# Decreased lipid storage in juvenile Bering Sea crabs (*Chionoecetes* spp.) in a warm (2014) compared to a cold (2012) year on the southeastern Bering Sea.

**Louise A. Copeman*[1,2,3], Clifford H. Ryer[1], Lisa B. Eisner[4], Jens M. Nielsen[4], Mara Spencer[1], Paul Iseri[1], Michele Ottmar[1]**

*indicates corresponding author

[1]Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, OR, 97365, USA

[2]College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Newport, OR 97365, USA

[3]Cooperative Institute for Marine Resources Studies, Oregon State University, Newport, OR 97365, USA

[4]Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, 98115, USA

## Abstract

The decline of eastern Bering Sea snow (*Chionoecetes opilio)* and Tanner (*Chionoecetes bairdi*) crab has coincided with loss of spring sea ice extent and northward contraction of the 'cold pool', a layer of cold (< 2 $^{o}$C) summer bottom water. We measured temperature-associated growth and lipid storage of lab-reared Tanner crab, as well as the fatty acid content of field-collected juvenile *Chionoecetes* spp. Field collections occurred during a cold, high sea ice year (2012) and a warm, low ice year (2014), representative of cold and warm climate stanzas in the southeastern Bering Sea. Lab-reared Tanner crab maintained the lowest growth rates but highest lipids under cold conditions (2 $^{o}$C). In the field, crabs contained higher fatty acids per wet weight (mg.g$^{-1}$) during 2012 than during 2014. Water column integrated chlorophyll a (chla, an indicator of phytoplankton biomass) from large particles (>10 µm) such as diatoms, was elevated in the colder year particularly over the central middle shelf. During the cold-year, crab storage of diatom-sourced fatty acids (16:1n-7 to 16:0, $r^2$=0.72) as well as a station-specific relationship between large size-fraction integrated chla and crab total fatty acids ($r^2$=0.5) points to the potential importance of diatoms to juvenile crab nutrition. Our results suggest that continued warming and loss of sea ice across the Bering Sea may reduce juvenile crab lipid storage through both direct thermal effects as well as through the reduction of large size phytoplankton delivered to the benthos.



## Key Words

Lipid, fatty acids, diatom, chlorophyll a, sea ice

## Introduction

Stocks of most major crab species in the North Pacific (red king crab, *Paralithodes camtschaticus*; blue king crab, *P. platypus*; snow crab, *Chionoecetes. opilio*, and Tanner crab, *Chionoecetes bairdi*) have been in decline for the last three decades (Armstrong et al. 1998; Orensanz et al. 1998; Woodby et al. 2005). Declining snow crab stocks have resulted in major fisheries reductions with a 50% drop in the total allowable catch for 2017, making this the lowest value for snow crab since 1982 (NPFMC 2018). The reason for Alaskan crab declines is poorly understood, but is generally thought to be due to both over-fishing and a changing climate (Szuwalski et al. 2020; Zheng and Kruse 2000; Zheng and Kruse 2006). On the southeastern Bering Sea (SEBS) shelf, south of 60N, two commercially important congener species of *Chionoecetes* overlap in their distributions. Snow crab is an Arctic species that occupies deep waters in the North Atlantic, North Pacific, and throughout the Arctic region; Tanner crab is a boreal species that ranges from Puget Sound, WA to the SEBS in the north. Recent climate warming (1982 to 2017) has resulted in a shift in the distribution of these species with adult snow crab moving northward and Tanner crab moving to deeper habitats to avoid rapidly warming bottom water and increased predation from northward moving ground fish (Landeira et al. 2018; Murphy 2020; Orensanz et al. 2004).

Temperature is the most important environmental variable controlling vital rates in ectotherms and has previously been shown to dramatically affect growth rates in many juvenile Alaskan crab species (Ryer et al. 2016; Stoner et al. 2013; Stoner et al. 2010). It has been suggested that juvenile snow crab have very narrow temperature tolerances, being generally restricted to bottom waters < 3 ℃ (Dionne et al. 2003), while Tanner crab juveniles prefer warmer conditions and avoid temperatures < 2 ℃ (Ryer et al. 2016), making both species

susceptible to climate-mediated changes in bottom water temperatures. The SEBS has experienced a number of warm (2002-2005 and 2014-2019) and cold stanzas (2006-2013) during the recent period of environmental monitoring (Duffy-Anderson et al. 2019; Eisner et al. 2016; Mueter and Litzow 2008; Stabeno and Bell 2019; Stabeno et al. 2012; Stevenson and Lauth 2019). The changing climate in the SEBS also influences sea ice dynamics and the resulting formation of the 'cold pool', a layer of cold (<2 °C) subsurface water (below the pycnocline) that forms over the middle shelf (50 to 100 m depth) during sea ice retreat in the spring (Wyllie-Echeverria and Wooster 1998). In cold years with extensive sea ice cover, the cold-pool can extend south to ~56 ºN while during warm periods with reduced sea ice cover the cold pool retreats northward to >60 ºN. In recent years (2018 & 2019), this retraction has been so extreme that the cold-pool has been completely absent from the SEBS and most of the north Bering Sea benthic system (Stabeno and Bell 2019; Stevenson and Lauth 2019).

The relative importance of climate-influenced, bottom up trophic cascades to juvenile crab condition and recruitment remains largely unknown. The Oscillating Control Hypothesis provides a framework to examine the complex, indirect food web effects on marine species dynamics in the Bering Sea, but focusses on pelagic food web dynamics. This theory links climate oscillation and variable sea ice extent to the timing of the spring bloom and subsequent energetic condition and recruitment of juvenile walleye pollock (*Gadus chalcogramma*) and Pacific cod (*Gadus macrocephalus*) (Coyle et al. 2011; Eisner et al. 2020; Farley et al. 2016; Heintz et al. 2013; Hunt et al. 2011; Hunt et al. 2002; Hunt et al. 2008; Sigler et al. 2014). However, we have less understanding of how these environmental processes affect early life history stages of juvenile crabs. This is because annual assessments of snow and Tanner crab over the SEBS focus on larger crabs with a mean carapace width of 48 mm and 4 to 7 years post

settlement age (Murphy 2020). Larger crabs likely have a nutritional condition that is integrated over multiple seasons and is less sensitive to short-term pulses in phytoplankton production. Juvenile stages of fish and crabs are characterized by lower energy storage and faster metabolic rates which makes them relatively more sensitive to changes in food quantity/quality and more vulnerable to starvation (Beder 2015; Copeman et al. 2014; Houde 2008; Hurst 2007).

Increased warming and loss of sea ice is forecast to decrease both food quality and quantity supplied to the benthos through decreased flux from ice-edge and pelagic phytoplankton blooms (Grebmeier 2012; Grebmeier et al. 2015; Renaud et al. 2015; Wassmann and Reigstad 2011). Benthic-pelagic coupling represents an essential source of energy, lipids and more specifically essential fatty acids for benthic fauna (Copeman and Parrish 2004; Ramos et al. 2003; Richoux et al. 2004). Characterization of fatty acid (FA) pools in benthic organisms has become increasingly important in ecological studies because FAs can provide time-integrated information about dietary utilization and trophic relationships (Budge et al. 2006; Dalsgaard et al. 2003; Parrish 2013). FA trophic markers are synthesized at lower trophic levels and can link consumers with various sources of primary production such as diatoms, dinoflagellates, terrestrial runoff, calanoid copepods and bacterial sourced organic matter (Budge and Parrish 1998; Copeman et al. 2009; Dalsgaard et al. 2003; Parrish 2013). Transfer of FAs from lower to higher trophic levels is generally conservative and therefore FAs are used to indicate dietary sources for invertebrates (Galloway et al. 2014; Kelly and Scheibling 2012; Spilmont et al. 2009), fish (Copeman et al. 2016; St John and Lund 1996), and mammals (Budge et al. 2008; Tucker et al. 2009). Sinking phytoplankton contain high proportions of polyunsaturated fatty acids (PUFA) that are essential to juvenile stages of many different benthic fauna (Kelly and Scheibling 2012; Richoux et al. 2005).

Recent laboratory and field observations have demonstrated the significance of both food quantity and food quality on the growth and lipid storage of newly settled Tanner crabs from shallow nearshore embayments in the Gulf of Alaska (Copeman et al. 2018). Here we provide the first data that examines trophic dynamics of juvenile *Chionoecetes* spp. across the SEBS. Our objectives were to examine crab lipid storage across offshore sites on the SEBS during two environmentally disparate years, 2012 (cold) and 2014 (warm). Specifically, we aimed to 1) determine the direct effect of temperature on lipid concentration and growth in newly settled juvenile Tanner crab in the lab, 2) determine spatial and annual differences in phytoplankton biomass (total integrated chla) and large particle phytoplankton biomass (>10 µm integrated chla) which is often indicative of diatoms, 3) determine spatial and annual differences in crab total fatty acid concentrations ($mg.g^{-1}$) and individual fatty acid proportions in relation to late summer phytoplankton biomass, and 4) discuss crab trophic dynamics and lipid storage in the context of continued warming across the sub-Arctic Bering Sea.

## Methods

*Live crab collection and laboratory temperature-growth experiment*

Details of crab collection protocols can be found in Ryer et al. (2015). Briefly, Tanner crabs (4.2 to 5.6 mm carapace width) were collected from shallow bays surrounding Kodiak Island, Gulf of Alaska, AK, USA using an epi-benthic sled in July of 2013. The codend of the sled was made of 3 mm mesh seine fabric, which retained C2 (molt stage 2) and larger juvenile Tanner crabs. The sled was towed along the seafloor at depths ranging from 10 to 30 m, parallel to shore, at a speed 0.5 $m.s^{-1}$ for ~30 m. Tanner crabs (~5 mm carapace width) were retained alive and shipped overnight in insulated containers to the Hatfield Marine Science Center (HMSC) in Newport, OR, USA.

At the laboratory, crabs were placed into individual growth cells immersed in temperature-controlled, flow-through seawater tanks as detailed in Copeman et al. (2018) and Ryer et al. (2016). Individual C2 crabs were gradually acclimated to 9 $^{o}$C and 2 $^{o}$C and fed a marine gelatinized food (diet composition as detailed in Copeman et al. (2018)). Crabs were fed a quantity of food that was more than their 24-hour satiation ration (based upon previous experiments). Three times per week, remaining food was removed and new food was added to growth chambers. Upon molting (C3) we measured crab carapace width using digital photography and this was considered the beginning of the temperature-growth experiment. Ten replicate crabs were maintained at 9 $^{o}$C and 2 $^{o}$C and the experiment was continued until the mid-molt point between the C4 and C5 stages. Mid-molt was estimated based upon prior data on the relative increase in intermolt periods from one stage to the next (Ryer et al. 2016). Growth cells, and hence crab placement within temperature controlled water baths were re-randomized on a weekly basis to preclude tank effects. All water baths were provided with continuous flow-through seawater (salinity ~33) and crabs were checked daily for molting activity. Crabs were re-measured 2 to 5 d after each molt to help insure that crab exoskeletons were sufficiently hard to resist damage during handling. At mid molt of the C4 stage, a randomly chosen subsample of 6 crabs from each temperature treatment was measured, weighed and placed in a vial with 2 mL of chloroform under a layer of nitrogen and frozen (-20 $^{o}$C) for later lipid extraction (<6 months). Intermolt period was determined in each temperature treatment using the days from C3 to C4. Molt increment, i.e. percent increase in carapace width from one stage to the next, was also analyzed across this same developmental stages. Intermolt period was analyzed to test for temperature effects using a Kruskal-Wallis one-way nonparametric ANOVA while, temperature

effects on molt increment and total lipids ($\sum$lipid, mg.g$^{-1}$) were analyzed using a one-way ANOVA with a significance of $\alpha > 0.05$.

*Crab sampling over southeastern Bering Sea 2012 and 2014*

Small mesh beam trawling was conducted over the SEBS shelf in 2012 and 2014 as detailed in Hurst et al. (2015) and Ryer et al. (2016). This sampling was conducted to target juvenile crabs on an exploratory basis as part of the larger NOAA Bering-Arctic-Subarctic Integrated Survey (BASIS). Crabs were sampled on the shelf (< 200m depth) from the Alaska Peninsula to 60 ºN in August to early October of 2012 and August to September of 2014. A 3-m beam trawl, with 7-mm mesh and a 4-mm mesh codend liner were used to make benthic tows. Global positioning system (GPS) coordinates were used to determine the length of each tow and were paired with the effective fishing width of the net (2.26 m) to calculate catch per unit effort (CPUE, crabs.100 m$^{-2}$). The speed and duration of the trawl was 1.3 m.sec$^{-1}$ for 5 to 10 minutes. *Chionoecetes* crabs < ~15 mm carapace width (C6 stages and smaller) were sorted, counted and then immediately frozen on-board.

To compare crabs across years but from within similar geographical regions, we divided crabs by latitude and into those from middle and outer shelf habitats. These regions are commonly used due to their distinct physical oceanography and ecosystem dynamics (Ortiz et al. 2016). The four crab sampling regions on the SEBS shelf included: 1) central middle (CM) between the 50 and 100 m bottom depth contours and from between 57 and 60 ºN, 2) south middle (SM) between the 50 and 100 m depth contours and from 57 ºN south to the Alaskan peninsula, 3) the central outer (CO) between the 100 and 200 m depth contours and offshore from 57 to 56 ºN, and 4) south outer (SO) between 100 and 200 m depth contours and from 56

177 ºN south to Unimak Pass. Sample sizes were based on availability and ranged from 12 to 37
178 crabs per year in a given sampling region (Table 1).

179 *Crab morphometrics and lipid analyses*

180 In 2012 and 2014, crab were sorted from the small mesh beam trawl and were frozen in a
181 -20 ℃ walk-in freezer on board the research cruise. Following the cruises, crabs were shipped
182 frozen overnight to the Hatfield Marine Science Center, where they were stored in a -80 ℃
183 freezer until they were identified, measure and weighed. All crabs were sampled within 6
184 months of storage at -80 ℃. They were placed directly into 2 mL of chloroform under a layer of
185 nitrogen and returned to a -20 ℃ freezer. All crabs were extracted for lipids within the
186 following 6 months (see below).

187 For the lipid laboratory analyses, crabs were first identified using the scores of carapace
188 characteristics developed by Urban et al. (2002) to differentiate Tanner crabs (score = 1), snow
189 crabs (score = 5) and possible range of intermediate morphology that represented hybrids (score
190 = 2 to 4). However, especially for the smaller juveniles, we found that typical carapace shape
191 was not sufficiently developed to be reliable, and eye color was not distinguishable, especially
192 after freezing. Therefore, we relied on epistome margin as the diagnostic character. Due to this
193 difficulty in distinguishing species from field sampled juveniles, we grouped all crabs as
194 *Chionoecetes* spp. for most statistical analyses of the effect of region and year on crab condition
195 and biomarker composition. The one exception, is a comparison of crab total fatty acid storage
196 on the central middle shelf, where we examined the differences between years as a function of
197 hybrid status (1- Tanner, 2-Tanner Hybrid, 3- snow hybrid). Here we had a high percentage of
198 stage 3 snow crab hybrids (Urban et al. 2002) which allowed us to look at annual differences as a
199 function of morphologically defined hybrid status. Carapace widths were measured with calipers

to the nearest 0.1 mm. The minimum carapace width in the 2012 samples was 4.33 mm (C3 stage) and 6.08 mm (C4 stage) in 2014. For the juvenile data analysis, we only included crabs <15.3 mm (C6 or under).

Once crabs were weighed and measured (both field samples and laboratory experiments) they were processed for lipid content in the Marine Lipid Ecology Laboratory at Oregon State University, Hatfield Marine Science Center. We did not have excess crabs to process for dry weights (DWT) or for ash-free DWT (AFDWT). The small size of C5 and C6 molt stages precluded splitting crab tissue between WWT, DWT and AFDWT measures. Therefore, we used conversion factors from a previous experiment on Alaskan Tanner crab to express crab total fatty acids per WWT (measured) into crab total fatty acids per DWT and AFDWT (estimated with conversion factors from Copeman et al. (2018), see Table 1). Lipids from whole individual crabs were extracted in chloroform and methanol according to (Parrish 1987) using a modified Folch procedure (Folch et al. 1956). Lipid class analyses were only completed on laboratory temperature experiment crabs while total fatty acids were measured on field collected crabs. The analyses of total fatty acids is faster and more efficient, and there is a strong positive relationship between total lipids and total fatty acids, as previously demonstrated in Tanner crabs collected around Kodiak Island, Alaska (Copeman et al. 2018).

Total lipids were determined using thin layer chromatography with flame ionization detection (TLC/FID) with a MARK V Iatroscan (Iatron Laboratories, Tokyo, Japan) as described by Lu et al. (2008) and Copeman et al. (2017). Extracts were spotted on duplicate silica-gel-coated Chromarods, and a three-stage development system was used to separate wax/steryl esters, triacylglycerols, free fatty acids, sterols and polar lipids. Polar lipid is mostly comprised of phospholipids with minor amounts of other acetone mobile polar lipids. The first rod

223 development was in a chloroform: methanol: water solution (5:4:1 by volume) until the leading
224 edge of the solvent phase reached 1 cm above the spotting origin. The rods were then developed
225 in hexane: diethyl ether: formic acid solution (99:1:0.05) for 48 min, and finally rods were
226 developed in a hexane: diethyl ether: formic acid solution (80:20:0.1) for 38 min. After each
227 solvent development, rods were dried (5 min) and conditioned (5 min) in a constant humidity
228 chamber (~32%) that was saturated with aqueous $CaCl_2$. Following the last development, rods
229 were scanned using Peak Simple software (ver. 3.67, SRI Inc.) and the signal detected in
230 millivolts was quantified with calibration curves using the following commercial standards from
231 Sigma (St Louis, MO, USA): cholesteryl stearate (wax ester), glyceryl tripalmitate
232 (triacylglycerols), palmitic acid (free fatty acids), cholesterol (sterols), L-alpha-
233 phosphatidylcholine (polar lipids). Calibrated relationships between lipid class areas and
234 standard lipid amounts (µg) had correlations with an $r^2$ >0.98 for all classes. Lipid class data did
235 not show significant proportional differences (Appendix 1) so only total lipids (∑Iatroscan total
236 lipids) are shown as absolute amounts per wet weight ($mg.g^{-1}$).

237 Prior to derivatization of field-collected crabs, an internal standard, tricosanoic acid
238 methyl ester (23:0), was added to lipid extracts in an amount that was ~10% of the total fatty
239 acids. Total lipid extracts were derivatized to form fatty acid methyl esters (FAME) using acid
240 transesterification in $H_2SO_4$ in MeOH (Budge et al. 2006). An HP 7890 GC FID equipped with
241 an autosampler and a DB wax GC column (Agilent Technologies, Inc., USA) was used to
242 analyze FAME samples. The DB wax column was 30 m in length, with an internal diameter of
243 0.25 mm and a film thickness of 0.25 µm. The column temperature began at 65°C, held for 0.5
244 min, and then raised to 195°C (40°C.$min^{-1}$), held for 15 min and then increased again (2 °C.$min^{-1}$)
245 ) to a final temperature of 220°C and held for 1 min. The hydrogen carrier gas was flowing at a

rate of 2 mL.min$^{-1}$ and the injector temperature was set at 250°C, while the detector temperature was held constant at 250°C throughout the 31-min run. Peaks were identified using retention times based on standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3). Nu-Check Prep GLC 487 (Elysia, MN, USA) quantitative FA mixed standard was used to check column function and chromatograms were integrated using Chem Station (version A.01.02, Agilent).

Statistical differences by year and region of collection were examined for crab total fatty acids per wet weight (WWT, mg.g$^{-1}$), crab storage of diatom indicator fatty acids (ratio of 16:1n-7 to 16:0, Viso and Marty (1993)) and crab storage of bacterial fatty acids per wet weight (mg.g$^{-1}$, ∑odd and branched chains, Kaneda (1991)) using 2-way ANOVAs with Tukey's pairwise comparisons ($p<0.05$, Minitab 19). We included individual fatty acid proportions > 0.5% in at least one region (Table 1) as well as total fatty acids per WWT in a multivariate analyses using PRIMER v.7 (Primer-E) with a Permutational ANOVA, PERMANOVA add-on package (Primer-E Ltd). We included ∑FA (mg.g$^{-1}$) in our multivariate analyses of crabs in order to demonstrate fatty acids associated with increased total lipid storage. Fatty acids were square-root transformed prior to analyses and were then used to calculate a triangular matrix of similarities (Bray-Curtis similarity) between each pair of samples. Non-metric multidimensional scaling (*n*MDS), an iterative process that uses ranks of similarities, was utilized to explore the effect of region and year of collection on the fatty acid composition of juvenile *Chionoecetes* spp.crabs. We performed a 2-way PERMANOVA with carapace width as a covariate to control for size and examined the significance of region of collection (CM, SM, CO, SO) and year (2012 or 2014) on the fatty acid composition of crabs.

*Integrated Chla concentrations across the southeastern Bering Sea Shelf, 2012 and 2014*

To compare crab condition and trophic biomarkers to an index of phytoplankton biomass we used water column integrated chla ($mg \cdot m^{-2}$) values collected in 2012 and 2014 from the same biennial BASIS survey that hosted crab collections. The BASIS fisheries oceanography surveys (2003 to present) provide valuable data on oceanography, and primary and secondary production across the Eastern Bering Sea from mid-August to October (details as in Eisner et al. (2016)). Variations in chla concentrations were used to evaluate spatial and inter-annual differences in total phytoplankton biomass. In addition, the ratio of large size-fraction to total phytoplankton biomass (>10 μm chla / total chla) was estimated from discrete water samples filtered through polycarbonate 10 μm and GF/F (nominal pore size 0.8 μm) filters, and analyzed with standard fluorometric methods (Parsons et al. 1984). Increases in the ratio of large sized phytoplankton can indicate higher proportions of diatoms and thus may be indicative of diet quality. Total integrated chla ($mg.m^{-2}$, over the top 50 m of the water column or to the bottom for shallower stations) was estimated from CTD fluorescence profiles, calibrated with discrete total chla (GF/F) samples. At each station, integrated chla > 10 μm was estimated by multiplying the mean large size fraction ratio (>10 μm chla/ total chla) from discrete samples by the total integrated chla value. Total and >10 μm integrated chla at each station were averaged over each of the four regions used to compare juvenile crabs (CM, SM, CO, SO) in both 2012 and 2014 (Table 1). Additionally, we looked at the station-specific relationship between late summer large size phytoplankton biomass and crab condition over the shelf in both years and just in 2012 alone. Specifically, we compared the integrated >10 μm chla to station-specific averages for crab ∑FA ($mg.g^{-1}$) and the fatty acid diatom indicator (ratio of 16:1n-7 to 16:0) in crab tissue using linear regressions (SigmaPlot version 14, $p<0.05$).

Spatial patterns in bottom temperatures and chla biomass data from survey sampling stations was visualized using Empirical Bayesian Kriging (Krivoruchko and Gribov 2019) using ArcGIS Desktop 10.7. Bottom temperature for the BASIS juvenile crab distribution maps was obtained from CTD casts conducted at survey stations as described in Eisner et al. (2016). Monthly average sea ice extents were obtained from the National Snow and Ice Data Center's Sea Ice Index version 3 (Fetterer et al. 2017 updated daily).

**Results**

Our laboratory experiments showed that temperature influenced the growth and lipid storage of juvenile Tanner crabs. Temperature increased the rate at which crabs molted with an average day to molt (C3 to C4 stages) of only 37 ± 1 (n = 9) days at 9 ℃ compared to 110 ± 5 (n = 10) days at 2 ℃ (C3: Kruskal-Wallis, $H_1$ = 13.58, p = 0.0002, Fig. 1a). The effect of temperature on the molt increment was also pronounced with a higher increase in size from C3 to C4 at 9 ℃ (38.5 ± 3.7, n = 9) than at 2 ℃ (26.5 ± 3.9, n = 10, C3: ANOVA, $F_{1,16}$, = 4.82, p=0.043, Fig. 1b). Although growth was faster at warmer temperatures, the effect on lipid storage was the opposite: C4 crabs cultured at 2 ℃ had significantly higher lipid densities (18.7 ± 3.1 $mg.g^{-1}$, n = 5) than those cultured at 9 ℃ (9.4 ± 3.0 $mg.g^{-1}$, n = 6, ANOVA, $F_{1,9}$=4.7, p = 0.050, Fig. 1c). Difference in the lipid class proportions were not significant although crabs at colder temperatures trended towards higher triacylglycerols and lower proportions of sterols than those reared at 9℃ (Table A1).

Throughout all four regions of the SEBS, bottom temperatures were warmer in 2014 than 2012 (Fig. 2). The average region-specific increase in bottom temperature was 2.1 ± 0.6 ℃ (n = 4) with the largest increase in temperature across the two central shelf regions (~2.5 ℃) and a

smaller increase in bottom temperature along the outer deeper shelf regions (~1.5 ℃, Table 1). In both years, juvenile Tanner crabs (species rank 1 & 2) were concentrated in the warmer deeper bottom waters of the outer shelf (100 to 200 m). This data from both years are in agreement with a previous reports for just 2012 where Ryer et al. (2016) noted the distribution of juvenile Tanner crab was concentrated along the outer shelf in avoidance of the cold-pool over the middle shelf. A similar distribution of Tanner crab was found in 2014, although generally CPUE was lower in the southern regions. Juvenile snow-hybrids (rank-3 as defined in Urban et al. (2002)) were only captured on the central middle shelf (Fig. 2), which historically is covered by the cold-pool (<2 ℃ water) during cold and moderate temperature years.

There was substantial spatial and inter-annual variation in chla across the SEBS during 2012 and 2014 (Fig. 3). The region-specific total integrated chla was higher in 2012 than in 2014 with an average region-specific difference of 42 $mg.m^{-2}$ (n = 4 regions, Fig. 3a & 3c) while chla in the large size fraction was 32 $mg.m^{-2}$ higher in 2012 than 2014 (Fig. 3b & 3d). Mean annual values for each regions showed the highest integrated chla in 2012 on the south outer (SO) shelf (143.7 ± 79.2 $mg.m^{-2}$, n = 4) and the lowest mean values in 2014 on the south middle (SM) shelf (27.7 ± 7.1 $mg.m^{-2}$, n = 8) (Table 1). The regional-specific decrease in integrated chla was highest over the SO shelf with a drop from 2012 to 2014 of 104 $mg.m^{-2}$. The least change in total integrated chla was measured across the central middle (CM) shelf where values decreased by 18 $mg.m^{-2}$ from 2012 to 2014. Region-specific large particle (>10 μm) chla ranged from a high of 28 $mg.m^{-2}$ on the CM shelf in 2012 to a low of 2 $mg.m^{-2}$ in 2014 on the SO shelf (Fig. 3b & 3d). The largest regional differences in chla from large particles was measured on the CM shelf between 2012 and 2014, where values in 2014 were only 21% on average of those measured in 2012 (a reduction from 28 $mg.m^{-2}$ down to 6 $mg.m^{-2}$, Table 1, Fig. 3).

There was a significant interaction between year and region (general linear model (GLM), $F_{3,178} = 13.90$, $p<0.001$) on the total fatty acid concentration of juvenile crabs. Crabs had the highest fatty acids per weight on the CM shelf in 2012 and the lowest fatty acids on the SO shelf in 2014. This region-specific difference in fatty acid tissue storage between 2012 and 2014 was the most significant on the CM shelf compared to other survey regions (Fig. 4a). There were significantly higher densities of bacterial fatty acids in crab tissues in 2012 than in 2014 across all regions (GLM, $F_{1,178} = 5.24$, $p<0.02$). Region of collection also had a significant effect on crab bacterial markers (GLM, $F_{3,178} = 28.04$, $p<0.001$, Fig. 4b) with crabs collected on the CM shelf having significantly higher levels than crabs from all other regions. Diatom markers in crab tissues were interactively affected by region and year of collection (GLM, $F_{3,178} = 19.95$, $p<0.001$) with crabs collected in 2012 from the CM region having the highest ratio of diatom indicator fatty acids while crabs collected on the outer shelf (SO & central outer (CO)) had significantly lower and less variable diatom indicators in both years. A significant decrease in the diatom indicator was measured in all regions from 2012 to 2014 except on the SO where levels did not significantly differ between years (Fig. 4c).

Correlations between the integrated chla in >10 μm particles and mean crab fatty acid storage ($mg.g^{-1}$ WWT) as well as crab storage of diatom indicator fatty acids (ratio of 16:1n-7 to 16:0) were evaluated across stations where crab were captured over the middle shelf (CM and SM) in 2012 and 2014. The outer shelf stations were excluded due to the lower numbers of stations sampled. Comparisons over both years showed a week relationship between >10 μm chla in late summer and crab lipid storage ($F_{1,22} = 6.59$, $p = 0.018$, $r^2 = 0.2$) as well as crab tissue storage of diatom markers ($F_{1,22} = 11.03$, $p = 0.003$, $r^2 = 0.3$, Fig. 5a & 5b). However, when this relationship was examined only in the cold year (2012) we saw a positive relationship between

361 station-specific >10 µm chla and crab total fatty acids ($F_{1,9}$ = 11.06, p = 0.001, $r^2$ = 0.50) and a
362 highly positive relationship with the diatom fatty acid indicators in crab tissue ($F_{1,9}$ = 26.75, p =
363 0.009, $r^2$ = 0.72). This relationship points to the importance of large size phytoplankton biomass
364 (conceivably diatoms) to juvenile crab lipid storage.

365 Juvenile *Chionoecetes* spp. from all four regions across the SEBS in two years were
366 distinguished based on individual fatty acids >0.5% and crab total tissue fatty acids ($mg.g^{-1}$)
367 using *n*MDS (non-metric multidimensional scaling, Fig. 6). Crabs from the CM shelf were
368 characterized by elevated fatty acids characteristic of diatoms (16:1n-7 and $C_{16}$ PUFA) and
369 elevated total fatty acids per WWT, compared to crabs from outer shelf regions which had lower
370 fatty acid concentrations. In particular, crabs from the CO shelf had higher proportions of long
371 chain $C_{20+22}$ monounsaturated fatty acids (MUFA) typical of calanoid copepods (i.e. 20:1 n-9 and
372 22:1 n-11) which could indicate that these lower lipid crabs were feeding at a higher trophic
373 level. There was a proportional increased in importance of bacterial fatty acids (i.e. *ai* 17:0 and
374 *ai* 15:0) in crabs from the CM and SM shelf regions in 2014 compared to 2012, likely due to the
375 relative decrease in diatom-sourced fatty acid in 2014. There was a significant interaction
376 between year and collection region on crab lipid biomarker composition (PERMANOVA,
377 pseudo $F_{3, 177}$ = 9.18, p <0.001) with larger annual differences in crabs collected on the CM shelf
378 then those from the SO shelf.

379 Tanner crab (ranks 1), Tanner hybrid (rank 2) and snow hybrid (rank 3, as defined in
380 Urban et al. (2002)) only overlapped geographically on the CM shelf (Fig. 2). Therefore, we
381 only analyzed crab lipid composition as a function of hybridization stage in the CM region while
382 for all other analyses we pooled data for *Chionoecetes* spp. In the CM region, we found a
383 significant interaction between year and hybrid status on total fatty acids per WWT ($mg.g^{-1}$) in

384 juvenile crabs (GLM, $F_{2,56} = 5.16, p = 0.009$). The decrease in total fatty acids from a cold
385 (2012) to a warm (2014) year was more significant for snow hybrids (rank 3) than it was for
386 Tanner crabs (rank 1, Fig. 7). Although sample sizes were small, this indicates potentially a
387 more dramatic effect of environmental warming and changes to food quality on snow crab lipid
388 storage then measured for Tanner crabs.

389 **Discussion**

390 Our combined laboratory and field-based analyses on the early juvenile stages of the
391 *Chionoecetes* spp. complex from across the SEBS show both direct thermal and indirect dietary
392 impacts of environmental change on juvenile crab lipid storage. Crabs in the warm year (2014)
393 had lower total fatty acids per weight, and had lower diatom fatty acid biomarkers than crabs
394 from the cold year (2012: one of the last major SEBS cold pool years that decade). These
395 findings give us a mechanistic framework through which to view changes in crab abundance and
396 energetic status during on-going environmental transformation and northward retraction of the
397 Bering Sea cold pool.

398 *Direct thermal effects on juvenile Chionoecetes spp.*

399 Temperature is the most important environmental factor controlling vital rates in
400 ectotherms (Hartnoll 2001) and consequently our finding of faster crab growth with warm (9 ℃)
401 compared to cold temperatures (2 ℃) is expected (Ryer et al. 2016; Stoner et al. 2013; Stoner et
402 al. 2010). Ryer et al. (2016) noted that slow growth rates of Tanner crabs at cold temperatures
403 (C3 to C4 stage, ~100 days at 2 ℃) likely explained their avoidance of the Bering Sea cold pool
404 with higher crab abundance found in warmer deeper outer shelf waters (C3 to C4 stage, ~50 days
405 at 5℃). Temperature-dependent growth rates of *Chionoecetes* spp. (Ryer et al. 2016; Yamamoto

et al. 2015) indicate that crabs in our study were in their second year on the bottom after setting, despite their comparative small size in relation to age-0 crabs from warmer nursery sites in the Gulf of Alaska (Copeman et al. 2018; Ryer et al. 2015). Warmer temperatures in 2014 may explain the general predominance of larger juvenile crabs in our collections from 2014 compared to 2012 (Table 1), but this variance was not extreme, and was within one molt stage (C5 to C6, estimated from the temperature-dependent growth relationship in Ryer et al. (2016)). Previous laboratory studies on juvenile Alaskan crab species have shown variable lipid densities with ontogeny during pelagic stages (Beder 2015; Copeman et al. 2014), but relatively stable lipids per weight across juvenile benthic stages (Copeman et al. 2012). Therefore, annual difference (2012 vs. 2014) in crab lipid storage here are likely not attributable to the minor annual differences in crab molt stages.

Understanding the mechanisms through which thermal effects act on vital rates (oxygen consumption, growth, lipid metabolism) can be improved by utilizing controlled laboratory studies with multiple physiological end points (Pörtner and Knust 2007). We found increased temperature caused direct, but opposing effects on juvenile Tanner crab growth and lipid storage. Vital rates of crustaceans, and ectotherms in general, have a dome-shaped relationship with temperature (Laurel et al. 2016; Schiffer et al. 2014; Storch et al. 2011). Ryer et al. (2016) noted a relatively eurythermal growth response in juvenile Tanner crabs as growth is positively correlated with a wide range of temperatures (ranging from 2 ℃ up to 12 ℃). In contrast, snow crab exhibit a colder and more stenothermal response with higher growth up to 4-5 ℃, but decreased growth and survival at warmer temperatures (8 ℃, Yamamoto et al. (2015)). However, neither study concurrently measured the variation in energy storage as a function of temperature. While temperature-dependent growth is quite well defined for many species of fish

and crabs, less is known about the tradeoffs between growth and lipid storage with thermal variation. In temperature-controlled experiments on larval and juvenile cod species, the thermal maximum for lipid storage has been found to be lower than that observed for growth (Copeman et al. 2017; Koenker et al. 2018). Similarly, we found reduction in lipid with increased growth in Tanner crabs at 9 ℃ compared to 2 ℃, results that suggests a lower thermal optimum for lipid storage than for growth. Further detailed species-specific experiments with more temperature treatments are required to parameterize the temperature-dependent trade-offs between lipid storage and growth (protein synthesis) in juvenile *Chionoecetes* crabs. Knowledge of these temperature-dependent vital rates could allow more accurate predictions of future effects of warming on crab growth, energetics, and ultimately recruitment potential.

*Indirect food web effects*

Expected indirect effects of warming and loss of sea ice for benthic invertebrates include diminished quantity and quality of resources fluxing to the benthos (Griffiths et al. 2017; Harada 2016; Hobson et al. 1995; Hunt et al. 2011). Particularly, a reduction in sea ice and associated ice-algae blooms (often diatoms) may substantially reduce the energy deposition to the seafloor. The mechanisms through which environmental change affect benthic-pelagic coupling have been more rigorously studied in the northeastern Bering and Chukchi Seas than in the SEBS likely because northern seas are more ice-dominated and have a greater benthic biomass (Grebmeier 2012; Lovvorn et al. 2005) than the more pelagic-dominated SEBS.

Across all four of our study regions and through both warm and cold years, we found that diatom fatty acid biomarkers in crab tissues were positively associated with increased total fatty acids ($mg.g^{-1}$ WWT) in juvenile crabs. Therefore, much of the excess lipid storage in juvenile crab tissues is of diatom origin and points to the importance of this primary producer for juvenile

crab metabolism and growth. We did not have samples of food items such as organic "fluff" material or small benthic prey to analyze for lipid biomarkers to directly link crab lipid compositions to their diet. Although we do not have explicit species identification of phytoplankton in our chla samples from 2012 and 2014, evidence from FLOWCAM imaging of phytoplankton undertaken in the Bering and Chukchi seas during summer in the same years noted a predominance of diatoms in 2012, that was much reduced in 2014 (Goes et al. 2014). Further, larger diatoms were more prevalent in late spring of 2012 than in 2011, a warmer year with less extensive sea ice (Stauffer et al. 2014). Our results for these SEBS crabs are also in agreement with previous work on nearshore Tanner crabs in the central Gulf of Alaska (Copeman et al. 2018). In four isothermal nearshore embayments, increased crab growth and lipid storage was positively related to the organic content and in particular to the concentration of bacterial- and diatom-sourced lipids in the top sedimentary layer (Copeman et al. 2018). However, unlike Tanner crabs from the Gulf of Alaska, crabs from the SEBS in cold years also likely store diatom lipids from early spring ice-associated blooms.

In 2012, extensive sea ice covered most of the SEBS throughout early spring with only the SO shelf remaining ice-free. This is in contrast to 2014, where March ice was absent from all regions except for partial coverage of the CM shelf (Fig. 3). The SO shelf was the only region that was not covered by March sea ice in either year and crabs from this region were the only group that did not show a significant difference in their diatom indicator fatty acids between 2012 to 2014 (Fig. 4c). This indicates that ice-associated, diatom production likely contributed significantly to higher condition of 2012 crabs across the middle and CO shelf regions. A potential proxy for late summer diatom production (>10μm chla $mg.m^{-2}$, discussed above) over the shelf in 2012 (cold year) was positively correlated with the diatom indicator (16:1n-7 to 16:0)

and total fatty acids ($mg.g^{-1}$) in crab tissues (Fig. 5d). This suggests that in cold years, both spring ice-edge and summer-fall pelagic diatom production may play significant roles in juvenile crab nutrition over the SEBS shelf. Future use of ice algae specific trophic markers such as compound specific isotopes of diatom fatty acids, sterols and isoprenoid 25 (Brown et al. 2017; Koch et al. 2020; Leu et al. 2020) could help to define the role of spring ice-associated versus pelagic diatom production in juvenile crab nutrition in the Alaskan Arctic.

There is a very little understanding of how crab lipid metabolism (i.e. fatty acid assimilation rates and tissue wash-out rates) can impact the lipid biomarker signatures in cold-water crab tissues (Copeman et al. 2012; Stoner et al. 2010). Generally, assimilation time for small crabs occurs quickly as exemplified by a recent dietary studies on juvenile Dungeness crabs (*Metacarcinus magister*) that showed tissue fatty acid assimilation and discrimination after only six weeks (Thomas et al. 2020). Alaskan red king crab (*Paralithodes camtschaticus*) fed live-food with different fatty acid compositions displayed significant differences in their fatty acid profiles after less than one month of feeding (Beder 2015), while differences in the lipids of juvenile Tanner crabs fed low, medium, and high lipid diets were evident after only one molt stage (C4 to C5, Copeman et al. (2018)). However, even less is known about the effect of reduced food availability or starvation on the measured fatty acid biomarkers in crab tissue. It is likely that crabs store excess lipids and retain these for long times at cold temperatures following the spring sympagic- and pelagic-blooms. The signature of ice-associated diatom production is probably retained throughout the summer months. Additionally, it is likely that spring diatom production sinks to the benthos and that this material serves as a 'food bank' which supplies the benthos well past the short spring production season, as previously described for Arctic (Schollmeier et al. 2018; Weems et al. 2012) and Antarctic (Mincks et al. 2005) benthic food

webs. The unknown crab tissue assimilation rates and turnover times for fatty acids make it directly difficult to partition ice-associated from pelagic-associated diatom dietary input. However, with continued warming of the entire water column, contraction of spring sea ice (2019, Fig. 3), and consequent northward shrinkage of the cold pool over the Bering Sea, it is conceivable that the persistence of this spring-deposited food bank may be decreasing both by reduced benthic-pelagic coupling but also internally by increased secondary consumer metabolic rates on the sea floor.

The late summer biomass of large sized chla (>10 µm) was elevated across the SEBS in 2012 compared to 2014, but there were also changes in the biomass of small sized chla (< 10 µm) between the two years. A large late summer coccolithophore bloom of the prymnesiophyte, *Emiliania huxleyi* (small cells, ~ 5 µm) formed over the middle shelf in 2014 (60,658 $km^2$) that was practically absent in 2012 (273 $km^2$)(Ladd et al. 2018). The presence of this extensive coccolithophore bloom in 2014 partially explains why total values for late summer chla ($mg.m^{-2}$) remained fairly constant across the two years (CM region, 72 $mg.m^{-2}$ to 55 $mg.m^{-2}$), but values for chla in large particles were dramatically lower (28 v. 6 $mg.m^{-2}$) in 2014 as was the ratio of biomass from large particles to total biomass (Table 1). As opposed to diatoms that have relatively large particle sizes, sink rapidly and are common during spring in high nutrient waters, small coccolithophore cells contribute little to the benthos and form blooms often in late summer nutrient-depleted waters (Eisner et al. 2016; Grebmeier et al. 2006; Ladd et al. 2018; Olson and Strom 2002). Coccolithophores likely contribute little to the diet of larger zooplankton and are not necessarily a preferred dietary source for microzooplankton in the SEBS, even given their small size (Olson & Strom 2002). As such, little of this production is likely transferred from

520 phytoplankton to secondary benthic consumers or to upper trophic level pelagic organisms such
521 as fish, seabirds and marine mammals (Hunt et al. 1999; Olson and Strom 2002).

522 Crabs collected from the CO shelf were distinguished in a multivariate analysis of their
523 fatty acid composition compared to crabs from other regions, particularly in 2014 (Fig. 6). This
524 differentiation was defined by generally low fatty acid storage ($mg.g^{-1}$) and higher concentrations
525 of calanoid copepod fatty acids. High proportions of $C_{20+22}$ chain length MUFA (16 to 22%) in
526 predators are characteristic of feeding on calanoid copepods with high wax ester lipid storage
527 (Dalsgaard et al. 2003; Lee et al. 2006; Stevens et al. 2004), but these fatty acids are also found
528 in high proportions in some other benthic macroinvertebrates, such as cold-water echinoderms
529 (Copeman and Parrish 2003). Given the small size of these juvenile crabs, the most logical
530 explanation for this elevated $C_{20+22}$ MUFA is from the direct consumption of copepod carcasses
531 or their fecal pellets. Large oceanic copepods on the SEBS outer shelf such as *Neocalanus* spp.
532 develop in spring and begin descending to depth to diapause as lipid-rich C5 stages in late May
533 (Miller 1993; Vidal and Smith 1986). *Neocalanus cristatus* collected in diapause from offshore
534 waters of southeast Hokkaido, Japan were found to contain approximately 80% of their lipids as
535 wax esters with a fatty alcohol composition that was ~81% $C_{20+22}$ MUFA (Yamada et al. 2016).
536 It is possible that *Neocalanus* on the outer shelf of the Bering Sea could reach the shallow shelf
537 bottom and be consumed by juvenile crabs during their attempt to reach diapause habitat at
538 greater depths (Miller 1993). However, it is noteworthy that these crabs which are potentially
539 feeding at a higher trophic level were in lower lipid-based condition than crabs from the
540 shallower shelf regions that had higher diatom indicator fatty acids.

541

*Caveats and future research*

Crab total fatty acid values here are expressed relative to WWT because we did not have enough animals to analyze individuals for dry weight (DWT) and ash-free DWT (AFDWT, organic mass). Expression of fatty acids per WWT is not ideal as it is impossible to distinguish differences in lipid content per organic weight from difference in lipid content due to variable shell weight. This can be an issue when comparing crabs that are of disparate size or ontogenetic stage, however, the crabs in our study only varied by one molt stage (Table 1). Previous studies on Tanner and red king crab from Alaska found no significant difference in the proportion of moisture or AFDWT in crab tissues as a function of their molt stage (C2 to C4 ) (Copeman et al. 2018; Stoner et al. 2010).

Crustaceans can also vary in the proportion of AFDWT as a function of their intramolt cycle and changes in association with ecdysis. (Copeman et al. 2012; Ouellet et al. 1992). Generally, there are 3 biochemical phases during the intramolt period which are typified by a short post molt period, a longer intramolt period, and another short non-feeding premolt period. Studies on juvenile crustaceans have documented a general energetic pattern of no increase in lipids during the postmolt period, a rapid accumulation of lipid during the feeding intramolt stage, and lastly, a small decrease in lipids during a nonfeeding premolt stage (Copeman et al. 2012; Ouellet et al. 1992; Sánchez-Paz et al. 2006; Zhou et al. 1998). We controlled for this intramolt energetic variability in our lab study by sampling at a set and temperature-adjusted mid-molt period. It is not possible to control for energetic variation due to intramolt stage in field collected crabs. Nevertheless, lab studies have shown that there is a large degree of variation in intramolt duration in juvenile snow crabs (i.e. C4 stages at 4 ℃ ranged from 59-192

d, Yamamoto et al. (2015)) which leads us to conclude that intramolt stage is unlikely to be uniformly different as a function of geographical region across the SEBS.

Through the use of both laboratory and field approaches, we have provided some of the first evidence linking both direct metabolic and indirect food web effects of warming to reduced lipid storage of juvenile *Chionoecetes* spp. Our understanding of factors affecting crab recruitment on the SEBS, could be greatly enhanced by definitive genetic differentiation of Tanner, snow and hybrids (Smith et al. 2005). Snow crabs were only collected on the central middle shelf but we noted that warming conditions appeared to have a more significant impact on their energetic condition than for Tanner crabs. Previous studies on the SEBS have shown that environmentally driven impacts on pelagic food webs are not identical in all warm stanzas (Duffy-Anderson et al. 2017; Eisner et al. 2019; Eisner et al. 2016) and the same may be true for cold stanzas. The addition of more years of crab collection and lipid analysis, with particular urgency focused on sampling during rapidly disappearing SEBS "cold" years, will help us better define the mechanisms driving variability in crab condition. Northward expansion of this type of annual ecosystem study with a focus on small juvenile crabs will provide greater insight into how environmental conditions are impacting the distribution, condition and resultant recruitment variability of *Chionoecetes* spp. across the northern Bering Sea and into the Chukchi Sea.

**Acknowledgements**

We would like to thank Janet Duffy-Anderson and Daniel Cooper and the crew of the 2012 and 2014 BASIS NOAA Ecosystem Survey for the collection of juvenile crab, chla and temperature data. We would like to thank Kayln Hubbard for technical assistance with lipid analyses at the Marine Lipid Ecology Lab at Oregon State University. Further, we thank Scott Haines for

assistance with laboratory experiments and help with crab hybrid identification. Benjamin Laurel, Jeffrey Napp, Thomas Hurst and Erin Fedewa provided helpful editorial reviews on earlier versions of this manuscript. Thanks also to Cynthia Sweitzer for providing help with procurement of permits for crab collections. We would like to thank two anonymous peer-reviewers as well as Dr. Patrick Mayzaud for helpful suggestions that greatly improved our manuscript.

## Author's Contributions

CR was the principle investigator on this grant. CR and LC contributed to the study conception and design. Data collection was performed by MO, CR, LC, MS, PI and LE. Data analysis was performed by LC. The first draft of the manuscript was written by LC and all authors commented on previous versions of the manuscript. All authors read and provided critical review to the final manuscript.

## Funding

This research was funded in part by an Essential Fish Habitat grant awarded to Dr. Clifford Ryer from the NMFS Alaska Region's Habitat Conservation Division.

## Declarations

The authors have no conflicts of interest to declare that are relevant to the content of this article. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service.

Figure Legends

**Fig. 1** The effect of temperature on mean (± SE) (a) inter-molt period in days from C2 to C3; (b) % intermolt increment from C2 to C3 based on carapace width; and (c) total body lipid by wet weight for C3 (2 degrees) and C4 (9 degrees) crabs, midway through their intermolt period. Tanner crabs (*Chionoecetes bairdi*) were fed to satiation 3X per week on a marine gelatinized diet.

**Fig. 2** Distribution of juvenile Tanner crab (*Chionoecetes bairdi*) and hybrid snow crabs (*Chionoecetes opilio*) molt stages C3 to C6 from the southeastern Bering Sea during September 2012 and 2014. CPUE are overlain on bottom temperatures collected from CTD casts conducted at the sampling sites (open circles). Tan symbols indicate Tanner and Tanner hybrid ranks (1-2) while red indicates snow crab and snow crab hybrids (3+, Urban et al. (2002)). Snow crab hybrids are found only in the colder central middle (CM) shelf while Tanners and Tanner hybrids are predominantly found in the warmer outer and southern regions. Shelf regions include: 1) central middle (CM), 2) south middle (SM), 3) the central outer (CO), and 4) south outer (SO). Ellipses include sampling sites where crabs were caught within the larger sampling region based on Ortiz et al. (2016).

**Fig. 3** Contours of total integrated chla in (a) 2012 and (b) 2014, and integrated chla in particles >10 µm in (c) 2012 and (d) 2014. Data are integrated over the top 50 m (methods as in (Eisner et al. 2016). Shelf regions include: 1) central middle (CM), 2) south middle (SM), 3) the central outer (CO), and 4) south outer (SO). For color bars, interpolated data values were stretched along a color ramp using minimum-maximum stretch type, such that high/low values could be edited to match between years. Monthly average sea ice extents are shown for 2012, 2014 as well as 2019, as an example of recent extremely low sea ice extent (Fetterer et al. 2017 updated daily). Ellipses include sampling sites where crabs were caught within the larger sampling region based on Ortiz et al. (2016).

**Fig. 4** Annual and regional differences in the total fatty acids ($mg.g^{-1}$), total bacterial fatty acids ($mg.g^{-1}$) as well as diatom fatty acid indicator in juvenile crabs (*Chionoecetes* spp.) from four geographical regions in the southeastern Bering Sea (2012-2014). Multiple comparisions of year*region, different letters indicate a significant difference $p<0.05$. Shelf regions include: 1) central middle (CM), 2) south middle (SM), 3) the central outer (CO), and 4) south outer (SO). ∑Bacterial markers per WWT include all odd and branched chained fatty acids (Table 1).

**Fig 5** Station-specific relationship between integrated Chla in particles > 10 µm across the SEBS shelf in late summer/fall and (a) crab total fatty acids per WWT in 2012 and 2014, (b) diatom indicator in crab tissues in 2012 and 2014, (c) crab total lipids per WWT in crabs from 2012 only, and (d) diatom indicator in crabs from 2012.

**Fig. 6** Nonmetric multidimensional scaling (*n*MDS) of individual juvenile crabs (*Chionoecetes* spp.) based on their fatty acid composition. Crabs were sampled in 2012 and 2014 from four regions across the SEBS: 1) central middle (CM), 2) south middle (SM), 3) the central outer (CO), and 4) south outer (SO). Fatty acids used for *n*MDS include all individual fatty acids >0.5% as shown in table 1 as well as total fatty acids per WWT ($mg.g^{-1}$). Vectors are shown for individual fatty acids that had a correlation > 0.5. PERMANOVA for the effects of region and year showed a significant interactive effect $p<0.001$ as illustrated by the larger annual effect (2012 versus 2014) in fatty acid composition of crabs on the CM shelf compared to overlapping

650 composition of crabs from SO region between the 2 years. Fatty acids indicative of diatoms
651 includes $C_{16}$ PUFA and 16:1n-7, fatty acids indicative of bacteria include odd and branched
652 chains and 18:1n-7, and fatty acids indicative of *Calanoid* copepods include $C_{20+22}$ MUFA
653 (Dalsgaard et al. 2003; Kelly and Scheibling 2012; Parrish 2013).

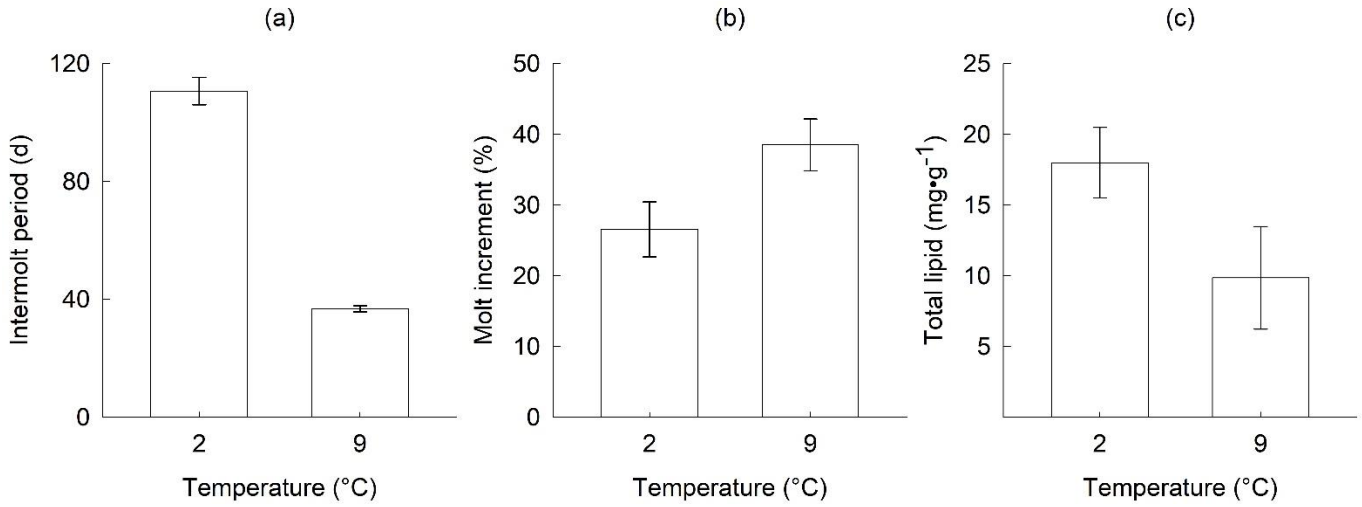
654 **Fig. 7** Annual and species differences in the total fatty acids ($mg.g^{-1}$) in juvenile crabs from the
655 central middle (CM) shelf of the SEBS (2012-2014). Samples sizes were Tanner crab
656 (*Chionoecetes bairdi*.) 2012 n = 6, 2014 n = 7, Tanner hybrid crabs 2012 n = 8, 2014 n = 11, and
657 snow crab (*Chionoecetes opilio)* hybrids 2012 n = 11, 2014 n = 19. Multiple comparisions of
658 year*region, different letters indicate a significant difference, $p<0.05$.

659

660

661

662

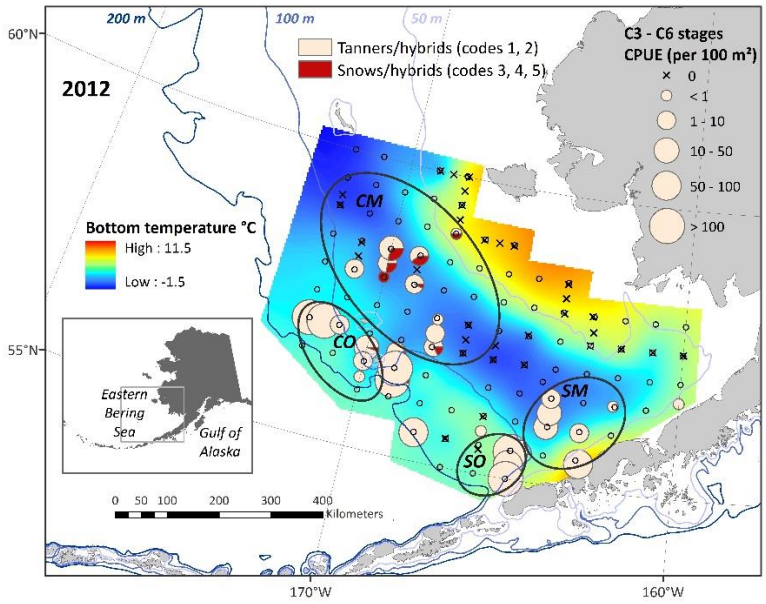



663

664

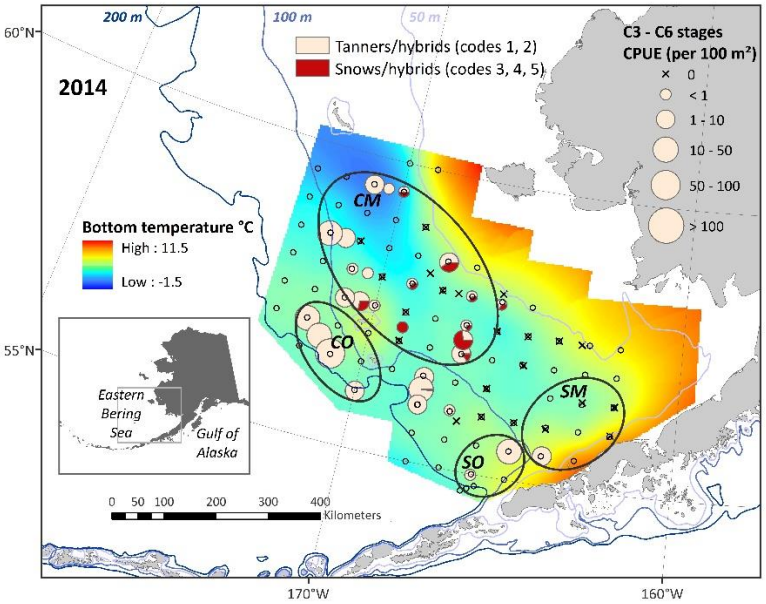
665

**(a)**



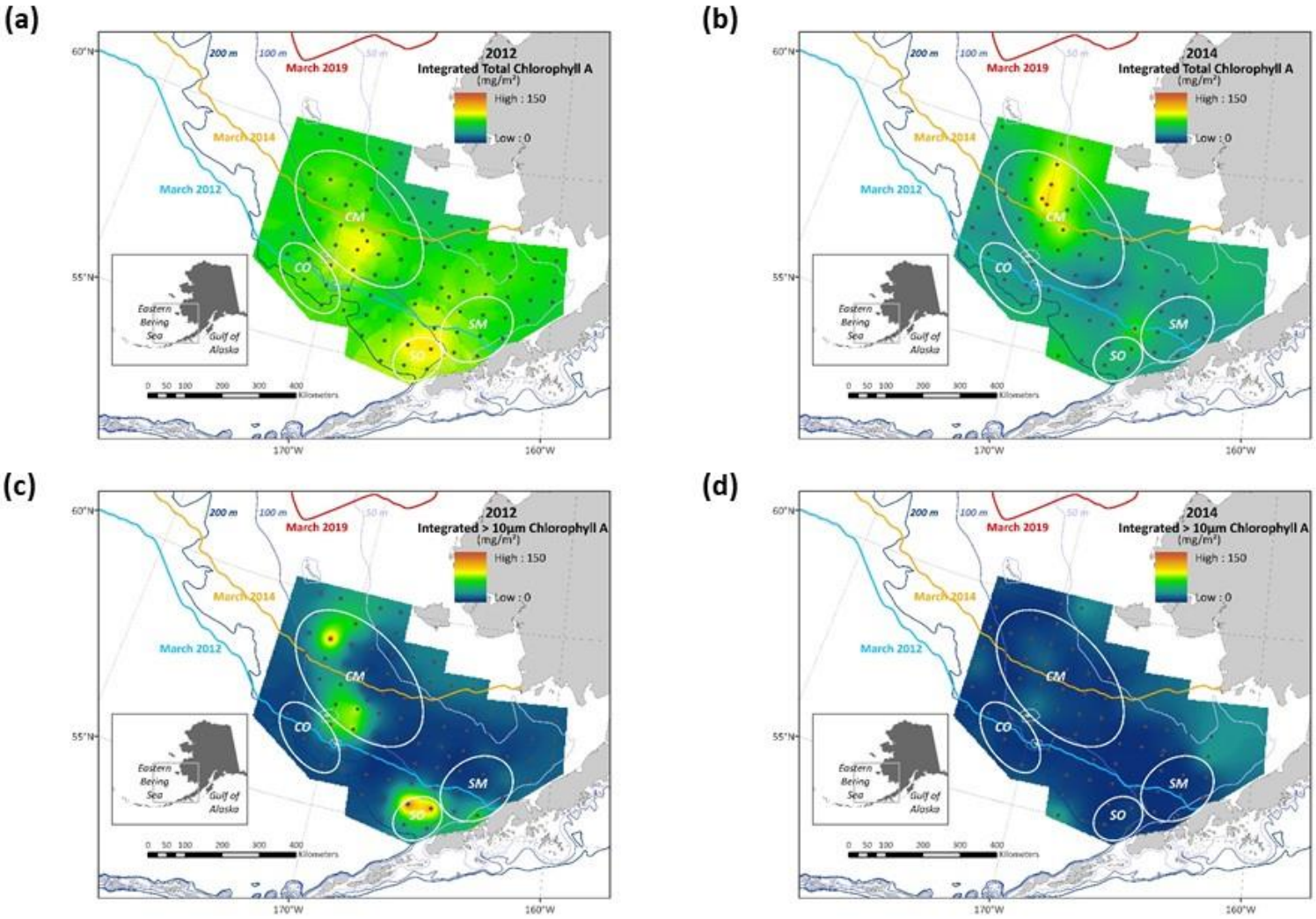

666

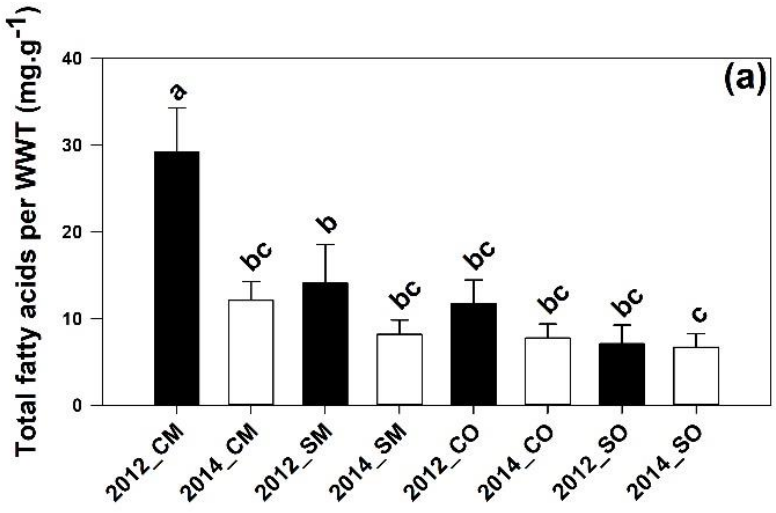
**(b)**



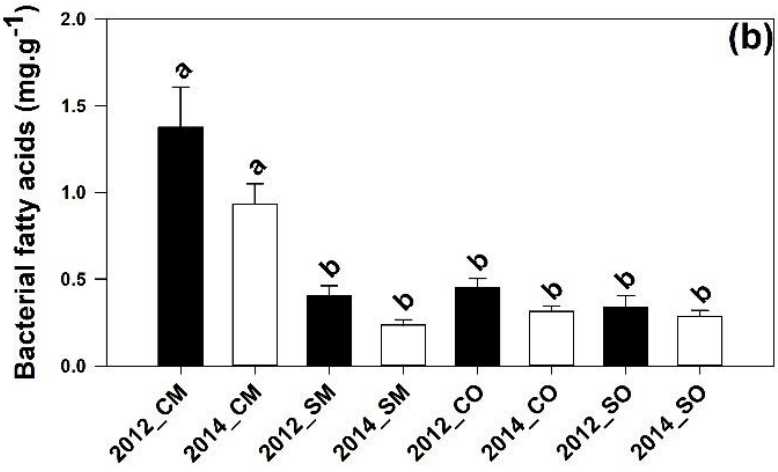

667

668

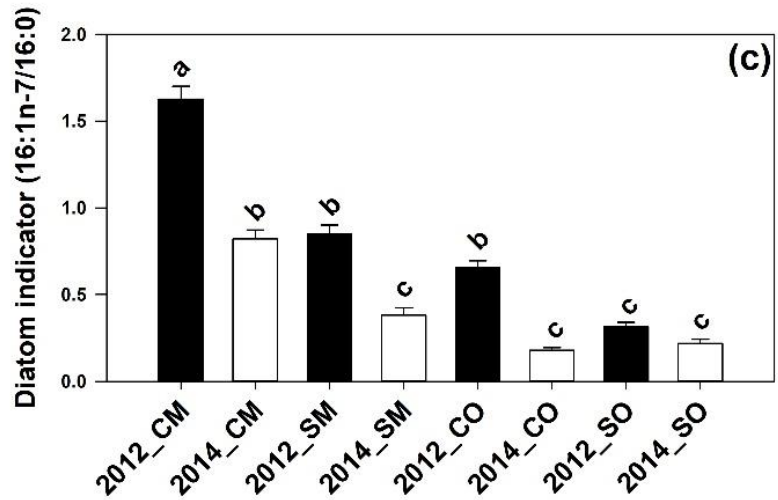

(a)
2012
Integrated Total Chlorophyll A
(mg/m²)
High : 150
Low : 0
March 2019
March 2014
March 2012
200 m
100 m
50 m
CM
CO
SM
SO
Eastern Bering Sea
Gulf of Alaska
0 50 100 200 300 400 Kilometers
60°N
55°N
170°W
160°W
(b)
2014
Integrated Total Chlorophyll A
(mg/m²)
High : 150
Low : 0
March 2019
March 2014
March 2012
200 m
100 m
50 m
CM
CO
SM
SO
Eastern Bering Sea
Gulf of Alaska
0 50 100 200 300 400 Kilometers
60°N
55°N
170°W
160°W
(c)
2012
Integrated > 10µm Chlorophyll A
(mg/m²)
High : 150
Low : 0
March 2019
March 2014
March 2012
200 m
100 m
50 m
CM
CO
SM
SO
Eastern Bering Sea
Gulf of Alaska
0 50 100 200 300 400 Kilometers
60°N
55°N
170°W
160°W
(d)
2014
Integrated > 10µm Chlorophyll A
(mg/m²)
High : 150
Low : 0
March 2019
March 2014
March 2012
200 m
100 m
50 m
CM
CO
SM
SO
Eastern Bering Sea
Gulf of Alaska
0 50 100 200 300 400 Kilometers
60°N
55°N
170°W
160°W



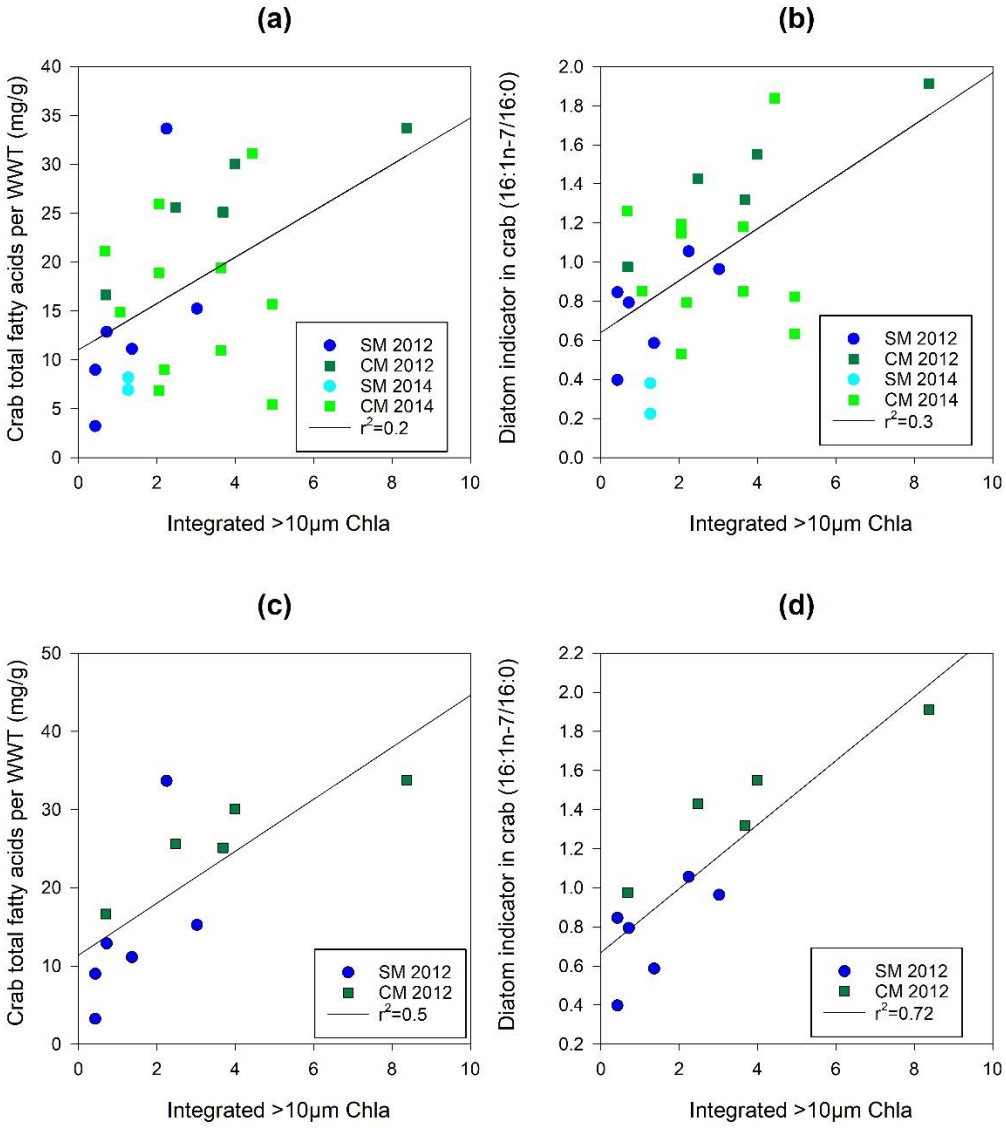

Year<0.001
Region<0.001
Year*Region<0.001

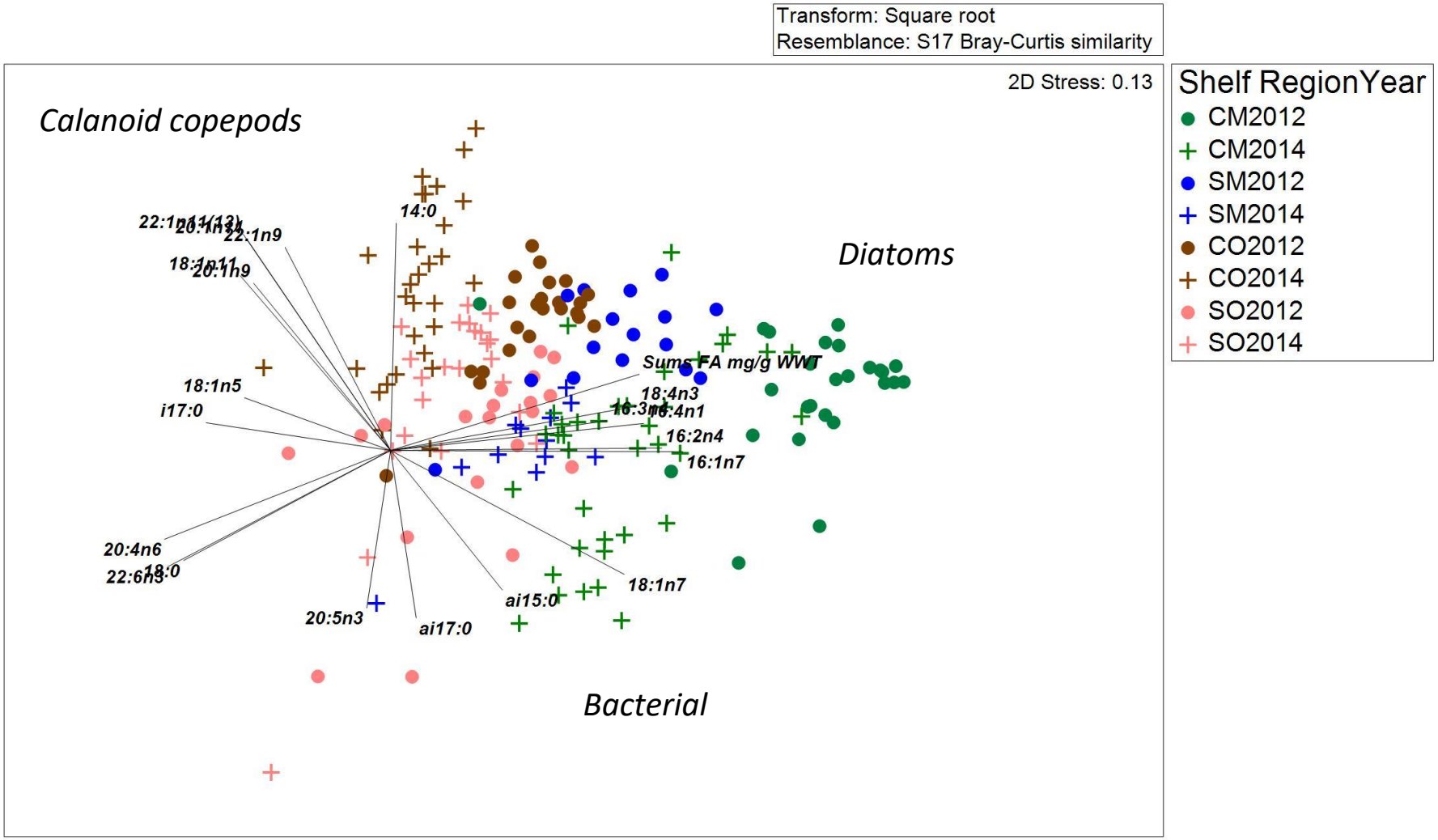



Year = 0.02
Region<0.001
Year*REgion=0.31




Year<0.001
Region<0.001
Year*Region<0.001


(a)
Crab total fatty acids per WWT (mg/g)
Integrated >10µm Chla
SM 2012
CM 2012
SM 2014
CM 2014
r²=0.2
(b)
Diatom indicator in crab (16:1n-7/16:0)
Integrated >10µm Chla
SM 2012
CM 2012
SM 2014
CM 2014
r²=0.3
(c)
Crab total fatty acids per WWT (mg/g)
Integrated >10µm Chla
SM 2012
CM 2012
r²=0.5
(d)
Diatom indicator in crab (16:1n-7/16:0)
Integrated >10µm Chla
SM 2012
CM 2012
r²=0.72


Transform: Square root
Resemblance: S17 Bray-Curtis similarity
2D Stress: 0.13
Shelf RegionYear
CM2012
CM2014
SM2012
SM2014
CO2012
CO2014
SO2012
SO2014
Calanoid copepods
Diatoms
Bacterial
14:0
22:1n9
20:1n9
18:1n5
i17:0
Sums FA mg/g WWT
18:4n3
16:4n1
16:2n4
16:1n7
20:4n6
22:6n3
18:0
20:5n3
ai17:0
ai15:0
18:1n7

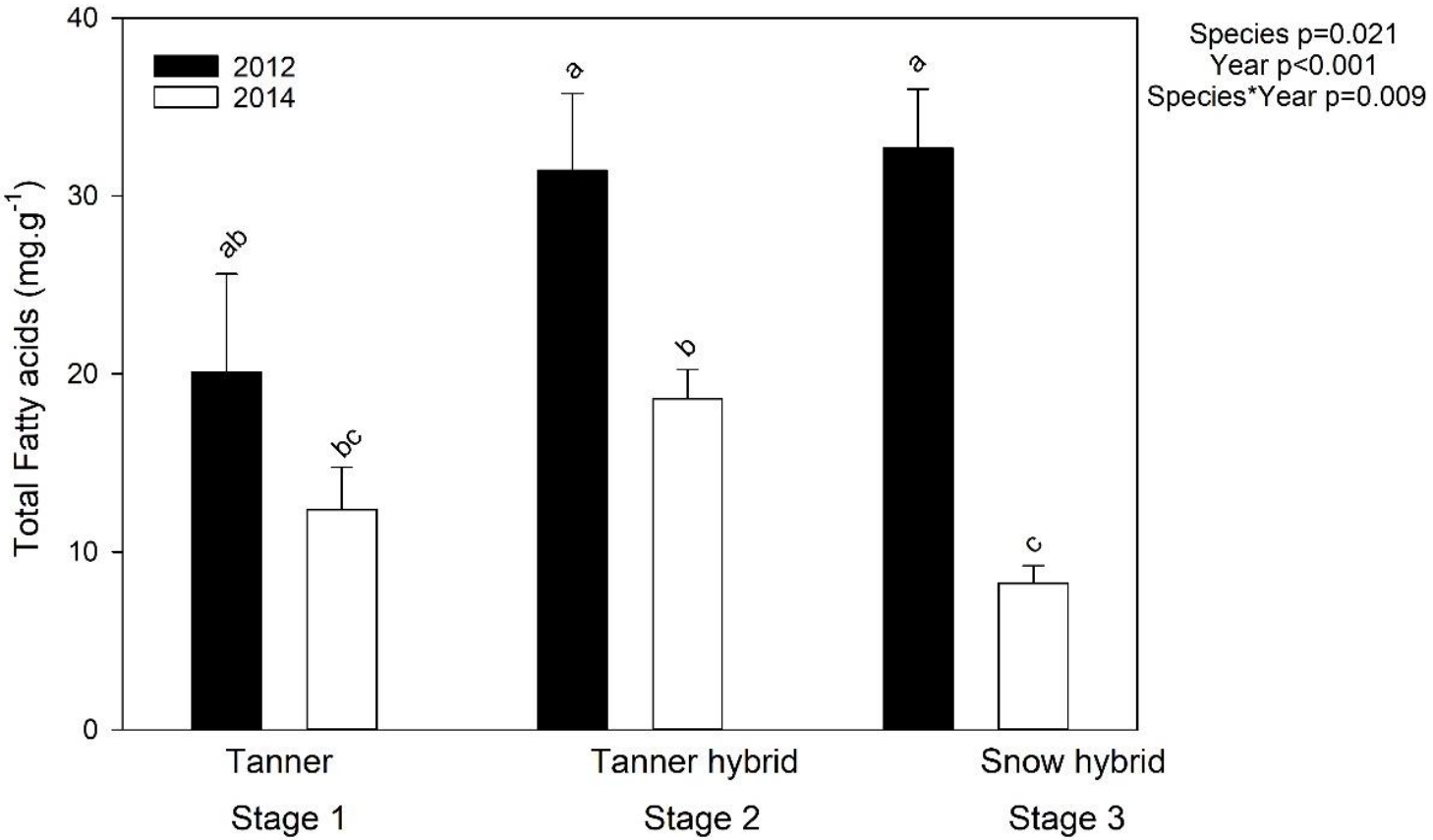

Species p=0.021
Year p<0.001
Species*Year p=0.009
2012
2014
Total Fatty acids (mg.g-1)
40
30
20
10
0
ab
bc
a
b
a
c
Tanner
Stage 1
Tanner hybrid
Stage 2
Snow hybrid
Stage 3

**Table 1:** Annual and spatial trends in near bottom temperature, mean integrated total and large size (>10 µm) chla, as well as total fatty acids per WWT and percentage fatty acids (>0.5%) in juvenile crabs (*Chionoecetes* spp.) from the southeastern Bering Sea.

| **Shelf Region** | **Central middle (CM)** | | **Central Outer (CO)** | | **South middle (SM)** | | **South outer (SO)** | |
|---|---|---|---|---|---|---|---|---|
| **Year** | **2012** | **2014** | **2012** | **2014** | **2012** | **2014** | **2012** | **2014** |
| **Station number oceanography** | **27** | **25** | **6** | **6** | **8** | **8** | **4** | **6** |
| Bottom temperature (August-September) BASIS ℃ | 1.55±1.78 | 3.26±1.44 | 3.02±0.48 | 4.12±0.19 | 3.03±2.62 | 5.94±2.04 | 4.49±0.54 | 5.10±0.76 |
| Total integrated chla $mg.m^{-2}$ | 72.86±40.05 | 55.16±37.43 | 54.35±21.08 | 33.97±10.86 | 54.07±23.81 | 27.66±7.07 | 143.73±79.21 | 39.05±13.47 |
| Integrated chla in particles >10 µm, $mg.m^{-2}$ | 27.93±38.8 | 5.63 ± 4.99 | 5.94±4.31 | 4.28 ± 3.11 | 15.37±25.54 | 2.06 ± 1.55 | 15.37 ± 25.54 | 3.18 ± 2.18 |
| Ratio of >10µm /total chla | 0.29±0.27 | 0.13±0.11 | 0.11±0.06 | 0.11±0.07 | 0.23±0.28 | 0.08±0.07 | 0.56±0.19 | 0.08±0.04 |
| | | | | | | | | |
| **Sample size crabs** | **25** | **37** | **25** | **29** | **16** | **12** | **20** | **23** |
| Carapace Width (mm) | 9.0±0.4 | 11.5 ± 0.4 | 12.5 ± 0.6 | 10.9 ± 0.5 | 9.0 ± 0.2 | 11.8 ± 1.1 | 9.0 ± 0.2 | 9.9 ± 0.4 |
| Molt Stage[1] | C5 | C6 | C6 | C5-C6 | C5 | C6 | C5 | C5 |
| Total FA per WWT $(mg.g^{-1})$ | 29.3±12.7 | 12.1±6.7 | 11.8±6.5 | 7.8±4.3 | 14.1±8.9 | 8.2±2.9 | 7.1±4.8 | 6.7±3.7 |
| FA per DWT $(mg.g^{-1})^d$ | 76.7 | 31.7 | 30.9 | 20.4 | 36.9 | 21.5 | 18.6 | 17.6 |
| FA per AFDWT $(mg.g^{-1})^d$ | 174.1 | 72.0 | 70.2 | 46.3 | 83.9 | 48.7 | 42.3 | 40.0 |
| % of total FA | | | | | | | | |
| 14:0 | 2.6±0.5 | 1.5±0.7 | 3.0±0.9 | 3.1±1.5 | 1.8±0.5 | 1.6±0.5 | 2.4±0.7 | 2.3±0.9 |
| *ai* 15:0 | 2.3±2.4 | 3.4±3.4 | 0.1±0.0 | 0.1±0.0 | 0.1±0.2 | 0.2±0.1 | 0.2±0.2 | 0.1±0.1 |
| 15:0 | 0.5±0.1 | 0.6±0.2 | 0.5±0.1 | 0.5±0.2 | 0.4±0.1 | 0.4±0.1 | 0.6±0.1 | 0.4±0.1 |
| *i* 16:0 | 0.2±0.9 | 1.6±1.4 | 0.4±0.1 | 0.4±0.1 | 0.2±0.1 | 0.4±0.1 | 0.6±0.3 | 0.5±0.2 |
| 16:0 | 12.3±1.2 | 10.6±1.9 | 11.1±1.3 | 10.9±1.8 | 12.1±0.8 | 13.6±1.4 | 15.9±1.8 | 13.6±1.6 |
| *i* 17:0 | 0.2±0.0 | 0.4±0.1 | 0.5±0.2 | 0.7±0.1 | 0.4±0.1 | 0.1±0.2 | 0.6±0.2 | 0.6±0.3 |
| *ai* 17:0 | 0.5±0.4 | 1.1±0.7 | 0.4±0.1 | 0.4±0.1 | 0.4±0.2 | 0.4±0.1 | 0.7±0.1 | 0.5±0.2 |
| 17:0 | 0.2±0.1 | 0.4±0.2 | 0.4±0.2 | 0.6±0.2 | 0.3±0.2 | 0.0±0.2 | 0.5±0.3 | 0.4±0.2 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 18:0 | 2.3±1.4 | 3.1±0.6 | 3.3±0.7 | 3.8±1.1 | 3.4±0.6 | 3.5±0.4 | 4.1±0.9 | 4.6±1.1 |
| **∑SFA[a]** | **17.9±2.1** | **16.7±2.2** | **18.5±1.9** | **19.3±2.2** | **18.1±1.2** | **19.3±1.5** | **24.9±5.8** | **21.5±2.2** |
| 16:1n-7 | 19.8±3.8 | 8.7±3.8 | 7.0±1.6 | 1.9±0.9 | 10.3±2.4 | 5.0±1.7 | 4.9±1.6 | 2.9±1.4 |
| 17:1 | 0.2±0.4 | 0.6±0.4 | 0.5±0.2 | 0.5±0.2 | 0.2±0.3 | 0.6±0.3 | 0.5±0.2 | 0.6±0.1 |
| 18:1n-11 | 0.1±0.0 | 0.2±0.2 | 0.8±0.3 | 0.9±0.1 | 0.3±0.1 | 0.2±0.1 | 0.1±0.2 | 0.5±0.2 |
| 18:1n-9 | 9.8±3.5 | 8.9±1.9 | 10.3±3.5 | 8.6±1.2 | 10.0±3.1 | 11.6±1.2 | 10.9±5.3 | 10.7±2.2 |
| 18:1n-7 | 11.6±1.0 | 9.3±0.9 | 8.2±1.4 | 4.9±1.2 | 9.4±1.1 | 7.7±0.5 | 7.1±1.1 | 6.7±1.1 |
| 18:1n-5 | 0.3±0.1 | 0.5±0.2 | 0.6±0.2 | 0.7±0.4 | 0.8±0.2 | 0.5±0.2 | 0.8±0.1 | 0.7±0.2 |
| 20:1n-11 | 0.9±0.3 | 1.5±0.9 | 5.2±1.5 | 8.4±4.0 | 2.5±0.8 | 1.3±0.5 | 2.0±1.2 | 3.4±1.5 |
| 20:1n-9 | 0.9±0.4 | 1.6±0.6 | 3.4±1.3 | 4.4±2.0 | 4.5±2.2 | 1.9±0.6 | 2.6±1.9 | 2.3±0.8 |
| 20:1n-7 | 1.2±0.3 | 2.0±0.9 | 2.4±0.6 | 1.3±1.0 | 3.2±1.1 | 1.1±0.4 | 1.7±0.9 | 1.3±0.5 |
| 22:1n-11 | 0.1±0.2 | 0.5±0.6 | 3.7±1.6 | 7.4±4.3 | 2.5±1.6 | 1.0±0.6 | 1.5±1.3 | 2.6±1.6 |
| 22:1n-9 | 0.1±0.1 | 0.2±0.3 | 1.0±0.5 | 1.0±0.5 | 0.2±0.3 | 0.2±0.3 | 0.1±0.2 | 0.9±0.7 |
| **∑MUFA[b]** | **46.0±3.5** | **35.2±4.6** | **43.6±3.5** | **40.8±8.2** | **44.4±3.9** | **31.9±3.3** | **32.8±5.9** | **33.6±4.5** |
| 16:2n-4 | 1.6±0.2 | 1.1±0.5 | 0.9±0.2 | 0.4±0.1 | 1.1±0.3 | 0.9±0.3 | 0.7±0.4 | 0.6±0.2 |
| 16:3n-4 | 0.6±0.4 | 0.1±0.3 | 0.0±0.2 | 0.0±0.0 | 0.4±0.3 | 0.1±0.2 | 0.0±0.2 | 0.0±0.0 |
| 16:4n-1 | 0.7±0.3 | 0.3±0.4 | 0.2±0.1 | 0.0±0.0 | 0.5±0.2 | 0.2±0.1 | 0.2±0.2 | 0.0±0.0 |
| 18:2n-6 | 0.6±0.1 | 0.8±0.3 | 0.8±0.2 | 0.7±0.0 | 0.6±0.1 | 1.2±0.2 | 0.1±0.3 | 0.9±0.3 |
| 18:3n-3 | 0.1±0.1 | 0.1±0.1 | 0.1±0.1 | 0.2±0.1 | 0.1±0.1 | 0.6±0.2 | 0.3±0.3 | 0.4±0.2 |
| 18:4n-3 | 1.9±0.4 | 0.9±0.9 | 0.8±0.3 | 0.2±0.2 | 1.3±0.7 | 0.8±0.3 | 0.7±0.5 | 0.6±0.3 |
| 20:2n-6 | 0.2±0.2 | 0.8±0.4 | 0.6±0.5 | 0.8±0.5 | 0.6±0.4 | 1.0±0.2 | 1.0±0.08 | 1.0±0.9 |
| 20:4n-6 | 1.4±0.4 | 2.8±0.7 | 4.0±1.6 | 4.2±1.4 | 2.6±0.9 | 4.1±0.5 | 5.2±1.5 | 5.9±2.6 |
| 20:5n-3 | 17.5±1.3 | 19.9±2.3 | 17.2±1.8 | 17.7±4.2 | 17.5±3.2 | 21.0±1.4 | 17.0±2.7 | 17.6±2.4 |
| 22:5n-3 | 0.4±0.1 | 1.0±0.3 | 1.3±0.5 | 1.0±0.3 | 1.5±0.5 | 1.2±0.7 | 0.8±0.7 | 1.2±0.6 |
| 22:6n-3 | 6.1±1.3 | 10.8±2.5 | 8.7±1.5 | 11.9±2.3 | 8.8±1.4 | 15.1±2.3 | 12.3±2.1 | 13.3±1.9 |
| **∑PUFA[c]** | **32.6±2.8** | **41.5±3.8** | **36.3±3.0** | **38.1±7.1** | **36.2±3.9** | **47.6±2.7** | **40.0±5.2** | **42.9±4.5** |

[1]Molt stage estimate based on Ryer et al. (2016) and Ryer et al. (2015).
[a]∑SFA, saturated fatty acids contains < 0.5% of *i*15:0, 20:0, 22:0, 24:0,

[b]∑MUFA, monounsaturated fatty acids contains<0.5% 14:1, 15:1, 16:1n-11, 16:1n-9,16:1n-5, 18:1n-5, 22:1n-7

[c]∑PUFA, polyunsaturated fatty acids contains<0.5% 16:4n-3,18:2n-4,18:3n-6, 18:3n-4, 20:3n-6, 20:3n-3, 20:4n-3, 21:5n-3, 22:4n-6, 22:5n-6, 22:4n-3

"*i*" refers to iso branched chains and "*ai"* refers to anti-iso branched chains.

[d] Average conversion factors were calculated for WWT to DWT =2.63 ± 3.49 (n=107) and WWT to AFDWT = 5.95 ± 8.64 (n=107) using values from wild C3 and C4 Tanner crabs collected near Kodiak Island in the Gulf of Alaska, USA as described in Copeman et al. (2018). Values are to be considered approximate and are given to allow comparison of total fatty acids per weight with published crab studies where fatty acid values are expressed per DWT or AFDWT

**Appendix 1:** Iatroscan-determined total lipids and lipid classes of juvenile Tanner crabs (*Chionoecetes bairdi*.) reared at 2 ℃ and 9 ℃ in individual growth cells in a controlled laboratory growth experiment.

| | 2℃ | 9℃ |
|---|---|---|
| | n=5 | n=6 |
| Iatroscan-determined total lipids ($mg.g^{-1}$) | 18.7 ± 3.1 | 9.4 ± 3.0 |
| | | |
| Steryl/Wax Esters | 0.2 ± 0.0 | - |
| Triacylglycerols | 48.1 ± 5.7 | 43.7 ± 11.0 |
| Free Fatty acids | 1.9 ± 0.3 | 2.3 ± 0.7 |
| Sterols | 6.1 ± 1.2 | 11.2 ± 4.8 |
| Polar Lipids | 43.6 ± 4.5 | 42.8 ± 6.8 |

**References:**


Armstrong J, Armstrong D, Hilborn R (1998) Crustacean resources are vulnerable to serial depletion–the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev Fish Biol Fisheries 8:117-176. https://doi.org/10.1023/A:1008891412756

Beder A (2015) The effects of dietary essential fatty acid enrichment on the nutrition and condition of red king crab (*Paralithodes camtschaticus*) larvae. Masters of Science Thesis, University of Alaska Fairbanks

Brown TA, Assmy P, Hop H, et al (2017) Transfer of ice algae carbon to ice-associated amphipods in the high-Arctic pack ice environment. J Plankton Res 39:664-674. https://doi.org/10.1093/plankt/fbx030

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. Mar Mamm Sci 22:759-801. https://doi.org/10.1111/j.1748-7692.2006.00079.x

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29:1547-1559. https://doi.org/10.1016/S0146-6380(98)00177-6

Budge SM, Springer AM, Iverson SJ, et al (2008) Blubber fatty acid composition of bowhead whales, *Balaena mysticetus*: Implications for diet assessment and ecosystem monitoring. J Exp Mar Biol Ecol 359:40-46. https://doi.org/10.1016/j.jembe.2008.02.014

Copeman L, Daly B, Eckert GL, et al (2014) Storage and utilization of lipid classes and fatty acids during the early ontogeny of blue king crab, *Paralithodes platypus*. Aquaculture 424-425:86-94. https://doi.org/10.1016/j.aquaculture.2013.12.025

Copeman L, Ryer C, Spencer M, et al (2018) Benthic enrichment by diatom-sourced lipid promotes growth and condition in juvenile Tanner crabs around Kodiak Island, Alaska. Mar Ecol Prog Ser 597:161-178. https://doi.org/10.3354/meps12621

Copeman LA, Laurel BJ, Boswell KM, et al (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39:1109-1126. https://doi.org/10.1007/s00300-015-1792-y

Copeman LA, Laurel BJ, Spencer M, et al (2017) Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic-Boreal interface: an experimental laboratory approach. Mar Ecol Prog Ser 566:183-198. https://doi.org/10.3354/meps12040

Copeman LA, Parrish CC (2003) Marine lipids in a cold coastal ecosystem: Gilbert Bay, Labrador. Mar Biol 143:1213-1227. https://doi.org/10.1007/s00227-003-1156-y

Copeman LA, Parrish CC (2004) Lipids classes, fatty acids, and sterols in seafood from Gilbert Bay, Southern Labrador. J Agric Food Chem 52:4872-4881. https://doi.org/10.1021/Jf034820h

Copeman LA, Parrish CC, Gregory RS, et al (2009) Fatty acid biomarkers in coldwater eelgrass meadows: elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 386:237-251. https://doi.org/10.3354/Meps08063

Copeman LA, Stoner AW, Ottmar ML, et al (2012) Total lipids, lipid classes, and fatty acids of newly settled red king crab (*Paralithodes Camtschaticus*): comparison of hatchery-cultured and wild crabs. J Shellfish Res 31:153-165. https://doi.org/10.2983/035.031.0119

Coyle KO, Eisner LB, Mueter FJ, et al (2011) Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fish Oceanogr 20:139-156. https://doi.org/10.1111/j.1365-2419.2011.00574.x

Dalsgaard J, St John M, Kattner G, et al (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225-340. https://doi.org/10.1016/s0065-2881(03)46005-7

Dionne M, Sainte-Marie B, Bourget E, et al (2003) Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Mar Ecol Prog Ser 259:117-128. https://doi.org/10.3354/meps259117

Duffy-Anderson JT, Stabeno PJ, Siddon EC, et al (2017) Return of warm conditions in the southeastern Bering Sea: Phytoplankton - Fish. Plos One 12:21. https://doi.org/10.1371/journal.pone.0178955

Duffy-Anderson JT, Stabeno P, Andrews III AG, et al (2019) Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. Geophys Res Lett 46:9833-9842. https://doi.org/10.1029/2019GL083396

Eisner L, Cieciel K, Gann J, et al (2019) Phytoplankton Biomass and Size Structure During Late Summer to Early Fall in the Eastern Bering Sea. In Siddon, E, and Zador, S 2019 Ecosystem Status Report 2019: Eastern Bering Sea, Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council, 605 W 4th Ave, Suite 306, Anchorage, AK

Eisner LB, Gann JC, Ladd C, et al (2016) Late summer/early fall phytoplankton biomass (chlorophyll a) in the eastern Bering Sea: Spatial and temporal variations and factors affecting chlorophyll a concentrations. Deep Sea Res Part II 134:100-114. https://doi.org/10.1016/j.dsr2.2015.07.012

Eisner LB, Yasumiishi EM, Andrews AG, et al (2020) Large copepods as leading indicators of walleye pollock recruitment in the southeastern Bering Sea: Sample-Based and spatio-temporal model (VAST) results. Fish Res 232:105720. https://doi.org/10.1016/j.fishres.2020.105720

Farley EV, Heintz RA, Andrews AG, et al (2016) Size, diet, and condition of age-0 Pacific cod (*Gadus macrocephalus*) during warm and cool climate states in the eastern Bering Sea. Deep Sea Res Part II 134:247-254. https://doi.org/10.1016/j.dsr2.2014.12.011

Fetterer F, Knowles K, Meier W, et al (2017 updated daily) Sea Ice Index, Version 3. Monthly Sea Ice Extent Data. National Snow and Ice Data Center (NSIDC), Boulder, Colorado USA. Accessed 5 May 2020

Folch J, Less M, Sloane Stanley GH (1956) A simple method for the isolation and purification of total lipids from animal tissues. The Journal of Biological Chemistry 22:497-509

Galloway AWE, Eisenlord ME, Dethier MN, et al (2014) Quantitative estimates of isopod resource utilization using a Bayesian fatty acid mixing model. Mar Ecol Prog Ser 507:219-232. https://doi.org/10.3354/meps10860

Goes JI, D'Sa EJ, Do H, et al (2014) Influence of the Bering Sea on Arctic Ecosystems experiencing rapid reductions in sea-ice. Paper presented at the Ocean Optics XXII, Portland, Maine, USA, 2014/10/25

Grebmeier JM (2012) Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. Annu Rev Mar Sci 4:63-78. https://doi.org/10.1146/annurev-marine-120710-100926

Grebmeier JM, Bluhm BA, Cooper LW, et al (2015) Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. Oceanography 28:116-133. https://doi.org/10.5670/oceanog.2015.61

Grebmeier JM, Cooper LW, Feder HM, et al (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331-361. https://doi.org/10.1016/j.pocean.2006.10.001

Griffiths JR, Kadin M, Nascimento FJA, et al (2017) The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. Glob Change Biol 23:2179-2196. https://doi.org/10.1111/gcb.13642

Harada N (2016) Review: Potential catastrophic reduction of sea ice in the western Arctic Ocean: Its impact on biogeochemical cycles and marine ecosystems. Glob Planet Change 136:1-17. https://doi.org/10.1016/j.gloplacha.2015.11.005

Hartnoll RG (2001) Growth in Crustacea – twenty years on. Hydrobiologia 449:111-122. https://doi.org/10.1023/a:1017597104367

Heintz RA, Siddon EC, Farley EV, et al (2013) Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. Deep Sea Res Part II 94:150-156. https://doi.org/10.1016/j.dsr2.2013.04.006

Hobson KA, Ambrose WG, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from δ13C and δ15N analysis. Mar Ecol Prog Ser 128:1-10. https://doi.org/doi:10.3354/meps128001

Houde E (2008) Emerging from Hjort's Shadow. J Northwest Atl Fish Soc 41:53–70. https://doi.org/10.2960/J.v41.m634

Hunt GL, Baduini CL, Brodeur RD, et al (1999) The Bering Sea in 1998: The second consecutive year of extreme weather-forced anomalies. Eos, Transactions American Geophysical Union 80:561-566. https://doi.org/10.1029/EO080i047p00561

Hunt GL, Coyle KO, Eisner LB, et al (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. Ices J Mar Sci 68:1230-1243. https://doi.org/10.1093/icesjms/fsr036

Hunt GL, Stabeno P, Walters G, et al (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Res Part II 49:5821-5853. https://doi.org/10.1016/S0967-0645(02)00321-1

Hunt GL, Stabeno PJ, Strom S, et al (2008) Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep Sea Res Part II 55:1919-1944. https://doi.org/10.1016/j.dsr2.2008.04.032

Hurst TP (2007) Causes and consequences of winter mortality in fishes. J Fish Biol 71:315-345. https://doi.org/10.1111/j.1095-8649.2007.01596.x

Hurst TP, Cooper DW, Duffy-Anderson JT, et al (2015) Contrasting coastal and shelf nursery habitats of Pacific cod in the southeastern Bering Sea. Ices J Mar Sci 72:515-527. https://doi.org/10.1093/icesjms/fsu141

Kaneda T (1991) Iso- and anteiso-fatty acids in bacteria: biosynthesis, function, and taxonomic significance. Microbiol Rev 55:288-302. https://doi.org/10.1128/mr.55.2.288-302.1991

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1-22. https://doi.org/10.3354/meps09559

Koch CW, Cooper LW, Lalande C, et al (2020) Seasonal and latitudinal variations in sea ice algae deposition in the Northern Bering and Chukchi Seas determined by algal biomarkers. PLOS ONE 15:e0231178.

https://doi.org/10.1371/journal.pone.0231178

Koenker BL, Copeman LA, Laurel BJ (2018) Impacts of temperature and food availability on the condition of larval Arctic cod (Boreogadus saida) and walleye pollock (Gadus chalcogrammus). Ices J Mar Sci 75:2370-2385. https://doi.org/10.1093/icesjms/fsy052

Krivoruchko K, Gribov A (2019) Evaluation of empirical Bayesian kriging. Spatial Statistics 32:100368. https://doi.org/10.1016/j.spasta.2019.100368

Ladd C, Eisner LB, Salo SA, et al (2018) Spatial and Temporal Variability of Coccolithophore Blooms in the Eastern Bering Sea. J Geophys Res-Oceans 123:9119-9136. https://doi.org/10.1029/2018jc014302

Landeira JM, Matsuno K, Tanaka Y, et al (2018) First record of the larvae of tanner crab *Chionoecetes bairdi* in the Chukchi Sea: A future northward expansion in the Arctic? Polar Sci 16:86-89. https://doi.org/10.1016/j.polar.2018.02.002

Laurel BJ, Spencer M, Iseri P, et al (2016) Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biol 39:1127-1135. https://doi.org/10.1007/s00300-015-1761-5

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306. https://doi.org/10.3354/meps307273

Leu E, Brown TA, Graeve M, et al (2020) Spatial and temporal variability of ice algal trophic markers—with recommendations about their application. J Mar Sci Eng 8:676. https://doi.org/10.3390/jmse8090676

Lovvorn JR, Cooper LW, Brooks ML, et al (2005) Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. Mar Ecol Prog Ser 291:135-150. https://doi.org/10.3354/meps291135

Lu YH, Ludsin SA, Fanslow DL, et al (2008) Comparison of three microquantity techniques for measuring total lipids in fish. Can J Fish Aquat Sci 65:2233-2241. https://doi.org/10.1139/f08-135

Miller CB (1993) Development of large copepods during spring in the Gulf of Alaska. Prog Oceanogr 32:295-317. https://doi.org/10.1016/0079-6611(93)90018-9

Mincks S, Smith C, DeMaster D (2005) Persistence of labile organic matter and microbial biomass in Antarctic shelf sediments: evidence of a sediment food bank. Mar Ecol Prog Ser 300:3-19. https://doi.org/10.3354/meps300003

Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol Appl 18:309-320. https://doi.org/10.1890/07-0564.1

Murphy JT (2020) Climate change, interspecific competition, and poleward vs. depth distribution shifts: Spatial analyses of the eastern Bering Sea snow and Tanner crab (*Chionoecetes opilio* and *C. bairdi*). Fish Res 223:105417. https://doi.org/10.1016/j.fishres.2019.105417

NPFMC (2018) Fishery Management Plan for Bering Sea and Aleutian Islands King and Tanner Crabs. Bering Sea Crab Plan Team North Pacific Fishery Management Council, Anchorage, AK, September 2018

Olson MB, Strom SL (2002) Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. Deep Sea Res Part II 49:5969-5990. https://doi.org/10.1016/S0967-0645(02)00329-6

Orensanz J, Ernst B, Armstrong DA, et al (2004) Contraction of the geographic range of distribution of snow crab (Chionoecetes opilio) in the Eastern Bering Sea: an environmental ratchet? California Cooperative Oceanic Fisheries Investigations Report 45:65

Orensanz JML, Armstrong J, Armstrong D, et al (1998) Crustacean resources are vulnerable to serial depletion - the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev Fish Biol Fish 8:117-176. https://doi.org/10.1023/a:1008891412756

Ortiz I, Aydin K, Hermann AJ, et al (2016) Climate to fish: Synthesizing field work, data and models in a 39-year retrospective analysis of seasonal processes on the eastern Bering Sea shelf and slope. Deep Sea Res Part II 134:390-412. https://doi.org/10.1016/j.dsr2.2016.07.009

Ouellet P, Taggart CT, Frank KT (1992) Lipid condition and survival in shrimp (*Pandalus borealis*) larvae. Can J Fish Aquat Sci 49:368-378. https://doi.org/10.1139/f92-042

Parrish CC (1987) Separation of aquatic lipid classes by chromarod thin-layer chromatography with measurement by Iatroscan flame ionization detection. Can J Fish Aquat Sci 44:722-731. https://doi.org/10.1139/F87-087

Parrish CC (2013) Lipids in Marine Ecosystems. ISRN Oceanography 2013:16. https://doi.org/10.5402/2013/604045

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical & biological methods for seawater analysis. Pergamon Press. doi:https://doi.org/10.1016/C2009-0-07774-5

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95-97. https://doi.org/10.1126/science.1135471
Ramos CS, Parrish CC, Quibuyen TAO, et al (2003) Molecular and carbon isotopic variations in lipids in rapidly settling particles during a spring phytoplankton bloom. Org Geochem 34:195-207. https://doi.org/10.1016/S0146-6380(02)00166-3
Renaud PE, Sejr MK, Bluhm BA, et al (2015) The future of Arctic benthos: Expansion, invasion, and biodiversity. Prog Oceanogr 139:244-257. https://doi.org/10.1016/j.pocean.2015.07.007
Richoux NB, Deibel D, Thompson RJ, et al (2004) Seasonal changes in the lipids of *Mysis mixta* (Mysidacea) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland). Can J Fish Aquat Sci 61:1940-1953. https://doi.org/10.1139/F04-139
Richoux NB, Deibel D, Thompson RJ, et al (2005) Seasonal and developmental variation in the fatty acid composition of *Mysis mixta* (Mysidacea) and *Acanthostepheia malmgreni* (Amphipoda) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland). J Plankton Res 27:719-733. https://doi.org/10.1093/plankt/fbi045
Ryer CH, Long WC, Spencer ML, et al (2015) Depth distribution, habitat associations, and differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska. Fish Bull 113:256-269. https://doi.org/10.7755/fb.113.3.3
Ryer CH, Ottmar M, Spencer M, et al (2016) Temperature-dependent growth of early juvenile southern Tanner crab *Chionoecetes bairdi*: implications for cold pool effects and climate change in the South Eastern Bering Sea. J Shellfish Res 35:259-267. https://doi.org/10.2983/035.035.0128
Sánchez-Paz A, García-Carreño F, Muhlia-Almazán A, et al (2006) Usage of energy reserves in crustaceans during starvation: Status and future directions. Insect Biochemistry and Molecular Biology 36:241-249. https://doi.org/10.1016/j.ibmb.2006.01.002
Schiffer M, Harms L, Lucassen M, et al (2014) Temperature tolerance of different larval stages of the spider crab *Hyas araneus* exposed to elevated seawater $PCO_2$. Front Zoo 11:87. https://doi.org/10.1186/s12983-014-0087-4
Schollmeier T, Oliveira ACM, Wooller MJ, et al (2018) Tracing sea ice algae into various benthic feeding types on the Chukchi Sea shelf. Polar Biol 41:207-224. https://doi.org/10.1007/s00300-017-2182-4
Sigler MF, Stabeno PJ, Eisner LB, et al (2014) Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during 1995-2011. Deep Sea Res Part II 109:71-83. https://doi.org/10.1016/j.dsr2.2013.12.007
Smith CT, Grant WS, Seeb LW (2005) A Rapid, High-Throughput Technique for Detecting Tanner Crabs *Chionoecetes bairdi* Illegally Taken in Alaska's Snow Crab Fishery. Trans Am Fish Soc 134:620-623. https://doi.org/10.1577/t04-007.1
Spilmont N, Meziane T, Seuront L, et al (2009) Identification of the food sources of sympatric ghost shrimp (*Trypaea australiensis*) and soldier crab (*Mictyris longicarpus*) populations using a lipid biomarker, dual stable isotope approach. Austral Ecol 34:878-888. https://doi.org/10.1111/j.1442-9993.2009.01994.x
St John MA, Lund T (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar Ecol Prog Ser 131:75-85. https://doi.org/10.3354/meps131075
Stabeno PJ, Bell SW (2019) Extreme Conditions in the Bering Sea (2017–2018): Record-Breaking Low Sea-Ice Extent. Geophys Res Lett 46:8952-8959. https://doi.org/10.1029/2019GL083816
Stabeno PJ, Kachel NB, Moore SE, et al (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res Part II 65:31-45. https://doi.org/10.1016/j.dsr2.2012.02.020

Stauffer BA, Goes JI, McKee KT, et al (2014) Comparison of spring-time phytoplankton community composition in two cold years from the western Gulf of Alaska into the southeastern Bering Sea. Deep Sea Res Part II 109:57-70. https://doi.org/10.1016/j.dsr2.2014.03.007

Stevens CJ, Deibel D, Parrish CC (2004) Copepod omnivory in the North Water Polynya (Baffin Bay) during autumn: spatial patterns in lipid composition. Deep-Sea Res Part I 51:1637-1658. https://doi.org/10.1016/j.dsr.2004.07.011

Stevenson DE, Lauth RR (2019) Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. Polar Biol 42:407-421. https://doi.org/10.1007/s00300-018-2431-1

Stoner AW, Copeman LA, Ottmar ML (2013) Molting, growth, and energetics of newly-settled blue king crab: Effects of temperature and comparisons with red king crab. J Exp Mar Biol Ecol 442:10-21. https://doi.org/10.1016/j.jembe.2013.02.002

Stoner AW, Ottmar ML, Copeman LA (2010) Temperature effects on the molting, growth, and lipid composition of newly-settled red king crab. J Exp Mar Biol Ecol 393:138-147. https://doi.org/10.1016/j.jembe.2010.07.011

Storch D, Fernandez M, Navarrete SA, et al (2011) Thermal tolerance of larval stages of the Chilean kelp crab *Taliepus dentatus*. Mar Ecol Prog Ser 429:157-167. https://doi.org/10.3354/meps09059

Szuwalski C, Cheng W, Foy R, et al (2020) Climate change and the future productivity and distribution of crab in the Bering Sea. Ices J Mar Sci 78:502-515. https://doi.org/10.1093/icesjms/fsaa140

Thomas M, Schram J, Clark-Henry Z, et al (2020) Juvenile Dungeness crabs (*Metacarcinus magister*) selectively integrate and modify the fatty acids of their experimental diets. Philos Trans R Soc Lond B Biol Sci 375:20200038. https://doi.org/10.1098/rstb.2020.0038

Tucker S, Bowen WD, Iverson SJ, et al (2009) Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). Mar Ecol Prog Ser 384:287-302. https://doi.org/10.3354/meps08000

Urban D, Pengilly D, Jadamec L, et al (2002) Testing carapace morphology characteristics for field identification of *Chionoecetes* hybrids. In: Paul AJ et al. (eds) Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp 97-113

Vidal J, Smith SL (1986) Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. Deep Sea Res Part A 33:523-556. https://doi.org/10.1016/0198-0149(86)90129-9

Viso AC, Marty JC (1993) Fatty-acids from 28 marine microalgae. Phytochemistry 34:1521-1533. https://doi.org/10.1016/s0031-9422(00)90839-2

Wassmann P, Reigstad M (2011) Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. Oceanography 24:220-231. https://doi.org/10.5670/oceanog.2011.74

Weems J, Iken K, Gradinger R, et al (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430:32-42. https://doi.org/10.1016/j.jembe.2012.06.015

Woodby D, Carlile D, Siddeek S, et al (2005) Commercial fisheries of Alaska. Alaska Dep. Fish Game Spec. Publ. 05–09, 66 p

Wyllie-Echeverria T, Wooster WS (1998) Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanogr 7:159-170. https://doi.org/10.1046/j.1365-2419.1998.00058.x

Yamada Y, Nishida S, Graeve M, et al (2016) Lipid and fatty acid/alcohol compositions of the subarctic copepods *Neocalanus cristatus* and *Eucalanus bungii* from various depths in the Oyashio region, western North Pacific. Comp Biochem Physiol B, Biochem Mol Biol 198:57-65. https://doi.org/10.1016/j.cbpb.2016.04.003

Yamamoto T, Yamada T, Kinoshita T, et al (2015) Effects of temperature on growth of juvenile snow crabs, *Chionoecetes opilio*, in the laboratory. J Crustac Biol 35:140-148. https://doi.org/10.1163/1937240x-00002309

Zheng J, Kruse GH (2000) Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. Ices J Mar Sci 57:438-451. https://doi.org/10.1006/jmsc.1999.0521

Zheng J, Kruse GH (2006) Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Prog Oceanogr 68:184-204. https://doi.org/10.1016/j.pocean.2006.02.002

Zhou SJ, Shirley TC, Kruse GH (1998) Feeding and growth of the red king crab *Paralithodes camtschaticus* under laboratory conditions. J Crustac Biol 18:337-345. https://doi.org/10.2307/1549328