Annual and spatial variation in the condition and lipid storage of juvenile Chukchi Sea gadids during a recent period of environmental warming (2012 to 2019).

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ABSTRACT

The Arctic is undergoing dramatic environmental change with decreasing sea-ice extent and increasing summer temperatures. The late summers of 2017 and 2019 on the eastern Chukchi Sea were anomalously warm, nearly 4°C warmer than the previous 30-year average. Increased ocean temperatures can affect the energetics of North Pacific fish by increasing their metabolic demands and via shifting fish prey assemblages. Here we describe the total lipids as well as fatty acid (FA) trophic markers in juveniles of two Arctic gadids (polar cod, *Boreogadus saida* and saffron cod, *Eleginus gracilis*) as well as two sub-Arctic gadids (walleye pollock, *Gadus chalcogrammus* and Pacific cod, *Gadus macrocephalus*) collected on recent ecosystem surveys spanning the north Bering and Chukchi seas. Fifty percent of the variance in the lipid composition of gadids was accounted for by species-specific differences, while ecosystem measurements such as bottom temperature, large > C3 stage *Calanus* abundance, and surface temperature were found to independently account for 25%, 12% and 10%, respectively. Allometric relationships in lipid storage revealed that polar cod have a different lipid storage profile than other gadids, suggesting a species-specific life-history strategy for high lipid storage that is an adaptation to Arctic environments. Both polar cod and saffron cod had reduced lipid storage in 2017 compared to fish collected in earlier years. Polar cod in 2017 were significantly lower in total lipid, triacylglycerols (TAG), diatom- (16:1n-7/16:0) and *Calanus*-sourced ($\sum C_{20}+C_{22}$) FA over the Chukchi Shelf. Juvenile gadids showed interspecific differences in the spatial distribution of high lipid individuals, with polar cod having the highest lipids in the northern ice-associated regions of the Chukchi Sea and walleye pollock in the southern Chukchi Sea. In 2019, polar cod's distribution had shifted north such that they were only abundant in the northern Chukchi Sea, where they maintained higher region-specific lipid storage than in 2017. It is concerning that reduced lipid content in polar cod was associated with elevated water temperatures, given predicted continued warming in the Chukchi Sea. Energetic changes in juvenile gadids may be associated with future increased natural mortality rates for regional populations (e.g. overwintering) and unstable foraging value for birds and mammals in the Arctic.

Keywords: Lipids, Fatty acids, Gadids, Chukchi Sea

Highlights

- Sub-Arctic gadids surveyed over the Chukchi shelf were in low energetic condition as evidenced by total lipid content per body wet weight
- Species-specific differences accounted for most of the variance in gadid lipids
- Age-0 polar cod had a unique lipid storage strategy compared to other gadids in the region
- Elevated lipids in polar cod were associated with increased storage of diatom- and *Calanus*-sourced fatty acids
- Bottom and surface temperature and salinity as well as the abundance of large *Calanus* explained 21% of the variation in polar cod lipid storage

1. Introduction

There are four commercially and/or ecologically important species of gadids (cod species) in Alaska waters. These include two sub-Arctic gadids, walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the Bering Sea and Gulf of Alaska, and two Arctic gadids, saffron cod (*Eleginus gracilis*) and polar cod (*Boreogadus saida),* in the eastern Chukchi Sea (ECS) and Beaufort Sea. As adults, polar cod and walleye pollock generally occupy pelagic, offshore habitats, whereas saffron cod and Pacific cod are more demersal in the nearshore and offshore regions, respectively (Hurst et al., 2015; Laurel et al., 2007; Logerwell et al., 2015). However, at early life stages, all species occupy pelagic habitats and serve as mid-trophic forage fish by facilitating energy transfer between zooplankton and upper trophic levels (Craig et al., 1982; Frost and Lowry, 1981; Heintz et al., 2013; Springer et al., 1996). Historically, these sub-Arctic and Arctic gadid assemblages had limited spatial overlap in the Alaska waters, but recent extreme warming and increased northward current flows through the Bering Strait have resulted in the co-occurrence of all four juvenile gadids in pelagic waters of the South ECS (SECS, 65.75 - 68.24 °N, Wildes et al., accepted; Levine et al., in review). Pacific cod in 2017 and walleye pollock in 2019 have also recently been surveyed in the ECS as far north as the North ECS (NECS, 70.75 - 73.00°N, Cooper et al., in review; Levine et al. in review), indicating a dramatic northward range shift for juveniles of these species into Arctic waters. Similar northward movement of gadid fish stocks has been documented for older life history stages concurrent with bottom warming in the Bering Sea (Baker, 2021; Stevenson and Lauth, 2019).

In the last ten years, unprecedented warming of the Chukchi Sea (Danielson et al., 2020; Huntington et al., 2020) and record low sea ice in the Bering Sea (Stabeno and Bell, 2019) have been documented. Small-bodied pelagic fish species are important biological indicators of climate change by way of direct temperature-dependent effects on their growth (Laurel et al., 2016; Peck et al., 2013) and lipid storage (Copeman et al., 2017). The direct effects of temperature on early survival and growth of gadids were recently described under common food environments (Laurel et al., 2017; 2018; 2016). However, the complex indirect effects of climate change on juvenile Arctic gadid survival and growth, such as through variable food quantity (Hurst et al., 2017; Koenker et al., 2018) and quality (Copeman and Laurel, 2010; Jonsson et al.,

2013) are less understood. Synchronized with recent oceanographic changes, there has been a measured reduction in *Calanus glacialis* abundance throughout the Chukchi Sea with small Pacific copepods increasing (i.e. *Pseudocalanus* spp.), particularly in the warm waters of the northeastern Bering Sea (NEBS, ~62 - 65.74 °N) and SECS (Huntington et al., 2020; Kim et al., 2020). In the most recent years surveyed (2017 and 2019), *C. glacialis* abundance was an order of magnitude lower than in the previous decade (Ashjian et al., 2017; Pinchuk and Eisner, 2017; Spear et al., 2019; Spear et al., 2020). Such changes may impact juvenile gadids, as *C. glacialis* is the major prey item for juvenile polar cod and other gadids, which could alter late summer energetic condition and potential overwintering success (Bouchard and Fortier, 2020; Buckley and Whitehouse, 2017; Heintz et al., 2013; Kohlbach et al., 2017b).

Measurement of lipids and fatty acids (FA) in juvenile fish provides temporally integrated (weeks) information on both trophic relationships and energetic status (Budge et al., 2012; Copeman et al., 2008; 2013; St John and Lund, 1996). Trophic biomarkers such as FA are produced at low trophic levels and are moved through the food web in a somewhat conservative manner, thus providing information about dietary origins when analyzed in consumers (Budge et al., 2006; Budge and Parrish, 1998; Dalsgaard et al., 2003). Here, we use a FA notation of A:B n-X, where A indicates the number of carbon atoms, B is the number of double bonds and X indicates the position of the first double bond relative to the terminal methyl group. Two specific fatty acid trophic markers are important in polar and upwelling food webs: diatom indicator FA (16:1n-7/16:0) and long chain monounsaturated FA (MUFA) indicative of calanoid copepod wax ester storage ($\sum C_{20+C22}$ MUFA) (Galloway and Winder, 2015; Graeve and Greenacre, 2020; Kattner et al., 2007; Lee et al., 2006; Viso and Marty, 1993). Conversely, phytoplankton from pelagic zones that are high in flagellates have been found to contain higher proportions of C_{18} PUFA and 22:6 n-3 (Budge et al. 2006, Falk-Petersen et al. 1998). Previous studies on polar cod and saffron cod have used these fatty acid trophic markers to show the degree of reliance on a diatom- and *Calanus* spp. -based food webs (Brewster et al., 2018; Budge et al., 2008; Copeman et al., 2016; Dissen et al., 2018; Graham et al., 2014; Kohlbach et al., 2017b).

The goal of our study was to characterize lipid storage in four species of juvenile gadids from the Alaska Arctic to better understand differences in observed fish lipids and energetic condition. Our objectives were: 1) to describe the species-specific variation in length-weight,

length-lipid, and morphometric condition using four years of survey data, 2) to use fatty acids per weight and fatty acid trophic markers to explore interspecific, annual and spatial differences in gadid food webs, and 3) to partition the variance in gadid lipids into relative contributions from species versus environmental conditions. We discuss annual and spatial variability in the lipid storage of sub-Arctic and Arctic gadids in relation to their potential responses to environmental warming, including overwintering success on the Chukchi Sea shelf.

2. Methods

2.1. Sample collections

Juvenile gadids for this study were collected using a variety of gear types with citations for detailed collection methodology, annual cruise names and sample numbers as presented in Table 1 and Fig. 1. Collection methods, fish handling techniques, and oceanographic temperatures for earlier years of saffron cod (2012) and polar cod (2013) sampling have previously been detailed in Copeman et al. (2016) and Copeman et al. (2020).

This manuscript uses fish sampled from the 2017 and 2019 Arctic Integrated Ecosystem Research Program (IERP) (https://www.nprb.org/arctic-program). For further information on the ecosystem-based approach and survey design, we encourage readers to reference Baker et al. (2020). Details of oceanography methods can be found in Danielson et al. (2020) and detail of juvenile gadid sampling in Levine et al. (in review) and Cooper et al. (in review).

2.2. Oceanographic and copepod abundance data

Water column temperatures and salinity for 2017 and 2019 are detailed in Danielson et al. (2020). Briefly, vertical profiles of temperature and salinity were collected from surface to near-bottom at each station using a Sea-Bird Electronics (SBE) 911+ CTD. All data are publicly available in the DataONE repository (https://doi.org/10.24431/rw1k5a0).

Zooplankton samples were collected in the Chukchi Sea between 8 August and 9 September in 2012 and 2013, 1 August to 27 September in 2017, and 27 August to 26 September

in 2019. For earlier years (2012 and 2013), sampling started in the Bering Strait and continued northward along zonal (east-west) transects up to 72.5 °N latitude (sampling details in Pinchuk and Eisner (2017)), while in later years (2017 and 2019), zooplankton sampling occurred at oceanographic stations as in Danielson et al. (2020).

Zooplankton were sampled with a 60-cm MARMAP-style bongo frame with a 505-µm mesh net. The net frame was equipped with an SBE 49 CTD transmitting real time tow data. The GPS location of the ship during the tow was recorded every 2 s to determine distance towed. Oblique tows from within 5-10 m off the bottom to the surface were conducted primarily during daylight hours. Volume filtered was measured with calibrated General Oceanics flowmeters mounted inside the nets. Volumes recorded from the flowmeter were compared with volumes estimated from the distance towed at each station to detect net clogging. In practice, little clogging occurred in the 505-µm mesh net during sampling. All samples were preserved in 5% formalin, buffered with seawater for later processing.

In the laboratory, each mesozooplankton sample was sequentially split using a Folsom splitter until the smallest subsample contained approximately 200 specimens of the most abundant taxa. Congener species *Calanus marshallae* and *C. glacialis* co-occurring in the Chukchi Sea (e.g. Nelson et al. (2009)) were not discriminated and are named as *C. glacialis* hereafter. All *C. glacialis* in the smallest subsamples were identified, staged and counted. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant *C. glacialis* copepodite stages and only *C. glacialis* copepodite stages C3 and older are included in our analyses.

2.3. Field fish sampling and tissue collections

Juvenile gadids from 2017 and 2019 surveys were collected during the North Pacific Research Board funded Arctic IERP and the 2017 Arctic Marine Biodiversity Observing Network (AMBON, https://ambon-us.org/) surveys (Mueter et al., 2021). Juvenile gadids from 2012, 2013, 2017 and 2019 surveys were sorted from the catch, immediately placed on ice, and then frozen at < -20 °C within 6 hours of capture. Samples were stored at -80 °C in the AFSC's Auke Bay Laboratories following the surveys and were later sorted and fin clipped for genetic analyses (Wildes et al., accepted). Fish 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. During dissections, fish were washed with filtered seawater, blotted dry, stomachs and intestinal tracts were removed and heads were frozen for later incremental otolith analysis. Within 2 months of sampling, fish were bisected along the dorsal–ventral plane and one-half of the remaining fish tissues, including both muscle and liver, were re-weighed, placed in chloroform under nitrogen and frozen at -20 °C until lipid extraction.

2.4. Lipid extraction and analysis

Tissues were homogenized in chloroform and methanol and total lipids were extracted in chloroform:methanol:water (8:4:3) according to Parrish (1987) using a modified Folch procedure (Folch et al., 1956).

Total lipids and lipid classes 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 glass rods (Chromarods), and a three-stage development system was used to separate wax esters, triacylglycerols (TAG), free FA, sterols and polar lipids. Polar lipids are mostly comprised of phospholipids (PL) with minor amounts of other acetone mobile polar lipids. The first rod development was in a chloroform: methanol: water (5:4:1 by volume) until the leading edge of the solvent phase reached 1 cm above the spotting origin. The rods were then developed in hexane: diethyl ether: formic acid solution (99:1:0.05) for 48 min, and finally rods were developed in a hexane: diethyl ether: formic acid solution (80:20:0.1) for 38 min. After each solvent development, rods were dried (5 min) and conditioned (5 min) in a constant humidity chamber (~32%) that was saturated with aqueous $CaCl_2$. Following the last development, rods were scanned using Peak Simple software (ver. 3.67, SRI Inc.) and the signal detected in millivolts was quantified with calibration curves using the following standards from Sigma (St Louis, MO, USA): palmitic acid (free FA), cholesterol (sterols), L-alpha-phosphatidylcholine (polar lipids). Specialized standards were purified by column chromatography to use for TAGs (from *B. saida* liver) following methods from Ohman (1997). Calibrated, regression relationships between lipid class areas and standard lipid amounts (µg) had coefficient of determination $r^2 > 0.98$ for all classes.

Following total lipid and lipid class analyses of fish tissues, samples were processed for fatty acid analyses. An internal standard (23:0 methyl ester) was added at approximately 10% of the total FA to all samples and total lipid extracts were derivatized into their fatty acid methyl esters (FAMEs) using sulfuric acid-catalyzed transesterification (Budge et al., 2006). Resulting FAMEs were analyzed on an HP 7890 GC FID equipped with an autosampler and a DB wax+ GC column (Agilent Technologies, Inc., U.S.A.). The column was 30 m in length, with an internal diameter of 0.25 mm and film thickness of 0.25 μm. The column temperature began at 65 °C and held this temperature for 0.5 min. Temperature was increased to 195 °C (40 °C min^{-1}), held for 15 min then increased again (2 °C min^{-1}) to a final temperature of 220 °C. Final temperature was held for 1 min. The carrier gas was hydrogen, flowing at a rate of 2 ml min^{-1}. Injector temperature was set at 250 °C and the detector temperature was constant at 250 °C. Peaks were identified using retention times based upon standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3) and in consultation with retention index maps performed under similar chromatographic conditions as our GC-FID (Wasta and Mjøs, 2013). Column function was checked by comparing chromatographic peak areas to empirical response areas using a quantitative FA mixed standard, GLC 487 (NuCheck Prep). Chromatograms were integrated using Chem Station (version A.01.02, Agilent).

2.5. Interspecific differences in age-0 weight and lipid storage

For each of the four juvenile gadid species, we examined length-weight (WWT, g) and length-fatty acid (total FA per animal, mg) relationships using a non-linear regression (Sigma plot 14.0). We used a power function ($Y = a * X^b$) with an approximate value of *b* equal to 3, indicating isometric growth. Whole body fish lipids (mg) were estimated by multiplying Iatroscan-summed lipid classes per WWT (mg g^{-1}) by whole body WWT (g). Length (mm, SL), WWT (g) and total FA (mg) data were log$_{10}$-transformed and differences in species weight and total FA were compared using a General Linear Model (GLM) with length as a covariate ($p <$ 0.05, Minitab 21.1; untransformed data shown in Fig. 2).

2.6. *Annual differences in condition metrics*

We calculated one morphometric condition measurement, Fulton's K condition index (K = ((WWT, g) / (SL, cm)[3]) * 100 (Nash et al. 2006), and used multiple lipid-based indices: total lipid concentration per WWT (mg.g^{-1}), total fatty acid per WWT (mg.g^{-1}), and the calanoid-specific fatty acid marker ($\sum C_{20} + C_{22}$ MUFA per WWT, mg.g^{-1}) to examine annual variation in each species. We used a GLM (Type III SS) to examine the effects of species and year (SPSS version 26) on condition metrics with significant within-species annual differences examined using Tukey's pair-wise test with a Bonferroni correction ($p < 0.05$).

Similarly, region-specific annual trends for each species were investigated (one-way ANOVA) and are shown in supplementary materials (S1). Regions of the eastern Chukchi Sea (ECS) were defined as southern (SECS), central (CECS, 68.25 - 70.74°N) and northern (NECS), areas of approximately equal latitudinal range, as used previously by Buckley and Whitehouse (2017) (Fig. 1).

2.7. *Multivariate fatty acid composition of juvenile gadids*

Multivariate differences among the fatty acid composition of juvenile gadid species were visualized using individual FAs present at $> 1\%$ in all gadid samples as well as the percentage of bacterial FAs ($\sum$odd and branched chains), calanoid FAs ($\sum C_{20}+C_{22}$ MUFA) and total fatty acids per WWT (mg.g^{-1}) in PRIMER v.7 (Primer-E) with a Permutational ANOVA, PERMANOVA add-on package. Data were square-root transformed prior to analysis and 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 show gadid fatty acid composition as a function of species and year. We used a 2-way PERMANOVA analysis ($p < 0.05$) to test for the significance of annual and interspecific differences in gadid multivariate lipid composition.

2.8. *Partitioning variation in gadid multivariate fatty acid composition*

Using transformed lipid data (outlined above) and a Bray-Curtis matrix, we performed distance-based linear model (DISLM) routines to quantify the relative contribution of fish species and ecosystem variables (surface and bottom temperature, surface and bottom salinity,

and > C3 stage *Calanus* abundance) on the realized fatty acid composition of juvenile Chukchi Sea gadids. We used a step-wise procedure (9999 permutations) with Akaike's Information Criterion (AIC) for model selection, and report results of marginal tests as well as total variation explained by each variable using a step-wise procedure. We also used distance-based redundancy analysis (dbRDA) to visualize the fitted model in multi-dimensional space (Anderson et al., 2008; Galloway and Winder, 2015). The position of the vector diagram relative to the first ordination axis was not centered on zero, but indicated the direction across the ordination plane in which the predictor variables increased. The length of the vector lines within the circle indicated the amount of total variation in each variable explained by that ordination plane. This same procedure was completed on polar cod alone, to examine the portion of lipid variance described by environmental variables.

2.9. Spatial trends in gadid lipids

Empirical Bayesian kriging (Krivoruchko and Gribov, 2019) was used to visualize spatial patterns in surface water temperatures and gadid lipid storage by interpolating data from survey sample stations (ArcGIS Desktop 10.7). Interpolated data values were stretched along a color ramp using the standard deviations stretch type.

3. Results

3.1 Mass and lipid allometry

The exponential regression coefficient *b*, for the relationship between length (mm) and WWT per fish (g) for all four species of juvenile gadids ranged between 2.85 and 3.22 (Fig. 2a, Table 2, 20-85 mm), indicating isometric growth. Analyses of log-transformed length-weight relationships indicated that both length ($p < 0.001$) and species (GLM, species $F_{3,709}=80.31$, $p < 0.001$) had a significant effect on the WWT (g) of juvenile gadids. For a given length, Pacific cod and saffron cod were significantly heavier than walleye pollock and polar cod had the lowest weight-at-length of all gadid species ($p < 0.05$ Tukey's pairwise comparison, untransformed data shown in Fig. 2a).

The exponential coefficient *b* for the relationship between length (mm) and total FA per fish (mg) ranged from a high of 3.85 in polar cod to a low of 2.19 in juvenile saffron cod, indicating distinct species-specific allometries of lipid accumulation (Fig. 2b, Table 2). Analyses of log- transformed length-fatty acid data indicated that both length ($p < 0.001$) and species (GLM, species $F_{3,707} = 58.66$, $p < 0.001$) had a significant effect on the fatty acid storage (mg) in juvenile gadids. For a given length, polar cod had significantly higher fatty acid storage, followed by walleye pollock, while Pacific cod and saffron cod had the lowest mean lipid storage of all gadids ($p < 0.05$; all contrasts, Tukey's pairwise comparison, untransformed data as in Fig. 2b).

3.2. Annual variability in body condition and lipid storage

Not all species were captured in all years, precluding a full-factorial analysis of condition across species, regions, and years (Fig. 1). We focused our statistical analysis on annual differences within species across our whole survey region. Where possible, species- and region-specific annual variation in condition metrics were explored and are presented in supplementary materials (S1 a-c). Generally, annual trends across the whole region are similar to region-specific comparisons.

As expected, Fulton's K morphometric condition factor (Fig. 3a) was species-specific (2-way GLM, Species, $F_{3,709,} = 89.42$, $p < 0.001$) but also varied across years (Year $F_{3,709,} = 27.91$, $p < 0.001$). Both polar cod and walleye pollock had higher ($p < 0.001$) Fulton's K in 2017 compared to other survey years but there was no significant annual difference in Fulton's K for saffron cod ($p = 0.252$).

Total lipids per WWT ($mg.g^{-1}$) were significantly different among species (Species, GLM, $F_{3,684} = 84.00$, $p < 0.001$) and across years (Year $F_{3,684} = 37.26$, $p < 0.001$, Fig. 3). Total lipid concentrations of polar cod and saffron cod were higher in 2013 and 2012, respectively, then in 2017. Polar cod collected in 2019 (NECS region only) were not significantly different in total lipid from those in 2013 ($p = 0.251$). There was no significant difference in the total lipid concentration of walleye pollock from 2017 and 2019 ($p = 0.331$). Total fatty acid concentrations in gadid tissues ($mg.g^{-1}$ WWT) generally showed the same significant differences as those

reported for total lipid. However, walleye pollock had a significantly higher level of fatty acid storage per WWT (p = 0.003) in 2019 than in 2017 (Fig. 3c).

Calanoid-copepod FA markers (mg.g^{-1} WWT) were significantly different among species (GLM, Species $F_{3,712,}$ = 90.26, p < 0.001) and years (Year $F_{3,712}$ = 41.32, p < 0.001), with much higher levels in polar cod than in all other species (Table 2, Fig. 3d). Polar cod from 2013 had significantly higher calanoid-sourced fatty acid storage than those from 2017 and a similar significant decrease was noted in saffron cod from an earlier cold year (2012) to 2017. Levels of calanoid FA in polar cod collected in 2019, only from the NECS, were not different from those sampled in 2013. Walleye pollock had slightly higher calanoid fatty acid storage in 2019 than in 2017 (p = 0.003) (region-specific comparisons in S1).

3.3. Inter-specific differences in lipid classes and fatty acids

Age-0 polar cod had twice the mean lipid concentration (total lipids per WWT, 20-35 µg.mg^{-1}) in their tissues compared to other juvenile gadids (Table 3, Fig. 2). Elevated lipids in polar cod were typified by higher proportions of the storage lipid class, TAGs (27-57%), and monounsaturated FA (MUFA, 38-50%, Table 3). Polar cod had more than five times the fatty acid concentration originating from calanoid copepods (4 to 6.5 mg.g^{-1}) as that observed in the other gadid species (0.2 to 1.2 mg.g^{-1}, Table 3). The diatom indicator ratio (16:1n-7/16:0) was also elevated in polar cod tissues compared to other species. Both saffron cod and polar cod had lower levels of the diatom indicator FA in 2017 and 2019 than in the earlier, colder sampling years (2012, 2013, Table 3).

Multivariate analyses of gadid lipids from all years (Table 3, Fig. 4) illustrate the large relative variation in polar cod compared to other species. Polar cod were spatially segregated in multivariate lipid space due to their high lipid content (FA per WWT, mg.g^{-1}) as well as their calanoid- ($\sum C_{20+22,}$ MUFA) and diatom-sourced (16:1n-7) fatty acid storage. Conversely, Pacific cod and saffron cod in 2017 were characterized by very low total FA and elevated proportional levels of FA indicative of membrane PLs rather than energy storage (i.e. 22:6n-3, 18:0). It was evident that saffron cod and polar cod had a significant shift in their lipid composition from

earlier cold years (2012, 2013) to warm conditions in 2017, with declining total and diatom-sourced lipids (Fig. 4). Compared to all other gadids, walleye pollock had an intermediate lipid storage level that was higher in 2019 than in 2017 and richer in C_{18} PUFA (18:4n-3, 18:3n-3 and 18:2n-6). A two-way PERMANOVA indicated that both species (pseudo-$F_{3,187}$ = 41.47, p = 0.0001) and year of sampling (pseudo-$F_{3,187}$ = 28.44, p = 0.0001) significantly affected the multivariate lipid composition of juvenile gadids. PERMANOVA for the effects of species and year showed a significant interactive effect (pseudo $F_{1,183}$ = 3.98, p = 0.01) as illustrated by the larger annual change in polar cod lipids (2017 versus 2019) than measured for walleye pollock over the same years.

3.4. *Partitioning variation in gadid fatty acids*

The marginal tests report the proportion of the variation in gadid lipid composition accounted for by the categorical species designation and each ecosystem variable (temperature, salinity, > C3 stage *Calanus* abundance) independent of the other explanatory variables (Table 4a). The species designation accounted for 50% of the total variation in gadid lipids with the ecosystem characteristics explaining much less of the variation. Bottom temperature, large *Calanus* abundance and surface temperature were the ecosystem measurements that explained accounted for most of the variation with 25%, 12% and 9.9%, respectively, on marginal tests. Salinity explained little of the variation either from surface (1.6%) or bottom measurements (8.1%). The results from the step-wise selection tests using AIC procedure, resulted in a model that accounted for 58% of the total variation in the gadid lipid data. Addition of ecosystem variables to the taxonomic grouping increased the cumulative variation accounted for by 8% (Table 4b).

The full model was visualized with a dbRDA where the symbols and colors represent year and species, respectively (Fig. 5). The first two axes in the model accounted for 93% of the variability in the fitted model and 54% of the variability in the entire lipid dataset. The first axis (dbRDA 1, 84%) accounted for most of the variation and polar cod were located on the positive side of the axis while all other gadids were on the negative side. The second axis (dbRDA 2) accounted for much less variability (8.7%) but separated Pacific cod along the positive and walleye pollock along the negative. The vectors show the relationships of the dbRDA axes to each of the explanatory variables, including the categorical species grouping and continuous

ecosystem variables. Polar cod segregation along dbRDA1 was associated with low bottom temperatures, reduced surface salinity and elevated *Calanus* copepod (> C3 stage) abundances. Walleye pollock lipid composition was associated with elevated surface temperatures and Pacific cod with elevated bottom temperatures and higher surface salinity relative to other gadids.

We next examined the impact of ecosystem factors on the lipid composition of just polar cod using 3 years of available survey data. Bottom temperature, large *Calanus* abundance and surface temperature were the ecosystem characteristics that accounted for most of the variation with 7.5%, 6% and 6%, respectively, on marginal tests (Table 4c). Again, surface salinity (4%) and bottom salinity (1%) explained less of the variation in lipids. The results from the step-wise selection tests using AIC criterion resulted in a model that accounted for 21% of the total variation in polar cod lipid composition with bottom and surface temperature accounting for 13% of that cumulative variation (Table 4d).

The first dbRDA axis accounted for 57% of the fitted variation and segregated fish from the NECS from the CECS (Fig. 6). Fish with negative values on the first axis were predominantly from the NECS and from collections in 2013 and 2019. They were associated with higher abundances of > C3 stage *Calanus* and lower bottom temperatures while fish from the CECS, particularly in 2017, were associated with warmer bottom temperature and weakly associated with higher bottom salinity. The second dbRDA axis only accounted for 29% of the fitted variation but separated NECS polar cod collected in 2013 on the negative side from those collected in 2019 on the positive side. Fish lipids in 2013 were segregated along this axis in association with lower surface salinity and decreased temperatures likely indicative of ice melt, compared to polar cod from 2019. The largest region-specific annual difference in multivariate lipid composition was seen in polar cod from the CECS between 2013 and 2017.

3.5. Spatial trends in juvenile gadid fatty acids

Spatial patterns in polar cod total FA per WWT scaled with patterns for total calanoid-sourced lipid storage, indicating the importance of this prey item to juvenile polar cod energetics (total fatty acids per WWT, mg.g^{-1}, Fig. 7). In 2013 and 2017, polar cod had the

highest fatty acid storage in the < 5 ℃ waters of the NECS, specifically surrounding Hanna Shoal, near the mouth of Barrow Canyon and in coastal regions off Icy Cape (Fig. 7). In southern waters with temperatures > 8 °C, polar cod were less abundant (Levine et al., in review), but also showed lower lipid storage and reduced calanoid-copepod fatty acid markers (Fig. 7). In 2019, polar cod were still in high lipid storage condition near the entrance to Barrow Canyon and in the ice-associated regions east of Hanna Shoal and north of Herald Shoal, but they had reduced lipid storage to the south of Hanna Shoal compared to 2013 and 2017.

In 2019, the regional distribution of polar cod and walleye pollock only overlapped at a few stations to the south and west of Hanna Shoal (Fig. 7), where lipid storage was high in polar cod but low in walleye pollock. Average surface water temperatures at polar cod stations in 2019 were 6.67 ± 0.16 °C while walleye pollock stations were 8.86 ± 0.8 °C. For walleye pollock, high total fatty acids were also associated with calanoid-sourced lipid storage, but at a much lower absolute level (Fig. 7). Walleye pollock generally had higher total FA and calanoid-sourced lipids in the SECS.

4. Discussion

The use of summer survey data from 2012, 2013, 2017 and 2019 has allowed us to examine age-0 gadid lipid storage during a period of rapid environmental warming and species redistribution. The among- and within-species variation in total lipids and fatty acid trophic markers during this period revealed several important observations. First, we observed significant species differences in allometric lipid storage, particularly emphasized by the unique high-lipid storage profile of polar cod. Second, most of the variance in the multivariate lipid composition of the four gadids was accounted for by species-specific differences (50%), but an additional 8% of the variation was accounted for by ecosystem measurements such as bottom temperature, large > C3 stage *Calanus* abundance, and surface temperature. Third, we observed spatial-temporal changes in lipid composition within each species. For example, Arctic gadids (saffron and polar cod) had low lipid storage over the central Chukchi Sea shelf in 2017 compared to 2012 and 2013. Unfortunately, a northward distributional shift of polar cod and the

extremely low catches of saffron cod in 2019, limited additional regional-annual comparisons. Sub-Arctic gadids (Pacific cod and walleye pollock) that were transported onto the Chukchi shelf during contemporary survey years had low lipid storage compared to polar cod and in relation to literature values from more southern habitats (Budge et al., 2022; Siddon et al., 2013). Below we discuss several potential mechanisms that explain observed differences in species' energetic condition over time and space. Understanding these mechanisms will aid in predicting gadid responses to warming in the Alaska Arctic.

4.1. Condition of juvenile gadids

Condition metrics, measures of morphometric proportions or physiological states, are broadly used in fisheries science due to their inferred correlation with nutritional status and potential links to recruitment success (Hurst et al., 2021; Wuenschel et al., 2019). Condition metrics are also specific to ontogenetic stage and cannot be broadly applied across taxonomic groups (Martin et al., 2017; Suthers, 1998), as exemplified here by the difference in Fulton's K observed even among similarly aged congeners. We found that this widely applied morphometric condition index (Fulton's K) exhibited opposite trends for annual variation compared to lipid storage metrics (Fig. 3). In 2017, polar cod, walleye pollock and saffron cod all had significantly lower lipid-based indices; however, when comparing to other years, Fulton's K-values for all species were highest in 2017. It is unclear what mechanisms led to reduced lipid storage in gadids in 2017, but it is not surprising that Fulton's K did not agree with lipid analyses. Previous studies on juvenile Atlantic cod (*Gadus morhua*) and cold-water Alaskan Tanner crabs (*Chionoecetes bairdi*) indicate that length-weight relationships like Fulton's K are less sensitive to energetic status compared to lipid-based metrics (Copeman et al., 2018; 2008). Conflicting results from different condition measures should be investigated further using laboratory studies that focus on explicitly evaluating which indicators are more closely tied to demographic outcomes.

4.2. Lipid storage in juvenile Chukchi Sea gadids

In highly seasonal environments, consumers must rapidly store lipids during times of high productivity to survive prolonged periods of low food availability (Copeman et al., 2016; 2021; Hurst, 2007; Renaud et al., 2018; Sogard and Olla, 2000). Lipids are the most efficient form of energy storage, providing at least two-thirds more energy per gram than proteins or carbohydrates (Lee et al., 2006; Parrish, 2013). Lipid storage in polar cod was higher than that of other Alaska gadids, both in terms of total lipids and the storage lipid class, triacylglycerols (TAG). Total lipid values that we report (~30 mg.g^{-1}) are in general agreement with those previously reported from the Alaska Arctic region (Dissen et al., 2018; Graham et al., 2014), Canadian Beaufort Sea (Brewster et al., 2018) and in laboratory experiments (Copeman et al., 2017). Similar to our findings, Brewster et al. (2018) noted that polar cod had approximately twice the tissue lipid concentration of co-occurring saffron cod and Greenland cod (*Gadus ogac*). Field studies indicate that saffron cod overwinter at smaller sizes in the Chukchi and Beaufort Seas (< 55 mm SL) than in their southern habitats in Gulf of Alaska and the southeastern Bering Sea (> 75 mm SL, Helser et al., 2017) and also have much higher lipid concentrations (19 mg.g^{-1} WWT) in northern habitat reaches than in the southern Bering Sea (12 mg.g^{-1} lipid) (Copeman et al., 2016). The high prioritization for energy storage observed in small-bodied polar cod and saffron cod at the northern extent of their latitudinal range suggests that there is a high winter mortality risk in the Arctic and that this risk is more likely due to starvation than predation (Ivan et al., 2015). Northern juvenile gadids seem to utilize a higher lipid storage strategy compared to southern juveniles, likely to optimize a short seasonal period of food availability and to maximize overwintering survival at a smaller size (Copeman et al., 2020; Copeman et al., accepted; Leu et al., 2011).

During the warm Arctic IERP survey years (2017 and 2019), an unprecedented northward expansion of juvenile sub-Arctic gadids was observed (Cooper et al., in review; Levine et al., in review; Wildes et al., accepted). Comparison of lipid storage in sub-Arctic gadids (Pacific cod and walleye pollock) collected in the Chukchi Sea with those from lower latitudes suggest that ecosystem conditions in new northern habitats may still be suboptimal for their growth and energy storage. Late summer/fall total lipid storage was low for both Chukchi Sea Pacific cod (~8 mg.g^{-1} WWT, 2017) and walleye pollock (~17 mg.g^{-1} WWT, 2017 and 2019) compared to collections from more southern Alaska regions. Cooper et al. (in review) compared the length-weight and length-fatty acid residuals of Pacific cod captured in the Chukchi Sea to

those from the Gulf of Alaska and found that Gulf of Alaska fish were heavier and had higher fatty acid storage than fish from the Chukchi Sea. Age-0 Pacific cod from the Gulf of Alaska sampled in 2011 to 2013 had almost two-fold the total lipids (~17 mg.g^{-1}) as Chukchi Sea juveniles (Budge et al., 2022). Similarly, walleye pollock from the Chukchi Sea contained very low lipids (~17 mg. g^{-1}) compared to pollock from both the southeastern Bering Sea (~34 mg. g^{-1}, calculated from Siddon et al. (2013)) and Gulf of Alaska (20-28 mg.g^{-1}, Heintz and Vollenweider (2010) and ~25 mg.g^{-1}, Budge et al. (2022)). Given the low lipid storage we found in sub-Arctic gadids captured in Arctic surveys, it seems unlikely that these juveniles can successfully overwinter in the cold, low productivity environments of the winter Chukchi Shelf.

4.3. *Fatty acid trophic markers*

Analyses of fish trophic links using fatty acid markers are ideally done with lipid from storage tissues such as liver that are rich in TAG (Budge et al., 2006; Dalsgaard et al., 2003). However, we were not able to obtain adequate liver tissues to perform tissue-specific lipid analyses due to the small size of fish examined in this study, < 60 mm SL. Therefore, we used homogenates representative of whole body lipids, as previously done in other studies focused on age-0 juvenile gadids (Budge et al., 2022; Copeman et al., 2008). Homogenate samples reflect both dietary FA in shorter-term TAG deposition and structural FA from phospholipids (PL). The fatty acid composition of PL is considered more species- and tissue-specific, but relative changes can also reveal patterns in dietary contributions (Bell and Dick, 1991; Copeman and Parrish, 2002). Controlled laboratory studies on juvenile Pacific cod and walleye pollock have previously revealed that dietary shifts are reflected more quickly in liver tissue TAG than in muscle tissue PL but that both tissues do significantly mirror dietary FA within a few weeks of consumption (Copeman et al., 2013).

The distinct fatty acid composition of polar cod was typified by elevated proportions of MUFA accumulated from specialized predation on calanoid-copepods (Kohlbach et al., 2017b; Loseto et al., 2009), which in turn have high levels of the $C_{20}+C_{22}$ MUFA originating from their unique seasonal wax ester storage (Copeman et al., 2020; Graeve et al., 2005; Hagen and Auel, 2001; Lee et al., 2006; 1971). Elevated diatom lipid storage in polar cod tissues gives support to

the theory that polar cod nutritional status is highly dependent on their feeding in cold, nutrient-rich waters that support both ice and later pelagic diatom-*Calanus* based food webs (Soreide et al., 2008; Soreide et al., 2007). Walleye pollock had an intermediate level of lipid storage compared to other gadid species, but had higher proportions of C_{18} PUFA that are elevated in flagellates (discussed in Nielsen et al. (in review)) compared to diatoms (Dalsgaard et al., 2003). These fatty acid markers suggest that walleye pollock were storing lipids resulting from their predation on smaller copepods that typically do not graze on diatoms. Pacific cod and saffron cod analyzed in 2017 were characterized by very low total FA and elevated proportional levels of 22:6n-3 and 18:0. These two FA are found at high percentages in the membrane lipids of gadids and 22:6n-3 is generally retained in tissues independent of diet (Bell and Dick, 1991; Copeman et al., 2002). The high proportion of these membrane FA combined with low total lipids per WWT and < 2% TAG storage, suggest that Pacific and saffron cod in 2017 were on the verge of starvation.

4.4. Gadid fatty acid composition and ecosystem variability

After accounting for species, ecosystem variables (i.e. temperature and large > C3 stage *Calanus*) contributed to 8% of the additional variation in the multivariate lipid composition among gadids. This was not surprising, considering that these species do not typically co-occur across a large range of ecosystem conditions. Within-species analysis revealed that ecosystem metrics accounted for 21% of the variation in FA of polar cod, with bottom temperature (7%), surface temperature (6%) and *Calanus* abundance (6%) accounting for the most variation on the marginal test. The co-variance of large *C. glacialis* with water mass characteristics (i.e. low temperature and low surface salinity) resulted in *Calanus* abundance accounting for very little additional variability in polar cod FA once physical variables were incorporated into the model (step-wise ~1.5%). However, we also recognize that there is a potential temporal mismatch between fatty acid integration time (weeks to months) and copepod sampling (one sample per station in late August-September). It is likely that *C. glacialis* was prominent in the diet of juvenile polar cod throughout the preceding months of July and August (Bouchard and Fortier, 2020; Buckley and Whitehouse, 2017) but were not present at the time of *Calanus* copepod sampling.

On a regional scale, we note that the *Calanus* MUFA signal was strongest in polar cod (2013, 2017, 2019) in the NECS where genetically distinct and localized *C. glacialis* populations have been documented and where their numbers were higher and persistent (i.e. Ashjian et al. (2017); Nelson et al. (2009); Pinchuk and Eisner (2017)). *Calanus* MUFA storage in polar cod was more variable in locations where *C. glacialis* is dependent on advection through the Bering Strait (i.e. 2013 and 2017 CECS). Interestingly, it has been proposed that polar cod in the NECS, especial near Hanna Shoal, may originate with a localized Arctic spawning population. Conversely, the majority of fish on the Chukchi Shelf are proposed to originate in southern spawning areas near the Bering Strait and Kotzebue Sound (Deary et al., 2021; Vestfals et al., 2019)(Chapman 2021). This difference in larvae origin could also partially explain the relative nutritional stability of fish from the NECS compared to polar cod in more southern regions.

4.5. Direct and indirect impacts of continued warming

This study spanned a period of intense environmental warming in the Chukchi Sea (Danielson et al., 2020; Huntington et al., 2020) and record low sea ice in the Bering Sea (Stabeno and Bell, 2019). The direct effects of temperature on fish vary with life history stage (Rijnsdorp et al., 2009). Of the species examined here, polar cod have the narrowest thermal tolerance during the egg (-1.5 to 3.0 ºC) and early larval (-1 to 5 ºC) stages, becoming more thermally tolerant during the late pelagic juvenile stage (-1 to 11 ºC) (Koenker et al., 2018; Laurel et al., 2017; Laurel et al., 2018). In recent years, the Chukchi Sea has been generally ice-free for much of the spring-summer and has surface waters that, in some areas, are already warming beyond the thermal limits of early stages of polar cod (Danielson et al., 2020; Laurel et al., 2017; Laurel et al., 2018). Long- term ecosystem surveys both in the Barents Sea and in the Canadian Arctic have reported decadal scale increases in size-at-age of juvenile polar cod (Bouchard et al., 2017; Dupont et al., 2020) concurrent with reductions in sea ice concentrations and earlier spring ice retreat. As a result, Bouchard et al. (2017) predicted that warming would cause a temporary increase in polar cod biomass, but that with further levels of borealization in the Arctic, that polar cod would be replaced by less specialized sub-Arctic fish. Laboratory studies on polar cod have shown that this species holds an energetic advantage (higher rate of lipid accumulation per weight) over Pacific cod and walleye pollock only at temperatures < 5 ºC

(Copeman et al., 2017). These laboratory data combined with evidence of declining abundances and lipid storage during warming events (> 8°C, Deary et al. (2021); Levine (2021)), may indicate that the SECS and CECS are currently episodically warming beyond the specialized thermal limits of polar cod.

Continued warming may have negative impacts on polar cod via changes in the quantity, quality and phenology of zooplankton production and thus the nutrition status of juvenile fish in the summer (Bouchard and Fortier, 2020; Bouchard et al., 2017). Large Arctic zooplankton have elevated lipid storage that is dependent on both sympagic (ice-associated) and open-water diatom lipid production, that is, seasonally elevated in cold nutrient-rich waters (Kattner et al., 2007; Kohlbach et al., 2017a; 2017b; Nielsen et al., in review; Soreide et al., 2010). Shifts in zooplankton dynamics during recent warming, such as increased abundance of small southern species concurrent with decreases in large Arctic ice-associated zooplankton (e.g. *C. glacialis*) have likely resulted in lower zooplankton lipids available in the diet of juvenile Chukchi Sea polar cod (Ashjian et al., 2017; Pinchuk and Eisner, 2017; Spear et al., 2019; Spear et al., 2020). However, there is some debate as to whether warming will decrease zooplankton resources in Arctic gateways. In the Barents Sea, it has been hypothesized that an increased northward influx of sub-Arctic copepods (i.e. *Calanus finmarchicus*) may actually buffer the lipid deficit to juvenile fish caused by declining ice-associated *C. glacialis* (Renaud et al., 2018). Apart from direct impacts of warming, polar cod may also be outcompeted if southern "invading" congeners can more efficiently utilize a more southern zooplankton assemblage.

4.6. Overwintering and summer lipid storage

Recent laboratory studies on the winter survival of juvenile polar cod (Copeman et al., accepted) indicate that pre-winter lipid content determines winter survival duration. The magnitude of annual differences in the mean lipid content of field-collected polar cod from the CECS (2013: 34.7 mg.g^{-1} WWT vs. 2017: 16.0 mg.g^{-1} WWT, S1) was particularly striking, despite the fish being similar in size (2013: 43.4 mm SL vs. 2017: 47.2 mm SL). Copeman et al. (accepted) developed a temperature-dependent lipid-loss model for polar cod to illustrate how winter thermal conditions are either highly important following summers that support fish in good condition (e.g. NECS 2013, 2019) or are potentially irrelevant when the preceding summer

conditions result in a poor energetic state for age-0 juveniles (e.g. CECS, 2017). They also note that small changes in fall/winter temperature between -1 and 2 °C have important implications for the survival of fish entering winter in a high energetic state. The importance of summer-fall prey availability and pre-winter condition have been shown to be vital processes regulating walleye pollock recruitment in the eastern Bering Sea (Heintz et al., 2013; Hunt et al., 2011; Mueter et al., 2011) and it is likely that similar processes dictate the survival of Arctic gadids on the Beaufort and Chukchi Sea shelves.

4..7 Future work

In contrast to long-term ecosystem surveys available from the Canadian and Norwegian Arctic (Aune et al., 2021; Bouchard and Fortier, 2020; Bouchard et al., 2017; Dupont et al., 2020), the pelagic Chukchi Sea fish community and ecosystem status remains poorly surveyed. Routine oceanographic and biological monitoring of the Chukchi Sea is needed to better account for annual variability and capture a broader range of seasonal environmental conditions that determine the abundance and nutritional condition of Arctic species and northward-moving sub-Arctic species. Increased annual replication could help us to understand climate-mediated mechanisms that drive measured variability in juvenile fish lipid storage and improve our ability to predict overwinter survival potential and resulting recruitment.

Despite the limited time series in our data, we document significant variability in juvenile gadid lipid storage during a period of rapid change in species distributions across the Chukchi Sea shelf (De Robertis et al., 2016; Levine, 2021; Wildes et al., accepted). Linking these changes to implications for population dynamics will require a better understanding of the survival and life history trajectories such variation imposes on these fish, for example, predation vulnerability, overwintering success, maturation, etc. Both lipid reserves and size-at-age will likely be critical metrics in determining species-specific recruitment of all four juvenile gadid species in Arctic waters.

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Ethical approval: All animal experiments were conducted at the National Oceanic and Atmospheric Administration facilities. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Louise Copeman: Conceptualization, formal analysis, writing-original draft, supervision, visualization, and investigation.: **Carlissa Salant**: investigation.: **Michelle Stowell**: investigation.: **Mara Spencer:** investigation.: **Benjamin Laurel**: writing-original draft, funding acquisition, **David Kimmel** writing-original draft and investigation, **Alexei Pinchuk:** writing-original draft and investigation.

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Fig. 4. Nonmetric multidimensional scaling (*n*MDS) of the annual fatty acid composition of four species of juvenile gadids: polar cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), Walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) collected on ecosystem surveys during 2012, 2013, 2017 and 2019. Data are square root transformed and a Bray-Curtis similarity matrix was used. Data points are annual station averages of ~ n = 5 fish. Species and sampling as detailed in Tables 1 and 2. Fatty acid vectors are shown for individual fatty acids > 1% (Table 2) as well as total fatty acids per WWT (mg.g^{-1}) and sum of calanoid-copepod fatty acids.

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Fig. 6. Distance-based redundancy analysis (dbRDA) ordination of juvenile polar cod lipids. The DISTLM partitioned the variances in polar cod lipids explained by ecosystem metrics for all 310 fish for which we have full station information. Data are square root transformed and a Bray-Curtis similarity matrix was used. The colors indicate years and symbols represent regions of the Chukchi Sea. The vector overlays show the strength of the relationship between the ecosystem variables and the dbRDA axes. Note that the position of the vector diagram relative to the first ordination axis is arbitrary, not centered on zero.

Fig. 7. Annual spatial interpolation maps for the total fatty acids per WWT (mg.g^{-1}) in juvenile polar cod from 2013, 2017 and 2019 as well as juvenile walleye pollock in 2019. Fish were collected on eastern Chukchi Sea Ecosystem surveys with data sources and cruise details as in Table 1.

Table 1: Four species of juvenile gadids were collected over the eastern Chukchi Sea and northeastern Bering Sea (NEBS) from seven different Arctic surveys during 2012, 2013, 2017 and 2019. Below are samples sizes, gear types and field collection citations as well as biochemical analyses performed to assess fish condition.

	Ecosystem survey	Year	Age	Number of fish for lipid classes	Number of fish for fatty acids	Number of fish for body size	Gear type	Region	Reference to collection methods
Polar cod	EIS	2013	0	38	67	66	Midwater/surface trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020)
	SHELFZ	2013	1	35	68	68	Bottom/Midwater trawls	Chukchi Sea	(Gunderson and Ellis, 1986; Logerwell et al., 2018)
	Arctic IERP	2017	0	112	112	110	Midwater/surface/beam trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020; Levine, 2021; Logerwell et al., 2018)
	Arctic IERP	2019	0	109	109	109	Midwater/surface trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020; Levine, 2021)
Saffron cod	EIS	2012	0	48	48	48	Midwater/surface/beam trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020)
	EIS	2012	1	33	33	33	Midwater/surface trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020)
	AMBON	2017	0	37	37	36	Isaacs-Kidd Midwater Trawl/ 3 m Plum staff beam trawl	Chukchi Sea	(Iken et al., 2019; Mueter et al., 2021)
	Arctic IERP	2017	0	29	29	29	Midwater/surface/beam trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020; Logerwell et al., 2018)
	NBS	2017	0	30	30	30	Surface trawls	NEBS	(Farley et al., 2020; Murphy et al., 2017)
Pacific cod	Arctic IERP	2017	0	117	117	117	Midwater/surface/ beam trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020; Logerwell et al., 2018) (Cooper et al. in review)
	NBS	2017	0	13	13	13	Surface trawls	NEBS	(Farley et al., 2020; Murphy et al., 2017)
Walleye pollock	Arctic IERP	2017	0	47	47	47	Midwater/Surface trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020) (Levine et al. in review)
	Arctic IERP	2019	0	111	111	111	Midwater/surface/beam trawls	Chukchi Sea	(De Robertis et al., 2016; Farley et al., 2020; Logerwell et al., 2018) (Levine et al. in review)

Table 2: Overview of the regression parameters (estimated mean ± SE) and the r^2 of the power functions ($Y = a\,L^b$) relating length (mm) to fish wet weight (WWT, g) and fish total fatty acids (mg) for four age-0 juvenile gadids collected in the Chukchi Sea between 2012 and 2019. Power functions were run on 10 mm increments of size-binned data.

	Wet weight (g)		
	Parameter a	Parameter b	r^2
Polar cod (*Boreogadus saida*)	$2.67 \times 10^{-6} \pm 1.26 \times 10^{-6}$	3.22 ± 0.11	0.99
Saffron cod (*Eleginus gracilis*)	$9.70 \times 10^{-6} \pm 8.19 \times 10^{-6}$	2.96 ± 0.21	0.99
Walleye pollock (*Gadus chalcogrammus*)	$1.12 \times 10^{-5} \pm 4.61 \times 10^{-6}$	2.89 ± 0.10	0.99
Pacific cod (*Gadus macrocephalus*	$1.73 \times 10^{-5} \pm 5.02 \times 10^{-6}$	2.85 ± 0.07	0.99
	Total fatty acids (mg)		
	Parameter a	Parameter b	r^2
Polar cod (*Boreogadus saida*)	$5.41 \times 10^{-6} \pm 1.57 \times 10^{-6}$	3.85 ± 0.07	0.99
Saffron cod (*Eleginus gracilis*)	$0.24 \times 10^{-2} \pm 0.43 \times 10^{-2}$	2.19 ± 0.44	0.92
Walleye pollock (*Gadus chalcogrammus*)	$0.06 \times 10^{-2} \pm 0.07 \times 10^{-2}$	2.58 ± 0.29	0.97
Pacific cod (*Gadus macrocephalus*	$0.03 \times 10^{-2} \pm 0.01 \times 10^{-2}$	2.61 ± 0.10	0.99

Table 3: Summary of lipid measures for juvenile saffron cod (*Eleginus gracilis*), polar cod (*Boreogadus saida*), walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) collected on ecosystem surveys during 2012, 2013, 2017 and 2019. Grey highlights indicate historical years representing a relatively 'cold' thermal phase of the Chukchi Sea, compared to the current 'warm' years (2017 and 2019).

Species	Saffron		Polar cod			Walleye pollock		Pacific cod
Year	2012	2017	2013	2017	2019	2017	2019	2017
Age	0 &1	0	0 &1	0	0	0	0	0
Surface temperature °C	7.5 ± 0.3	7.0± 0.2	4.0 ± 0.2	5.5 ± 0.1	6.7 ± 0.2	5.6 ± 0.1	8.9 ± 0.1	6.0 ± 0.1
Standard length, mm	59.0 ± 2.4	58.1 ± 1.7	67.5 ± 2.3	43.6 ± 0.8	48.3 ± 0.9	58.5 ± 1.2	49.6 ± 1.0	67.0 ± 0.8
Sample size	81	96	73	112	109	47	111	130
Total lipids per WWT	17.3 ± 1.0	8.8 ± 0.2	34.4 ± 2.0	19.7 ± 1.0	30.2 ± 1.1	15.9 ± 1.0	17.3 ± 0.6	8.2 ± 0.1
%Triacylglycerols (TAG)	12.7 ± 1.6	2.0 ± 0.4	57.3 ± 1.6	32.7 ± 2.0	27.8 ± 1.5	21.5 ± 2.1	17.4 ± 1.6	1.9 ± 0.3
% free fatty acids	27.6 ± 0.9	15.5 ± 0.9	14.7 ± 0.5	8.3 ± 0.2	16.0 ± 0.5	9.6 ± 0.3	21.9 ± 0.5	16.8 ± 0.6
% sterols	11.6 ± 0.5	12.9 ± 0.3	4.8 ± 0.2	6.7 ± 0.3	5.5 ± 0.2	7.5 ± 0.2	7.3 ± 0.3	12.9 ± 0.2
% Polar lipids (PL)	47.1 ± 1.2	69.6 ± 1.2	22.1 ± 1.2	52.3 ± 1.7	50.8 ± 1.1	61.4 ± 1.9	53.3 ± 1.2	68.4 ± 0.7
Sample size	81	96	137	112	109	47	111	128
Total FA per WWT	16.2 ± 0.7	7.4 ± 0.2	26.9 ± 0.9	18.2 ± 0.9	27.1 ± 1.0	12.0 ± 0.8	16.0 ± 0.7	7.0 ± 0.2
% 14:0	2.7 ± 0.1	1.3 ± 0.0	3.8 ± 0.1	2.8 ± 0.1	4.2 ± 0.1	2.7 ± 0.1	1.3 ± 0.0	1.1 ± 0.0
% 16:0	16.9 ± 0.3	17.7 ± 0.2	13.7 ± 0.2	14.4 ± 0.3	16.7 ± 0.2	16.9 ± 0.3	17.7 ± 0.2	17.5 ± 0.1
% 18:0	3.8 ± 0.1	4.5 ± 0.1	1.7 ± 0.0	2.1 ± 0.1	1.9 ± 0.1	3.8 ± 0.1	4.5 ± 0.1	4.0 ± 0.1
∑ % SFA	25.0 ± 0.4	24.6 ± 0.2	19.8 ± 0.2	19.9 ± 0.3	24.5 ± 0.2	24.7 ± 0.3	28.7 ± 0.3	23.5 ± 0.1
% 16:1 n-7	7.8 ± 0.5	2.7 ± 0.1	13.6 ± 0.4	8.5 ± 0.4	8.8 ± 0.3	4.2 ± 0.3	4.6 ± 0.2	2.3 ± 0.1
% 18:1 n-7	4.9 ± 0.2	3.6 ± 0.1	3.4 ± 0.1	2.9 ± 0.1	2.8 ± 0.0	3.4 ± 0.1	3.4 ± 0.1	3.9 ± 0.1
% 18:1 n-9	9.6 ± 0.2	7.2 ± 0.1	7.3 ± 0.1	6.4 ± 0.1	6.8 ± 0.2	8.7 ± 0.2	9.9 ± 0.2	7.4 ± 0.1
% 20:1 n-9	5.0 ± 0.3	1.4 ± 0.1	13.2 ± 0.4	11.0 ± 0.5	11.5 ± 0.4	3.2 ± 0.4	3.4 ± 0.2	1.5 ± 0.1
% 22:1 n-11	1.3 ± 0.1	0.6 ± 0.1	7.2 ± 0.2	5.4 ± 0.3	6.5 ± 0.4	1.4 ± 0.2	1.2 ± 0.1	0.5 ± 0.1
∑ % MUFA	32.7 ± 0.8	18.0 ± 0.3	50.2 ± 0.5	38.2 ± 1.1	42.0 ± 1.1	23.5 ± 1.0	25.2 ± 0.6	17.7 ± 0.2
% 20:4 n-6	1.0 ± 0.1	1.0 ± 0.1	0.2 ± 0.0	0.6 ± 0.0	0.2 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	1.0 ± 0.2
% 20:5 n-3	13.2 ± 0.3	15.0 ± 0.3	11.9 ± 0.2	14.0 ± 0.3	10.7 ± 0.2	17.9 ± 0.3	14.8 ± 0.4	15.7 ± 0.2
% 22:6 n-3	20.0 ± 0.6	33.4 ± 0.4	11.6 ± 0.3	19.5 ± 0.7	15.1 ± 0.6	25.1 ± 0.9	22.5 ± 0.7	35.4 ± 0.4
∑ % PUFA	41.3 ± 0.7	56.5 ± 0.3	29.4 ± 0.4	41.1 ± 0.9	33.5 ± 0.9	51.1 ± 0.8	46.0 ± 0.5	58.1 ± 0.2
Diatom: 16:1n-7/16:0	0.5 ± 0.0	0.2 ± 0.0	1.0 ± 0.0	0.7 ± 0.0	0.6 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0
Calanus ∑ % C_{20+22} MUFA	7.5 ± 0.4	2.7 ± 0.2	23.7 ± 0.6	18.2 ± 0.9	20.5 ± 0.9	5.7 ± 0.7	5.3 ± 0.3	2.8 ± 0.1
Calanus ∑ mg/g C_{20+22} MUFA	1.2 ± 0.1	0.2 ± 0.0	6.5 ± 0.3	4.0 ± 0.3	6.4 ± 0.5	0.8 ± 0.1	0.9 ± 0.1	0.2 ± 0.0

Table 4: Results of the DISTLM sequential and step-wise tests for all 650 gadids and 309 polar cod for which we have matching lipid composition and ecosystem metrics. Selection criterion using AIC for all gadids included all 6 variables.

(a) all gadids, marginal tests

Group	SS(trace)	Pseudo-F	P	Proportion
Species	34538	161.64	0.0001	0.50
Log >C3 *Calanus*	8567	92.00	0.0001	0.12
Surface temperature	6872	71.78	0.0001	0.099
Bottom temperature	16965	211.51	0.0001	0.25
Surface salinity	1091	10.43	0.0001	0.016
Bottom salinity	5592	57.24	0.0001	0.081

(b) all gadids, step-wise

Group	SS(trace)	Pseudo-F	P	Proportion	AIC	Delta AIC	Cumulative r^2
Species	34538	161.64	0.0001	0.50	2598.7	110.5	0.50
Log >C3 *Calanus*	2662.9	53.93	0.0001	0.039	2548.4	60.2	0.54
Surface temperature	1219	25.63	0.0001	0.018	2525	36.8	0.56
Bottom temperature	860.09	18.58	0.0001	0.012	2508.5	20.3	0.57
Surface salinity	759.25	16.80	0.0001	0.011	2493.7	5.5	0.58
Bottom salinity	332.16	7.42	0.0002	0.0048	2488.2		0.58

(c) polar cod, marginal tests

Group	SS(trace)	Pseudo-F	P	Proportion
Log >C3 *Calanus*	1224.7	19.50	0.0001	0.059
Surface temperature	1190.5	18.92	0.0001	0.058
Bottom temperature	1544.6	25.00	0.0001	0.075
Surface salinity	839.12	13.10	0.0001	0.041
Bottom salinity	243.77	3.70	0.0267	0.012

(d) polar cod, step-wise

Group	SS(trace)	Pseudo-F	P	Proportion	AIC	Delta AIC	Cumulative r^2
Bottom temperature	1544.6	24.47	0.0001	0.075	1288.5	41.5	0.075
Surface temperature	1138.4	17.36	0.0001	0.055	1271.4	24.4	0.13

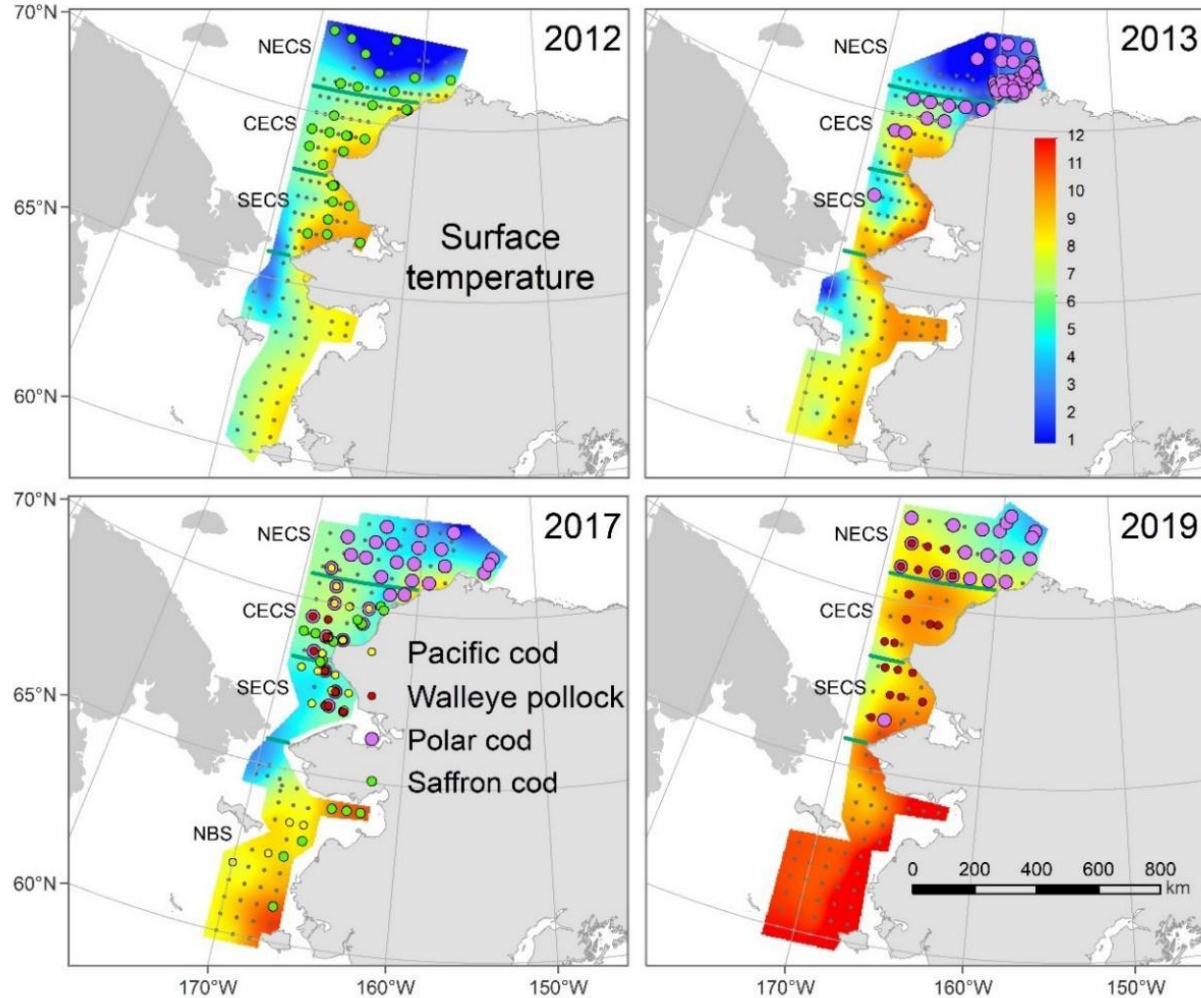|							
Bottom salinity	669.19	10.21	0.0002	0.032	1261.6	14.6	0.16
Surface salinity	677.53	9.65	0.0002	0.034	1251.2	4.2	0.19
Log >C3 *Calanus*	324.51	6.21	0.0047	0.016	1247		0.21

Fig. 1. Distribution of juvenile gadids collected on annual ecosystem surveys as detailed in Table 1. Species-specific stations are indicated for fish that were analyzed for detailed condition and lipid biomarker analyses. Stations were plotted with surface temperature (°C, color scale in upper right panel) at the time of sampling to illustrate the dramatic warming in 2017 and 2019 compared with earlier sampling years. Symbol size does not infer abundance but rather allows for a stacked presentation of multiple species at a given station.

Fig. 2. Relationships between standard length (SL, mm) and wet weight (WWT, g) as well as SL and total fatty acids (mg per fish) for all age-0 juvenile Chukchi Sea gadids processed for lipid analyses (2012, 2013, 2017 and 2019). Data are shown for (a) 10 mm increments of size-binned WWT and (b) size-binned total fatty acids. Power function equations are in Table 2.
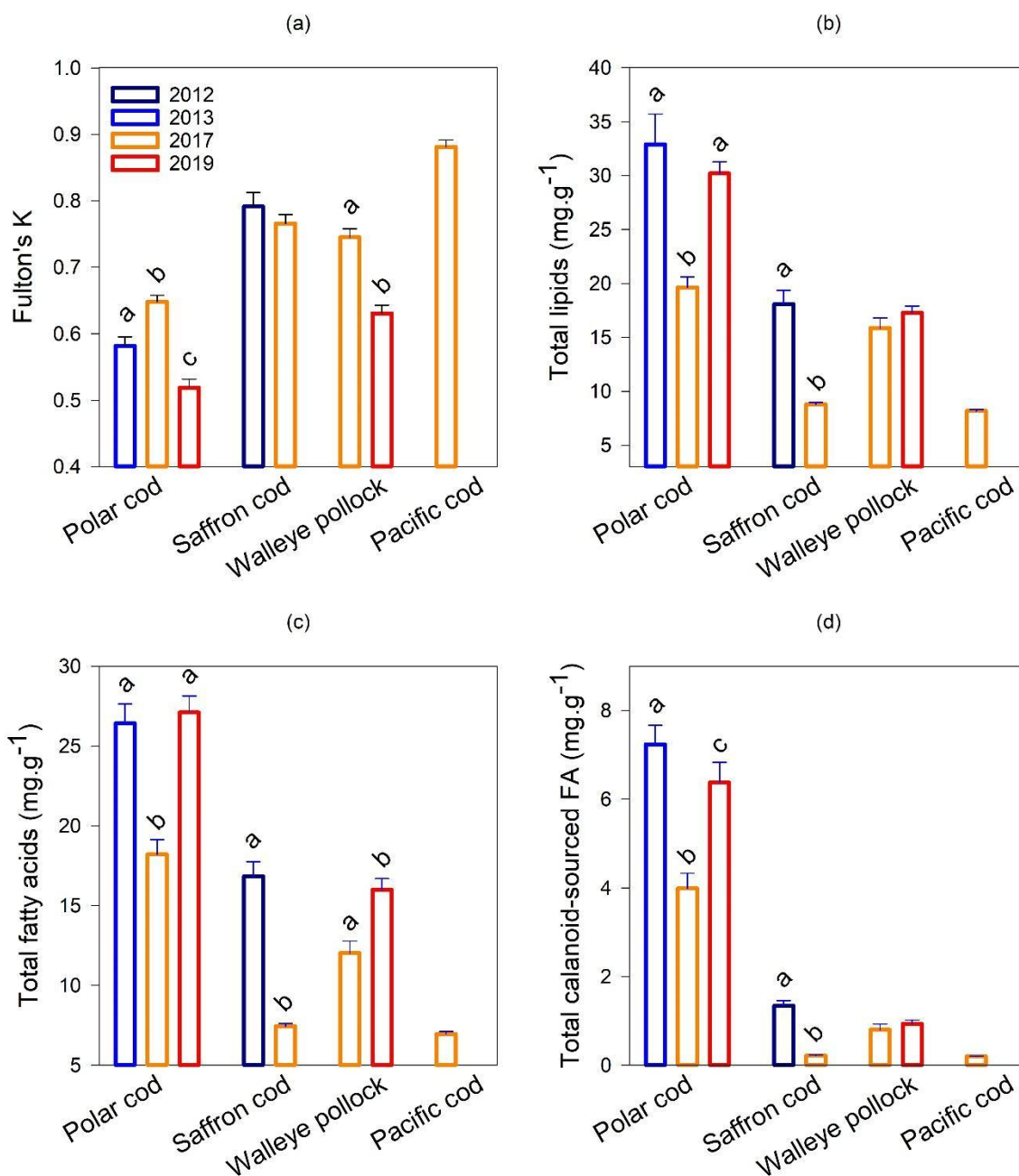
Fig. 3. Annual differences in body condition and lipid storage of age-0 polar cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) collected on ecosystem surveys during 2012, 2013, 2017 and 2019. Data shown for (a) Fulton's K, (b) total lipids (mg.g^{-1} WWT), (c) total fatty acids (mg.g^{-1} WWT), and (d) total calanoid copepod fatty acid storage ($\sum$ C$_{20}$+C$_{22}$ MUFA mg.g^{-1} WWT). Data are mean + SE displayed by species and year with sample sizes as in Table 1. Different letters represent significant differences between years within a species, ANOVA with LSD test, p < 0.05. Species-specific regional comparisons are shown in S1.
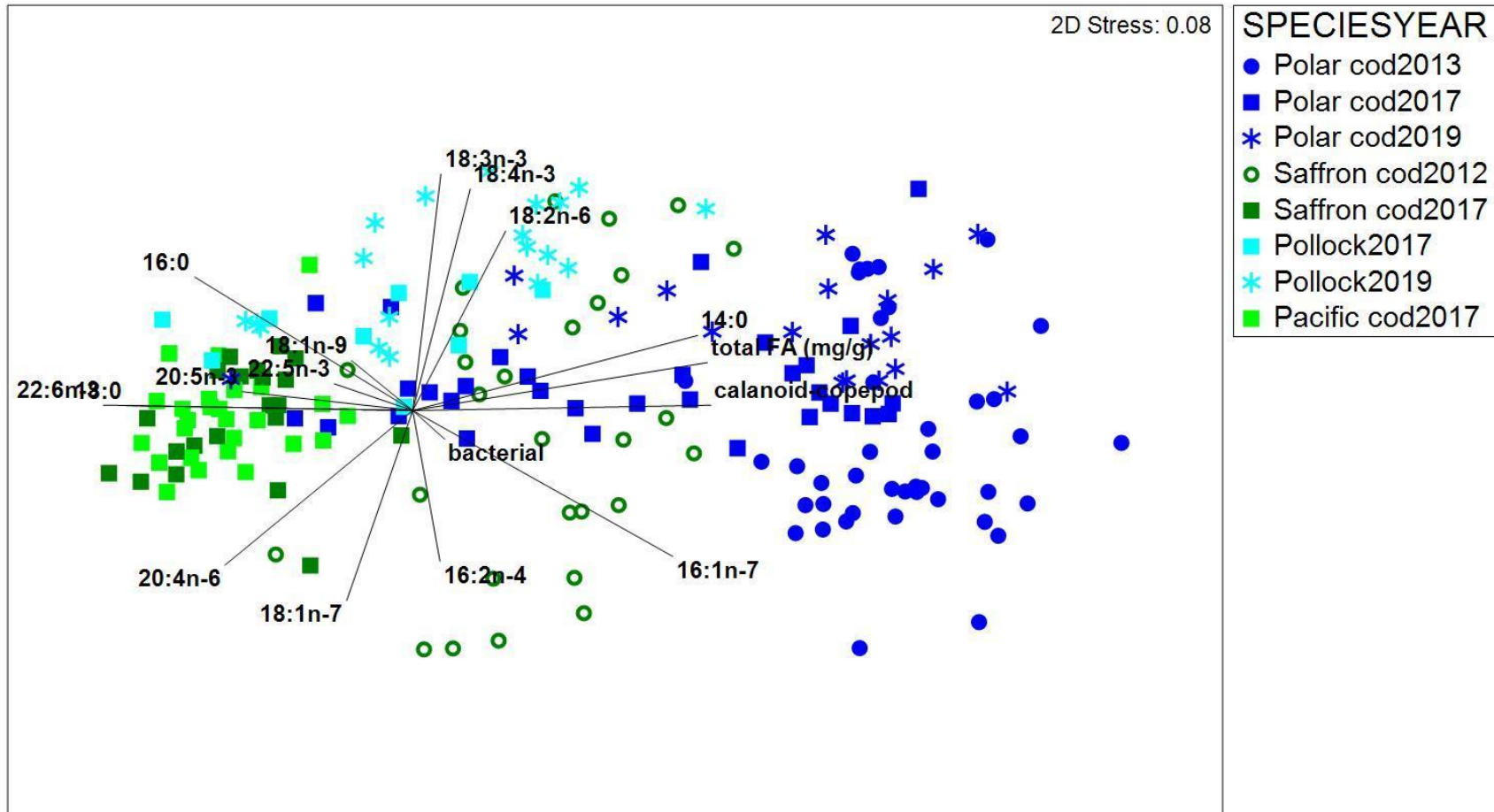
Fig. 4. Nonmetric multidimensional scaling (*n*MDS) of the annual fatty acid composition of four species of juvenile gadids: polar cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), Walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) collected on ecosystem surveys during 2012, 2013, 2017 and 2019. Data are square root transformed and a Bray-Curtis similarity matrix was used. Data points are annual station averages of ~ n = 5 fish. Species and sampling as detailed in

Tables 1 and 2. Fatty acid vectors are shown for individual fatty acids > 1% (Table 2) as well as total fatty acids per WWT (mg.g^{-1}) and sum of calanoid-copepod fatty acids.
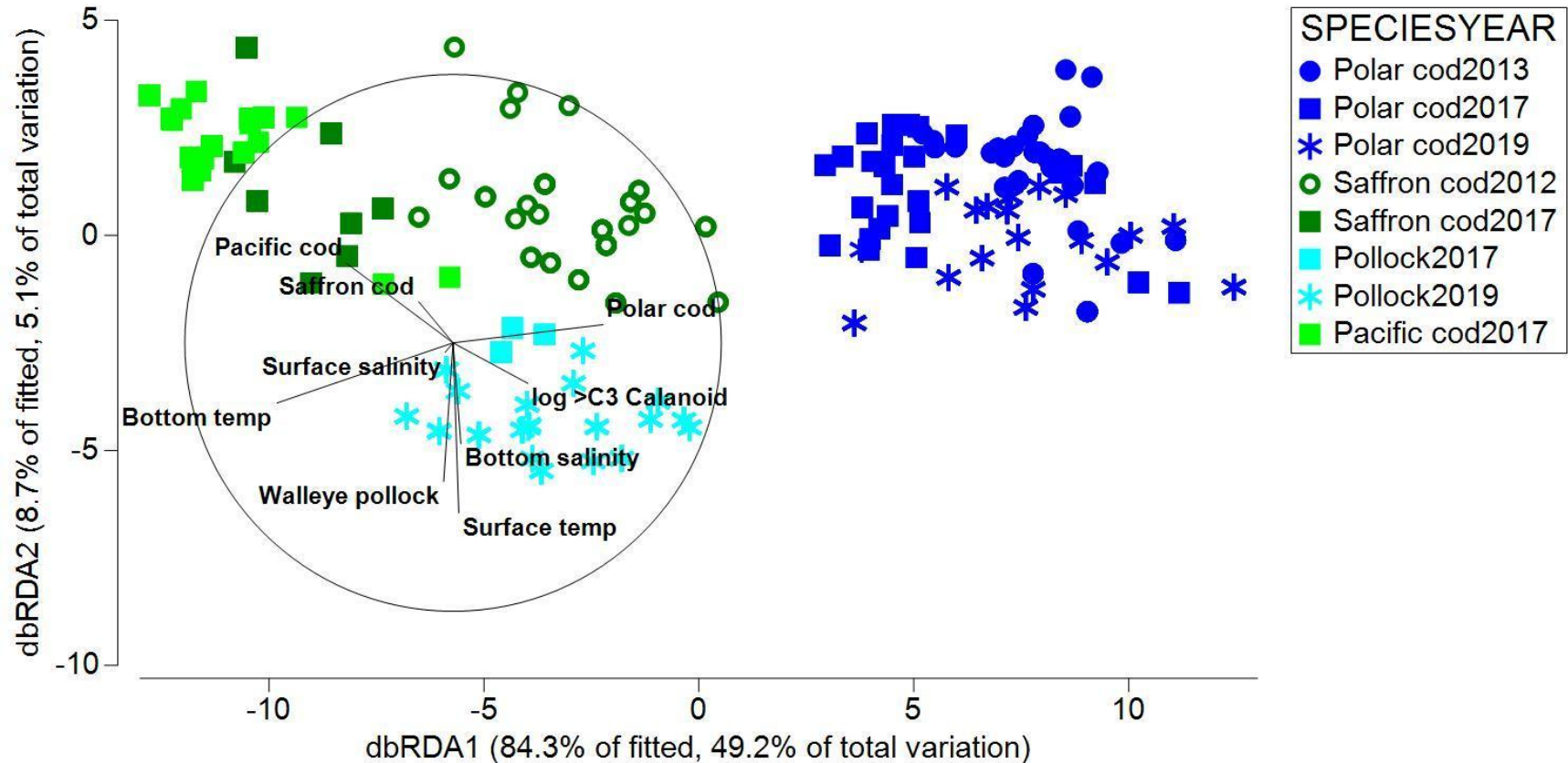

Fig. 5. Distance-based redundancy analysis (dbRDA) ordination of the full multivariate juvenile gadid data set. The DISTLM partitioned the variances in gadid lipids explained by species and those explained by ecosystem factors for all 650 gadid samples for which we have full information. Data are square root transformed and a Bray-Curtis similarity matrix was used. The top ranked variable, species, is indicated by different colors. The vector overlays show the strength of the relationship between the predictor variables (species and ecosystem metrics) and the dbRDA axes. Note that the position of the vector diagram relative to the first ordination axis is arbitrary, not centered on zero.
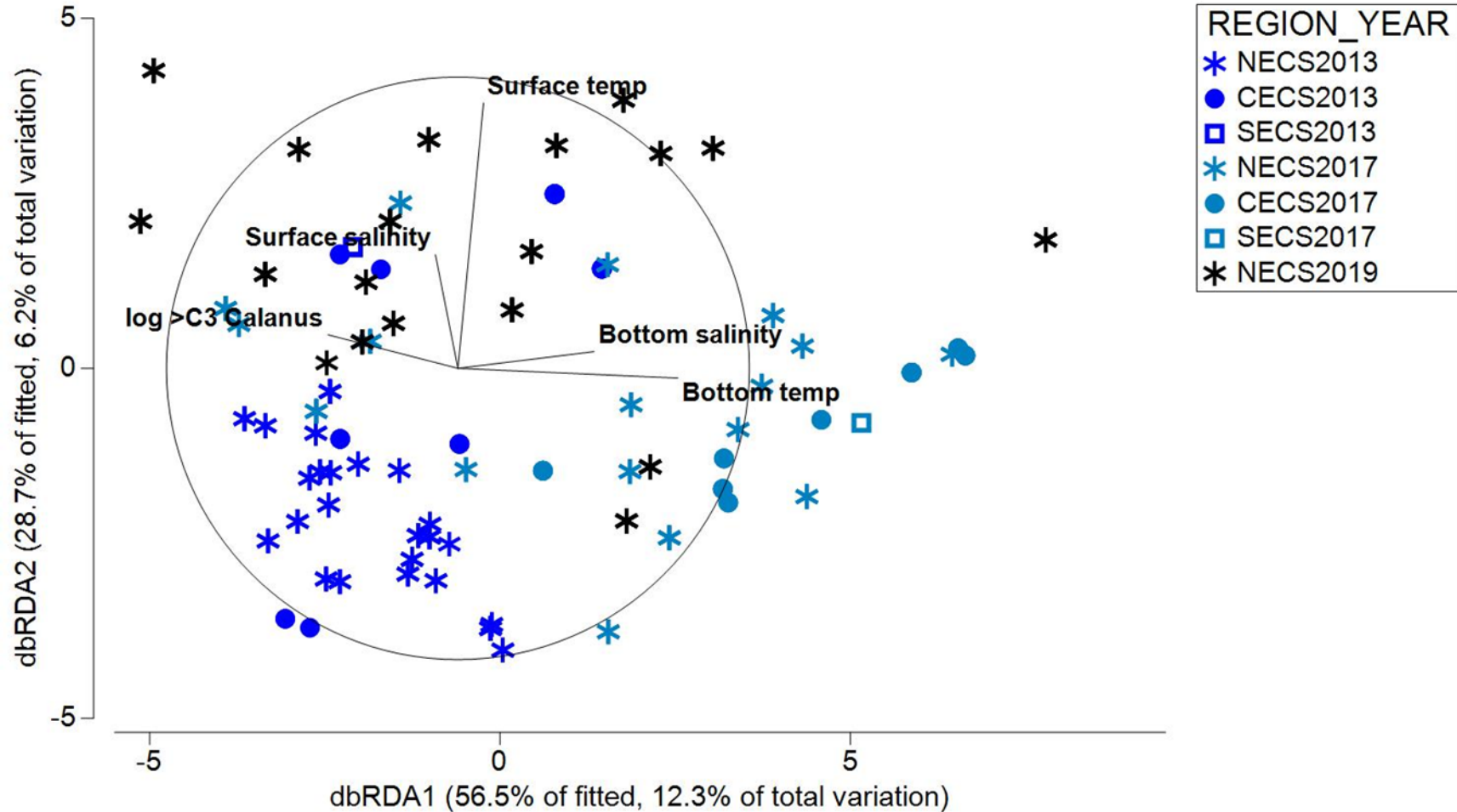
Fig. 6. Distance-based redundancy analysis (dbRDA) ordination of juvenile polar cod lipids. The DISTLM partitioned the variances in polar cod lipids accounted for by ecosystem metrics for all 310 fish for which we have full station information. Data are square root transformed and a Bray-Curtis similarity matrix was used. The colors indicate years and symbols represent regions of the Chukchi Sea. The vector overlays show the strength of the relationship between the ecosystem variables and the dbRDA axes. Note that the position of the vector diagram relative to the first ordination axis is arbitrary, not centered on zero.
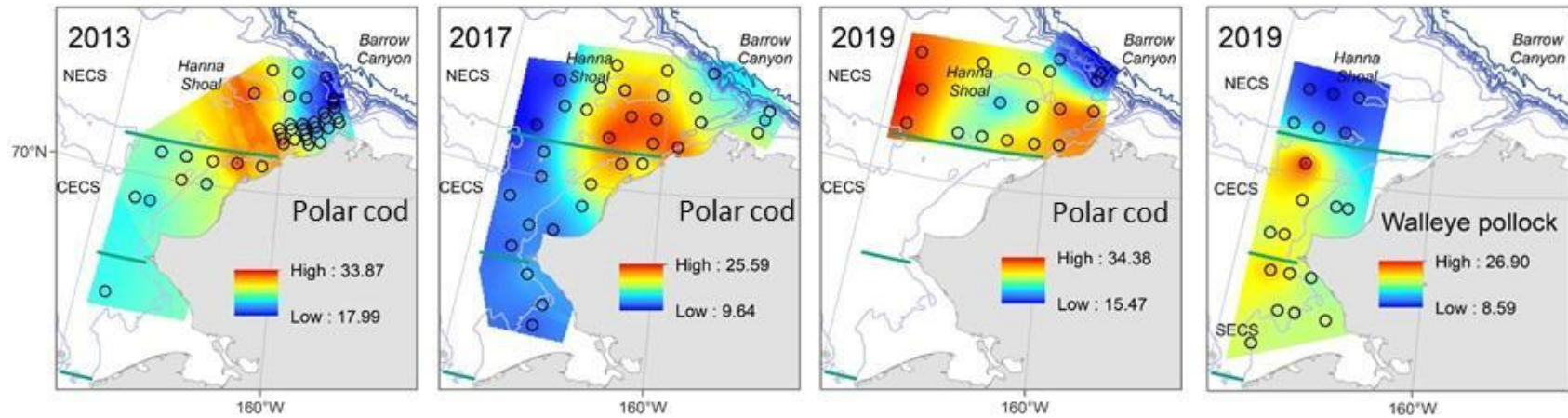
Fig. 7. Annual spatial interpolation maps for the total fatty acids per WWT (mg.g^{-1}) in juvenile polar cod from 2013, 2017 and 2019 as well as juvenile walleye pollock in 2019. Fish were collected on eastern Chukchi Sea Ecosystem surveys with data sources and cruise details as in Table 1.

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