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Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic–Boreal interface: an experimental laboratory approach

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ABSTRACT: Climate change impacts on Arctic fish communities will largely be determined by temperature-dependent vital metabolic rates of resident and invading species. In this study, we experimentally measured total lipids and lipid class storage in the liver and muscle of 2 juvenile Arctic gadids (Arctic cod *Boreogadus saida* and saffron cod *Eleginus gracilis*) and 2 juvenile boreal gadids (walleye pollock *Gadus chalcogrammus* and Pacific cod *Gadus macrocephalus*). Experiments were conducted over a 4 wk period across 5 temperatures (0, 5, 9, 16 and 20°C) at the Hatfield Marine Science Center in Newport, OR, USA. Results indicated clear species-specific non-linear effects of temperature on lipid accumulation. Arctic cod demonstrated a cold-water, stenothermic response with relatively high lipid storage (28 mg lipid g^{-1} WWT) and growth at 0°C. In contrast, saffron cod demonstrated a warmer-water, eurythermic response with elevated growth at temperatures beyond 16°C but comparatively low lipid storage across all thermal habitats (10 to 17 mg lipid g^{-1} WWT). Lipid storage and growth in the boreal species was dome-shaped and notably higher at intermediate temperatures (maximum lipid values of 44 mg lipid g^{-1} WWT for walleye pollock, 28 mg lipid g^{-1} WWT for Pacific cod). Further, the combined effects of temperature on both growth and lipid storage led to elevated lipid accumulation rate (LAR) indices in boreal species (4 to 11) compared to Arctic species (<3) at temperatures above 4°C. These results suggest that warming in the Arctic will lead to decreased condition in the resident mid-trophic fish assemblage in the absence of replacement by more boreal-type species shifting poleward.

KEY WORDS: Temperature · Climate change · Arctic-Boreal · Cod · Lipid storage · Condition index

INTRODUCTION

Arctic marine ecosystems are undergoing rapid change as the result of warming and loss of sea ice (Hoegh-Guldberg & Bruno 2010) and will likely experience higher rates of species invasions and species turnover than lower-latitude regions (Cheung et al. 2009). Highly migratory boreal fish species can potentially make rapid shifts poleward and impact Arctic marine food web connections and energy transfer (Smetacek & Nicol 2005, Cheung et al. 2009, Kortsch et al. 2015). Observational data indicate that climate-related shifts in the distribution of temperate and boreal marine fish species are occurring and expected to continue into the near future (Mueter & Litzow 2008, Fossheim et al. 2015, Montero-Serra et al. 2015), but our ability to predict the timing and consequences of such change is limited by a lack of physiological data on both boreal and resident Arctic species. Current models concerning warming in the

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Arctic have emphasized that the extra input of energy will lead to a boreal-type polar region and a warmer, less-productive temperate zone (Hunt et al. 2013, Arrigo & van Dijken 2015, Holt et al. 2016). However, testing and forecasting these predictions will require temperature-dependent bioenergetic data for species residing at the Arctic-Boreal interface.

Fish are poikilotherms, and the degree to which fish populations will respond to changing temperatures depends on their thermal preferenda (i.e. the temperature at which physiological processes are optimal). These physiological processes include a suite of cellular activities that are manifested in fish by way of growth rate, condition and survival. Temperature and food availability are important in determining the energy budget of fish, with energy allocated to growth and basal metabolism and excess energy deposited into energetic storage (i.e. lipids). Whereas growth and metabolic activity can often be characterized in hours to days, energy allocation (i.e. namely lipids) might be manifested in weeks of thermal exposure (Copeman et al. 2013) and go unnoticed or uncharacterized in scientific studies. Both growth and energy allocation represent important adaptations for surviving and persisting in local environments, especially in seasonal systems where food availability is punctuated by high production in the spring and low production during the winter. Therefore, the ability of the fish to both grow and store energy under varying thermal environments has important implications, both on species survival and for the animals that forage on them.

Characterizing the energetic status of fish can be done in numerous ways (e.g. Fulton's *K*, hepatosomatic index) but is most accurately achieved by measuring the amount of lipids in different body tissues. The major lipid classes in fish include triacylglycerols (TAG), sterols (ST) and phospholipids (PL). TAG is generally considered as the major storage lipid class in fish, while PL and ST are important in regulating cellular membrane fluidity (Parrish 1988). However, PL is also important as an energy source for low-lipid juvenile gadids as well as for marine eggs and larvae (Copeman et al. 2008, Laurel et al. 2010). Elevation in either the absolute amounts of total lipid or the relative proportion of storage lipid (TAG) to membrane lipid (ST) have previously been used to indicate improved energetic condition in multiple species of cold-water larval and juvenile fish (Lochmann et al. 1995, Amara et al. 2007, Copeman & Laurel 2010).

The liver is considered to be a primary energetic storage region in fish, most notably in gadids, because the liver is larger in size relative to the rest of the body (hepatosomatic index [HSI]) when compared to other species (Jobling et al. 1998, Kjesbu et al. 2014). The HSI of gadids is relatively low until juveniles achieve a weight of 1 g (60 mm standard length [SL]), after which it becomes relatively isometric and is often used as a condition index in fisheries ecology (Grant & Brown 1999, Kjesbu et al. 2014). The summer growth potential of gadids in the Arctic is much lower than that of gadids in the Bering Sea and Gulf of Alaska. This results in smaller size-at-age for gadids going into their 1st overwintering period in Arctic regions at <1 g (saffron and Arctic cod; Copeman et al. 2016, Helser et al. 2017) versus 1 to 5 g in the Bering Sea (walleye pollock and saffron cod; Siddon et al. 2013a, Copeman et al. 2016) versus >10 g in the Gulf of Alaska (Pacific cod and walleye pollock; Heintz & Vollenweider 2010, Laurel et al. 2007b).

Younger age classes of marine fish from the family Gadidae serve an important energetic link between plankton and upper trophic level animals (Craig et al. 1982, Sekerak 1982, Welch et al. 1992). Although typically lower in energetic density compared to other pelagic schooling fish (e.g. Clupeids and Osmerids), the energetic value of juvenile gadids can vary tremendously within and among species (Copeman et al. 2008, 2016, Heintz et al. 2013) to the point that general taxonomic characterizations are unreliable (Anthony et al. 2000). Across the lifespan of the individual, energetic density will change predictably with ontogeny and reproductive status (Jorgensen & Fiksen 2006) as well as seasonally (Vollenweider et al. 2011, Kooka & Yamamura 2012). However, variance within an ontogenetic stage is more poorly understood. Energy density is especially important during the pelagic juvenile phase when gadids are important forage fish to nesting seabirds and piscivorous fish species (Gaston & Hipfner 1998, Whitehouse et al. 2014). In addition, the amount of energetic stores during the juvenile phase determine overwintering survival and regulate recruitment dynamics in important gadid fisheries (Heintz et al. 2013, Siddon et al. 2013a).

In Alaskan waters, there are 4 ecologically important species of gadids. These include Arctic cod *Boreogadus saida* and saffron cod *Eleginus gracilis* in the Chukchi and Beaufort Seas (hereon referred to as 'Arctic gadids') and walleye pollock *Gadus chalcogrammus* and Pacific cod *Gadus macrocephalus* in the Bering Sea and Gulf of Alaska (hereon referred to as 'boreal gadids'). As adults, these species use a variety of habitats. Arctic cod and walleye pollock are more pelagic and remain in the offshore region for much of their life history, whereas saffron cod and Pacific cod are more demersal and are commonly found in both the nearshore and offshore regions, respectively (Laurel et al. 2007b, Hurst et al. 2015, Logerwell et al. 2015). However, during the juvenile phase, all 4 species use pelagic habitats and serve as important energetic links between the plankton and upper trophic level species in the spring and summer (Frost & Lowry 1981, Craig et al. 1982, Springer et al. 1996). Small-bodied pelagic fish species are already well-recognized as being important biological indicators of climate-driven changes by way of temperature-dependent effects on growth (Peck et al. 2013). However, no studies to date have directly examined how warming will impact the lipid content of these fish under similar climate scenarios.

In this study, we experimentally measure the temperature-dependent lipid allocation in 2 juvenile Arctic gadids and 2 juvenile boreal gadid species. Using standardized husbandry protocols, we examine (1) whether environmental regulation of lipid allocation is similar within and among related species from boreal and Arctic regions and (2) how modest warming scenarios could impact the quality of mid-trophic fish assemblages at the Pacific-Arctic interface. These data will be useful in predicting how living marine resources, particularly in the Arctic, will respond to climate change scenarios.

MATERIALS AND METHODS

Temperature-growth rate experimental methodology has been previously described in detail by Laurel et al. (2016). Briefly, laboratory experiments were conducted at the NOAA, Alaska Fisheries Science Center's Arctic Laboratory at the Hatfield Marine Science Center in Newport, Oregon, USA. Live juvenile fish ranging in size between 20 and 85 mm SL were collected by either fyke net (Arctic and saffron cod, Beaufort Sea, 70.383° N, 148.552° W), beach seine (Pacific cod, Gulf of Alaska, 57.882° N, 152.626° W), or light and lift net (walleye pollock, Puget Sound, 48.135° N, 122.760° W) and shipped to Newport, Oregon, during the spring and summer of 2012 (Table 1). Fish were held in the laboratory at 6 to 8°C for a period of 2 to 3 mo and fed a combination of thawed krill and herring for the first 3 wk of captivity. At Week 4, fish were gradually weaned onto a 'gel diet' that would be used for each of the growth experiments (see below for details).

Growth experiments on all 4 species were conducted on similarly sized juveniles (weights ranged from 3 to 9 g across all species; see lengths in Table 1) in a series of experimental tanks (66 × 46 × 38 cm) supplied with flow-through, temperature-controlled seawater. All fish were initially measured and stocked into experimental tanks at a density of 4 individuals per tank. Small size differences among individual fish (2 to 4 mm in SL) within each tank were purposefully established in lieu of marking individuals to track individual growth (Hurst et al. 2012). After establishment of experimental groups, temperatures were adjusted to treatment temperatures (0, 5, 9, and 16°C) at a rate of 1.5°C d^{-1}. This temperature range was chosen to reflect the variation in summer temperatures ranging from cold offshore Arctic regions (0 to 2°C, Crawford et al. 2012) to nearshore shallow boreal and Arctic habitats (>14°C; Craig et al. 1982, Hurst et al. 2010). Replicate tanks (n = 2) of each temperature treatment (n = 4) were assigned for each species (n = 4) to comprise a total of 32 tanks. Fish were allowed to acclimate an additional 2 wk in the experimental tanks, after which fish were weighed to the nearest 0.01 g (wet weight mass [WWT]) and measured to the nearest 1 mm (SL) to

Table 1. Region of collection, length range-at-capture (SL, mm), length range used for the growth experiment, and length range of gadid fish used for lipid analyses

Species	Region of capture	Latitude Longitude	Length at capture (mm SL)	Length at start of growth experiment (mm SL)	Length at time of lipid sampling (mm SL)
Arctic cod *Boreogadus saida*	Beaufort Sea (Prudhoe Bay, AK)	70.383° N 148.552° W	70–85	81–125	85–135
Saffron cod *Eleginus gracilis*	Beaufort Sea (Prudhoe Bay, AK)	70.383° N 148.552° W	70–85	86–123	93–155
Pacific cod *Gadus macrocephalus*	Gulf of Alaska (Kodiak, AK)	57.882° N 152.626° W	50–60	69–107	92–155
Walleye pollock *Gadus chalcogramma*	Puget Sound (Port Townsend, WA)	48.135° N 122.760° W	20–30	60–91	62–116

establish 'Time 0' and again at 2 wk and 4 wk to determine growth rates (Laurel et al. 2016). Fish were fed daily to satiation using a combination of thawed krill and a gelatinized combination of squid, krill, herring, commercial fish food, amino acid supplements and vitamins ('gel food'; recipe and lipid content as in the control diet details from Copeman et al. 2013). Lights were maintained on a 12 h light:12 h dark photoperiod for all experiments. Tanks were checked daily for mortalities, and dead fish were removed, weighed and measured. At the end of the experiment, an additional 20°C trial was conducted for species able to survive and maintain growth at 16°C. Specific growth rates (SGR) based on the mass of juvenile fish were determined using the following equations: $\text{SGR} = 100 - (e^{g} - 1)$ as in Laurel et al. (2016). Here, g is the instantaneous growth coefficient obtained by the equation $g = (\ln \text{WWT}_i - \ln \text{WWT}_0)/(t_i - t_0)$ where WWT_i is the wet weight of an individual fish at time t_i. At the end of the 4 wk experiment, all fish (n = 6 to n = 8 per temperature) were frozen (−80°C) for subsequent lipid analyses. All lipid analyses were done within 3 mo of the end of the laboratory experiment.

At the time of lipid sampling, fish whole bodies were weighed (WWT, 0.1 mg) and measured for SL (0.1 mm). Fish were then dissected on ice and the liver was removed and weighed for lipid sampling. Further, fish heads were removed and preserved for temperature-dependent growth studies using otoliths. Internal organs and digestive tracks were removed and remaining muscle tissues were then reweighed in order to calculate total muscle lipids. Muscle tissue was sampled by first removing the skin above the anus up to the dorsal margin and then dissecting a 300 mg portion of muscle along the dorsal margin. Liver lipid samples were taken by dissecting a 100 mg portion of tissue from random sites within the organ. A hepatosomatic index was calculated using the following equation: $\text{HSI} = (H/M) \times 100$, where H is the liver mass (0.1 mg), and M is the total wet mass (0.1 mg). Tissue samples of muscle and liver were immediately placed in chloroform under nitrogen at −20°C for later extraction and lipid class analyses, within 2 mo of sampling.

Lipid extraction and analysis

Tissues were homogenized in chloroform and methanol, and total lipids were extracted according to Parrish (1987) using a modified Folch procedure (Folch et al. 1956). Lipid classes were determined using thin layer chromatography with flame ionization detection (TLC/FID) with a MARK V Iatroscan (Iatron Labratories, Tokyo) and modified from those methods described by Lu et al. (2008). Extracts were spotted on duplicate silica gel-coated Chromarods, and a 3-stage development system was used to separate lipid classes (lipid classes quantified were wax esters, triacylglyerols, free fatty acids, sterols and polar lipid, as in Copeman et al. 2016). Following the last development, rods were scanned using Peak Simple software (ver. 3.67, SRI), and the signal detected in millivolts was quantified using lipid standards (Sigma, St Louis, MO). A specific triacylglycerol standard was purified from walleye pollock liver using column chromatography following the methods of Miller et al. (1998) with the addition of a final elution of 15 ml of hexane:diethyl ether:formic acid solution (80:20:0.1) as in Copeman et al. (2016). Lipid classes were expressed both in relative (% of total lipids) and absolute amounts (lipid per WWT, mg g^{-1}).

Data analysis

Temperature-dependent models for liver lipid storage, total body lipid storage and condition indices, as well as lipid accumulation rate (LAR) indices were constructed using best fit models limited to 3 parameters in Sigma Plot 12.5. The relationship between whole body total lipid (TL) storage (mg g^{-1}) and SGR was examined on individual fish using both linear and non-linear (2 parameter) best fit models. Tank replicates were used as the level of observation for models of temperature-dependent lipid storage and condition. Two-way ANOVAs (Minitab general linear model ver. 16) were used to determine statistical differences among species and temperature for each lipid parameter.

RESULTS

Mortality occurred only in the highest temperature treatments (16 and 20°C) for all gadids. As reported in Laurel et al. (2016), Arctic cod were visibly stressed after 2 wk of exposure to 16°C, suggesting that such conditions can only be tolerated for short periods of time, and mortality (n = 3) was observed at 2 wk after Time 0. For this reason, Arctic cod were not analyzed for lipids at the 16°C and higher temperature treatments. In the 20°C treatment, Pacific cod mortality started 2 wk past Time 0, with only 3 fish surviving through the end of the experiment.

The 20°C treatment for walleye pollock was discontinued after the first growth measurement (Week 2) due to mortalities shortly after acclimation (n = 2 in Week 1 and n = 2 just after Week 2).

Muscle lipids

Compared to liver tissue, muscle tissue accounted for the majority of the body mass (~70%) in these small juvenile fish. Further, muscle tissue was characterized by high proportions of polar lipid (~90% phospholipids, PL), a low percentage of storage lipid (triacylglycerols, TAG), and relatively stable total lipid (TL) content both between species and with variable temperatures (Fig. 1, Table 2). At temperatures ≤9°C, there was a significant interactive effect of temperature and species on the TL (mg lipid g^{-1} WWT) content of the muscle tissue (ANOVA, $F_{6,23}$ = 5.78, p = 0.005). Arctic cod had significantly higher TLs in their muscle tissues than all other gadids, at both 0 and 9°C (see Table 2a, and pooled temperatures Fig. 1a; ANOVA, $F_{3,20}$ = 6.11, p = 0.004). Similarly, at temperatures ≥16°C (which Arctic cod did not survive), there was no significant effect of species (ANOVA, $F_{2,11}$ = 0.96, p = 0.43) or temperature (ANOVA, $F_{1,11}$ = 1.49, p = 0.27) on the TL in the muscle (Table 2a). The proportion of TAG in muscle lipids showed an interactive effect of species and temperature (ANOVA, $F_{6,23}$ = 3.47, p = 0.03, Table 2a). Generally, proportions of TAG in muscle tissues were elevated in Arctic cod relative to all other species at low temperatures whereas saffron cod had the lowest proportions of TAG (Fig. 1b). This pattern changed for saffron cod at the highest temperature (20°C), when saffron cod had greater TAG than the other 2 boreal species (Table 2a). At temperatures ≤9°C, the proportions of free fatty acid (FFA) in fish muscle was significantly affected by species (ANOVA, $F_{3,23}$ = 70.15, p < 0.001) but not by temperature. FFA proportions were highest in boreal species with walleye pollock significantly elevated (12.7%) compared to Pacific cod (7.6%), and the 2 Arctic species had significantly lower proportions that ranged from 1.0 to 1.2% (Table 2a). Sterols (ST) in fish muscle at temperatures ≤9°C were significantly affected by species (ANOVA, $F_{3,23}$ = 28.94, p < 0.001) but not by temperature. Arctic cod had much lower proportions of ST (~4.9%) than seen in the other gadid species (~10%). At temperatures ≥ 16°C, there was a significant interaction between species and temperature (ANOVA, $F_{2,11}$ = 5.35, p < 0.05) with elevated proportions of ST at 20°C in boreal species but not at 16°C. Lastly, there was as significant interaction between temperature and species (ANOVA, $F_{6,23}$ = 5.98, p = 0.004) on the proportions of PL in muscle tissues of juvenile gadids. PL values in all gadids at all temperatures ranged from 60 to 83% of TL (Table 2). Absolute values of PL (mg lipid g^{-1} WWT) were significantly elevated in Arctic cod compared to the other gadid species (Fig. 1c, averaged across temperatures).

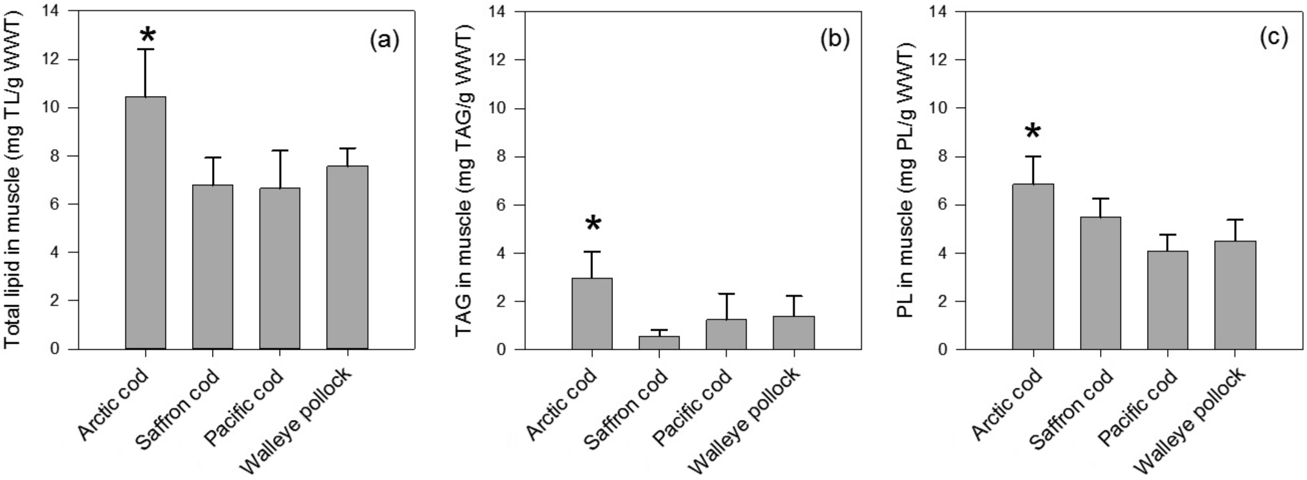

Fig. 1. Lipid class composition of 4 species of marine juvenile gadids: Arctic cod *Boreogadus saida*, saffron cod *Eleginus gracilis*, Pacific cod *Gadus macrocephalus* and walleye pollock *Gadus chalcogrammus*. (a) Density of total lipid (TL) in the muscle (mg TL g^{-1} WWT), (b) density of triacylglycerols (TAG) in the muscle (mg TAG g^{-1} WWT), (c) density of polar lipid (PL) in the muscle (mg PL g^{-1} WWT). There was no significant effect of temperature on muscle lipids, and therefore, bars represent the mean of all tanks averaged across all temperatures for a given species (n = 6 to 10 tank means per species; duplicate tanks per temperature, 3 to 5 temperatures depending on the species thermal limits). *Significant difference between species with (a) TL, ANOVA, $F_{3,32}$ = 9.34, p < 0.001; (b) TAG, ANOVA, $F_{3,32}$ = 9.46, p < 0.001; and (c) PL, ANOVA, $F_{3,32}$ = 11.21 , p < 0.001)

Table 2. Total lipid (mg lipid g^{-1} WWT tissue) and percentage lipid class composition in (a) muscle and (b) liver of 4 species of juvenile gadids reared at 5 temperatures. AC: Arctic cod *Boreogadus saida*; SC: saffron cod *Eleginus gracilis*; PC: Pacific cod *Gadus microcephalus*; WP: walleye pollock; TL: total lipid; TAG: triacylglycerols; FFA: free fatty acids; ST: sterols; PL: polar lipids. Dash indicates that fish were not analyzed at temperatures >9°C due to elevated mortality in treatment tanks. Treatment values represent means of 6 to 8 fish except at temperatures >9°C where sample sizes dropped due to mortality (n = 4 to 7)

Temp	Species	TL (mg g^{-1})	% TAG	% FFA	% ST	% PL
(a) Muscle						
0°C	AC	11.5 ± 0.6	24.5 ± 2.4	1.0 ± 0.2	4.8 ± 0.3	69.6 ± 2.3
	SC	8.3 ± 1.2	9.7 ± 2.2	1.6 ± 0.3	9.7 ± 0.8	79.0 ± 2.3
	PC	6.3 ± 0.4	10.9 ± 2.4	7.4 ± 0.5	9.6 ± 0.5	71.9 ± 2.1
	WP	7.4 ± 0.7	17.9 ± 4.9	14.4 ± 1.4	10.1 ± 1.4	56.9 ± 3.2
5°C	AC	8.2 ± 1.0	24.1 ± 3.1	0.9 ± 0.3	5.8 ± 0.8	68.8 ± 3.3
	SC	6.8 ± 0.5	5.8 ± 2.0	1.4 ± 0.2	9.1 ± 0.8	83.7 ± 1.7
	PC	9.4 ± 0.9	30.6 ± 3.6	7.0 ± 1.0	7.8 ± 0.5	54.4 ± 3.3
	WP	8.3 ± 1.0	23.7 ± 3.9	13.1 ± 0.8	10.6 ± 1.7	52.3 ± 2.5
9°C	AC	11.6 ± 0.7	34.2 ± 4.3	1.0 ± 0.2	4.0 ± 0.3	60.6 ± 4.2
	SC	5.4 ± 0.4	5.5 ± 1.3	0.6 ± 0.2	12.6 ± 1.6	81.1 ± 1.7
	PC	5.6 ± 0.5	17.0 ± 2.1	8.4 ± 0.5	9.8 ± 0.6	64.8 ± 1.6
	WP	7.9 ± 0.5	25.0 ± 4.9	10.5 ± 1.2	10.5 ± 1.2	54.0 ± 2.8
16°C	AC	–	–	–	–	–
	SC	6.2 ± 1.6	7.5 ± 1.9	0.6 ± 0.2	11.7 ± 1.4	80.1 ± 2.5
	PC	5.6 ± 0.7	19.5 ± 5.7	5.5 ± 0.4	11.4 ± 1.3	63.6 ± 4.3
	WP	6.4 ± 0.6	20.6 ± 4.0	8.8 ± 0.4	9.9 ± 0.6	60.7 ± 3.2
20°C	AC	–	–	–	–	–
	SC	7.4 ± 0.4	10.6 ± 4.0	2.4 ± 0.3	7.7 ± 0.6	79.3 ± 3.4
	PC	5.9 ± 0.4	1.4 ± 1.4	19.2 ± 4.6	15.5 ± 2.1	62.4 ± 5.4
	WP[a]	8.0 ± 0.4	0.7 ± 0.4	12.1 ± 1.2	11.7 ± 0.6	75.5 ± 1.9
(b) Liver						
0°C	AC	310.5 ± 25.8	89.8 ± 1.8	0.4 ± 0.3	0.5 ± 0.1	9.3 ± 1.7
	SC	126.3 ± 33.4	67.3 ± 6.7	4.8 ± 1.0	2.0 ± 0.6	25.7 ± 5.6
	PC	204.8 ± 46.2	61.8 ± 13.3	6.6 ± 3.1	1.9 ± 1.5	29.7 ± 9.2
	WP	272.0 ± 53.1	65.7 ± 5.2	13.0 ± 1.1	2.7 ± 0.5	18.6 ± 4.3
5°C	AC	342.6 ± 24.4	90.9 ± 11.1	1.5 ± 0.4	0.6 ± 0.3	7.0 ± 0.8
	SC	119.4 ± 25.0	67.3 ± 6.6	5.0 ± 0.7	1.9 ± 0.5	25.8 ± 5.9
	PC	415.8 ± 26.7	81.4 ± 0.5	2.4 ± 0.5	0.3 ± 0.1	15.9 ± 0.8
	WP	420.8 ± 44.7	80.4 ± 1.9	5.5 ± 0.8	1.7 ± 0.4	12.2 ± 1.9
9°C	AC	305.7 ± 17.3	85.5 ± 8.1	1.4 ± 0.3	0.9 ± 0.8	11.7 ± 7.5
	SC	142.5 ± 31.1	69.3 ± 2.6	3.0 ± 0.5	2.3 ± 0.8	25.3 ± 2.1
	PC	395.3 ± 20.9	80.8 ± 2.5	2.3 ± 0.4	0.3 ± 0.1	16.4 ± 2.3
	WP	486.2 ± 41.1	78.0 ± 3.9	3.5 ± 0.9	1.2 ± 0.2	17.2 ± 3.0
16°C	AC	–	–	–	–	–
	SC	294.1 ± 54.9	74.9 ± 2.9	3.0 ± 0.3	1.1 ± 0.2	20.9 ± 3.1
	PC	360.4 ± 60.8	78.1 ± 5.6	1.5 ± 0.1	0.7 ± 0.3	19.6 ± 5.1
	WP	530.9 ± 41.8	82.7 ± 3.2	2.8 ± 0.9	0.6 ± 0.3	14.0 ± 3.5
20°C	AC	–	–	–	–	–
	SC	355.3 ± 89.6	62.4 ± 5.1	3.8 ± 0.6	0.9 ± 0.4	32.4 ± 6.1
	PC	89.1 ± 33.0	59.0 ± 20.2	15.6 ± 10.8	6.7 ± 3.6	18.6 ± 6.5
	WP[a]	307.3 ± 49.9	84.0 ± 3.2	6.3 ± 1.4	2.0 ± 0.4	7.6 ± 1.8

[a] WP were sampled after only 2 wk of the growth experiment at 20°C

Liver lipids

For all species examined, liver tissue accounted for on average only 4 % of the wet weight, and liver lipids were much denser and showed higher variability with temperature and species than muscle lipids. The TL (mg lipid g^{-1} WWT) in gadid livers as well as the proportional (%) lipid class composition for all species at all temperature combinations is shown in Table 2b. Clearly, TLs in gadid livers (mg lipid g^{-1} WWT) were significantly affected by the interaction of species and temperature (Fig. 2a, Table 2b). Both boreal species demonstrated a Gaussian peak relationship between both TL storage (Fig. 2a) and TAG storage (Fig. 2b) with temperature. This significant relationship (Pacific cod r^2 = 0.84, walleye pollock $r^2 \geq 0.85$; Table 3) had maximum lipid storage values at mid temperature ranges and minimum lipid values at cold and warm extremes. Both TL and TAG showed maximum values for Pacific cod at ~9°C, while walleye pollock had maximum liver lipid storage at ~11.5°C. Saffron cod had a very different relationship between liver lipid storage and temperature that was best described by a quadratic relationship (TL r^2 = 0.97, TAG r^2 = 0.89). Highest levels of TL and TAG (mg lipid g^{-1} WWT) were measured in the liver at 20°C (Fig. 2, Table 3). Arctic cod liver storage did not vary statistically between 0 and 9°C (Table 2, Fig. 2 where the line is just for visual purposes).

At 0°C, elevated lipid storage in the liver (mg lipid g^{-1} WWT) of Arctic cod relative to the other gadids was associated with elevated proportions of TAG (~90 %) and low proportions of the other lipid classes, FFA, ST and PL (∑ ~ 10 %; Table 2b). However, maximum liver lipid densities in boreal species were higher (531 mg lipid g^{-1} WWT in walleye pollock and 416 mg lipid g^{-1} WWT in Pacific cod) than those seen in Arctic species (maximum values of ~350 mg lipid g^{-1} WWT at 5°C and 20°C for Arctic cod and saffron cod, respectively; Fig. 2). Relationships between TLs and TAG densities with temperature were basically identical. This indicates that lipid storage in the liver is largely driven by the accumulation or depletion of TAG.

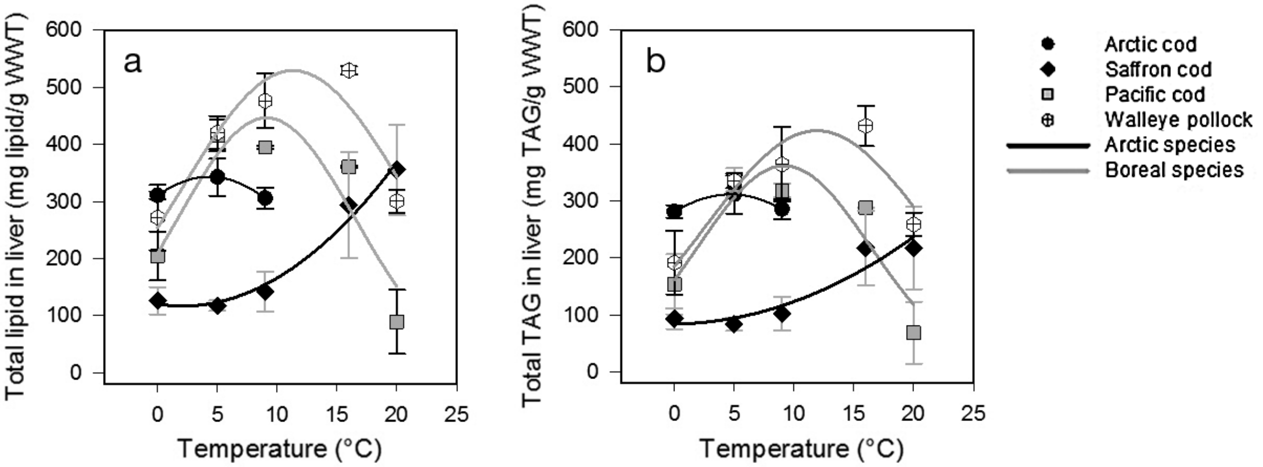

Fig. 2. Temperature-dependent lipid storage as (a) total lipids and (b) total triacylglycerols (TAG) in the liver of the 4 species of juvenile gadids. Values (as mg g^{-1} liver WWT) represent the mean values of duplicate tanks (n = 2) with 4 individuals per tank. Arctic cod showed too few points to statistically define the relationship, and therefore, the line is just used to visually illustrate the lipid density in this species relative to 3 other gadids. Model parameters are given in Table 3

Table 3. Parameters for the relationship between the density (mg lipid g^{-1} WWT) of (a) total lipids (TL) in the liver and (b) triacyglycerols (TAG) per WWT in the liver relative to culture temperature for 4 species of juvenile gadids. Boreal species (Pacific cod and walleye pollock) were described by the 3 parameter Gaussian peak relationship. Here, Y refers to the lipid density, a is the maximum fish lipid density (mg g^{-1}), T_0 is the temperature at which the slope is zero or the maximum peak in lipid density (°C), T_i is the temperature of a given treatment (°C), and b is the width of the lipid density peak (°C). A non-linear quadratic equation was used to explain the positive relationship between saffron cod lipid storage and culture temperature; here, Y refers to the total lipid or TAG density in fish livers, Y_0 is the lipid density at 0°C, a and b are constants, and T_i is the temperature of a given treatment (°C)

Gaussian peak relationship $Y = a \cdot \exp\{-0.5 \cdot [(T_i - T_0)/b]^2\}$

	a	T_0	b	r^2
Pacific cod TL in liver (Fig. 2a)	446.63 ± 65.88	9.11 ± 1.26	7.40 ± 1.45	0.84
Pacific cod TAG in liver (Fig. 2b)	361.70 ± 54.44	9.18 ± 1.24	7.22 ± 1.24	0.84
Walleye pollock TL in liver (Fig. 2a)	529.30 ± 50.83	11.32 ± 0.98	9.34 ± 1.57	0.85
Walleye pollock TAG in liver (Fig. 2b)	423.25 ± 41.81	11.92 ± 1.02	9.26 ± 1.62	0.86

Quadratic relationship $Y = Y_0 + (a \cdot T_i) + (b \cdot T_i^2)$

	a	Y_0	b	r^2
Saffron cod TL in liver (Fig. 2a)	−3.29 ± 5.30	120.37 ± 21.55	0.78 ± 0.25	0.97
Saffron cod TAG in liver (Fig. 2b)	0.21± 7.36	84.42 ± 29.93	0.37 ± 0.35	0.89

Condition indices

The hepatosomatic index (HSI), the ratio of TLs in the liver (mg):TLs in the muscle (mg), and the density of TLs in the combined muscle and liver (mg g^{-1}) were used as indicators of animal condition. Generally, all 3 indices showed similar patterns to each other (Fig. 3) and to the trends that were previously described for liver lipid content (Fig. 2). For both boreal species, all the condition indices were described using a Gaussian peak relationship. The peak temperature at which maximum condition values were observed for Pacific cod ranged from 8.6°C (TL in the combined muscle and liver, mg lipid g^{-1} WWT, $r^2 = 0.88$; Fig. 3c) to 10.0°C (liver to muscle ratio, $r^2 = 0.95$; Fig. 3b). Walleye pollock had maximum condition indices at higher temperatures that ranged from 12.1°C (TL in combined muscle and liver, mg lipid g^{-1} WWT, $r^2 = 0.91$; Fig. 3c) to 13.3°C (liver to muscle ratio, $r^2 = 0.86$; Fig. 3b).

Arctic cod had elevated condition indices at 0°C (Fig. 3), but with increased temperatures up to 9°C, we observed a decrease in their condition relative to trends for the other 2 boreal gadid species. This elevated condition at low temperatures was apparent in the HSI and total lipids in muscle and liver combined (mg g^{-1}) but not in the liver:muscle lipid ratio. Saffron cod had the lowest condition value among both

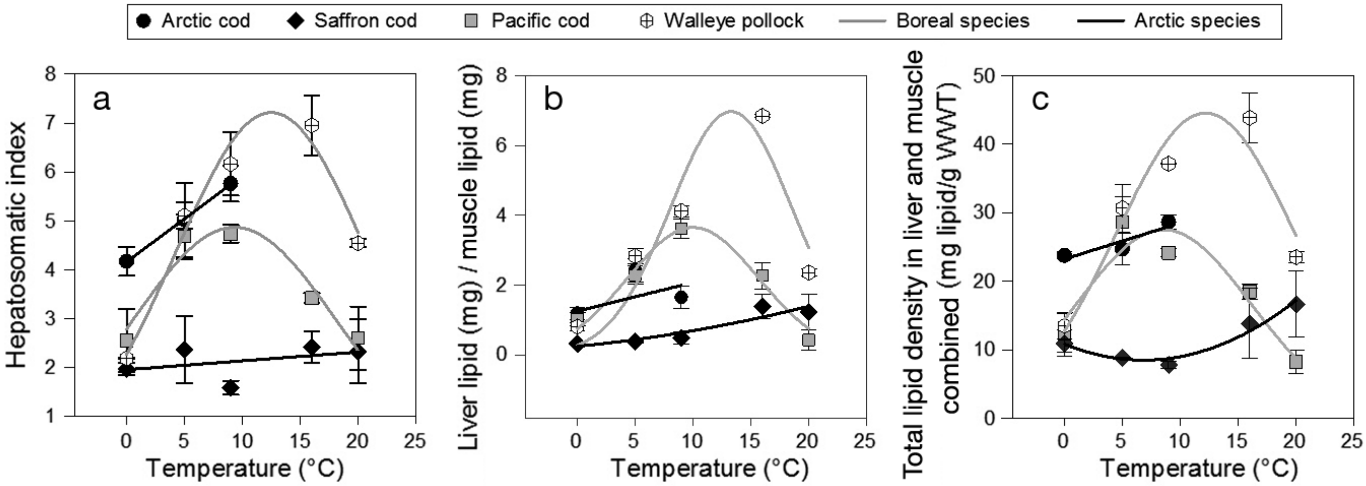

Fig. 3. Temperature-dependent condition indices of the 4 species of juvenile gadids. Values represent the mean values of duplicate tanks (n = 2) with 4 individuals per tank. (a) Hepatosomatic index, (b) total liver lipids (mg):total muscle lipids (mg), and (c) total lipid in the liver and muscle combined (mg lipid g^{-1} WWT). Model parameters are given in Table 4

the Arctic and boreal gadids. The effect of temperature on saffron cod condition was also relatively minor, with the exception of 20°C, where saffron cod increased in condition but the other gadids showed a significant decrease in condition (Fig. 3c). The effects of temperature on saffron cod condition were positive up to 20°C, based on both liver to muscle lipids ($r^2 = 0.86$) and TL density in liver and muscle ($r^2 = 0.95$; Table 4). There was a very weak relationship between temperature and HSI in saffron cod ($r^2 =$

Table 4. Parameters for the relationship between the condition indices and culture temperature in 4 species of juvenile gadids. Boreal species (Pacific cod and walleye pollock) were described by a 3 parameter Gaussian peak relationship. Here, Y refers to a condition index, a is the maximum fish condition, T_0 is the temperature at which the slope is zero or the maximum peak in condition (°C), T_i is the temperature of a given treatment (°C), and b is the width of the condition peak in °C. A non-linear quadratic equation was used to explain the positive relationship between saffron cod condition and culture temperature; here, Y refers to a condition index, Y_0 is the condition at 0°C, a and b are constants, and T_i is the temperature of a given treatment. A linear relationship was used to explain the relationship between Arctic cod condition and temperature; here, Y refers to a condition index, Y_0 is the condition index at 0°C, c is the slope of the line, and T_i is the temperature of a given treatment (°C)

Gaussian peak relationship $Y = a \cdot \exp\{-0.5 \cdot [(T_i - T_0)/b]^2\}$

	a	T_0	b	r^2
Pacific cod HIS, (Fig. 3a)	4.87 ± 0.32	9.33 ± 0.68	8.85 ± 0.96	0.93
Pacific cod liver:muscle (Fig. 3b)	3.65 ± 0.34	10.00 ± 0.55	5.63 ± 0.56	0.95
Pacific cod TL density in liver and muscle (Fig. 3c)	27.50 ± 3.32	8.57 ± 1.10	7.54 ± 1.25	0.88
Walleye pollock HIS (Fig. 3a)	7.22 ± 0.44	12.50 ± 0.53	8.23 ± 0.78	0.96
Walleye pollock liver:muscle (Fig. 3b)	6.97 ± 1.44	13.30 ± 0.88	5.23 ± 1.14	0.86
Walleye pollock TL density in liver and muscle (Fig. 3c)	44.52 ± 4.44	12.19 ± 0.77	7.71 ± 1.09	0.91

Quadratic relationship $Y = Y_0 + (a \cdot T_i) + (b \cdot T_i^2)$

	a	Y_0	b	r^2
Saffron cod liver:muscle (Fig. 3b)	0.032 ± 0.06	0.24 ± 0.25	0.001 ± 0.003	0.86
Saffron cod TL density in liver and muscle (Fig. 3c)	−0.7 ± 0.3	10.8 ± 1.1	0.05 ± 0.01	0.95

Linear relationship $Y = Y_0 + (c \cdot T_i)$

	Y_0	c		r^2
Arctic cod HSI (Fig. 3a)	4.16 ± 0.03	0.18 ± 0.00		0.99
Arctic cod liver:muscle (Fig. 3b)	1.25 ± 0.50	0.08 ± 0.10		0.27
Arctic cod TL density in liver and muscle (Fig. 3c)	23.22 ± 1.31	0.52 ± 0.22		0.85
Saffron cod HSI (Fig. 3a)	1.96 ± 0.28	0.02 ± 0.02		0.17

0.17; Fig. 3a). The relationship between temperature and condition in Arctic cod was described using a simple linear relationship. This relationship was stronger for HSI ($r^2 = 0.99$) and TL density in liver and muscle ($r^2 = 0.85$) than in the liver to muscle ratio ($r^2 = 0.27$; Fig. 3, Table 4).

Specific growth rate and lipid storage

Boreal species showed a significant positive relationship between combined muscle and liver lipid density (mg lipid g^{-1} WWT) and specific growth rate (SGR, % d^{-1}) (Fig. 4). In contrast, there was no relationship between SGR and TLs in Arctic species. Higher SGRs and TL storage were noted in walleye pollock with warmer temperatures up to 16°C ($r^2 = 0.50$); however, increased variability was observed in TL storage and growth at 20°C. Similarly, Pacific cod showed elevated TL storage with increased SGRs up to 9°C but lower TL and SGR at 16°C ($r^2 = 0.48$).

Lipid accumulation rate

The lipid accumulation rate (LAR) index incorporates changes in individual fish SGR and lipid density as a function of temperature. LAR index is an indicator of the ability of juvenile fish to accumulate lipid over time (% lipid in the liver and muscle combined × specific growth rate). Here, we show the model extrapolated to −2°C and finishing at the maximum species-specific temperature at which we did not observe excessive mortality. We used Gaussian peak

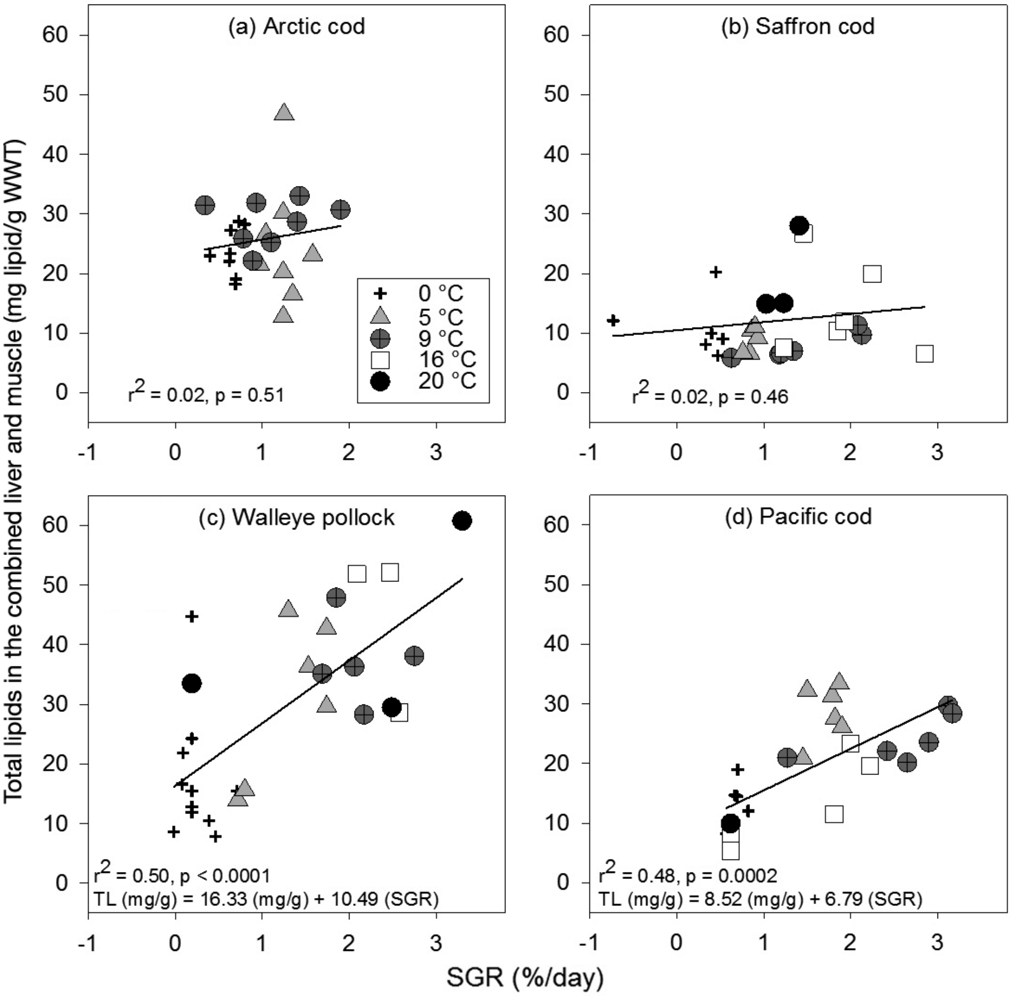

Fig. 4. Relationship between total lipids in the combined liver and muscle (mg lipids g^{-1} WWT) and specific growth rate (SGR, % d^{-1}) for the 4 species of juvenile gadids. Values represent individual fish that were measured for growth and lipid composition at the end of the experiment

relationship models to explain how LAR varied with temperature for both boreal species and for saffron cod, while a linear relationship described Arctic cod (Table 5, Fig. 5). Maximum LAR indices for Pacific cod were observed at 10.0°C (r^2 = 0.97) compared to 14.4°C (r^2 = 0.99) for walleye pollock and 16.2°C (r^2 = 0.97) for saffron cod (Table 5, Fig. 5). The LAR index for Arctic cod was linear up to a maximum value of 9°C. The most apparent differences in these LAR indices among species were in their modeled maxima; with species rank order (highest to lowest) going from walleye pollock (11.6) to Pacific cod (6.8) to Arctic cod (3.4) and saffron cod with very low accumulation indices (2.5). However, these rank orders changed within different thermal ranges. For example, at temperatures <1.3°C, Arctic cod had the highest LAR index compared to other gadids (Fig. 5). Between 1.3 and 6.7°C, Pacific cod and walleye pollock were ranked highest which was then superseded by just walleye pollock under warmer conditions (i.e. 6.7 to 16°C). At the highest temperature range, representing 'estuarine conditions' (>16°C), saffron cod were ranked highest by the fact that they are the only species in the group with the thermal tolerance to survive at such temperatures. However, saffron cod showed very little variation in this index overall despite having the physiology to grow and survive across the broadest range of temperatures.

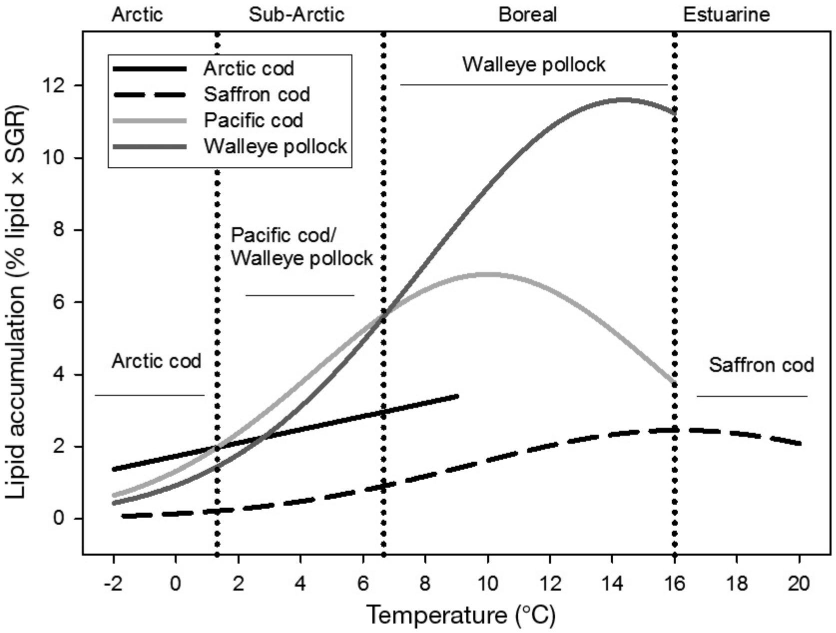

Fig. 5. Temperature-dependent lipid accumulation rate (LAR) index for the 4 species of juvenile gadids. Model parameters are given in Table 5. The species that had the highest LAR in each of the idealized thermal ranges is noted on the figure: Arctic cod in the Arctic range (−2 to 1.3°C), Pacific cod and walleye pollock in the sub-Arctic range (1.3 to 6.7°C), walleye pollock in the boreal range (6.7 to 16°C) and finally saffron cod in the extreme estuarine warm range (>16°C). Late summer thermal habitat transitions are idealized and were defined when the species range order changed

Table 5. Parameters for the relationship between lipid accumulation rate (LAR) index and temperature in 4 species of juvenile gadids. Saffron cod, walleye pollock and Pacific cod were described by a 3 parameter Gaussian peak relationship. Here, Y refers to the LAR, a is the maximum accumulation rate, T_0 is the temperature at which the slope is zero or LAR is maximum (°C), T_i is the temperature of a given treatment (°C), and b is the width of the accumulation peak (°C). For Arctic cod, Y_0 is the LAR index at 0°C, and c is the slope of the line

Gaussian peak relationship $Y = a \cdot \exp\{-0.5 \cdot [(T_i - T_0)/b]^2\}$	a	T_0	b	R^2
Pacific cod LAR (Fig. 5)	6.77 ± 0.69	10.00 ± 0.64	5.53 ± 0.70	0.97
Walleye pollock LAR (Fig. 5)	11.60 ± 0.78	14.37 ± 1.13	6.39 ± 1.10	0.99
Saffron cod LAR (Fig. 5)	2.45 ± 0.18	16.16 ± 0.89	6.73 ± 0.90	0.97

Linear relationship $Y = Y_0 + (c \cdot T_i)$	Y_0	c		R^2
Arctic cod LAR (Fig. 4)	1.73 0.46	0.18 ± 0.07		0.85

DISCUSSION

The results of this study indicate that lipid content is highly variable among gadids and that temperature directly impacts their lipid density in a species-dependent manner. As such, the relative energetic content of forage fish in these regions is poised to change significantly with continued warming, which has implications for both the survival of these species and the piscivorous fish, marine seabirds and mammals that depend on them for forage. We discuss these results in terms of the mechanisms, life-history strategies and ecosystem consequences of variable energetic allocation within and among gadids at the Pacific-Arctic interface.

Species-specific temperature response in lipid allocation: Boreal vs. Arctic

We focused on the 60–120 mm size range of juveniles (Age 1 for Arctic species and Age 0 for boreal species) because this ontogenetic stage represents a phase of development when lipid storage patterns reflect environmental variability that is not confounded by sexual maturity (Mello & Rose 2005). Further, analyzing all gadids at this common size standardized all species to the smallest size at which liver could easily be dissected and organ-specific lipids could be measured (pers. obs.). This size also reflects the stage at which all species transition from a solely copepod-dominated diet to one based on a more diverse assemblage of larger prey (Renaud et al. 2012, Strasburger et al. 2014, Gray et al. 2016). Therefore, the species differences observed in this study most likely reflect species-specific physiology at a common ontogenetic stage and, therefore, some index of fitness under variable thermal environments. At 60–120 mm, juvenile gadids can be highly variable in lipid content in the late summer and early fall (Grant & Brown 1999, Copeman et al. 2008, Heintz et al. 2013, Copeman et al. 2016). Such variability has obvious implications for upper trophic level predators but can also have implications for overwintering survival and recruitment dynamics within fish populations (Heintz et al. 2013, Siddon et al. 2013a). Nothing is currently known about the importance of lipid storage to overwintering survival in Arctic gadids.

Arctic cod have become the focus of several recent studies because they are highly abundant (Crawford & Jorgenson 1993, Benoit et al. 2008, 2014, De Robertis et al. 2017), are energetically richer than saffron cod (Nahrgang et al. 2010, L. A. Copeman et al. unpubl.) and appear to be more temperature sensitive than other gadids in the Pacific Arctic Region (Laurel et al. 2016). Here, we show that the loss of Arctic cod in Alaskan waters by way of climate change could result in a 'fat deficit' in the forage fish community without an accompanying range shift of boreal gadids further north. Current models suggest that poleward shifts of walleye pollock and Pacific cod will be hampered by persistent ice coverage during winter months in the Northern Bering Sea (Hollowed et al. 2011, Sigler et al. 2011, Hollowed & Sundby 2014). Melting sea ice during the spring results in a <2°C cold pool that effectively acts as a thermal barrier for boreal Pacific gadids shifting northward during summer months, despite the presence of warmer conditions existing in the surface and bottom waters of the Chukchi Sea during summer. The scenario in which Arctic cod are absent and energetically equivalently gadids cannot invade their niche sets up a poor scenario for marine sea birds and mammals that rely upon lipid-rich forage fish.

The correlation of temperature-dependent specific growth rate and body lipid content was only observed in the boreal species, possibly indicating unique life history strategies for survival in Arctic gadids living in severe over-wintering environments, where winter temperatures are <0°C (Bouchard & Fortier 2011). Juvenile cold-water gadids rapidly accumulate lipids during the late summer and autumn in order to store excess lipids for prolonged overwintering (Hurst 2007, Laurel et al. 2007a, Heintz & Vollenweider 2010, Copeman et al. 2016). We propose that surviving severe overwintering in the Arctic could require more lipid reserves be accumulated in a shorter growing season than in boreal regions, whereas larger body sizes in boreal regions may be required to reduce size-dependent predation mortality (overwintering processes reviewed by Sogard 1997, Sogard & Olla 2000, Hurst 2007). Copeman et al. (2016) found a latitudinal gradient in saffron cod size and lipid storage with age-0 fish from the Chukchi Sea over-wintering at a smaller size (<60 mm) and higher lipid density than age-0 fish from the Bering Sea that were larger (~100 mm) and had lower lipid density.

Investigation of the tissue-specific lipid class composition of Arctic and boreal gadids can provide insight into a potential mechanism through which small fish are able to overwinter in the Arctic. Classic condition indices such as HIS showed similar trends to condition indices we describe here based on lipid classes in the whole body or in the liver. However, indices such as HIS and length-weight residuals do not take into account the importance of lipid storage in muscle tissue (Copeman et al. 2008). Therefore, gross condition indices may underestimate the energetic storage of small juvenile Arctic gadids. We have shown that Arctic cod stored higher amounts of TL and TAG (mg lipid g^{-1} WWT) in their muscle tissues than other gadid species at temperatures <9°C. High lipid density in the muscle of Arctic cod shown here may be an alternative strategy to compensate for the short Arctic growing season and the allometric constraints of liver formation (Kamisaka & Ronnestad 2011). Elevated lipid levels in the muscle of Arctic cod may be an adaptation to unique Arctic habitats that allow cod to successfully overwinter during the first year of life, perhaps in a torpid state.

Our research has focused on the realized physiology (growth rate and lipid accumulation rates) of juveniles, and we have presented these results in the context of climate change and fisheries. Further study is required to understand the underlying physiological mechanisms that define Arctic cod's limited thermal tolerance. Future experiments looking at the ability of Arctic and boreal gadids to change their membrane fluidity in response to temperature and diet would be particularly interesting. These experiment should focus on examining the molecular species composition of the phospholipid membranes and membrane fluidity as measured by electron spin resonance (Bell & Dick 1991, Hall et al. 2002). Regardless of the mechanisms, the unique thermal responses and detrended lipid-growth pattern among Arctic species emphasize the need for species-specific biological data in order to understand climate impacts on fish from different ecosystems. In addition, there should be increased attention to examining the effects of lipid content on overwintering survival of these fish under varying environmental scenarios (*sensu* Hurst 2007). Although summer environmental conditions are projected to change in the Arctic with warming, winters will still be cold, dark, long and ice-covered.

Climate change impacts on the mid-trophic fish assemblage

Climate impacts on future fisheries are complicated by the indirect effects of warming on marine food webs that will accompany the direct physiological responses (i.e. growth and lipid storage) of individual species in response to changes in temperature. For example, the direct effects of temperature on fish metabolism may exacerbate or offset associated changes in food webs dynamics resulting from warming (Hixson & Arts 2016) that are now evident in both the Pacific (Venrick et al. 1987, Ershova et al. 2015) and Atlantic (Barton et al. 2016, Defriez et al. 2016) regions. Warming ocean temperatures can lead to changes in the timing, quantity and quality of zooplankton available to juvenile fish (Reygondeau et al. 2015, Sydeman et al. 2015). More specifically, thermally induced changes in food webs have been shown to negatively impact juvenile gadid recruitment into adult populations and have resulted in decreased abundances both in Atlantic cod (Beaugrand & Kirby 2010) and Pacific walleye pollock (Mueter et al. 2011, Stabeno et al. 2012, Siddon et al. 2013b) during warmer years. The energy density of juvenile gadids is affected by way of changes in prey assemblages, fish size-at-age and changes in foraging habitat (Sigler et al. 2016).

Increased recruitment of gadids has been observed in cold years when fish growth and survival during the larval and juvenile phases has been linked to matches in the abundance of large, cold-water, high-fat zooplankton species (Beaugrand & Kirby 2010, Heintz et al. 2013). Conversely, warm years have been characterized by decreased condition and survival of gadids with concurrent decreases in high-fat copepod species. Annual temperature oscillations in Alaskan waters shift the zooplankton assemblages from small copepods of low energetic density (warm years) to large boreal copepods of high energetic density (cold years; Sigler et al. 2011). The corresponding changes in the late summer energetic status of walleye pollock in warm (2005, upper 30 m water temperatures ranged from 5 to 14°C) and cold years (2010, ranged from 3 to 11°C) have been attributed to these changes in the prey field energy density (Mazur et al. 2007, Heintz et al. 2013, Siddon et al. 2013b), but our results indicate that temperature also plays a direct role on the energetic status of gadids when their food is kept constant and they are fed to satiation. During warm years, such as 2005, the upper range of temperatures experience by walleye pollock in the field were above the thermal maximum for lipid condition that we measured in the lab (12 to 13°C). With predicted future warming of the Bering Sea in late summer, walleye pollock and Pacific cod could more frequently experience late summer temperatures that exceed their laboratory-determined ideal temperatures for maximum condition and growth (WP ≈ 13°C and PC ≈ 10°C). The direct impact of temperature on the energetic status of fish offers a new interpretation to observed patterns in the field where it has been assumed to be wholly food-related (sensu Jobling et al. 1991). Decreased juvenile gadid condition during warm years could result from not only reduced food quality but also a concurrent higher metabolic rate.

Chukchi Sea August sea surface temperatures are warming at a rate of about +0.5°C per decade, correlating with declining trends in summer sea-ice extent in the region (Jeffries et al. 2014). Recent field surveys in the Bering and Chukchi seas have provided some of the first comprehensive information on the size, abundance, age and habitat temperature profiles for juvenile Arctic cod and saffron cod in this region (De Robertis et al. 2017, Helser et al. 2017). Both Arctic gadid species showed a strong association with oceanographic conditions, with Arctic cod juveniles found at high abundances on the Chukchi shelf in colder, saltier water. In contrast, saffron cod had larger populations in warmer, fresher waters, often in coastal embayments and areas affected by Alaska Coastal Water (Danielson et al. 2017). Laurel et al. (2016) measured maximum temperature-dependent growth for Arctic cod and saffron cod at 7.3 and 14.8°C, respectively. These laboratory-generated growth rates agree well with the field distribution of the 2 species; Arctic cod were found in the highest abundances between 4 and 7°C, while saffron cod juveniles were generally found in warmer waters above 8°C (De Robertis et al. 2016). This indicates that fish are selecting water temperatures that maximize growth and energy storage. With continued warming, the direct effects of temperature on growth rates of Arctic cod could lead to further range constriction into northern regions that are below 7°C in late summer. From an energetic perspective, Arctic cod can only accumulate lipids at rates faster than other gadids at temperatures below <1.3°C (Fig. 5) and have much lower ability to grow and store energy at temperatures above the sub-arctic range, ~1.3 to 6.7°C. Saffron cod showed very little temperature sensitivity in their lipid storage patterns in the laboratory. Both field and laboratory results indicate that saffron cod are less sensitive to the effects of increased warming than juvenile Arctic cod.

CONCLUSION

In conclusion, the effects of climate warming on fish populations have been largely understood by way of bioclimatic envelope models that heavily depend on the fish growth response in relation to temperature and do not account for environmental impacts on the condition of the fish (e.g. Heikkinen et al. 2006, Attrill & Power 2002). However, qualitative changes within a species may precede actual changes in the species assemblage as the result of climate change. With increased warming in the Arctic, further research is required to examine the interaction between food web change (food quantity and quality) and higher temperatures on the physiology of both Arctic and boreal gadids. It is likely that gadids will be more sensitive to food quantity and quality at elevated temperatures when metabolic rates are high. Therefore, warm temperatures coupled with decreased availability of high-lipid prey may interact to decrease the condition of juvenile gadids under warming scenarios. Boreal gadids were able to achieve higher lipid accumulation rates at warm temperatures (>4°C) than Arctic gadids; however, the success of boreal gadids in the Arctic will be highly dependent on their overwintering physiology, about which very little is known. The importance of marine lipids for overwintering survival of fish, birds and mammals is well-established, but this study provides some of the only direct links of temperature to tissue-specific lipid allocation and lipid accumulation rates in marine fish. Incorporating temperature effects on marine lipid content of ecologically important gadids will be an important consideration when examining marine regime shifts, biogeographical changes and bioenergetic relationships resulting from climate change in marine ecosystems.

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