Heintz et al. 2013; Siddon et al. 2013), suggesting that the common mechanisms regulating gadid recruitment on the eastern Bering Sea shelf are climate condition, prey quality and quantity, and caloric density of gadids prior to winter.

5.7 Acknowledgments

We thank all of the people involved in collecting, sorting, and processing the samples used in this study. This includes the crews of the FV Sea Storm, FV Northwest Explorer, and NOAA ship Oscar Dyson. This research is contribution NPRB XXX and BEST-BSIERP XXX. References to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA. The findings and conclusions in this paper are those of the authors do not necessarily represent the views of NMFS or NOAA.
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   Res. II 49, 5821-5853.

   345.


Table 1. Sampling summary

<table>
<thead>
<tr>
<th>Year</th>
<th>Vessel(s)</th>
<th>Start Date</th>
<th>End Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>Sea Storm</td>
<td>31-August</td>
<td>28-September</td>
</tr>
<tr>
<td>2004</td>
<td>Sea Storm</td>
<td>14-August</td>
<td>28-September</td>
</tr>
<tr>
<td>2005</td>
<td>Sea Storm</td>
<td>14-August</td>
<td>06-October</td>
</tr>
<tr>
<td>2006</td>
<td>Sea Storm/Northwest Explorer</td>
<td>16-August</td>
<td>20-September</td>
</tr>
<tr>
<td>2007</td>
<td>Sea Storm</td>
<td>15-August</td>
<td>08-October</td>
</tr>
<tr>
<td>2008</td>
<td>Oscar Dyson</td>
<td>11-September</td>
<td>27-September</td>
</tr>
<tr>
<td>2010</td>
<td>Oscar Dyson</td>
<td>18-August</td>
<td>24-September</td>
</tr>
<tr>
<td>2011</td>
<td>Oscar Dyson</td>
<td>23-August</td>
<td>15-September</td>
</tr>
</tbody>
</table>
Table 2. Prey taxa identified in all stomachs analyzed and the associated diet categories used for construction of Bray-Curtis similarity matrix.

<table>
<thead>
<tr>
<th>Diet categories</th>
<th>Prey taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barnacle</td>
<td>Cirripedia cyprid</td>
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<tr>
<td>Barnacle</td>
<td>Balanidae</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Bivalvia</td>
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<tr>
<td>Chaetognath</td>
<td>Chaetognatha</td>
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<tr>
<td>Chaetognath</td>
<td><em>Parasagitta elegans</em></td>
</tr>
<tr>
<td>Crab zoea</td>
<td>Brachyura</td>
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<tr>
<td>Crab zoea</td>
<td>Decapoda</td>
</tr>
<tr>
<td>Crab zoea</td>
<td>Decapoda larvae</td>
</tr>
<tr>
<td>Crab zoea</td>
<td>Paguridae</td>
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<tr>
<td>Crab zoea</td>
<td>Paguridae zoea</td>
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<tr>
<td>Crab zoea</td>
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</tr>
<tr>
<td>Crab zoea</td>
<td><em>Chionoecetes opilio</em></td>
</tr>
<tr>
<td>Euphausiid</td>
<td>Euphausiacea</td>
</tr>
<tr>
<td>Euphausiid</td>
<td>Euphausiacea eggs</td>
</tr>
<tr>
<td>Euphausiid</td>
<td><em>Thysanoessa inermis</em></td>
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<tr>
<td>Euphausiid</td>
<td><em>Thysanoessa inspinata</em></td>
</tr>
<tr>
<td>Euphausiid</td>
<td><em>Thysanoessa longipes</em></td>
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<td>Euphausiid</td>
<td><em>Thysanoessa raschii</em></td>
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<tr>
<td>Euphausiid</td>
<td><em>Thysanoessa</em> sp.</td>
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<tr>
<td>Euphausiid</td>
<td><em>Thysanoessa spinifera</em></td>
</tr>
<tr>
<td>Category</td>
<td>Species Name</td>
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<td>Gammaridae</td>
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<td>Gammarid</td>
<td>Gammaridea</td>
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<td>Cnidaria</td>
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<td>Gelatinous</td>
<td>Cumacea</td>
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<tr>
<td>Hyperiid</td>
<td><em>Hyperia sp.</em></td>
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<td>Hyperiid</td>
<td><em>Themisto libellula</em></td>
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<td>Hyperiid</td>
<td><em>Themisto pacifica</em></td>
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<td>Large copepod</td>
<td><em>Neocalanus flemingeri</em></td>
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<tr>
<td>Large copepod</td>
<td><em>Neocalanus plumchrus</em></td>
</tr>
<tr>
<td>Large copepod</td>
<td><em>Neocalanus sp.</em></td>
</tr>
<tr>
<td>Mysid</td>
<td>Mysidacea</td>
</tr>
<tr>
<td>Other fish</td>
<td>Digested fish</td>
</tr>
<tr>
<td>Other fish</td>
<td>Fish</td>
</tr>
<tr>
<td>Pollock</td>
<td><em>Gadus chalcogrammus</em></td>
</tr>
<tr>
<td>Polychaete</td>
<td>Polychaeta</td>
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<tr>
<td>Pteropod</td>
<td><em>Limacina helicina</em></td>
</tr>
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<td>Shrimp</td>
<td>Caridea</td>
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<td>Small copepod</td>
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<td>Small copepod</td>
<td>Centropages abdominalis</td>
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<tr>
<td>Small copepod</td>
<td>Copepoda</td>
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<td>Small copepod</td>
<td>Oithona similis</td>
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<tr>
<td>Small copepod</td>
<td>Pseudocalanus minutus</td>
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<td>Small copepod</td>
<td>Pseudocalanus newmani</td>
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<tr>
<td>Small copepod</td>
<td>Pseudocalanus sp.</td>
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Table 3. Sample size (n) for length, diet, and energetic status of juvenile cod sampled in the Bering Sea during August - September 2003 - 2011. The year 2009 is omitted due to low sample size.

<table>
<thead>
<tr>
<th>Year</th>
<th>Length</th>
<th>Diet</th>
<th>Energy</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>102</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>2004</td>
<td>603</td>
<td>35</td>
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<tr>
<td>2005</td>
<td>1,480</td>
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<td>2006</td>
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<td>2007</td>
<td>587</td>
<td>195</td>
<td>28</td>
</tr>
<tr>
<td>2008</td>
<td>421</td>
<td>105</td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td>2013</td>
<td>326</td>
<td>18</td>
</tr>
<tr>
<td>2011</td>
<td>368</td>
<td>40</td>
<td>18</td>
</tr>
</tbody>
</table>
Table 4. R statistics representing the multivariate distance between Pacific cod diets in pairs of domains from the Bering Sea in warm and cool years. Domains prefixed with W were sampled in warm years (2003-2005) and those prefixed with C were sampled in cool years (2007-2011).

* indicates $p < 0.01$, “a” indicates there were < 999 permutations possible.

<table>
<thead>
<tr>
<th></th>
<th>W-Outer</th>
<th>W-Middle</th>
<th>W-Inner</th>
<th>C-Outer</th>
<th>C-Middle</th>
</tr>
</thead>
<tbody>
<tr>
<td>W-Middle</td>
<td>0.091a</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>W-Inner</td>
<td>0.071a</td>
<td>0.048a</td>
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<td>C-Outer</td>
<td>-0.151a</td>
<td>0.365*</td>
<td>0.663*</td>
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<td>C-Middle</td>
<td>0.009a</td>
<td>0.490*</td>
<td>0.765*</td>
<td>0.019</td>
<td></td>
</tr>
<tr>
<td>C-Inner</td>
<td>-0.039a</td>
<td>0.351*</td>
<td>0.578*</td>
<td>-0.037a</td>
<td>0.238*</td>
</tr>
</tbody>
</table>
Figure 1. Survey grid (core stations) for the 2003 to 2011 Bering-Aleutian Salmon International Survey. Contour lines are associated with the 50 m and 100 m bottom depths delineating the inner (< 50 m depth), middle (50 m to 100 m depth), and outer (> 100 m depth) domains.
Figure 2
Figure 3. Mean lengths (mm) and 95% confidence intervals of juvenile cod captured during 2003 to 2011 in the eastern Bering Sea.
Figure 4. Mean lengths (mm) and 95% confidence intervals of juvenile cod within cool (C), average (A), and warm (W) climate periods and among domains (inner (I), middle (M), and outer (O)).
Figure 5. MDS plots of juvenile cod diets from warm, average, and cool years in the Bering Sea, showing comparisons among domains. Each point represents the average diet of juvenile cod sampled at a specific station within the domain during the appropriate climatic condition. The MDS model was fit to all domains simultaneously with an overall stress = 0.17. R statistics indicate the distance between warm and cool years in each domain.
Figure 6. Average diets of juvenile cod sampled in the Bering Sea in warm (2003-2005) and cool (2007-2011) years. Diet categories account for > 90% of the overall dissimilarity between climatic states and are listed from the bottom in order of their contribution to dissimilarity.
Figure 7. Correlation between juvenile cod and pollock energy densities in one warm (2005) and three cool (2007, 2010 and 2011) years. Symbols reflect the mean energy density each year, error bars are ± 1 s.e.. Symbols may obscure error bars.
6.1 Abstract

Arrowtooth flounder (*Atheresthes stomias*) and Kamchatka flounder (*A. evermanni*) are closely related flatfish species that co-occur in the eastern Bering Sea. The inability to distinguish larvae and early juveniles of these species has precluded studies of ecology for the early life stages of both species in the eastern Bering Sea. In this study, we developed a genetic technique to identify the larvae and early juveniles of the two species using mtDNA cytochrome oxidase subunit I (COI). Genetically identified specimens were then examined to determine a visual identification method based on pigment patterns and morphology. Specimens 6.0–12.0 mm SL and ≥ 18.0 mm SL can be identified to the species level, but species identification of individuals 12.1–17.9 mm SL by visual means alone remains elusive. The distribution of larvae (< 25.0 mm SL) of both arrowtooth flounder and Kamchatka flounder is similar in the eastern Bering Sea; however, juvenile (≥ 25.0 mm SL) Kamchatka flounder occur closer to the shelf break and in deeper water than juvenile arrowtooth flounder. Condition was measured in larvae and juveniles of each species as analyzing lipid content (%) and energy density (kJ/g dry mass). Kamchatka flounder larvae on average had higher lipid content than arrowtooth flounder larvae, but were also larger on average than arrowtooth flounder larvae in the summer. When corrected for length, both species had similar lipid content in the larval and juvenile stages.
6.2 Introduction

Arrowtooth flounder are large (max. size 86 cm total length), predatory flatfish that occur from off the coast of central California, north to the Bering Sea, and west to the Kamchatka Peninsula, Russia (Mecklenburg et al., 2002). Kamchatka flounder are similar in size, but occur primarily in the western Bering Sea with lesser occurrence in the eastern Bering Sea and along the Aleutian Islands (Mecklenburg et al., 2002). In the Bering Sea, arrowtooth flounder have been documented to feed primarily on juvenile and adult walleye pollock (Gadus chalcogrammus), euphausiids, and various shrimps (Yang and Livingston, 1986). They, in turn, are consumed by Alaska skates (Bathyraja parmifera) and sleeper sharks (Somniosus pacificus) as adults, and by Pacific cod (Gadus macrocephalus) and walleye pollock as juveniles (Spies et al., 2011). The diet of Kamchatka flounder is similar and often considered identical to arrowtooth flounder (Yang and Livingston, 1986). Both their predation impact and their role as prey for other organisms indicate that arrowtooth flounder and Kamchatka flounder are important constituents of the Bering Sea ecosystem (Aydin et al., 2007). The directed fishing effort for arrowtooth flounder has increased in recent years, as has the retention of adults caught in other commercial fisheries, possibly in response to an approximate eight-fold increase in adult arrowtooth flounder biomass in the Bering Sea since the early 1980s (Spies et al., 2011). Kamchatka flounder also experience some fishing pressure as directed commercial fishing has developed in recent years (Wilderbuer et al., 2011). Despite their many similarities, these two species can be separated as adults by the number of gill rakers on the second upper gill arch (one in Kamchatka flounder, two to three in arrowtooth flounder) and the visibility of the dorsal-most eye from the blind side (top of eye is visible in arrowtooth flounder, no part of eye visible in Kamchatka flounder) (Yang, 1988). Using electrophoretic examination of alleles at different loci, Ranck et al. (1986) determined that arrowtooth flounder and Kamchatka flounder were two genetically-distinct species and, based on the distinct distributions of certain alleles, there was no hybridization between the two species. However, adults of arrowtooth flounder and Kamchatka flounder collected in scientific and commercial catches were often recorded as either all arrowtooth flounder or the genus Atheesthes (Yang and Livingston, 1986; Spies et al., 2011). In 1991, adult arrowtooth flounder and Kamchatka flounder individuals began to be separated as distinct species by the Alaska Fisheries Science Center (AFSC) Groundfish Assessment Program (Zimmerman and Goddard, 1996). As of summer 2011, fishing management regulations dictated that arrowtooth flounder and Kamchatka flounder must be separated and recorded as distinct species in commercial fishing hauls due to the emergence of a directed fishery for adult Kamchatka flounder (Wilderbuer et al., 2011). While adults of both species have been well described, the early life stages in the eastern Bering Sea have not been. High recruitment success may be the cause of the increase in population size of arrowtooth flounder in recent years (Spies et al., 2011). Understanding the early life stages is
important to understanding recruitment and the first step to understanding recruitment in arrowtooth flounder is to identify and separate the early life stages from Kamchatka flounder. Our current study had the following objectives: 1) use genetic methods to identify to the species level larval and early juvenile *Atheresthes* collected in the eastern Bering Sea, 2) use the genetically identified individuals to develop a visual identification method that allows identification of historical and future samples, 3) describe the distribution and abundance of the early life stages of both arrowtooth flounder and Kamchatka flounder, and 4) examine condition as indicated by length adjusted dry mass, lipid content (%), and energy density of larvae and juveniles to determine differences in nutritional quality between species.

**6.3 Materials and Methods**

**6.3.1 Specimen collection**

All specimens in this study were either directly collected at sea or were sorted from previously collected preserved samples collected on previous AFSC ichthyoplankton surveys. The specimens collected at sea were obtained on spring and summer cruises from 2006 to 2010 by scientists on AFSC, Bering Ecosystem Study (BEST), and Bering Sea Integrated Ecosystem Research Program (BSIERP) cruises (Table 1). Specimens were collected opportunistically, resulting in varied collection and preservation methods during the study. Methods of collection included using bongo nets (60-cm; 500-µm mesh), Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; 1- m with 500-µm mesh; Wiebe et al., 1976), and surface and midwater trawls. Specimens removed from the bongo net were either placed directly into 100% non denatured ethanol or into 5% formalin after an eyeball was removed. Sampling from the MOCNESS involved removing specimens only from the drogue net, which was open for the duration of the tow; all specimens were immediately frozen at -80º C. The surface and midwater rope trawls sampled above and below the pycnocline; all specimens collected were immediately frozen at -80º C. Specimens sorted from previously collected preserved samples were chosen from cruises occurring from 1994 to 2010 (Table 1). The samples were collected on previous AFSC ichthyoplankton surveys using 60-cm bongo nets, MOCNESS tows, Methot trawls (Methot, 1986), Tucker trawls (1-m with 500-µm mesh; Tucker, 1951), and a modified bottom trawl (which samples the midwater). Sampling protocol during the cruises, along with sample handling and sorting, follows Matarese et al. (2003). All specimens used in this study were classified as either larvae (3.0–24.9 mm SL) or juveniles (≥ 25.0 mm SL) (Matarese et al., 1989).

**6.3.2 Genetic identification**

Species determination was based on a restriction enzyme digest that cuts DNA at a specific nucleotide sequence that is present in arrowtooth flounder but not Kamchatka flounder. The
The test was based on an initial sequencing of three adult specimens from each species, followed by testing on 20 adult specimens of which the species identification was known. Fin tissue was used for DNA extraction in all adults and was performed using Qiagen DNA extraction kits (Qiagen, Inc. Valencia, CA). For larval and early juveniles, a single eyeball (from either side of head) removed from either fresh, frozen, or 100% non-denatured ethanol preserved specimens was used for DNA extraction. The rest of the specimen body was placed back in its original preservative or, if frozen, photographed for future visual identification work. Larval DNA was extracted from a single eyeball using a standard Chelex DNA extraction protocol. The eyeball was submerged in 150 µl of 10% (w/v) Chelex ® 100 resin (BIO126 RAD Laboratories, Hercules, CA), heated to 60° C for 20 min followed by 103° C for 25 min. A 750 bp segment of cytochrome oxidase subunit I (COI) was amplified using the following primers: COI_RajaF (5’-CCGCTTAACTCTCAGCCATC-3’) and COI_RajaR (5’-TCAGGGTGACCAAAGAATCA-3’; Spies et al., 2006). Polymerase chain reactions (PCR) were conducted in a 10 µl volume, with approximately 100 ng DNA (1 µl taken from the Chelex supernatant), 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 3.0 mM MgCl2, 1.5 mM dNTPs, 0.5 pM of each primer, and 0.5 U Bioline Taq polymerase (Bioline USA, Inc., Boston, MA). PCR amplification using Chelex extractions can fail if the supernatant contains impurities such as proteins. Therefore, failed samples were repeated with a 1:10 135 or 1:100 dilution of the DNA, which typically resulted in success. The thermal cycling protocol consisted of 94° C for 2 min, followed by 40 cycles of 94° C (30 seconds), 57°C (30 sec), and 72° C (30 sec). DNA sequencing of amplified DNA from adult specimens was performed using COI_Raja primers at the University of Washington High Throughput Genomics Center (www.htseq.org). Following PCR, DNA was digested using Bmt1 (New England Biolabs, Ipswich, MA) according to manufacturer’s instructions, in a total volume of 10:l with 2:l PCR product and4Uof Bmt1 at 37° C for 1 h. Identification was based on either the presence of a single 750 bp fragment (Kamchatka flounder) or two fragments consisting of 450 and 300 bp (arrowtooth flounder).

This protocol was performed in a laboratory or at sea using an Agilent 2100 Bioanalyzer with a DNA 1000 kit (Agilent Technologies, Santa Clara, CA) and a BIO-RAD DNA Engine Thermalcycler.

6.3.3 Visual identification
Specimens identified using genetic methods were examined to develop a visual identification method based on morphological and pigmentation characters. Specimens were examined both with and without knowledge of their genetic identification to determine species-specific characters. Each specimen was critically evaluated with regards to morphology and pigment (such as the number of melanophores in a patch or the general shape and pattern of melanophore patches). Only specimens preserved in the same preservation medium were directly compared to one another. This was to minimize the identification of preservation artifacts as distinguishing species characters.
Morphometric measurements were taken from arrowtooth flounder and Kamchatka flounder larvae chosen from a single cruise. Only specimens initially preserved in formalin were used for morphometric measurements because the other preservation methods (100% ethanol and immediate freezing) shrink tissues and distort morphology. The following measurements were taken: standard length (SL), preanal length (tip of snout to anus), head length, snout length, eye diameter, and body depth (vertical measurement taken at pectoral fin; BD). The measurements were taken using a calibrated digital image analysis system consisting of a video camera attached to a stereo microscope and a computer with image analysis software. All measurements were recorded to the nearest 0.1 mm. A two sample t-test was used to identify statistically significant differences ($p < 0.05$) between each morphological measurement for the two species. Developmental stage terminology follows Kendall et al. (1984).

### 6.3.4 Distribution

Selected larval *Atheresthes* collected on previous AFSC cruises conducted from 1994 to 2010 (Table 1) were identified to the species level using pigmentation and morphological characters identified with the visual identification method. The locations of all specimens identified to species were mapped and a mean distribution based on abundance was calculated for each species using ArcGIS software.

### 6.3.5 Measures of Condition

### 6.3.6 Biological sampling

Larval and juvenile *Atheresthes* were collected from five research surveys conducted in the summer and early fall from 2008 to 2010 (Table 1). All specimens were measured to the nearest 0.01 mm SL. Specimens < 30.0 mm SL were identified to species using the genetic methods previously described, while specimens > 30.0 mm SL were identified morphologically using the number of gill rakers on the upper arch of the second gill raker. All specimens had an eyeball removed, even if identified visually. Stomach contents were removed prior to chemical analysis.

### 6.3.7 Dry mass

Larvae were individually dried at 60°C in a drying oven until their weight was stabilized. Juveniles were dried at 135°C using a LECO Thermogravimetric Analyzer (TGA) 601 or 701, which provided percent moisture values used to convert wet mass to dry mass equivalents.

### 6.3.8 Estimation of lipid content (%)

For larvae, a sulfo-phospho-vanillin (SPV) colorimetric analysis (Van Handel, 1985) was performed to determine lipid content (%). Dried material was sonicated in 2:1 (by 196 volume) chloroform:methanol solvent in glass centrifuge tubes for 60 min. Washes of 0.88% KCL and 1:1 (by volume) methanol:water were performed on the extracts as in the modified Folch extraction method (Vollenweider et al., 2011). Resulting chloroform extracts were evaporated.
in a LabConco RapidVap for 30 min at 40 ºC and 250 mbar 200 until reduced to approximately 1 ml in volume. Extracts were evaporated to dryness in 12 mm test tubes on a heating block at 75 ºC and then allowed to cool. Concentrated sulfuric acid was added to the tubes prior to incubation at 100 ºC for 10 min with subsequent cooling. The SPV reagent (1.2 mg/ml vanillin in 80% phosphoric acid) was added to each tube and allowed to develop for 10 min. Absorption was measured on an Agilent 8453 Spectrophotometer at 490 nm and extrapolated from species-specific calibration curves determined prior to analysis. For juveniles, lipid extraction was performed on dried material using a previously described method (Vollenweider et al., 2011) derived from the Folch extraction procedure.

6.3.9 Energy density
Energy density (kJ/g dry mass) was estimated using bomb calorimetry. Homogenized dry tissue was pressed into a pellet form and a Parr Instrument 6725 Semimicro Calorimeter with 6772 Precision Thermometer and 1109A Oxygen Bomb was used to measure the energy released from combustion of the sample pellets. The minimum pellet weight was set at 0.025 g of dry material based on the limits of instrument detection; individual larvae were composited within stations as needed to attain sufficient dry mass.

6.3.10 Statistical analysis
A general linear model was used to identify differences in the nutritional state of arrowtooth flounder and Kamchatka flounder. Lengths were compared by a nested analysis of variance (ANOVA) to account for differences in the numbers of fish collected. Species was the main factor with life stage nested in species and year nested in life stage. Post-hoc comparisons of species were conducted among the life stages using Bonferonni’s adjusted t value. Analysis of covariance (ANCOVA) was employed to compare dry mass and lipid content between species. This approach permitted comparisons when length distributions differed between species and the responses covaried with length. The ANCOVA used species, year, and their interaction as main factors and length as covariate. Analyses were conducted separately for larvae and juveniles because the response variables were heteroscedastic when pooled across life stages. Variables were transformed prior to analysis using logarithms (base 10), and the assumption that both species had equivalent slopes was tested. Student’s t was used to compare energy densities of larvae and juveniles.

6.4 Results
6.4.1 Genetics
Using mtDNA COI restriction analysis proved successful in identifying Atheresthes larvae and early juveniles to species in the laboratory (n = 337) and at sea (n = 78). Of the 415 total specimens, 165 were identified as arrowtooth flounder, 194 as Kamchatka flounder, and 56
failed to amplify properly resulting in an unknown identity. Size of specimens examined was 6.0–38.0 mm SL, with the majority of specimens 6.0–11.5 mm SL.

6.4.2 Visual identification

Visual examination of genetically-identified specimens was successful in determining key pigmentation differences between arrowtooth flounder and Kamchatka flounder larvae of 6.0–12.0 mm SL and ≥ 18.0 mm SL. These key pigmentation differences are size specific but not stage specific. Specimens 12.1–17.9 mm SL remain indistinguishable at this time because of the small sample size and a high degree of variation in pigmentation patterns.

Recently hatched Kamchatka flounder larvae (6.0–7.4 mm SL) can be distinguished from arrowtooth flounder of the same size by the presence of pigment dorsal to the gut at the anus and an anterior dorsal pigment patch located halfway between the anus and the caudal fin (Fig. 1a). Arrowtooth flounder begin to develop the same pigment patterns at about 7.5 mm SL, resulting in these characteristics no longer being able to be used. Larvae of 7.5–12.0 mm SL can be identified by two characters. Kamchatka flounder larvae of 7.5–10.5 mm have pigment on the crown of the head, beginning as a few melanophores and developing to numerous melanophores that cover the entire crown of the head by approximately 9.0 mm SL (Fig. 1a). In general, arrowtooth flounder larvae do not begin to develop head pigment prior to 10.5 mm SL, however, a few individuals do develop one or two small melanophores on the crown of the head beginning at approximately 8.5 mm SL (Fig 1b). Thus, specimens 8.5–10.5 mm SL with only 1–3 melanophores on the head cannot be identified to species. In addition to crown pigment, the second character by which Kamchatka flounder larvae 7.5–12.0 mm SL can be identified is the pigment dorsal to the gut that starts at mid gut and extends to the anus (Fig. 1a). Arrowtooth flounder larvae also have pigment dorsal to the gut, but it starts at ¾ gut length and extends to the anus. The combination of these two characters allows larvae 7.5–12.0 mm SL to be identified to species.

Few genetically identified specimens were larger than 12.0 mm SL. Identification methods for larger specimens began with the use of adult characters to identify specimens > 25.0 mm SL. These identified specimens were then used as a guide to begin identifying smaller specimens. The adult characters used to determine the larger specimens was the number of gill rakers on the second upper gill arch: Kamchatka flounder have one gill raker, arrowtooth flounder have two or three. While these structures are not fully formed in specimens of 25.0–27.0 mm SL, fleshy protrusions that are the precursors to the gill rakers are evident. After numerous specimens were separated based on gill raker counts, a pattern in the dorsal pigment bands was seen to be different between the two species.

The anterior dorsal patch on Kamchatka flounder is generally longer (> 5 melanophores long) and the individual melanophores in the patch are close together, often touching and at times
coalescing. Additionally, Kamchatka flounder develop melanophores between the anterior and posterior bands, which eventually connect the two bands at a smaller size than arrowtooth flounder (beginning as early as approximately 13.0 mm SL, but generally by 18.0 mm SL) (Fig. 1a). In contrast, arrowtooth flounder tend to have a short (< 5 melanophores long) anterior dorsal band with melanophores that are widely spaced apart. Melanophores do not develop between the anterior and posterior dorsal bands until approximately 25.0 mm SL (Fig. 1b). The few large larvae and early juveniles used in the genetic technique confirmed the validity of these visual differences.

Morphological measurements were taken on 20 arrowtooth flounder larvae and 19 Kamchatka flounder larvae. Specimens ranged in length from 6.3 to 12.6 mm SL. Head length and eye diameter were not statistically different between the two species, but body depth and preanal length were. Larvae of Kamchatka flounder have a stouter body (BD = 12.0 ± 1.1% SL) than arrowtooth flounder larvae (BD = 9.8 ± 1.4% SL; p < 0.05). In addition to a stouter body, Kamchatka flounder larvae also have a slightly longer preanal length than arrowtooth flounder larvae (36.3 ± 1.8% SL vs. 35.1 ± 1.8% SL; p < 0.05).

**6.4.3 Distribution**

Examining formalin-preserved specimens from previous AFSC cruises, a total of 1,928 larvae and juveniles were identified to species using pigmentation and morphological characters identified above, with individuals identified to genus because of ambiguous characters or damage. A total of 1,315 arrowtooth flounder larvae and 480 Kamchatka flounder larvae were identified; 125 arrowtooth flounder juveniles and eight Kamchatka flounder juveniles were identified.

The majority of larval arrowtooth flounder and Kamchatka flounder were collected along the shelf break in the southeastern Bering Sea between Unimak and Umnak Pass (Fig. 2). There were also individuals collected farther north in Pribilof Canyon along the shelf break near deep water. The calculated mean distribution for both species is similar (Fig. 2). Juveniles of both species were collected primarily north of where the majority of the larvae were collected. The calculated mean distribution of the two species showed that arrowtooth flounder juveniles appear to be located farther east and over shallower waters than Kamchatka flounder juveniles, which have a mean distribution close to Pribilof Canyon and deeper water (Fig. 2). However, fewer Kamchatka flounder juveniles were collected and identified (n = 8) than arrowtooth flounder juveniles (n = 125), so caution should be used when interpreting this result.

**6.4.4 Biological sampling**

Length analysis was restricted to larvae collected in 2009 and 2010 and juveniles collected in 2010. These were stages and years in which sufficient numbers of specimens were collected. No significant difference was found in the lengths of larvae or juveniles sampled in 2009 and
2010 ($F_{2.154} > 0.77, p = 0.466$), and larvae were significantly smaller than juveniles ($F_{2.154} > 1000, \ p < 0.001$). Pairwise comparisons of larvae and juveniles between the two species averaged across years indicated that Kamchatka flounder larvae averaged approximately 25% longer than arrowtooth flounder larvae ($t = 4.6, p < 0.001$), but no difference was detected among juveniles ($t = 0.31, p = 0.991$) (Table 2). Differences between the two sets of larvae therefore accounted for the overall difference detected between species ($F_{1.154} = 6.71, p = 0.010$).

### 6.4.5 Dry mass

The dry weights of larvae did not depend on year nor was there an interaction between year and species ($F_{1.96} < 0.15, p > 0.700$). However, larval arrowtooth flounder of a fixed length were approximately 25% lighter than similarly sized Kamchatka flounder ($F_{1.96} = 4.16, p = 0.044$; Fig. 3a). No difference in dry mass was detected among juvenile specimens in 2010 ($F_{1.53} = 1.68, p = 0.20$; Fig 3b). It was not possible to test for year effect due to an inadequate number of samples in 2008 and 2009.

### 6.4.6 Lipid content

In 2009 and 2010 the average lipid content of arrowtooth larvae was $7.5 \pm 0.3\%$ ($n = 39$) of dry mass compared with $10.8 \pm 0.7\%$ for Kamchatka flounder larvae ($n = 11$; Fig. 4a). While the lipid content of Kamchatka flounder larvae averaged approximately 30% more than that of arrowtooth flounder larvae, this difference was not significant after controlling for the differences in average length ($F_{1.45} = 3.15, p = 0.083$). Additionally, there was not an effect of year or interaction between year and species on larval lipid content ($F_{1.45} < 2.37, p > 0.130$). In 2010, there was no difference between juveniles ($F_{1.25} = 0.03, p = 0.857$). Arrowtooth flounder juveniles averaged $10.2 \pm 0.5\%$ lipid ($n = 21$) in 2010 compared with $10.7 \pm 0.7\%$ ($n = 7$) for Kamchatka flounder juveniles.

### 6.4.7 Energy density

Energy density in juveniles was only measured in 2010 and in larvae only in 2009. Only a few larvae could be measured because samples required compositing. There was no statistically significant difference between the energy densities of the two species. Only six measurements of larval energy density were taken and the difference between species was not statistically significant ($t = 1.06, p = 0.366$) (Fig. 4b). Arrowtooth larvae averaged $19.2 \pm 0.8$ kJ/g dry mass; Kamchatka flounder larvae averaged $19.8 \pm 0.7$ kJ/g dry mass. Energy densities between juveniles of the two species were nearly identical ($t = 1.19, p = 0.244$), averaging $20.5 \pm 0.2$ kJ/g dry mass for arrowtooth flounder ($n = 16$) and $20.8 \pm 0.2$ kJ/g dry mass for Kamchatka flounder ($n = 12$).

### 6.5 Discussion

With the increasing population size of arrowtooth flounder and interest for increased directed fishing effort for both arrowtooth flounder and Kamchatka flounder, there is a need to fully
identify and study both species in all life stages for management and ecological purposes.

Adults of arrowtooth flounder have been studied with regard to their distribution (Zimmerman and Goddard, 1996), predation effects on walleye pollock (Ianelli et al., 2009), and their role as prey for other organisms (Livingston and Jurado Molina, 2000). The early life stages in the Gulf of Alaska have been described by Blood et al. (2007); however, efforts to conclusively identify larvae and juveniles in the Bering Sea have been confounded by the overwhelming physical similarities between arrowtooth and Kamchatka flounder.

6.5.1 Genetics
Genetic methods have proven to be useful tools in identifying unknown specimens to the species or family level using the mtDNA gene COI (Hebert et al., 2002; Dawnay et al., 2007; Rocha et al., 2007). In Alaskan waters, Spies et al. (2006) also successfully used mtDNA COI to identify 15 different skate species. In this current study we have demonstrated that this genetic technique is valid for identifying specimens of *Atheresthes* to the species level. In addition, the technique developed in this study proved effective for use both in the laboratory and at sea aboard a research vessel. In particular, this ability to conclusively identify specimens to the species level while at sea is quite useful as it can enable a timely adjustment to sampling location or procedure in order to maximize collection of the target species.

6.5.2 Morphology
In the marine environment closely related species are often indistinguishable as larvae due to overlap in pigmentation and morphological characters. Prior to this study, all larval and early juvenile *Atheresthes* collected in the Bering Sea were identified only to the genus level. Despite numerous physical similarities, unique pigmentation and morphological differences were noted between the two *Atheresthes* species in the size ranges of 6.0–12.0 mm SL and ≥ 18.0 mm SL. In general, it appears that Kamchatka flounder acquire certain pigmentation characters at smaller sizes than arrowtooth flounder, thus the distinguishing characters noted in this paper can only be used for the specific size ranges to which they correspond. Specimens of 12.1–17.9 mm SL are indistinguishable at this time due because of a high degree of variability in pigment amongst individuals and a low number of genetically identified specimens in this size range. In addition to pigment, Kamchatka flounder larvae are stouter than arrowtooth flounder larvae (BD 12.0% SL vs. 9.8% SL) and have a slightly longer snout to anus length (36.3% SL vs. 35.1% SL). These are modest morphological differences and can be difficult to determine but can be helpful when used in conjunction with pigmentation characters to support species identification. Using the pigment characteristics described in this study, two specimens illustrated by Blood et al. (2007; Fig. 13) should be re-examined as both specimens were collected in the Bering Sea. The 13.4 mm SL specimen is most likely Kamchatka flounder, not arrowtooth flounder, based on the large amount of pigment present on the head and the pigment present on the dorsal midline between the two dorsal bands. While arrowtooth
flounder do develop pigment on the crown of the head, the amount of pigment present at this size is more indicative of Kamchatka flounder. In addition, the presence of pigment on the dorsal midline between the two dorsal bands at this size can only be Kamchatka flounder as arrowtooth do not develop this pigment until approximately 25.0 mm SL. The 10.0 mm SL specimen (Blood et al., 2007; Fig. 12) may also be a Kamchatka flounder due to the large amount of pigment located on the crown of the head and within the two dorsal patches. However, complete identification is difficult from the illustrations alone; a close visual examination of the original specimens is needed.

6.5.3 Distribution
The larval distributions of arrowtooth flounder and Kamchatka flounder in the eastern Bering Sea are similar. Most of the larvae collected were located in the southern part of the eastern Bering Sea in water > 200 m along the shelf break (Fig 2a, b). This may indicate that in the eastern Bering Sea both arrowtooth and Kamchatka flounder adults spawn in deep water, similar to that described for arrowtooth flounder in the Gulf of Alaska by Blood et al. (2007). The distribution of juveniles collected does appear to be different between the two species, but this result is tenuous due to the low number of juvenile Kamchatka flounder collected (n = 8). However, this result may indicate that juvenile Kamchatka flounder are migrating to their adult habitat. In general, the majority of adult Kamchatka flounder are collected in deeper waters and farther to the west than adult arrowtooth flounder, which often occur in shallower waters to the east (Zimmerman and Goddard 1996; Wilderbuer et al., 2011). It is possible that the low number of juvenile Kamchatka flounder collected is due to limited sampling in deeper waters to the west of the shelf break.

6.5.4 Condition
Differences in the condition between arrowtooth flounder and Kamchatka flounder larvae collected in the summer may relate to differences in timing of development. For years in which sufficient numbers of larvae were collected for analysis, Kamchatka flounder larvae were significantly larger than arrowtooth flounder larvae in the summer. Comparison of the lengths of larvae sampled in the summer indicates that the bulk of arrowtooth flounder larvae were in the preflexion or flexion stages (Blood et al., 2007). Assuming stage designation is similar for Kamchatka flounder, the majority of Kamchatka flounder sampled in the summer were in the flexion and postflexion stages. The difference in developmental stage could account for the differences in the length adjusted dry mass of the two species and the trend towards increased lipid content in larval Kamchatka flounder. Energy allocation strategies can differ among developmental stages during the early life stages. This study suggests that postflexion larvae of Atheresthes may invest more energy accreting tissue mass than earlier stages. Comparison of the lengths of juveniles sampled indicates that the majority of the fish sampled from both species were in the transformation stage (Blood et al., 2007). Hence there were no differences
in condition between juveniles of either species. The results presented here are the first
estimates of lipid and energy density in larval and juvenile arrowtooth flounder and Kamchatka
flounder. Lipid content values of juveniles in this study are similar to those reported for Atlantic
halibut (Hippoglossus hippoglossus) fed a diet that promoted growth and survival (Hamre et al.,
2002). Energy densities of larvae were similar to those of juveniles and suggests no change in
energy allocation strategy between these two stages. This is in contrast to walleye pollock
which undergo significant changes in both lipid content and energy density between lengths of
20 and 60 mm (Siddon et al., 2012), which is when walleye pollock undergo and complete
transformation to the juvenile stage (Brown et al., 2001). The only evidence of a shift in lipid
content among both species of Atheresthes sampled here is associated with ontogeny in the
larval stages.

6.6 Conclusion
This study has provided a method to genetically identify larval and early juvenile arrowtooth
flounder and Kamchatka flounder both in the field and in the laboratory, and has provided
morphological and pigmentation characters to visually identify these two species at small (6.0–
12.0 mm SL) and large sizes (≥ 18.0 mm SL). Future sampling effort during June–August when
arrowtooth flounder and Kamchatka flounder larvae 12.1–17.9 mm SL are in the water column
could aid in completing the visual identification of these two species. Once all arrowtooth
flounder and Kamchatka flounder between 6.0 mm SL to the juvenile stage can be identified, all
historical samples of Atheresthes collected in 1991–2010 (19 years) by the AFSC from the
eastern Bering Sea can be re-identified to the species level. This collection contains
approximately 5,065 individuals that, when identified to the species level, will greatly increase
our knowledge of distribution and abundance for these two species. Additionally, increased
sampling effort in the deeper water off the shelf break during summer and fall would help
define the distribution of the larger sizes of these two species and determine if there is a
difference in timing of development for larvae in the summer.

6.7 Acknowledgements
The authors would like to thank all the scientists that collected Atheresthes spp., larvae over the
years and the officers and crews of the following ships: NOAA ship Miller Freeman, NOAA ship
Oscar Dyson, R/V Thomas G. Thompson, USCGC Healy, and the R/V Knorr. We would also like to
thank Dan Cooper for his help with genetic identification of specimens while on the May 2010
cruise and for reviewing a draft of this manuscript, Melanie Paquin for her help with genetic
identification and sequencing in the laboratory, Ashlee Overdick for her illustrations of both
species, and Debbie Blood for also reviewing a draft of this manuscript. This is BEST-BSIERP
Bering Sea Project 476 publication number XX. This research is contribution EcoFOCI-XXX to
NOAA’s Fisheries-Oceanography Coordinated Investigations. The findings and conclusions in
this manuscript are those of the authors, and do not necessarily represent the views of the National Marine Fisheries Service.

6.8 Literature Cited


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Res. II. 94: 140-149.


### 6.9 Figure and table legends

**Figure 1.** Illustrations of eastern Bering Sea a) Kamchatka flounder (*Atheresthes evermanni*) and b) arrowtooth flounder (*A. stomias*). Arrows point to key identifying characters between the two species. Illustrations by Ashlee Overdick.

**Figure 2.** Distribution of abundance (catch/10m²) for formalin preserved larval and juvenile *Atheresthes* identified to species using visual identification techniques. a) arrowtooth flounder (ATF: *Atheresthes stomias*). b) Kamchatka flounder (KF: *A. evermanni*). In both maps, circles depict larvae (<25 mm SL), triangles depict juveniles (≥25 mm SL), X depicts calculation of mean distribution generated by ArcGIS software of larvae based on abundance, and diamond depicts calculated mean distribution of juveniles based on abundance. The size of circles and triangles is proportional to abundance.

**Figure 3.** Length-dry mass relationships for arrowtooth flounder (*Atheresthes stomias*) and Kamchatka flounder (*Atheresthes evermanni*) of larvae (a) and juveniles (b). Lines depict 573 the least-squares relationships for all species combined.

**Figure 4.** Measures of condition for arrowtooth flounder (*Atheresthes stomias*) and Kamchatka flounder (*A. evermanni*) collected in June/July (larvae) and September (juveniles) 2008–2010. a) % lipid (dry mass) and b) energy density (kJ/g). Sample sizes are indicated above each bar.
Figure 1. a)

Figure 2.

251
Figure 3.
Figure 4.

a)

b)
Table 1. Year and sampling date of cruises on which larval and juvenile *Atheresthes* specimens were collected. Number of specimens used listed.

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Table 2. Lengths of specimens used to measure condition. Measurements are mean ± standard error (number sampled).

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<thead>
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<td>2008</td>
<td>Larvae</td>
<td>14.4 ± 1.0 (6)</td>
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<td>2009</td>
<td>Larvae</td>
<td>12.4 ± 0.3 (57)</td>
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<td>Juveniles</td>
<td>37.2 ± 0.8 (9)</td>
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<td>2010</td>
<td>Larvae</td>
<td>11.9 ± 0.8 (11)</td>
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<td>Juveniles</td>
<td>48.7 ± 0.5 (39)</td>
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Conclusions:

The primary conclusion from this project is that the energy content of age-0 pollock during their first fall predicts their survival to age-1 (Heintz et al. 2013). Energy content is measured as the total energy content of the fish. It is the product of the energy density of the fish and it’s mass. Fish that are likely to survive winter must achieve a sufficient size and store a sufficient amount of lipid in order to maximize their probability of surviving winter. Their ability to achieve large size depends on water temperature. Development rate is accelerated in warmer water and fish are able to metamorphose sooner than in cool water (Smart et al. 2012). This early transition to the juvenile stage increases the time available for provisioning lipid stores prior to winter (Siddon et al. 2013). While warm conditions might be expected to maximize growth (Hurst et al. 2011) and the provisioning period, prey are less available under warm conditions (Coyle et al. 2011) and their overall lipid content is low (Heintz et al. 2013). In addition, there may be a poor spatial match between pollock and their prey (Siddon et al. 2013) in warm conditions. These observations are in direct contrast to the Oscillating Control Hypothesis (Hunt et al. 2008) and suggest that cool conditions are more likely to support high production of pollock than warm conditions. A similar story may exist for Pacific cod (Farley et al. in press), but there were too few samples to provide adequate detail.

Analysis of the energy content of arrowtooth flounder and Kamchatka flounder indicated flatfishes have different life history constraints from gadids. Both flatfish species had similar lipid and energy contents through all their developmental stages in contrast to walleye pollock and Pacific cod. However, it is unknown if their energy allocation strategies changes once they settled out of the water column. In addition it appears that arrowtooth and Kamchatka flounder partition their habitats temporally, with the latter species settling out of the water column earlier than the former.

BSIERP and Bering Sea Project connections:

This project would not have been possible without contributions from the ichthyoplankton and fish projects. Both of those projects conducted surveys and provided this study with laboratory samples. In addition, analyses conducted by those projects were important to understanding the data collected here. The ichthyoplankton study provided data on the distribution and diet of larval fishes and one of the graduate students ended up processing samples for this study and leading manuscripts. The fish study performed a similar role, providing diet and distribution data for juvenile forms. A difficulty associated with the structure of the overall program is that seasonal bioenergetics project was not wholly subsumed into one of the larger study groups (fish or ichthyoplankton). This hampered communication between this project and the others, particularly when they conducted independent meetings. Nevertheless, all the groups were receptive to the efforts of the bionenergetics project and willing to supply any and all requested data.

The laboratory studies were more ambitious than anticipated and we only were able to complete the RNA/DNA calibration and Pacific cod growth studies with the funds available. There were
insufficient numbers of fish available to conduct energetic studies during the developmental
process. However, these data have proven to be useful and provide a basis for understanding
observations of RNA/DNA made on field samples. Following this study we acquired three years of
RNA/DNA data from the field, this was insufficient for establishing environmental impacts. However,
today we now have five years of data and will collect a sixth set in the summer of 2014. This latter
set should provide insight into the growth under warm conditions. These latter samples will be the
subject of an upcoming manuscript.

Management or policy implications:

This study establishes a link between climate and the recruitment of age-0 pollock. It provides a
basis for understanding the recruitment process for walleye pollock in the eastern Bering Sea.
Beyond simply establishing a correlation, it develops from a theoretical underpinning and
demonstrates a way to link environmental variation to biological endpoints. The understanding
accrued in this project is important for explaining variability in the biomass of fishable populations.
By establishing this link it is now possible to predict how pollock biomass is likely to change in the
future in response to a warming climate. Consequently, the data are now considered in the pollock
stock assessment (e.g. Ianelli 2012) and NOAA’s annual Alaska Marine Ecosystems Considerations
Report for the North Pacific Fisheries Management Council (Zador 2013).

Publications:

Data or conclusions drawn from this project appear in the following publications.

De Forest, L., Duffy-Anderson, J.T., Heintz, R. A., Matarese, A. C., Siddon, E.C., Smart, T. I.,
Spies, I. B. (Submitted). Ecology and taxonomy of the early life stages of arrowtooth
flounder (Atheresthes stomias) and Kamchatka flounder (A. evermanni) in the
eastern Bering Sea. Deep Sea Research II.

Duffy-Anderson, J.T., Barbeaux, S., Farley, E., Heintz, R., Horne, J., Parker-Stetter, S. Petrik,
C., Siddon, E.C., Smart, T.I. (Submitted). A review and ecological synthesis of the first
year of life of walleye pollock (Gadus chalcogrammus) in the eastern Bering Sea and
comments on implications for recruitment. Deep Sea Research II.

Farley, Jr., E. V., Heintz, R. A., Andrews, A. G., Hurst, T. P. (Submitted). Size, diet, and
condition of age-0 Pacific cod (Gadus macrocephalus) during warm and cool climate
states in the eastern Bering Sea. Deep Sea Research II.

recruitment and fall condition of age-0 pollock (Theragra chalcogramma) from the
Hunt, G. L., Jr., Stabeno, P. J., Strom, S., and Napp, J. M. 2008. Patterns of spatial and
temporal variation in the marine ecosystem of the southeastern Bering Sea, with

Hunt GL Jr, Coyle KO, Eisner L, Farley EV, Heintz R, Mueter FJ, Napp JM, Overland JE, Ressler
PH, Salo S, Stabeno PJ (2011) Climate impacts on eastern Bering Sea foodwebs: A
synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES

pollock (Theragra chalcogramma) from age-0 to age-1 in the southeastern Bering

Siddon, EC, Kristiansen T, Mueter FJ, Holsman KK, Heintz RA, Farley EV. 2014. Spatial match-
mismatch between juvenile fish and prey provides a mechanism for recruitment
variability across contrasting climate conditions in the eastern Bering Sea. PLoS One
8(12) doi:10.1371/journal.pone.0084526

(Submitted). A mid-trophic view of subarctic productivity: Lipid storage, location

Sreenivasan, A. (2011) Nucleic acid ratios as an index of growth and nutritional ecology in
Pacific cod (Gadus macrocephalus), walleye pollock (Theragra chalcogramma), and
Pacific herring (Clupea Pallasii). PhD Dissertation. University of Alaska, Fairbanks,
Alaska. 112 p.

Poster and oral presentations at scientific conferences or seminars

Oral presentations:
Growth and Energy Allocation in Larval Pollock from the Bering Sea. 2009 Larval Fish
Conference. Portland, OR.

Bioenergetic Constraints on Winter Survival in Subadult Walleye Pollock (Theragra

Climate related changes in the nutritional condition of young-of-the-year pollock
(Theragra chalcogramma) from the eastern Bering Sea. 2011. Ecosystem Studies of
Subarctic Seas Open Science Meeting. Seattle, WA.

Climate Effects on the Nutritional Condition and Productivity of Marine Fish Populations.


Posters

Differences between observed growth and a physiological growth index (RNA/DNA ratio) in larval Pacific cod (*Gadus macrocephalus*) at different temperatures. 2009. Alaska Marine Sciences Symposium, Anchorage, AK


Seasonal patterns of energy content and allocation in walleye pollock (*Theragra chalcogramma*). 2011. Alaska Marine Sciences Symposium, Anchorage, AK

Age-1 walleye pollock in the eastern Bering Sea: distribution, abundance and energy density. 2011. Alaska Marine Sciences Symposium, Anchorage, AK

Variability in energetic status, diet and size of age 0 Pacific cod during warm and cold climate states in the eastern Bering Sea. 2013. Alaska Marine Sciences Symposium, Anchorage, AK

An individual-based model for growth of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea: implications for bottom-up control of recruitment success. 2013. Alaska Marine Sciences Symposium, Anchorage, AK

**Outreach**

Samples and concepts derived from this project formed the basis of several high school science fair projects, a Dartmouth University Steffanson Internship Grant and work conducted by a NOAA Hollings Scholar. One of the science fair projects advanced to the Intel International Science and Engineering Fair. It was titled “Applications of Bioelectrical Impedance Analysis to Predict Energy Content of Walleye Pollock”. The Hollings scholar examined seasonal variation in the energy content of *Thysanoessa raschii*. The Dartmouth intern conducted a latitudinal analysis of the energy content of capelin.

**Acknowledgements**

I wish to thank all of the technical staff at the Auke Bay Laboratories for receiving, maintaining and processing the samples. The efforts of Robert Bradshaw, Andrew Eller, Lawrence Schaufler, Ann Robertson, Kevin Heffern, and Elizabeth Parker were particularly helpful. Thanks are due to the staff of the NOAA-AFSC laboratory at the Hatfield Marine Science Laboratory in Newport OR for their help in developing the RNA/DNA studies.
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(Submitted). A mid-trophic view of subarctic productivity: Lipid storage, location  

influence walleye pollock early life stages in the southeastern Bering Sea. Marine  
Ecology Progress Series 455:257-267. DOI:10.3354/meps09619

Sreenivasan, A. (2011) Nucleic acid ratios as an index of growth and nutritional ecology  
in Pacific cod (Gadus macrocephalus), walleye pollock (Theragra chalcogramma),  
and Pacific herring (Clupea Pallasii ). PhD Dissertation. University of Alaska,  
Fairbanks, Alaska. 112 p.

Evaluation Report, North Pacific Fisheries Management Council, 605 W 4th Ave,  
Suite 306, Anchorage, AK 99501