Hatch timing, growth, and condition of juvenile Arctic cod (*Boreogadus saida*) in a warming Arctic: insights into overwinter survival strategies

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Abstract

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Arctic cod (*Boreogadus saida*) is a highly abundant fish species with a circumpolar distribution and is generally considered to be an energetically key component of the Arctic food web. Warming conditions and corresponding shifts in sea-ice extent and timing, prey composition, and predator/competitor interactions pose a risk to this cold-adapted species. Laboratory studies have demonstrated that critical early life stages have a narrow thermal tolerance and are particularly vulnerable to warming conditions. Here I examine how growth and hatching dynamics differed across and within years, with a particular emphasis on the role of temperature on these processes. I compared the pre-winter size and lipid storage of juvenile Arctic cod, which impact overwinter survival and recruitment dynamics, during a period of dramatic warming. Fish were captured during 2013, 2017, and 2019 summer surveys in the northern Bering and Chukchi Seas. Otoliths were processed to provide age and growth information and total fatty acids were assessed separately as a metric of lipid storage. Water temperatures during the summers of 2017 and 2019 were warmer than in 2013, and fish from 2017 and 2019 were larger and older on average. The summer growth and lipid storage of juvenile Arctic cod were similar among years, with the exception of 2017 fish having markedly lower concentrations of total fatty acids. We fit a series linear models to evaluate the effect of capture date, temperature, and sample year on both growth and lipid storage, and judged the weight of evidence using likelihood ratios. There was some evidence that earlier in the sampling season, temperature affected both the growth ($\chi^2_{(2)}$ = 7.99, p = 0.018) and lipid storage ($\chi^2_{(2)}$ =

8.61, p = 0.014) of juvenile Arctic cod, but exerted little to no influence at later stages. The results of this study suggest that sampled fish were able to attain larger pre-winter sizes in 2017 and 2019 because they hatched earlier and thus had longer growth periods, not because they grew faster. Temperature explained little of the variation in the growth or lipid storage of juvenile Arctic cod, despite their exposure to thermally distinct conditions during the weeks preceding capture. This suggests that other ecological factors, such as diet and water mass dynamics, that tend to covary with temperature, are currently exerting a greater influence on pre-winter survival than temperature alone.

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Dedication

To my grandmother who was full of grit and mirth, who gave when she had nothing to give, saw beauty in everything, and cared deeply for the individuals and world around her. She was more inspirational than she could ever know and I owe so many of my core values to her existence.

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1. Introduction

Conditions in the Pacific Arctic marine ecosystem are rapidly shifting, with warming temperatures and diminishing sea ice initiating a cascade of effects throughout the system (Huntington et al. 2020; Baker et al. 2020b). The rate and magnitude of these changes are among the highest in the world and are approaching irreversible levels of change for the foreseeable future under all warming scenarios (Constable et al. 2022). Central to the concerns brought about by these changes are if, how, and to what extent Arctic species will cope with these new conditions. Arctic cod (*Boreogadus saida*) is a prime example of a species at risk of such warming, given a specialized ability to thrive in polar conditions (Laurel et al. 2016; Mueter et al. 2016; Drost et al. 2016). Arctic cod is highly abundant, with a circumpolar distribution, and is generally considered to be an energetically critical component of the Arctic food web (Hop and Gjosaeter 2013; Whitehouse et al. 2014; Dupont et al. 2021). Given the ubiquity of Arctic cod and its importance for energy transfer in the food web, it is important to expand what we know of Arctic cod ecology in the context of climate change.

While Arctic cod has received increasing attention from the scientific community in recent years (Mueter et al. 2020), the inherent difficulties associated with studying mobile aquatic organisms that spend large portions of their life history beneath sea ice or in the darkness of polar night, have made it challenging to study this species throughout the entirety of its life history. Much of the uncertainty regarding this species is centered around the long, dark, ice-covered periods in the Arctic. Not only is this a time notoriously challenging to directly observe fish in the region (though see Benoit et al. 2010), it is also considered to be a major survival bottleneck for the fish themselves as they fight to survive the long, cold, unproductive period. While overwinter survival is a challenge for all high latitude fish, it is most critical for fish in their first year of life (Beamish and Mahnken 2001; Hurst 2007).

Arctic cod spawn during the winter months beneath the sea ice and produce ice-associated, buoyant eggs (Graham and Hop 1995). This is followed by a protracted hatch season that varies by region but generally extends from January to July (Bouchard and Fortier 2011; Chapman et al. 2022). To survive the extended overwintering period characteristic of northern latitudes, young-of-the-year Arctic cod must rapidly grow and store energy during a brief productive period to maximize the likelihood of overwinter survival (Copeman et al. 2022b). Obtaining a larger pre-winter size confers a survival advantage for juvenile Arctic cod via enhanced predator avoidance, resistance to starvation, and physiological tolerance to extreme conditions (Bouchard & Fortier 2008; Bouchard et al. 2017; Sogard, 1997). Additionally, any energy stores they are able to amass must be sufficient to sustain them through the long, unproductive winter period characteristic of the region. Any external factors that affect the ability of juvenile Arctic cod to grow and store energy can affect overwinter survival and, therefore, recruitment success.

Summer sea surface temperatures in the Pacific Arctic are currently warming at a rate of approximately +0.5°C per decade, and temperatures surpassing 9°C have been observed in the Chukchi Sea in recent years (Baker et al. 2023; Timmermans & Labe 2023). In warmer thermal regimes, the quality of zooplankton prey shifts from larger, lipid rich copepods that Arctic cod prefer to smaller, less energetically dense boreal species (Walkusz et al. 2011; Bouchard and Fortier 2020; David et al. 2022) and the northward expansion of more boreal fish species have resulted in increased predator and competitor overlap for Arctic cod (Baker 2021, Levine et al. 2023a). Warmer temperatures also cause changes in sea ice dynamics, freshwater inputs from inland sources, and water mass and wind dynamics—changes that are disruptive to established early life history patterns for Arctic cod (Spencer et al. 2020; Geoffroy et al. 2023; Goldstein et al. 2023). While warming conditions in the Arctic and corresponding shifts regional biological and environmental trends inherently affect the early life history strategies of Arctic cod, there are also a number of ways that increasing temperatures can directly affect both the pre-winter size and lipid storage of young-of-the-year Arctic cod.

Laboratory studies have evaluated the effect of temperature on larval and juvenile Arctic cod and have demonstrated that egg development and hatch success (Laurel et al. 2018), growth (Laurel et al. 2016, 2017; Koenker et al. 2018), and lipid accumulation and conservation (Copeman et al. 2017, 2022b) are all highly sensitive to temperature. Differences in hatch timing and hatch success are an important consideration for pre-winter size (along with growth rates) as they determine the length of the growing season and a longer growing season is often associated with a larger pre-winter size (Bouchard & Fortier 2011). Generally, time-to-hatch for Arctic cod decreases with increasing temperature, though hatch success declines markedly beyond 3°C (Laurel et al. 2018). The conditions post-hatch are also important to consider, and early hatchers are at risk of inadequate access to food and exposure to non-optimal conditions if they hatch before the ice break up and productive bloom in the spring (Fortier et al. 1996; Siddon et al. 2013b; Vikebo et al. 2021). Specific growth rates and lipid accumulation of juvenile Arctic cod in a laboratory setting exhibit positive relationships with temperature up to approximately 7-8°C and 9°C, respectively, when fish are fed daily to satiation (Laurel et al. 2016; Copeman et al. 2017). However, in the warmer temperature treatments of these studies (9°C+) growth and lipid accumulation declined, fish became visibly more stressed, and in some instances increased mortality was observed. A more recent study found that juvenile Arctic cod under simulated winter conditions (food deprived, 24-hr darkness) depleted energy stores more rapidly and experienced increased mortality at warmer temperatures (Copeman et al. 2022b). These studies have provided invaluable insight regarding the potential responses of Arctic cod to climate warming, though it remains unclear whether the thermal sensitivities observed in young captive fish translate to comparable responses for wild fish and what this means in terms of overwinter survival. To fully realize the value of these laboratory studies, it is important to compare the hatch dynamics, growth, and condition of laboratory fish to that of wild fish under comparable thermal conditions. Doing so improves understanding of how to apply these laboratory findings to wild populations and enhances our ability to monitor Arctic cod moving forward. Though it is important to note that the complexity of the system and the covariance of temperature with a number of other ecological factors, makes it challenging to disentangle the effect of temperature on these parameters.

While the effect of water temperature on the above parameters remains the primary focus of this work, the influence of salinity and sea ice dynamics on Arctic cod egg and larval development, and thus hatch dynamics, are significant and also considered here. Salinity varies seasonally as a function sea ice dynamics, freshwater input from inland riverine and glacial sources, precipitation, and local water mass dynamics, all of which are considered to be important factors affecting Arctic cod hatch dynamics (Bouchard and Fortier 2008; Schembri et al. 2021; Goldstein et al. 2023). Arctic cod eggs are tolerant to a wide range of salinities, but are characterized by specific densities meant to retain them under or near the sea-ice. Regional changes in salinity affect the buoyancy of Arctic cod eggs and their vertical distribution in the water column during the incubation and post-hatch time frames (Spencer et al. 2020). Furthermore, more saline water has a lower freezing point that results in a lower quality habitat for Arctic cod eggs and larvae than fresher water masses with slightly elevated temperatures (Schembri et al 2021). This relationship between salinity and temperature brought about “the freshwater winter refuge hypothesis”, and subsequent tests suggest that Arctic cod do in fact hatch sooner and survive better as larvae in regions with increased freshwater input (Bouchard and Fortier 2011; Bouchard et al. 2015; Schembri et al. 2021). We also consider sea ice dynamics due to the critical ecosystem services it provides to Arctic cod eggs and larvae in the form of complex habitat for predator avoidance, ice-associated prey for newly-hatched larvae, turbulence reduction, and UV protection for developing eggs to name a few (Bouchard and Fortier 2008; Geoffroy et al. 2023). Due to these associations Arctic cod hatch has historically been intimately tied to the timing of the sea ice break up (Bouchard & Fortier 2008). We contextualized inter-annual differences in hatch by assessing how these two variables, along with temperature, differed among years.

This work aims to evaluate the association between temperature and the pre-winter size and lipid storage of Arctic cod entering their first winter across three years characterized by distinct seasonal patterns of temperature, salinity and ice melt. Effects of temperature on pre-winter size were considered through two lenses: 1) the association between temperature dynamics on hatch dates of sampled fish (which dictates the length of the growing season), and 2) the association between recent temperature experience and individual growth rates. The pre-winter condition and lipid storage of these fish have been previously evaluated by Copeman et al. (2022a). The impetus for including the findings of Copeman et al. (2022a) in this work (apart from it being a major overwinter consideration) is that juvenile fish in highly seasonal, northern latitude ecosystems face competing energy demands of maximizing somatic growth and energy storage (Post & Parkinson 2001; Mogensen & Post 2012). Often, energy allocation for young-of-the-year fish in this context is structured around seasonal and ontogenetic demands and favors more allocation to growth and development in earlier life history stages and a shift to allocation into energy stores preceding the first winter (Post & Parkinson 2001; Mogensen & Post 2012; Siddon et al. 2013a). With access to both growth and lipid information, we explored whether there was any evidence of preferential allocation of energy reserves into storage tissues versus growth tissues as the fish enter their first winter and whether temperature seemed to influence this allocation strategy. Clarifying how temperature affects these life history parameters improves our understanding of how continued warming may affect juvenile Arctic cod overwinter survival and recruitment dynamics.

2. Materials and Methods

2.1 *Sample Collection Methods*

Juvenile Arctic cod were collected from the northeastern Bering and Chukchi Sea regions during the late summer of 2013, 2017, and 2019 with collection dates ranging from August 13 to September 27 (Figure 1). The fish used for this study were collected via midwater and surface trawls in the 2013 Arctic Ecosystem Integrated Survey (Arctic EIS) and 2017 and 2019 Arctic Integrated Ecosystem Research Program (Arctic IERP) surveys using a variety of gear types. Information regarding the background and specifics of the EIS and Arctic IERP surveys can be found in Mueter et al. (2017) and Baker et al. (2020, 2023) respectively. Detailed information regarding collection specifics, fish handling techniques, and lipid analyses are provided in Copeman et al. 2020 and Copeman et al. 2022 and are briefly outlined here.

Upon capture, Arctic cod were immediately placed on ice and frozen at < −20 °C within 6 h of capture. Samples were stored at −80 °C in the Alaska Fisheries Science Center (AFSC) Auke Bay Laboratories following the surveys and until they were shipped frozen overnight from Alaska to the Marine Lipid Ecology Laboratory at the Hatfield Marine Science Center (HMSC) in Newport, OR, USA.
At the time of tissue sampling, standard length (SL, ± 0.1 mm) and wet weight (WWT, ± 0.0001 g) were recorded. Fish were then washed with filtered seawater, blotted dry, stomachs and intestinal tracts were removed and heads were frozen and sent to the AFSC Resource Ecology and Fisheries Management Division (REFM) Age and Growth Program in Seattle, WA for otolith analysis. Fish were then bisected along the dorsal–ventral plane and one-half of the fish tissues, including both muscle and liver, were re-weighed, placed in chloroform under nitrogen and frozen at −20 °C. Lipid samples were extracted within 2 months of dissection (Copeman et al. 2022a).

A random subset of the age-0 Arctic cod analyzed in Copeman et al. (2022a) for lipids were used in this project to examine the daily age, growth, hatch dates, and lipid storage in the same fish under different conditions. To filter out fish older than age-0, only fish with a SL < 70 mm were selected for otolith removal using known age-length relationships for Arctic cod (Stone et al. 2019). Otoliths were removed in the laboratory under a dissecting microscope using acid-washed forceps, wiped and rinsed with ethanol to remove tissue residue, and stored in ethanol. Prior to preparation for age estimation, each otolith was checked using surface examination under a dissecting microscope to confirm an age of 0 (Stone et al. 2019). From the confirmed age-0 fish, one otolith was reserved for other analysis and the second was prepared for daily growth increment enumeration and measurements.

2.2 *Laboratory Methods*

We used the larger sagittal otoliths, to estimate age and growth for a minimum of 20 fish from each target year. In former studies examining Arctic cod daily increment formation, the smaller lapillar otoliths have commonly been used (Bouchard and Fortier 2011; Bouchard et al. 2015). However, a number of studies have compared age estimates from sagittal and lapillar otoliths in other gadid species and found that they produced reliably similar age estimates (Campana and Hurley 1989; Hüssy et al. 2003; Narimatsij et al. 2007). More recently, Chapman et al. (2022) validated the use of Arctic cod sagittal otoliths for daily increment analyses by comparing the sagittal and lapillar larval otoliths from a small sample of known-age, laboratory-reared Arctic cod.

Each otolith was polished transversely using various grades of sandpaper and lapping film to create a thin section that included the primordium and was thin enough to view daily growth increments at 100x magnification with transmitted light (Figure 2). This was done by mounting each otolith to a glass slide using clear thermoplastic glue so that either the anterior or posterior tip (excluding the core) hung over the slide edge. The slide was then held vertically (with the otolith side down) and gently ground up to the slide edge using a Buehler EcoMet Grinder/Polisher (Buehler, Lake Bluff, IL, USA) with 800 grit sandpaper. The otolith was then rotated 180° and the same was done for the other side to produce a thick transverse section that included the primordium. This section was then mounted onto a new slide with either the anterior or posterior end flush with the slide and the remainder of the polishing was done by hand using extremely fine grit lapping paper. In instances where the core was over-polished or missed altogether, that fish was excluded from subsequent age determination and new samples were selected in its place.

All otolith sections were imaged with a Nikon Eclipse Ti2E compound microscope using a 90x oil immersion objective lens. Age estimates were obtained by counting daily increments along the proximal-distal axis under a compound microscope with transmitted light at 100x magnification and annotating increments using an image analyzer system Image Pro 10® (Media Cybernetics). Each otolith was aged a at least twice by the primary analyst and a third time if the two ages were not within a 10% coefficient of variation (CV). Had any of the third estimates still not been with in a 10% CV of either of the initial two ages, that fish would have been excluded from further analyses. This did not occur for any of the aged samples in this project, and all samples were kept. Each age estimate was conducted using separate images, with a minimum of 7 days between estimates. One quarter of the otoliths were randomly subsampled, and independently aged by a second experienced analyst to test precision and bias using the same CV thresholds listed above. Using all available ages and annotations for each otolith (including the test ages from the secondary analyst), discrepancies were resolved and a final age was determined for each fish and used in all subsequent analyses. All otolith increment widths were measured using ImagePro 10 (Media Cybernetics).

2.3 Hatch Dates

The hatch dates for each fish were estimated by subtracting the daily age from the capture dates. Annual hatch date distributions of sampled Arctic cod were visually compared using density plots. We compared both the mean and variance in hatch dates of sampled fish by and fit kernel density smoothers to describe the distribution of hatch dates of sampled fish. These distributions provide information on the hatch timing of individuals that survived to the day of capture. Therefore, it combines information about timing of hatching events and how survivorship varied depending on timing of hatching.

Hatch distributions of sampled Arctic cod were visually compared to the daily temperature, salinity, and sea ice fraction time series in the northern Bering Strait region (see Station A3 in Figure 1) from January through mid-June to characterize the oceanographic conditions during the plausible Arctic cod incubation and post-hatch time frames (Geoffroy et al. 2023). Such visual comparisons were made to clarify the factors that may have influenced observed differences in hatch timing. This particular region was selected based on recent research findings that suggest spawning of Arctic cod in the Pacific Arctic likely occurs in the northern Bering Sea, southern Chukchi Sea, and/or Kotzebue Sound and that the fish sampled during the summer surveys in the Chukchi are largely advected north from these regions (Vestfals et al. 2021; Deary et al. 2021; Levine et al. 2023b).

To assess the association between temperature and the development and survival of Arctic cod eggs and larvae, we compared the thermal trends during the range of potential winter-spring incubation and post-hatch time frames to the hatch distributions of the sampled Arctic cod. Temperature data pertaining to hatch was obtained from the A3mooring time series data set (Woodgate 2018; Woodgate & Ferriz 2021). Because Arctic cod eggs are buoyant and incubate near the surface in association with the sea ice (Graham and Hop 1995), the ideal characterization of temperatures during incubation would have been in the form of SST. In fact, SST (°C) time series data were initially obtained from JPL NASA Level 4 sea surface temperature database at a resolution of 0.5° latitude and 0.5° longitude from January through mid-June between 66° N and 71° N and between 176° W and 157° W for each sample year (JPL MUR MEaSUREs Project, 2015). Unfortunately, cloud cover and sea ice hindered the continuity and precision of these values. As such, we opted to use available mooring data that was more continuous and less affected by such environmental factors. The Bering Strait climate site A3 mooring data set is generally considered to be the best available representation of the mean properties of the non-Alaska Coastal Current waters of the region (Woodgate 2018; Woodgate and Peralta-Ferriz 2021) and was thus chosen as the primary source of temperature data in the Bering Strait region. Average daily temperatures were calculated and used in subsequent comparisons with hatch distributions. Salinity values were obtained from the same Bering Strait A3 mooring dataset described above and average daily values were plotted during the time frame of interest. Daily sea ice fractions were obtained from JPL NASA Level 4 SST database at a resolution of 0.5° latitude and 0.5° longitude from January through mid-June between 66° N and 71° N and between 176° W and 157° W for each sample year (JPL MUR MEaSUREs Project, 2015).

2.4 Summer Thermal Experience

Temperature values to characterize the recent (relative to time of capture) summer thermal experience of Arctic cod in the Chukchi Sea were obtained from three sources: CTD casts at the time of capture, near-bottom mooring data from 5 stations in the Chukchi Sea (Fig.1.), and satellite-derived SST data for the region. The most direct measure of near-term thermal experience came in the form of temperature values obtained from CTD casts at the time of capture. However, as we were interested in characterizing the thermal experience for longer periods of time beyond the snapshot provided by CTD data, oceanographic information was also obtained from the Icy Cape mooring data set for all three sample years (Stabeno and McCabe 2023). Each Icy Cape mooring device was located near-bottom (located at approximately ~39m) and recorded oceanographic data, including temperature, hourly. Because mooring data for 2013 was temporally and spatially sparse, only 2017 and 2019 mooring data were used to estimate the recent thermal experience for each fish. For 2017 and 2019, the inverse distance weighted mean temperature was calculated for each fish for the 30 days preceding capture using temperature data from all 5 mooring stations as follows:

$$\bar{T}_i = \sum_{j=1}^{n} w_j T_j \text{ where } w_j = \frac{1/x_j}{\sum_{j=1}^{n} (1/x_j)} \qquad \text{Equation 1}$$

Where $\bar{T}_i$ represents the weighted mean temperature for fish_i, w_j is the weight for station j, T_j is the temperature for the 30 days pre-capture of fish_i at station j, and x_j indicates the distance between each station j and the capture location for each fish_i. The 30 days preceding capture were selected to better align with presumed integration times for the lipid data (L. Copeman, personal communication, 2023).

Given the temporal and spatial constraints of the CTD and mooring data, satellite-derived SST data was also used to further characterize the thermal experience of age-0 Arctic cod from all three sample years and capture locations. Daily SST (°C) time series data were obtained from JPL NASA Level 4 sea surface temperature database at a resolution of 0.5° latitude and 0.5° longitude between 66° N and 75° N and between 170° W and 156° W for the time period of interest (JPL MUR MEaSUREs Project, 2015). Interannual comparisons of temperature by depth in the region were made using mooring and satellite temperature data at the location of mooring station C2 as this site was both centrally located in the survey region and was the only mooring that had complete data for all three sample years. Summer monthly trends of SST in the northern Bering and Chukchi Seas were also mapped to visualize latitudinal and longitudinal differences in temperature by year. For each fish, SST was averaged for the 30 and 7 days preceding capture in a 1° latitude x 1° longitude (~ 111 km x 111 km) grid centered on the capture location.

2.5 Size and Growth

To determine if the size-at-age relationship differed between individuals caught in the three sample years, we fit several multiple linear regression models with the response variable of individual standard length (SL, mm) as a function of age, age and year, and age and year with an age-year interaction to account for the variable hatch date distributions. We evaluated degree of support using likelihood ratio tests.

Otolith increment widths are considered roughly proportional to the growth of the fish when the fish length:otolith length relationship is linear (Fey and Węsławski 2017; Fey and Greszkiewicz 2021). Given the adequately linear relationship between otolith diameter (measured through the core from the anterior to the posterior tip) and standard length for the fish used in this study ($R^2 = 0.92$, $P < 0.001$), we felt justified in using otolith measurements as a proxy for growth. Recent growth rates were calculated for two time periods: one for 30 days preceding capture to provide a growth metric that more accurately aligned with the time frame reflected in the lipid assays (Copeman et al. 2013) and another for 7 days preceding capture to allow for more confidence in the thermal comparisons under the assumption that the fish were closer to their respective capture locations during this narrower time window. In each instance, recent growth rate refers to the average otolith growth rate (μm/day) that occurred during the 30 or 7 days pre-capture and was calculated as follows:

$$g = (w_t - w_0)/t$$

Where g is the growth rate for a given fish during the specified pre-capture period, w_t is the otolith radius (from the core to the distal edge) at the time of capture, w_0 is the otolith radius from the core to the daily increment 30 or 7 days prior to the date of capture (e.g. the otolith edge), and t is the amount of time that spans this increment width (in this case, t = 30 or t = 7 days). Two different models of growth were initially considered: a linear growth model and an exponential growth model. We used maximum likelihood estimation to find the best-fitting parameters for both and found that the linear model had a much lower sum of squares than the exponential model. This indicated that the linear model was a better fit for the data and was thus used for all growth calculations. Recent growth rates were plotted against age and standard length and a linear regression was performed to check whether there were any age- or size-dependent influences on recent growth. In both instances, there were no detectible relationships between growth and these metrics during these time windows (Figure 3). As such, we used growth rate as our dependent variable without standardization for size or age, to explore how it differed in relation to sample year, time of year, and thermal experience.

We conducted several tests to identify sources of variation in recent growth. For this portion of the growth analysis, we used only growth values for the 7 days pre-capture. Growth rates for the 30-days pre-capture were used only in comparisons with lipid storage below. Because sampling days varied across survey years, seasonally-dependent growth might impede our ability to robustly estimate whether growth differed across years. For that reason, we fit two linear models and judged the weight of evidence using likelihood ratios. In the first model, growth rate was a function of sample day of year, and in the second, growth rate was a function of both sample day of year and a categorical year effect. As the sample years chosen for this work were selected on the basis of their unique temperature qualities, we also opted to more specifically evaluate whether individual differences in growth were related to temperature during this time frame. Because temperature varied seasonally, three linear models were fit to assess whether growth varied as a function of recent temperatures while considering seasonality: in the first model, growth rate was a function of sample day of year (null model), in the second, growth rate was a function of both sample day of year and the mean SST during the 7 days preceding capture, and in the third model growth rate was modeled as a function of sample day of year, mean SST during the 7 days preceding capture with a sample day of year-SST interaction term. We evaluated degree of support using likelihood ratio tests (package "lmtest").

2.6 Lipid Storage and Growth

Total fatty acids (mg/g fish wet weight) sampled from fish liver and muscle tissue by Copeman et al. (2022a) were used to evaluate differences in lipid storage across the sample years and in relation to somatic growth rates. We used a one-way ANOVA to determine whether total fatty acids varied significantly among the three sample years. To account for variation that may be due to differences in sampling time frames, we fit models using the same predictors and formats used for recent somatic growth. We compared two models, the first with sample day of year and the second with both sample day of year and capture year, evaluating degree of support using likelihood ratio tests. We then sought to test whether there was a relationship between total fatty acids and recent temperatures (in this case, during the 30 days preceding capture). To determine whether total fatty acids varied with recent temperatures, we fit three models, the first with sample day of year (null model), the second with both sample day of year and mean SST for the 30 days preceding capture, and a third model with sample day of year, mean SST, and a sample day of year-SST interaction term. We evaluated degree of support using likelihood ratio tests.

Finally, a linear regression of total fatty acids and recent (30 day) somatic growth was performed to evaluate if any relationship existed between the two important pre-winter growth metrics.

All data analysis and visualization were performed using R Statistical Software (v4.2.2; R Core Team 2022).

3. Results

3.1 Hatch Dates

Hatch distributions of sampled Arctic cod were markedly different between the three sample years. Hatching of fish sampled in 2013 began later than the other two sample years, with hatch beginning in early April and followed by larger pulses in mid-April and May (Figure.4). In contrast, the earliest sampled hatch dates were observed in the 2019 cohort, where hatching began in mid-February, and continued through the spring and into early summer. Sampled hatched dates in 2017 were intermediate to these two years, beginning in late March and peaking April through mid-May.

Examination of temperatures during the incubation and post-hatch time frames revealed similarities and some minor differences among the three study years. Temperatures from January through mid-June were generally similar (~-2°C) in all years for fish that hatched before May (Figure 4). However, in January of 2017 and 2019, there was a pulse of warmer water (approximately 0°C) that was absent in 2013. Once seasonal warming began in late April, the thermal profiles of the three years were markedly different. As such, later hatching fish (predominantly from May onwards) experienced different incubation and post-hatch temperatures, with 2013 generally being cooler than 2017 and 2019. Fish that hatched after May 2017 experienced the warmest conditions of all years and months considered.

The salinities during potential incubation and post-hatch time frames were markedly different and highly variable. The water during the potential incubation time frames were much fresher from January to late May in 2017 and 2019 than in 2013 (Figure 4). After May, salinities were more comparable in all three years. Seasonal patterns of sea ice concentration also differed among the sample years. Sea ice retreat (as indicated by lower or declining fraction values) in the region began the earliest in 2019, followed by 2017 and was the latest in 2013 (Figure 4).

3.2 Summer Thermal Experience

All three sources of temperature data for the Chukchi summer months supported the initial premise that 2013, 2017 and 2019 were thermally distinct years. Binned surface and bottom CTD temperature values indicated that at the time of capture, 2013 was cooler on average than the other two years both at the surface and at depth (Figure 5). For the remaining two years, CTD data indicated that 2019 had warmer average surface temperature but cooler average near-bottom temperature than 2017. Mooring and satellite temperature data generally confirmed these patterns but also revealed differences in the seasonal pattern of temperature. Mooring and satellite temperatures at the Chukchi C2 mooring site were always lower in 2013 than in the other years, regardless of depth (Figure 6). Thermal trends in 2017 and 2019 varied by season and depth. From July through early September, mooring data indicated that 2017 was consistently warmer than 2019 at depth. Interannual trends at the surface were more complex. Surface waters in the central Chukchi were the warmest in 2017 until the end of July. In August, 2019 SST surpassed 2017 SST, increasing to upwards of 9°C. Maps displaying larger scale, regional trends in the Northern Bering/Chukchi Sea summer SST revealed that that surface temperatures in 2017 and 2019 were consistently warmer than in 2013, and this pattern was strongest in July in the northern Bering Sea Region (Figure 7). As the summer progressed, surface waters in 2019 was generally warmer than the other two years, particularly in the southern Chukchi Sea).

The recent temperature values assigned to individual Arctic cod for growth analyses (based on capture location) varied by year, by depth, and depended on the temperature data source (Figure 8). The temperature at capture (mean water column temperature from CTD cast) was similar across years, though 2013 had a wider range of temperatures at capture. Mooring data for the available years suggested that 2017 was warmer at depth than in 2019. SST data during the 7 and 30 days preceding capture suggested a gradual warming trend over time with 2013 again having the widest range of temperatures. For all subsequent growth and lipid analyses, only the satellite-derived SST values were used as it was the only temperature data source that had complete spatio-temporal information for all three years.

3.3 Size and Growth

Size-at-age for sampled Arctic cod was similar in the three sample years, though a greater number of larger, older fish were observed in 2017 and 2019 than in 2013. Of the three models tested to explore differences in size-at-age for the three sample years, there was no evidence that models including the year in which the fish were captured performed better than the simpler model that included only age as a predictor. In both instances, the alternative hypothesis that a more complex model that includes sample year or a model that includes the sample year and a sample year – growth interaction term was rejected ($\chi^2_{(2)}$ = 2.42, p = 0.298 and $\chi^2_{(4)}$ = 7.38, p = 0.117, respectively; Figure 9).

Recent growth rates during the 7 days preceding capture did not differ among the sample years (Figure 10). Similarly, growth rates were similar regardless of the day a fish was captured (likelihood ratio test: $\chi^2_{(2)}$ = 4.78, p = 0.092). When we considered growth as a function of recent temperatures and the day of capture, we saw evidence for a seasonally-dependent association between growth and these parameters. Each of the models with SST predictors were tested against the null model with capture day as the only predictor. The alternative hypothesis was accepted only for the model that included day of capture, SST and a capture day-SST interaction term ($\chi^2_{(2)}$ = 7.99, p = 0.018) and rejected for the model that included capture day and SST alone ($\chi^2_{(1)}$ = 1.29, p = 0.256). Model predictions suggest an inverse effect of temperature on growth early in the sampling frame with little no effect on growth for the mid to late sampling time frames (Figure 11). Model predictions for the accepted alternative model above were plotted for fish sampled in the early (August 13 – 23), mid (August 30 – September 9), and late (September 17-27) time frames. As the later sampling time frame had fewer fish and exhibited the same prediction pattern as the mid capture time frame, it was excluded here. An early sampled fish from 2017 (white diamond in plot 11, early capture panel) was tested to determine whether it was leveraging the negative relationship between growth and SST for fish captured in the early time frame given its positionality. When this fish was removed, the seasonal relationship between growth SST did not change.

3.4 Lipid Storage and Growth

Total fatty acid content of Arctic cod differed among the three sample years (p = 0.015; Copeman et al. 2022a), and there was evidence for a seasonal association between temperature on lipid storage. Fish caught in 2017 generally had lower total fatty acids than fish caught in either 2013 or 2019 (Figure 12). An alternative model of total fatty acids as a function of day of capture and sample year was tested against a null model of total fatty acids as a function of day of capture alone. The null model was rejected in favor of the alternative model of total fatty acids that included both capture day of year and capture year ($\chi^2_{(2)}$ = 7.72, p = 0.021). In models testing whether total fatty acids varied as a function of the recent temperatures experienced by the fish, two different models were tested against a null model that included only the day of capture as the single predictor: Model 1 included day of capture and the mean SST for the 30 days preceding capture as predictors and Model 2 included day of capture, mean SST, and a day of capture-SST interaction term as predictors. In the first comparison of the null model to Model 1, the null hypothesis was accepted ($\chi^2_{(1)}$ = 0.036, p = 0.849). In the second comparison of the null model to Model 2, the alternative model that included day of capture, SST, and a day of capture-SST interaction term was accepted ($\chi^2_{(2)}$ = 8.61, p = 0.014). Model 2 predictions suggest a strong direct effect of temperature on total fatty acids that is only evident early in the sampling frame and little no effect on total fatty acids for the later sampling time frames (Figure 13). Model predictions suggest a positive effect of temperature on growth that is only evident early in the sampling frame and little no effect on growth for the mid to late sampling time frames. Model predictions for the accepted alternative model were similarly plotted for fish sampled in the early (August 13 – 23), mid (August 30 – September 9), with the late time frame being excluded for the reasons mentioned above. The same early sampled fish from 2017 (white diamond in plot 13, early capture panel) was again tested to determine whether it was leveraging the positive relationship between total fatty acids and SST for fish captured in the early time frame. When removed, the relationship between fatty acids and SST did not change. There was no apparent relationship between total fatty acids and growth rates during the 30 days preceding capture (p = 0.408) (Figure 14).

4. Discussion

This work helped to clarify the associations between environmental variables and the pre-winter size obtained by juvenile Arctic cod in the Alaska Arctic. We identified large differences in Arctic cod young-of-the-year sizes across three years with different environmental conditions. Despite different thermal experiences, the growth rates of fish from all three sample years were similar during the week and month preceding capture and there was little evidence that thermally-mediated summer growth rates made a significant contribution to the larger pre-winter size of 2017 and 2019 fish. Thus, differences in hatch timing were primarily responsible for the larger sizes at catch of juvenile Arctic cod in 2017 and 2019 compared to 2013. This distinction is in line with similar findings in other regions of the Arctic where hatch-date explained 90% of the variance in pre-winter size in Arctic cod and lends increasing support to the notion that Arctic cod rely primarily on maximizing the duration of the first growth season to achieve a large pre-winter size (Bouchard and Fortier 2011). Earlier hatch timing of sampled fish could arise through favorable environmental conditions that promote incubation and hatching, and/or through favorable conditions that promote survivorship of early-hatched fish. There was a seasonally-dependent association between temperature on both the growth (negative) and lipid storage (positive) of juvenile Arctic cod that was only evident for fish captured earlier on in the sampling period. There was no indication of preferential allocation into either storage or growth tissues for these late-summer captured juveniles regardless of when they were captured.

Early hatch, the environment, and pre-winter size

The most striking finding of this work was the unique hatch distributions of Arctic cod sampled in the three oceanographically distinct years. We found that Arctic cod captured in 2017 and 2019 generally hatched earlier and had more protracted hatch distributions than those captured in 2013. Two distinct hatch patterns have formerly been observed in Arctic cod throughout their range as follows: 1) a short hatching period from May to June/July centered on the ice break-up and the onset of biological production (Bouchard and Fortier 2008), and 2) a protracted hatching season (January to July/August) with many larvae emerging well before the ice break-up (Bouchard and Fortier 2008; Chapman et al. 2022). The later, more condensed hatching period observed in 2013 is similar to that observed for Arctic cod in other regions that are centered on the ice break-up and the onset of biological production (Bouchard and Fortier 2008). Recently in the Alaska Arctic, Arctic cod often have exhibited an extended hatching season with peak hatch dates ranging from January to June (Chapman et al. 2022), which means that some larvae are hatching under the ice in winter and early spring—a time when light, temperature, and prey availability are notoriously low. It has been suggested that this reproductive strategy increases the likelihood that at least some portion of the cohort will encounter favorable survival conditions in a highly variable system, and in the case of early hatchers, provides an opportunity for Arctic cod to maximize their pre-winter size through an increase in the growing season (Bouchard and Fortier 2011; Chapman et al. 2022). A number of environmental factors ultimately determine whether early hatchers survive and are rewarded with the survival advantage conferred by a larger pre-winter size (Bouchard and Fortier 2008, 2011; Bouchard et al. 2017). Given the extended hatch season of Arctic cod in the Alaska Arctic (Chapman et al. 2022), it is possible that early hatchers were present in 2013 and simply did not experience post-hatch conditions that were conducive to survival. The higher abundance of Arctic cod throughout the survey region in 2017 relative to 2013 supports this notion, though the northward transport and unique distribution of Arctic cod in 2019 precludes us from including this year in any such comparisons (Levine et al. 2023a, 2023b).

The sample years with earlier hatch dates were characterized by earlier ice retreat, fresher incubation and post-hatch conditions, and to a lesser extent slightly warmer temperatures in the Bering Strait region. We considered the differences in hatch timing through two lenses: the first being the conditions that affect incubation, and the second as the conditions post-hatch that influence larval survival. Generally, the incubation and post-hatch temperatures experienced by fish were that hatched from late-

March through mid- to late-April were similar for all three years. Fish that hatched outside of this range in 2017 and 2019 experienced warmer incubation and post-hatch conditions than 2013 fish. Trends in salinity with relation to hatch timing were a bit simpler. Winter and spring salinities in the Bering Strait region have been freshening in recent years due to increased glacial melt and precipitation from mainland Alaska, and this was evident in our incubation time series (Cooper et al. 2022; Woodgate and Peralta-Ferriz 2021). The range of salinities experienced during the incubation and post-hatch period for fish that hatched before mid-May were much fresher in 2017 and 2019 than in 2013. Salinities were comparably fresh for fish that hatched after mid-May, which coincides with the time frame that increased sea ice melt freshwater input from more local inland sources (i.e. river discharge) seasonally alter the salinity dynamics in the region. Although the timing and magnitude of sea ice retreat in the region differed by year, ice retreat did begin the soonest in 2019, followed by 2017 and 2013 in that order. This order also coincides with the timing of the first hatchers observed by year in this study. In other regions of the Arctic, similar observations of older (earlier hatched), more abundant, and larger juveniles during this time frame have been associated with years of earlier ice breakups and warmer spring-summer SST have been documented (Bouchard et al. 2017). Bouchard et al. (2017) hypothesized that warmer spring temperatures and an earlier ice break up favored a large pre-winter size by enhancing survival of early hatchers through hastening the production of important sources of prey, improved visibility for Arctic cod larvae to capture prey, and provided warmer, more optimal growing temperatures (when temperatures remain below physiological limits). Largely, these findings along with the work of Chapman et al. (2022) seem to corroborate this.

Temperature and Growth

While the hatch dates for Arctic cod were markedly different among the three sample years, the growth rates during the week and month preceding capture were similar. There was some evidence of an inverse relationship between temperature and growth detected in wild age-0 Arctic cod though the relationship was highly seasonal and only significant for fish sampled earlier on. Our findings of a negative relationship between growth and temperature (even if only on a seasonal basis) are at odds with laboratory observations of temperature and growth potential (maximum growth achievable when fed to satiation). This discrepancy suggests that although temperature clearly influences growth, alternative ecosystem factors (such as food quality and quantity) may govern the effect of temperature on fish growth dynamics (Dupont et al. 2020). It is also possible that the detection of a distinct thermal signature in growth was confounded by the inherent challenges of characterizing the thermal experience of these Arctic cod. At the age these Arctic cod were captured, they were occupying most of the water column and experiencing temperatures throughout the available vertical range (Levine et al. 2023b), and the best available temperature data (in terms of spatio-temporal coverage) for interannual comparisons only included temperatures at the surface.

While summer surface temperatures in the Chukchi are rapidly approaching critical physiological thresholds for larval and juvenile Arctic cod as identified in laboratory studies, at the ontogenetic stage evaluated in this study it is possible that they are able to seek thermal refugia at depth if not moving to new locations altogether. Temperature limits do appear to have shifted Arctic cod distributions in the Bering Sea system immediately south (Stevenson and Lauth 2019; Baker 2021), which suggests a need for continued monitoring. Access to more temperature data at depth in the region would have greatly improved our ability to characterize the temperatures experienced by these fish. Given access to more temperature data at depth, one could use this knowledge of their vertical distribution and best assumptions about how far from the capture location they may have traveled in the week and month preceding capture to more accurately characterize their individual thermal experience. Lacking access to such data, a possible alternative would be to use stable oxygen isotopes signatures in otoliths to back-calculate the temperatures of the water experienced by a given fish, though such analyses were beyond the scope of the current study (Kastelle et al. 2022).

Energy allocation into growth and storage tissues

While recent somatic growth of juvenile Arctic cod did not differ among these three years, lipid storage did vary, with 2017 fish having lower energy densities than 2013 and 2019 fish (Copeman et al. 2022a). As the summers 2017 and 2019 were comparably warm, the mechanism for the markedly lower lipid storage in 2017 remains unclear and does not seem to be temperature specific (Copeman et al. 2022a). Rather, it is likely that differences in other oceanographic conditions and corresponding differences in the spatial distribution between 2017 and 2019 fish played a role (L. Copeman, personal communication, 2023). Differences in a number of conditions such as wind and current dynamics, temperature, and sea ice between the two years resulted in a northward constriction of juvenile Arctic cod in 2019 compared to a more diffuse 2017 population with fish occupying the full latitudinal sampling gradient (Copeman et al. 2022a; Levine et al. 2023b, a; Goldstein et al. 2023). Unique distributions of fish during these years imply exposure to different conditions (outside of the thermal ones we consider here) and prey assemblages that could affect energetic density the more northerly-oriented population of Arctic cod sampled in 2019 may have had access to a more stable local population of the more energetically dense prey *Calanus glacialis* than 2017 fish did (L. Copeman, personal communication, 2023). Copeman et al. (2022) evaluated the contribution of a number of factors to the lipid storage of these Arctic cod and found that lipids were strongly associated with increased storage of diatom- and *Calanus*-sourced fatty acids, and that temperature, salinity and large *Calanus* abundance explained 21% of the variation in the storage of those lipids. Copeman et al. (2022) also suggest that *C. glacialis* was likely prominent in the diet of juvenile Arctic cod throughout the preceding months of July and August and its relative contribution to Arctic cod fatty acid variability may have been underestimated due to covariance with environmental variables and limited a temporal mismatch between sampling and fatty acid integration. While the major differences in fatty acids observed between years did not appear to be predominantly or directly linked to temperature, our results do suggest a positive relationship between ambient temperature and fatty acids earlier on in the sampling season (with little to no effect of temperature on total fatty acid content later on). This positive relationship is in line with laboratory measurements of temperature-mediated lipid accumulation in juvenile Arctic cod for the range of temperatures observed in this study (Copeman et al. 2017).

Comparisons of growth versus lipid storage suggest that juvenile Arctic cod on the cusp of their first winter were not preferentially allocating energy into either structural or storage tissues. Despite temperature exerting a negative seasonal effect on growth and a positive seasonal effect on lipid storage, there was no indication of allocation tradeoffs between growth and storage tissues in a seasonal context either. This corroborates similar observations in captive juvenile Arctic cod where no correlation between temperature-dependent specific growth rate and body lipid content was observed (Copeman et al. 2017). Maximizing somatic growth and energy storage are critical to successfully overwintering, and it could be that during this time frame they are doing both in equal measure. Even if earlier on in their ontogeny these Arctic cod subscribed to the aforementioned energy allocation by stages strategy, evidence that they were doing so in the late summer to early fall timeframe was not evident here (Post and Parkinson 2001; Mogensen and Post 2012). It is also important to consider that differing pressures and resource availability at the individual level may have limited our ability to see larger scale trends in allocation.

Overall, this work highlights the challenges in disentangling the effects of temperature from other covarying environmental variables. It has been suggested that some initial climate warming will indirectly benefit Arctic cod in the near-term (Bouchard et al. 2017), and our findings seem to be in line with this. Fish entering their first winter were able to obtain larger sizes in categorically warmer years and were capable of maintaining adequate energy stores, as indicated by the comparable lipid storages observed in 2013 and 2019 fish, a “cold” and “warm” year, respectively—though in this case, the flow dynamics and northern distribution of fish in 2019 likely played a role in the higher lipid stores. Despite this, a clear link between temperature and these measures was not clear (apart from some evidence of a seasonal effect of temperature on growth and lipid storage), which indicates that climate warming is primarily acting on young Arctic cod indirectly through other environmental variables. However, as water temperatures in many Arctic regions, including the region considered here, continue to warm and begin approaching the thermal thresholds identified in laboratory settings, it remains uncertain how young Arctic cod will respond. The sensitive early life stages of this species are less able to actively seek thermal refugia (both in terms of motility and habitat requirements) than their older counterparts, and at some point, the deleterious effects of warm temperatures will likely overwhelm the other environmental factors currently governing Arctic cod during their first year of life.

Generally, the effects of climate change are more pronounced in the region examined in this work than in the High Arctic, as the Bering Strait functions as one of the Arctic gateways—the Pacific Arctic gateway. In the Pacific Arctic gateway, advection of warmer, fresher Pacific waters through the Bering Strait intensifies borealization of the ecosystem and amplifies the changes already taking place (Geoffroy et al. 2023). Here, at the southern extent of its range, Arctic cod is experiencing the effects of warming and the corresponding cascade of effects (both abiotic and biotic) the most and is already at the limit of its tolerance range. While years with an earlier ice break-up and generally warmer conditions in the spring and summer did result in more and larger Arctic cod captured during the late summer surveys, it remains unclear what happens during the winter months and just how much the differences in pre-winter size and lipid stores actually affected overwinter survival and thus, recruitment. Moreover, the conditions during these warmer years that seem to be tenuously and conditionally favorable for larval and juvenile Arctic cod, also seem to be favorable for more boreal competitor and predator species as evidenced by higher proportions of other fish in the region during "warm" years (Baker 2021; Levine et al. 2023a). With this increased overlap, the question then becomes not just how will Arctic cod cope with the warmer temperatures and corresponding environmental changes, but how will they cope with them relative to more boreal species that are better suited to them? There is also evidence that increasingly earlier ice breakups could disconnect the herbivorous zooplankton (that age-0 Arctic cod rely on) from its food source, resulting in a mismatch cascade that could counteract the benefits gained from a longer growing season in early hatchers (Gonzalez et al. 2023; LeBlanc et al. 2020; Leu et al. 2011). Continued monitoring of such phenological interactions in this region, where the effects of warming are more rapid and intense, will help to clarify what challenges Arctic cod in non-gateway regions may face in the years to come and how the Arctic food web may shift as a result.

5. Conclusions

For the three years examined in this study, the most important process related to achieving large body size was hatching date, and the environmental conditions that promote early hatching and subsequent survival. Fish captured in 2017 and 2019 obtained larger pre-winter sizes because they hatched earlier, not because they grew faster. Despite experiencing thermally distinct conditions, temperature explained little of the variation in the growth or lipid storage of juvenile Arctic cod during the weeks preceding capture, though did exert some influence on these metrics on a seasonal basis. This finding is at odds with laboratory studies that revealed clear temperature-mediated trends in the somatic growth and lipid storage of age-0 Arctic cod. Such discrepancies suggest that temperature interacts with many other environmental variables to affect Arctic cod young-of-the-year body size and lipid storage. Surface temperatures in 2017 and 2019 in the Chukchi Sea were approaching a number of laboratory-identified physiological thresholds for larval and juvenile Arctic cod, and it will be increasingly important to monitor responses as temperatures surpass these limits in the years to come. Once the functional thermal thresholds for these early life stages are surpassed, it is possible that the other ecological factors currently steering the growth and condition of these fish will be outpaced by the detrimental direct effects of temperature on Arctic cod physiology. Characterizing and disentangling the direct and indirect effects of warming on Arctic cod remains a challenge, and given the complexity of these interactions, continued efforts to simultaneously look at the effect of multiple ecosystem factors on overwinter survival strategies will prove the most beneficial. Further clarification regarding the processes that take place during the winter months (namely, spawning and overwintering behavior) will be important to incorporate into future work.

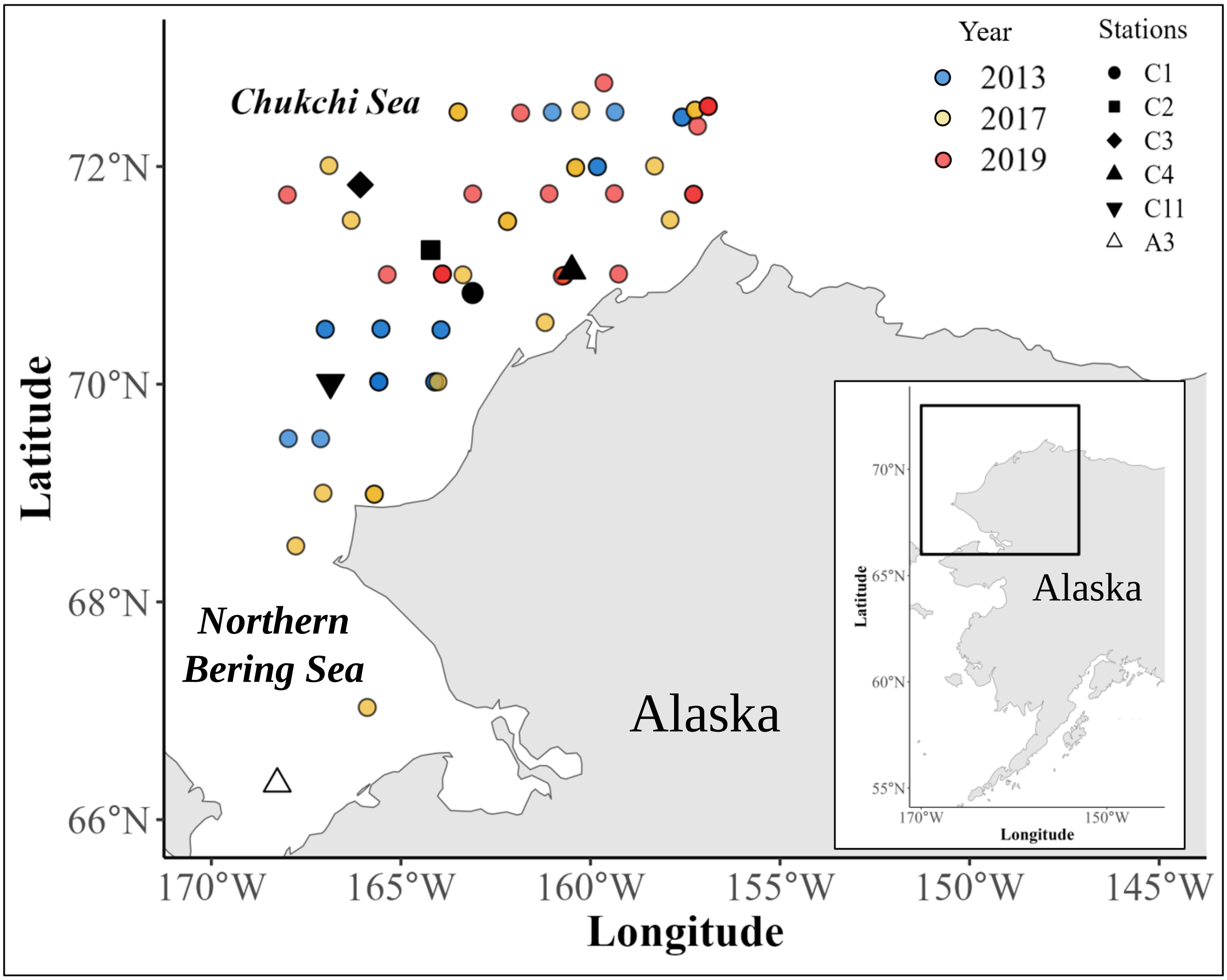

Figure 1. Arctic cod capture locations for the three sample years (colored points). Black symbols indicate mooring station locations oceanographic data was sourced from.

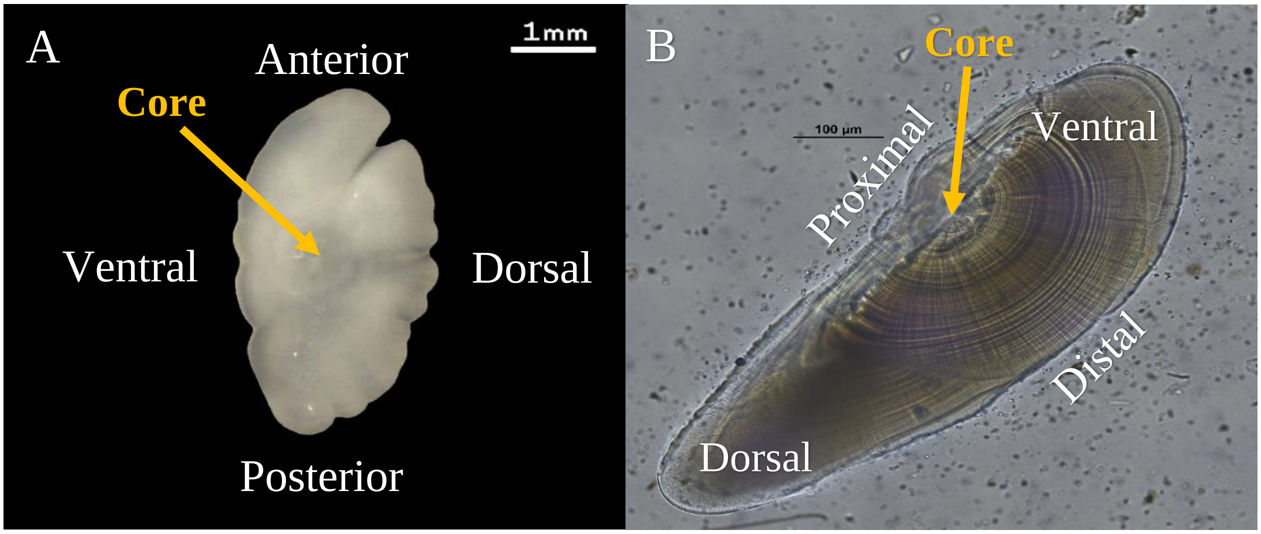

Figure 2. Surface and thin-section images of age-0 Arctic cod otolith. The first image (A) shows a proximal view of a whole sagittal otolith viewed with reflected light at 1.6x magnification under a dissecting microscope. The second image (B) shows the polished transverse cross section viewed with transmitted light using a compound microscope at 90x magnification.

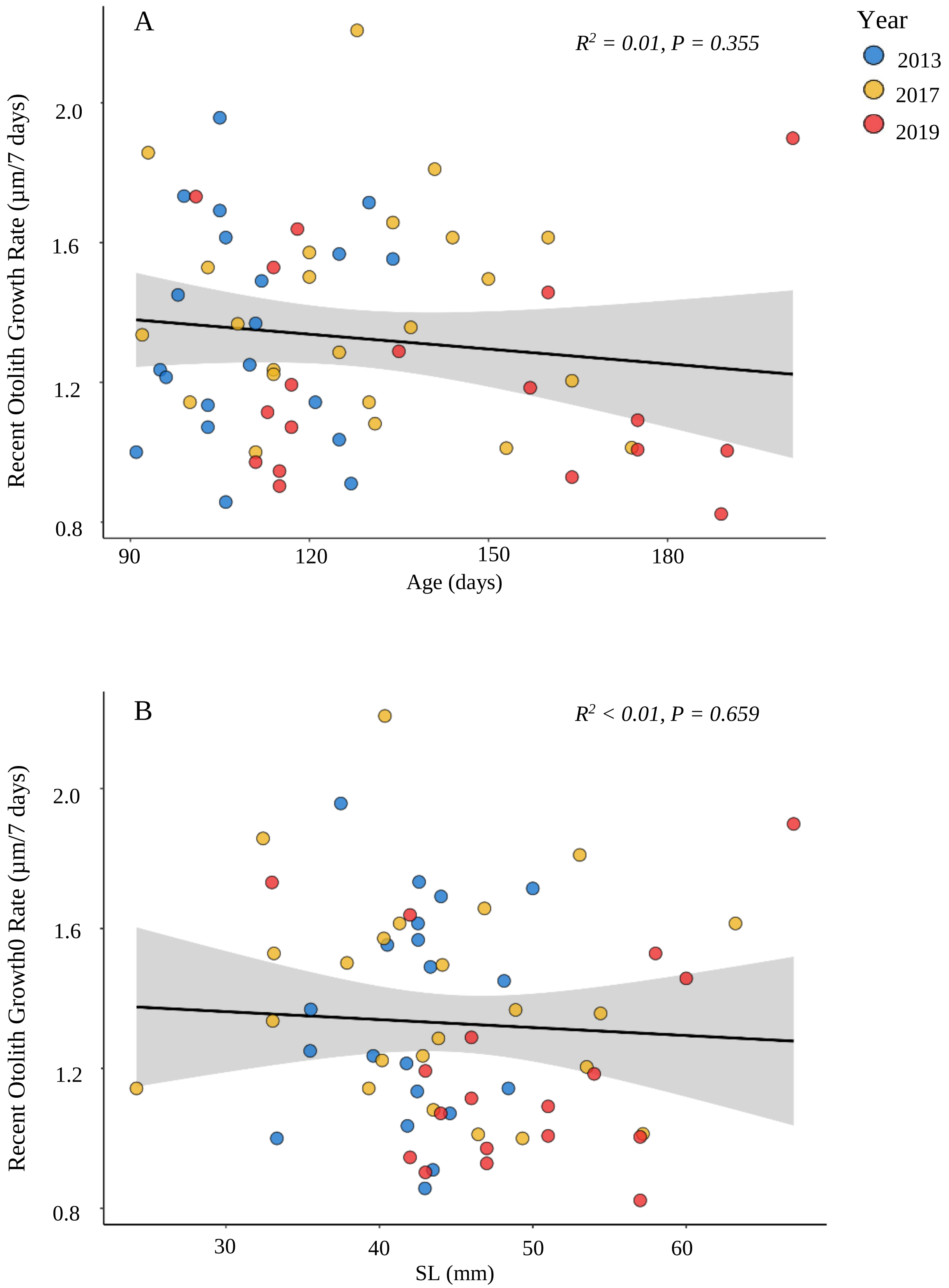

Figure 3. Linear regression of *Boreogadus saida* recent growth rates during the 7 days pre-capture versus both daily age (A) and standard length (B). Blue points represent 2013 fish, yellow points represent 2017 fish, and red points represent 2019 fish.

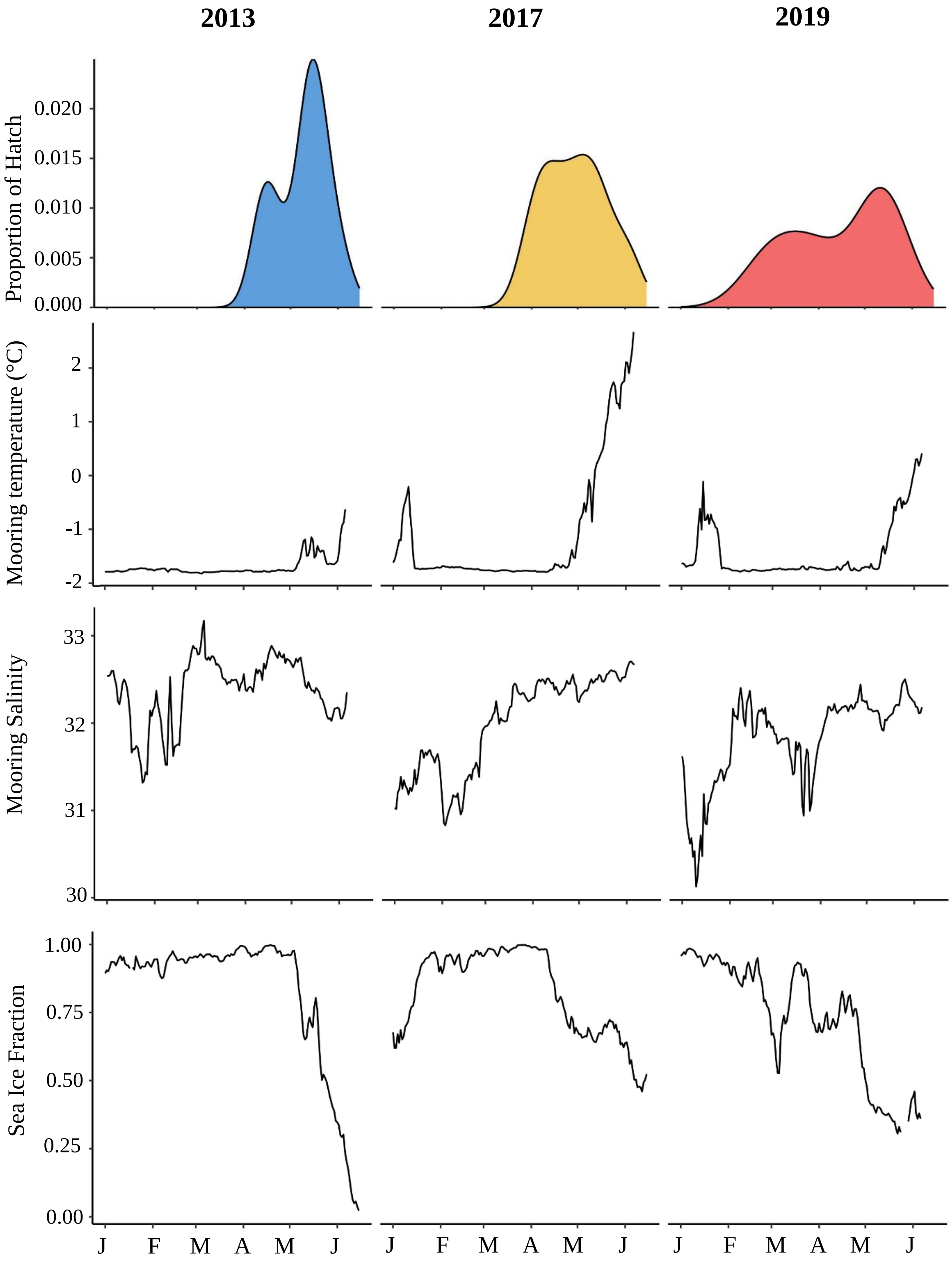

Figure 4. Bering Strait A3 mooring temperature and salinity and satellite-derived Bering Strait region sea ice fraction data from January through June in relation to 2013, 2017, and 2019 sampled Arctic cod hatch distributions.

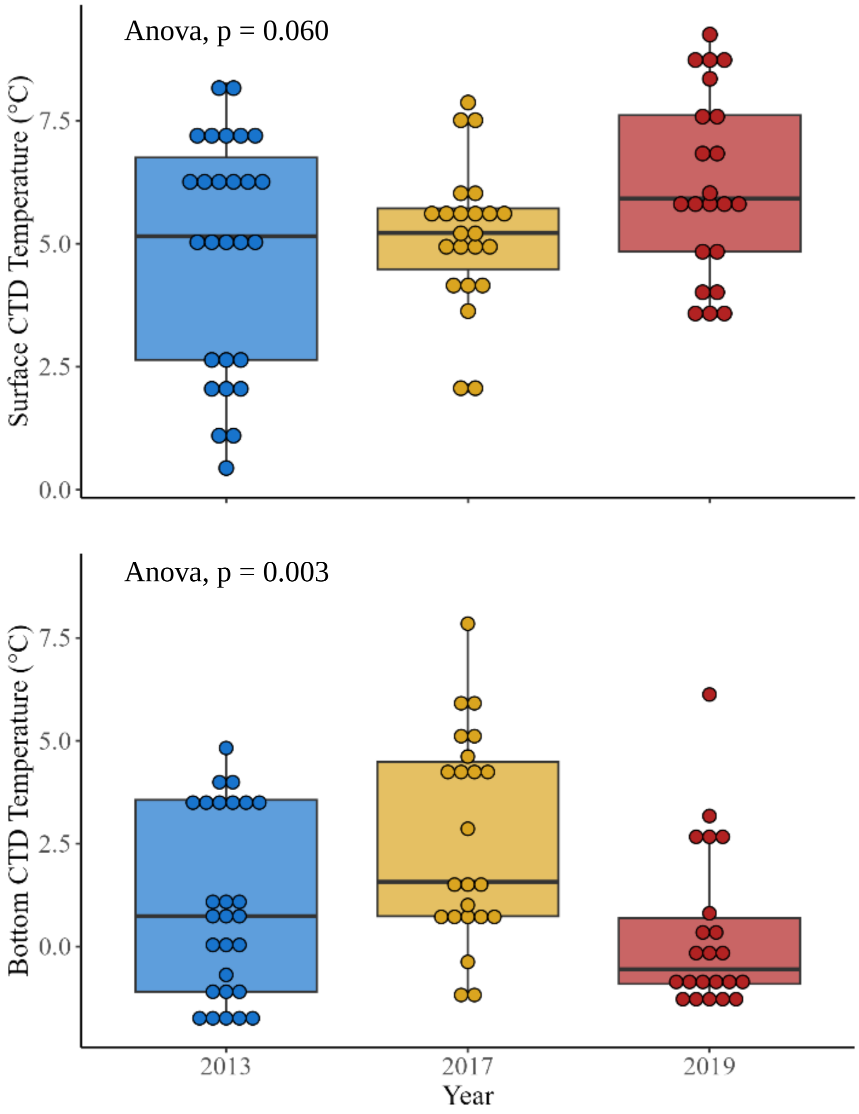

Figure 5. Box plots of CTD temperature values at the surface (top panel) and at depth (bottom panel) showing the range of temperatures at the time of capture in 2013, 2017, and 2019. The box represents the interquartile range of the data, the lower whisker shows the smallest value within 1.5 times the interquartile range below the 25th percentile, the upper whisker shows the largest value within 1.5 times the interquartile range above the 75th percentile. Horizontal lines within each box display the median value. Points beyond the whiskers indicate outliers.

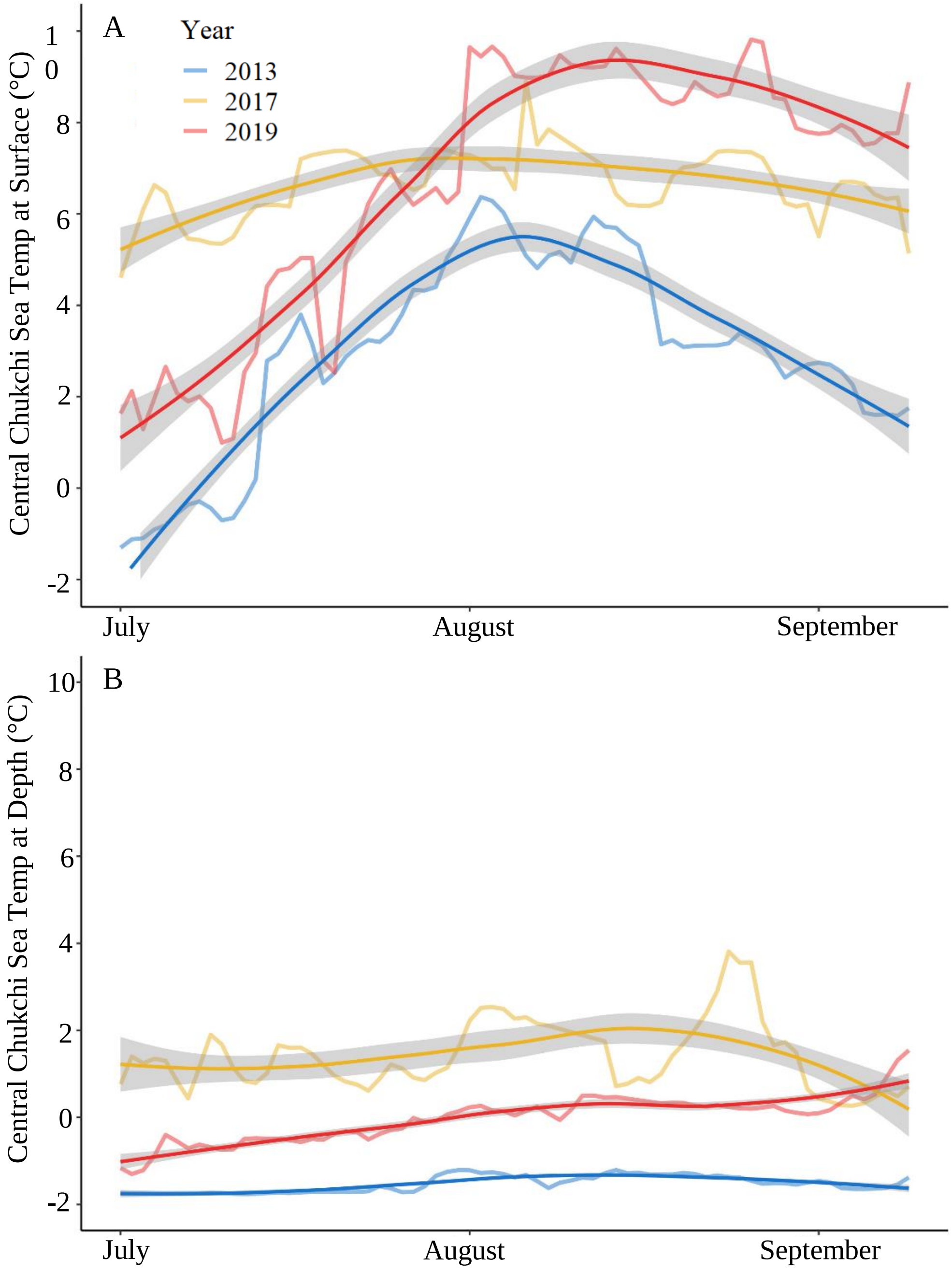

Figure 6. Overview of daily mean temperatures in the Chukchi Sea during the summer growth months in 2013, 2017, and 2019. Panel A shows SST in central Chukchi Sea at the location of mooring station C2. Panel B displays the mooring temperatures at depth in the central Chukchi Sea at mooring station C2. The actual data is plotted along with a LOESS smooth of the data. Gray bars depict the 95% confidence interval confidence intervals

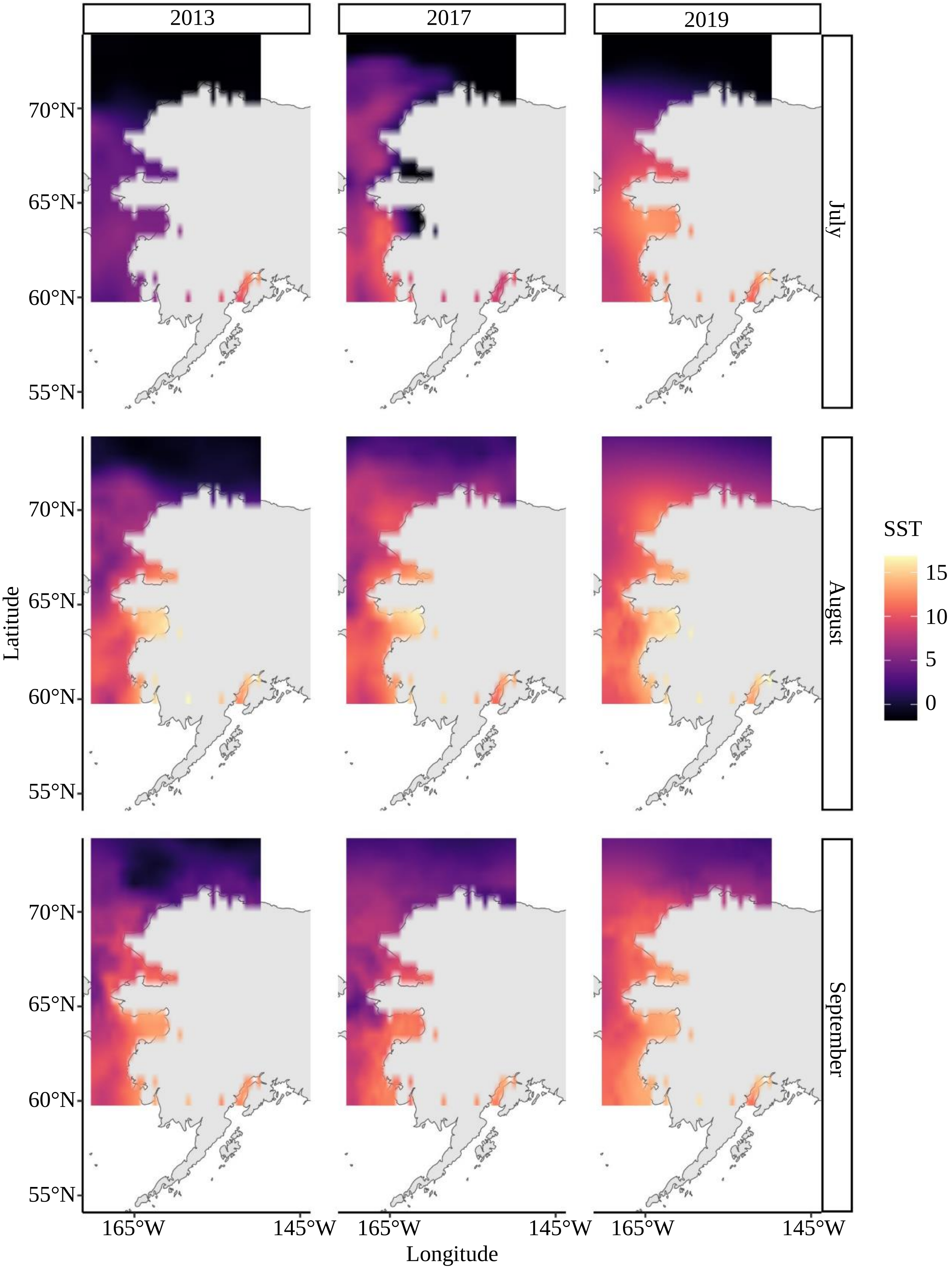

Figure 7. SST monthly averages for the summer months of 2013, 2017, and 2019 in the Northern Bering and Chukchi Seas.

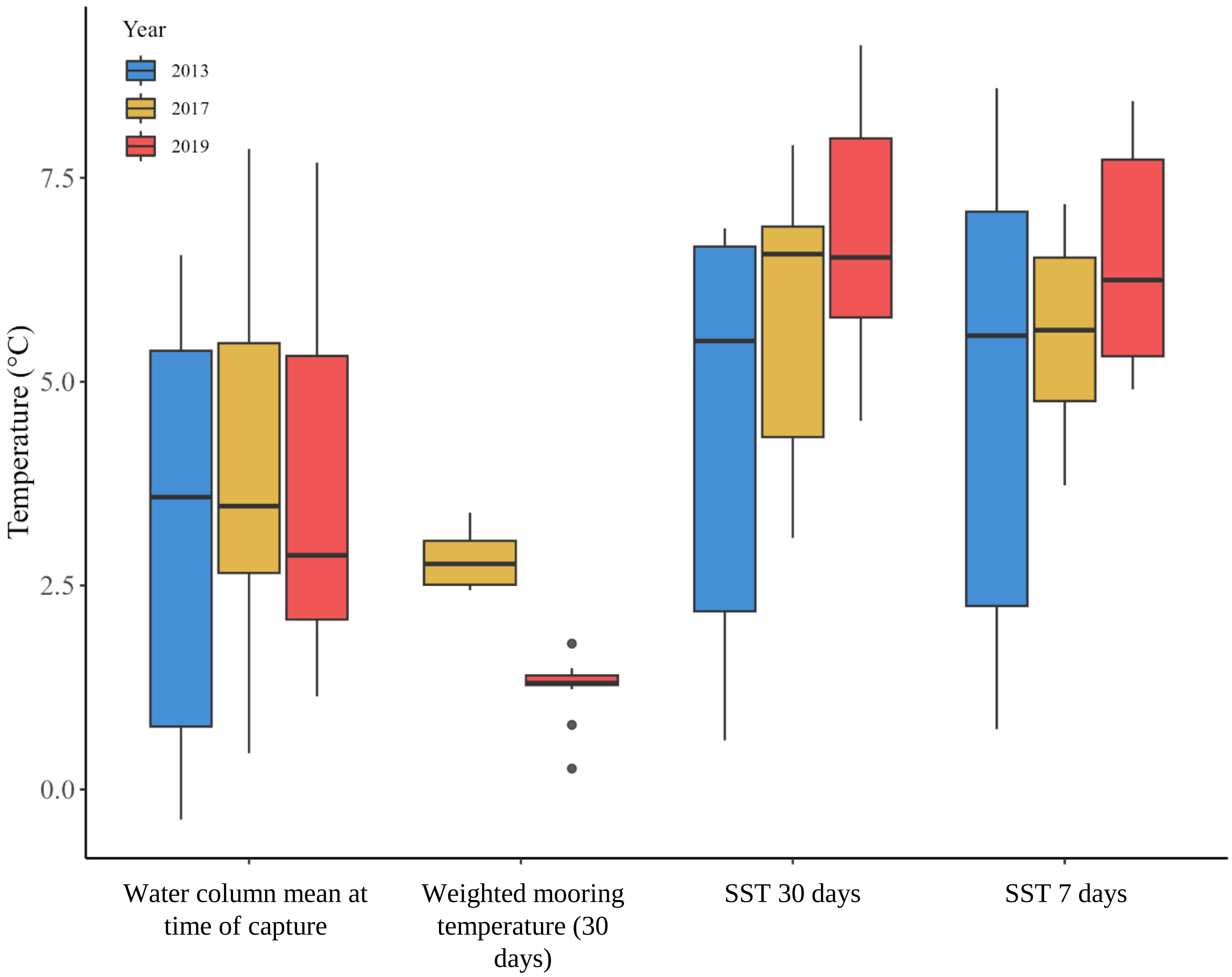

Figure 8. Range of values from individual Arctic cod derived from the 3 different information sources The first grouping is the mean temperature value from the CTD cast at the time of sampling, the second group is the weighted mean mooring temperature for each fish for the 30 days pre-capture, and SST 30 days and SST 7 days are the mean SST values for each fish for the 30 and 7 days pre-capture, respectively. The box represents the interquartile range of the data, the lower whisker shows the smallest value within 1.5 times the interquartile range below the 25th percentile, the upper whisker shows the largest value within 1.5 times the interquartile range above the 75th percentile. Horizontal lines within each box display the median value. Points beyond the whiskers indicate outliers.

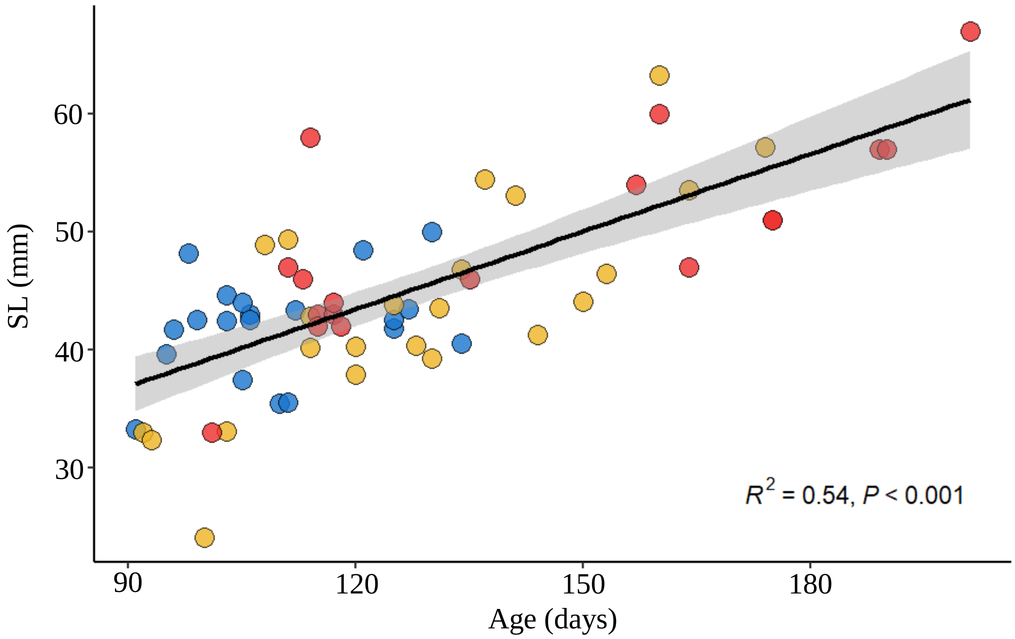

Figure 9. Length-at-age for Arctic (*Boreogadus saida*) caught in 2013 (blue points), 2017 (yellow points), and 2019 (red points). The gray band depicts the 95% confidence interval.

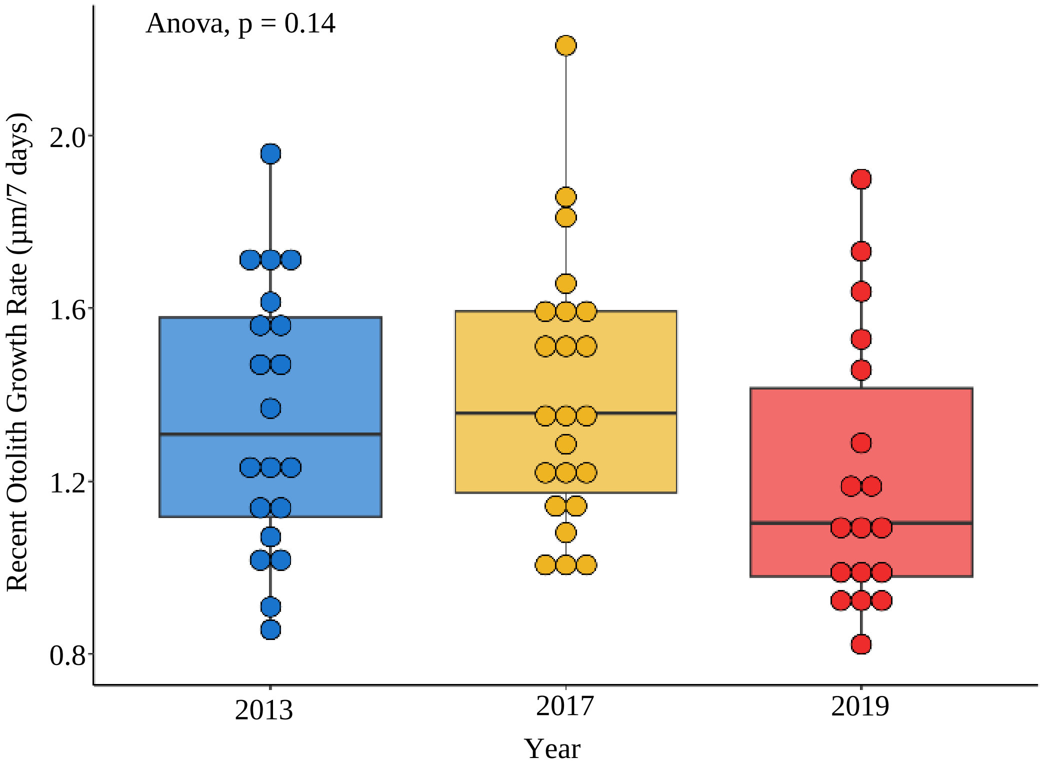

Figure 10. Recent growth rates of Arctic cod by sample year for the 7 days preceding capture. The box represents the interquartile range of the data, the lower whisker shows the smallest value within 1.5 times the interquartile range below the 25th percentile, the upper whisker shows the largest value within 1.5 times the interquartile range above the 75th percentile. Horizontal lines within each box display the median value. Points beyond the whiskers indicate outliers.

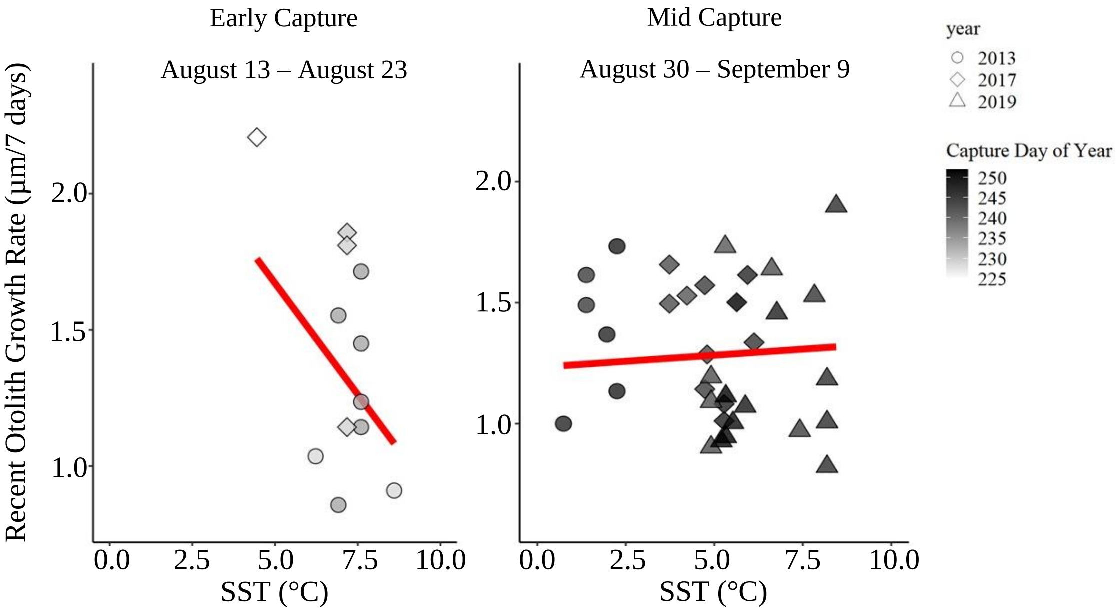

Figure 11. Model predictions for the interactive effect of temperature and capture time frame on Arctic cod growth rates during the week preceding capture. Each prediction line represents a different capture period as follows: The Early Capture panel displays model predictions of growth for fish captured on August 18 across the range of SST measured from August 13-August 23, the Mid Capture panel shows the model predictions of recent growth in the week preceding capture for fish captured on September 5 across the range of SSTs observed from August 30-September 9, few fish were captured in the late time frame (September 17-27) and are thus excluded in this plot. Points represent the measured recent growth rate of captured Arctic cod versus the SST during the week preceding capture. Point fill colors represent the fish capture day of year and point shape represents capture year.

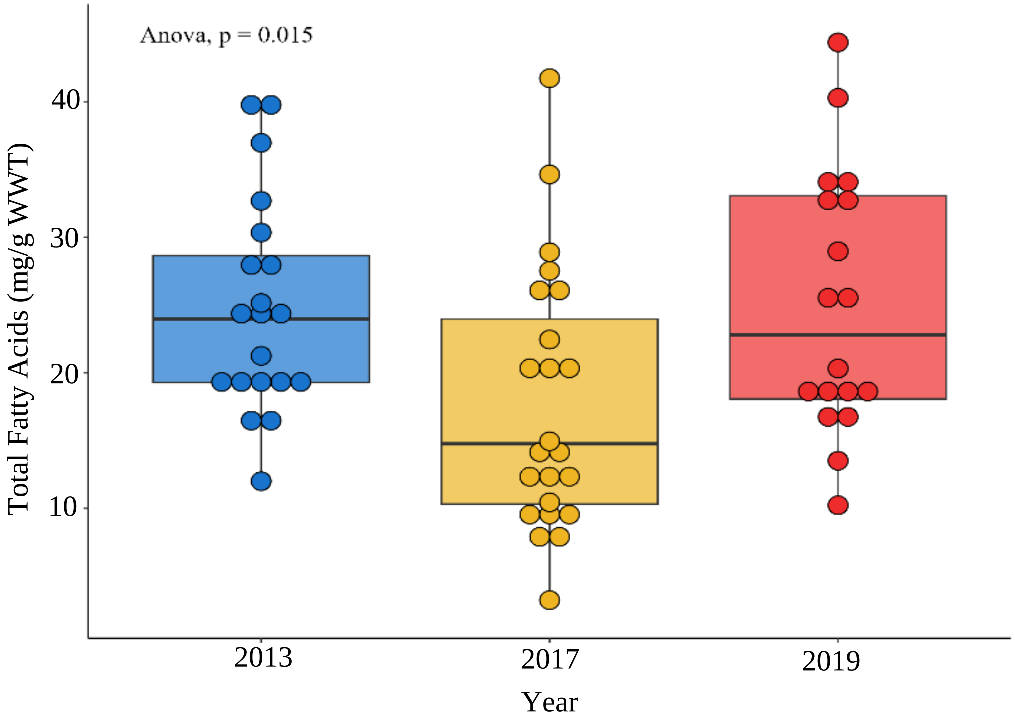

Figure 12. Total fatty acid content (mg/g WWT) of Arctic cod caught in the Chukchi during the summers of 2013, 2017, and 2019. The box represents the interquartile range of the data, the lower whisker shows the smallest value within 1.5 times the interquartile range below the 25th percentile, the upper whisker shows the largest value within 1.5 times the interquartile range above the 75th percentile. Horizontal lines within each box display the median value. Points beyond the whiskers indicate outliers.

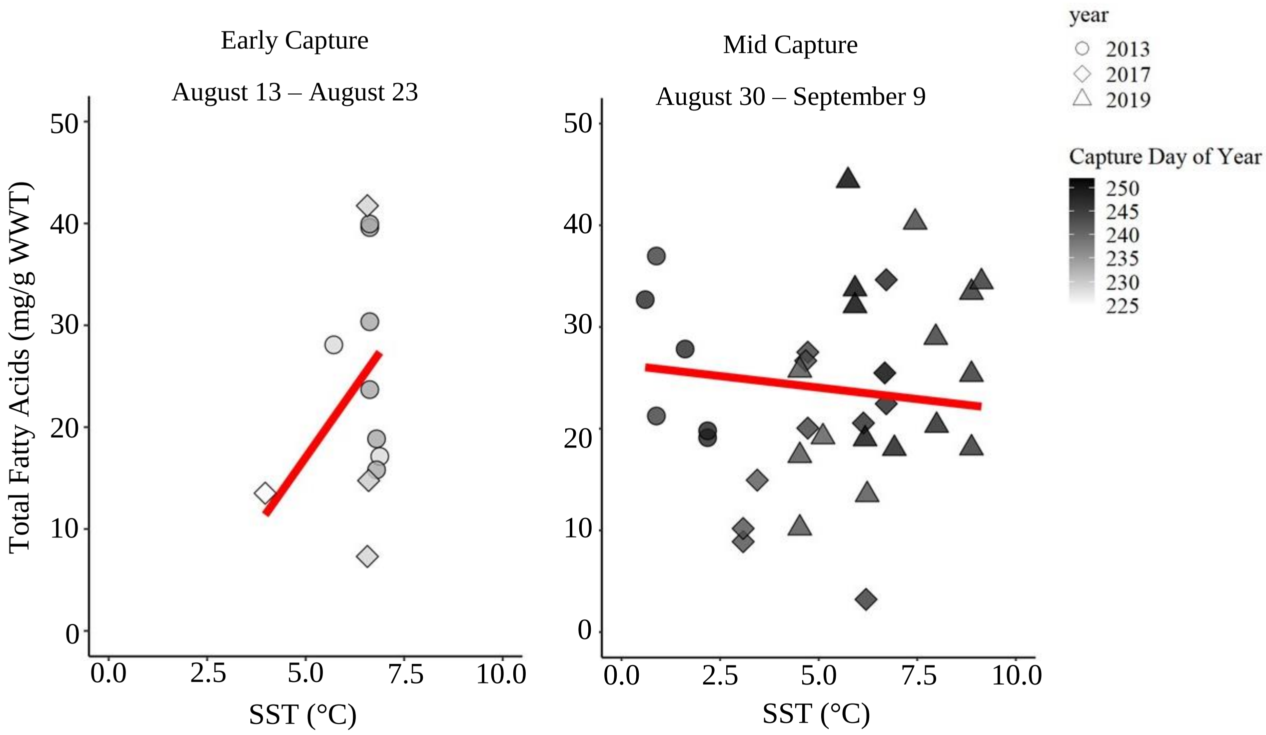

Figure 13. Model predictions for the interactive effect of temperature and capture time frame on Arctic cod total fatty acids during the week preceding capture. Each prediction line represents a different capture period as follows: The Early Capture panel displays model predictions of total fatty acids for fish captured on August 18 across the range of SST measured from August 13-August 23, the Mid Capture panel shows the model predictions of total fatty acids for fish captured on September 5 across the range of SSTs observed from August 30-September 9, and because few fish were captured in the late time frame (September 17-27) and it mirrored the mid capture time frame, it was excluded from this plot. Points represent the measured recent growth rate of captured Arctic cod versus the SST during the week preceding capture. Point fill colors represent the fish capture day of year and point shape represents capture year.

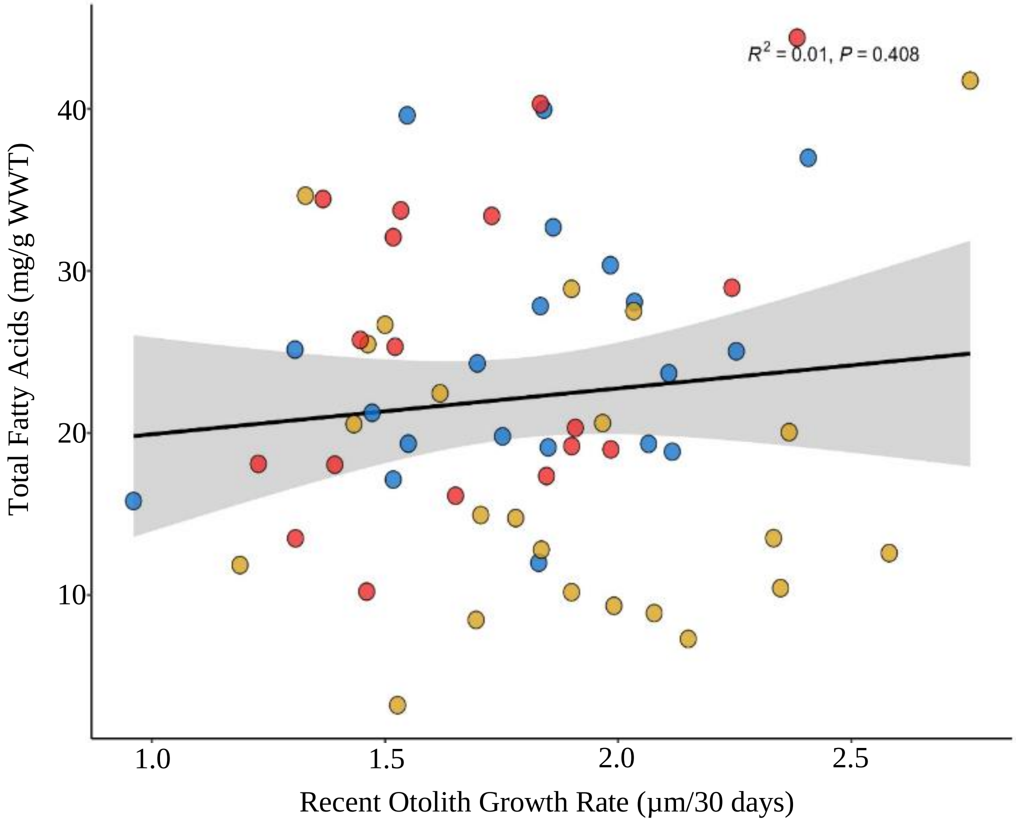

Figure 14. Total fatty acids (mg/g WWT) versus recent growth during the 30 days preceding capture in Chukchi Arctic cod captured in 2013 (blue points), 2017 (yellow points), and 2019 (red points). The gray band depicts the 95% confidence interval.

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