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Original Article

Impacts of temperature and food availability on the condition of larval Arctic cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*)

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The Arctic marine environment is rapidly changing with rising sea surface temperatures, declining sea ice habitat and projected increases in boreal species invasions. The success of resident Arctic fish will depend on both their thermal tolerance and their ability to cope with changing trophic interactions. Larval fish energetic condition is closely associated with mortality rates and therefore provides an indicator of overall well-being or fitness. In this study, we experimentally determined larval morphometric and lipid-based condition in an Arctic gadid (Arctic cod, *Boreogadus saida*) and a boreal gadid (walleye pollock, *Gadus chalcogrammus*) in response to different temperatures and food rations. Our results suggest that larval condition is highly sensitive to both factors but varies in a species- and ontogenetic-dependent manner. Results indicated that condition metrics based on length–weight relationships were not as sensitive as those based on lipid storage. Further, condition metrics changed with ontogeny and were best used within a developmental stage rather than across developmental stages. As expected, larval condition in first-feeding Arctic cod was higher at colder temperatures (2–5°C) than in the boreal gadid (5–12°C). However, at more developed larval stages the peak condition for Arctic cod was at warmer temperatures (7°C), while walleye pollock had the same thermal optimum as during earlier stages. Arctic cod were more sensitive to food ration at first feeding than walleye pollock, however; at later larval stages both species had a negative condition response to low food ration, especially at elevated temperatures (5 vs. 7°C). The lower thermal tolerance of Arctic cod, coupled with a higher sensitivity to food availability indicates that Arctic cod are particularly vulnerable to on-going environmental change. Arctic cod is a lipid-rich keystone species and therefore a reduction in their energetic condition during summer has the potential to affect the health of higher trophic levels throughout the Alaskan Arctic.

Keywords: Arctic cod, climate change, condition index, lipid storage, thermal sensitivity, walleye Pollock.

Introduction

Rapid ecosystem-level change is occurring throughout the Arctic because of rising temperatures in combination with declining sea ice volume and extent (Hoegh-Guldberg and Bruno, 2010). This, coupled with accelerated local extinction and invasion by North Pacific species, may result in higher species turnover rates and reorganization of the Arctic community structure (Cheung *et al.*, 2009; Fossheim *et al.*, 2015). Furthermore, sea ice reduction will potentially alter the regional primary productivity regime to the extent that a mismatch occurs between high-quality food production and key Arctic grazers (Søreide *et al.*, 2010; Leu *et al.*, 2011). The success of key Arctic species throughout the lipid-rich Arctic marine food web may largely be dictated by changing trophic interactions resulting from this mismatch (Falk-Petersen *et al.*, 2007; Søreide *et al.*, 2010).

The latitudinal range of marine ectotherms is mainly dependent upon their thermal tolerance. Arctic cod (*Boreogadus saida*) is an ecologically important species in the Arctic where it plays a critical role as a mid-trophic prey item to marine mammals, seabirds, and other fish (Bluhm and Gradinger, 2008; Logerwell *et al.*, 2015). As an ice-obligate species, Arctic cod will likely be impacted by sea ice retraction throughout the region (Fossheim *et al.*, 2015). Walleye pollock (*Gadus chalcogrammus*) is a sub-Arctic species, which occupies a similar role throughout the Bering Sea shelves and the Gulf of Alaska (Bacheler *et al.*, 2010). Climate warming and sea ice loss could result in the poleward migration of non-ice-obligate North Pacific species, such as walleye pollock (Rand and Logerwell, 2011; Fossheim *et al.*, 2015). However, apparent avoidance of the Bering Sea cold pool by adult pollock (Overland and Stabeno, 2004) and continued formation of winter ice in the North Bering and Chukchi Seas (Sigler *et al.*, 2011) may limit the potential for walleye pollock to become established in the Arctic (Hollowed *et al.*, 2013).

The early larval stage represents a critical period for marine fish species, often characterized by highly variable growth and survival (Letcher *et al.*, 1996; Houde, 2008). This is particularly true in Polar Regions characterized by low light, cold temperatures, and reduced prey availability where mortality risks are enhanced and recruitment is ultimately impacted by overwintering success (Hurst, 2007). Under these conditions, larval survival depends largely on maximization of growth prior to overwintering (Fortier *et al.*, 2006). Furthermore, developmental limitations of larval fish make this stage particularly sensitive to environmental stress and limit their ability to seek out suitable habitat under changing conditions (Rijnsdorp *et al.*, 2009). Currently, basic understanding of the larval physiology of Arctic cod is largely lacking due to limitations in the logistics of under-ice sampling during the ice-covered Arctic winter and spring (Graham and Hop, 1995). This absence of physiological and ecological information on the early life stages of Arctic cod severely limits our ability to determine its survival potential in the face of ongoing climate change (Christiansen *et al.*, 2014). Improved understanding of Arctic cod sensitivity to different environmental scenarios could help elucidate the factors that affect larval survival, population success, and eventual recruitment with changing ocean conditions.

The nutritional condition of larval fish can have major impacts on mortality through direct (e.g. starvation) and indirect (e.g. prolonged stage duration and vulnerability to predation) mechanisms (Ehrlich *et al.*, 1976, Shepherd and Cushing, 1980; Folkvord *et al.*, 1996). As such, nutritional condition is a useful metric that can serve as an indicator of overall well-being or fitness (Jones *et al.*, 1999). Condition indices have traditionally been based on the analysis of morphometric data, typically relating the actual weight of an individual to some "expected weight" or analysing a length–weight relationship (Bolger and Connolly, 1989). With these indices, it is assumed that at a given length, heavier fish are in better condition (Jones *et al.*, 1999). Despite their widespread use, the inherent assumptions and limitations of these methods have been widely recognized.

A range of condition indices (e.g. morphometric, biochemical, histological, etc.) with varying sensitivity to environmental stress exist (Suthers *et al.*, 1992). Though morphometric indices (e.g. Fulton's condition factor, *K*) are common (e.g. Neilson *et al.*, 1986; Brodeur *et al.*, 2000) in marine fish studies, direct condition measures (lipids) have been shown to be more sensitive to physiological stress in certain cases (Copeman *et al.*, 2008). One advantage of lipid condition indices is the fact that lipid classes, particularly triacylglycerols (TAGs), quickly adjust to changes in feeding and so they can indicate shorter-term change in nutritional status (Lochmann *et al.*, 1995). Conversely, morphometric or histological alterations are observed over longer time periods.

Lipids are a limiting nutrient in cold-water marine ecosystems (Litzow *et al.*, 2006) and affect the growth and survival of fish during early life stages (Lochmann *et al.*, 1995; Copeman *et al.*, 2002; Park *et al.*, 2006). The energy storage of gadids during their early ontogeny is impacted by a number of factors (e.g. temperature, prey availability/quality), which are directly and indirectly tied to changing environmental conditions (Siddon *et al.*, 2013). High temperatures increase metabolic demands and reduce the physiological ability of fish to store lipids (Jobling, 1988), in addition to altering the availability of prey and, thus, influencing the energy density of juvenile gadids (Heintz *et al.*, 2013).

By examining lipid class composition, it is possible to quantitatively measure energy reserves in an individual. TAGs are an energy storage lipid class that serve as an indicator of physiological state as they are the first lipids mobilized by fish during environmental stress (Fraser, 1989). To account for size dependency, TAG content can be measured relative to sterol (ST) compounds, a structural lipid class that serves as an adequate proxy for body size or dry weight (DWT) (Lochmann *et al.*, 1995). The resultant TAG:ST ratio provides an index, which has been successfully used to measure larval fish, bivalves and crustacean condition (Fraser, 1989; Copeman and Laurel, 2010). As with growth, lipid condition has been shown to decrease near the upper thermal limit in four species of North Pacific juvenile gadids (Copeman *et al.*, 2017).

An experimental investigation of the nutritional condition of larval Arctic cod under various temperature and productivity scenarios has not previously been completed. In this study, total lipid and relative lipid class metrics were used to assess larval Arctic cod and walleye pollock condition in relation to changes in temperature and food availability. These lipid metrics were compared with morphometric condition indices based on length–weight residuals and body depth(BD):length ratios to determine the sensitivity of each. Specific objectives of this study were to (i) assess species-specific condition of Arctic cod and walleye pollock at two larval stages across a range of temperatures (Arctic cod: −1 to 9°C; walleye pollock: 0–12°C), (ii) determine how the interaction of temperature and food availability act on the species-specific condition of gadid larvae, and (iii) compare the sensitivity of different larval condition indices to changes in temperature and food availability.

Methods

Information on the lipid allocation and nutritional condition of larval Arctic cod and walleye pollock was obtained from laboratory experiments conducted at the Alaska Fisheries Science Center's (AFSC) cold-water facilities at the Hatfield Marine Science Center (HMSC) in Newport, OR, USA. The results of these experiments also contributed to temperature-dependent growth and survival information (Koenker *et al.*, this issue). The experimental methodology for eggs sources, egg incubation, live food preparation, general experimental design and husbandry as well as growth metrics have been previously described in detail (Koenker *et al.*, this issue).

Experimental design

Briefly, laboratory experiments utilized larvae from the AFSC gadid broodstock programme. Broodstock were sourced from live juvenile fish collections of Arctic cod (70–85-mm SL) and walleye pollock (30–50-mm SL) collected during the spring or summer of 2011–2013. Juveniles were reared for over three years in the laboratory until they became active spawners (age 3+ fish) (collection details as in Laurel *et al.*, 2016).

Arctic cod adult broodstock were strip spawned in March of 2015 (for later stage experiment) and 2016 (for first-feeding experiment) and eggs from a single female were fertilized with milt from three males. Eggs were incubated at 1°C in a 4-L mesh pan suspended in a water bath until reaching ∼75% hatch level, at which time all hatched and unhatched larvae were transferred to 400-L stock tanks held at 2–3°C. Walleye pollock adult broodstock holding temperatures were reduced from 9 to 5°C in the fall and spawned naturally from February to late April 2015 (for both experiments). Eggs were retained in an egg basket from which the highest quality eggs were transferred directly to 100-L stock tanks and incubated at 5–6°C.

Growth experiments were carried out in 38-L glass aquaria supplied with flow-through, temperature-controlled seawater. First-feeding Arctic cod larvae (mean 5.9-mm SL) were slow-acclimated to their corresponding temperature treatment and gently transferred to twelve aquaria for high food ration treatments (−1, 2, 5, and 9°C; $n = 3$ replicate tanks/temperature) and six for low food ration treatments (2 and 5°C; $n = 3$ replicate tanks/temperature) stocked at a density of ∼12 larvae per litre. First-feeding walleye pollock larvae (mean 4.7-mm SL) were acclimated in the same manner to twelve aquaria for high food ration treatments (0, 2, 5, and 12°C; $n = 3$ replicate tanks/temperature) and six for low food ration treatments (2 and 5°C; $n = 3$ replicate tanks/temperature) stocked at a density of ∼12 larvae per litre.

Later stage larvae of both species remained in stock tanks and fed enriched rotifers (*Brachionus* sp.) twice daily at a density of 5 prey ml^{-1}, before being gradually transitioned onto a diet of enriched brine shrimp (*Artemia* sp.) at a prey density of 2 prey ml^{-1} (see below for enrichment protocols). Later stage Arctic cod (78 dph; mean 11.3-mm SL) were transferred to twelve aquaria for high food ration treatments (0, 2, 5, and 7°C; $n = 3$ replicate tanks/temperature) and six for low food ration treatments (2 and 5°C; $n = 3$ replicate tanks/temperature) stocked at a density of ∼3 larvae per litre. A fourth replicate tank at 0 and 7°C was set up after 1 week to account for particularly high mortality in one of the replicate tanks at each temperature. An additional 9°C trial was conducted for later stage Arctic cod to assess the upper thermal limit for survival ($n = 1$ tank due to high mortality). Later stage walleye pollock (84 dph; mean 8.6-mm SL) were transferred to fifteen aquaria for high food ration treatments (0, 2, 5, 9, and 12°C; $n = 3$ replicate tanks/temperature) and nine for low food ration treatments (2, 5, and 9°C; $n = 3$ replicate tanks/temperature) in July 2015.

First-feeding larval experiments received enriched rotifers (*Brachionus* sp.), while later stage experiments received enriched brine shrimp (*Artemia* sp.). Rotifers were cultured at 26°C in a high-density rotifer culture system from Aquatic Eco-Systems. Rotifers were harvest and enriched twice daily with Algamac 3050 (0.3 g per million rotifers; Aquafauna, Hawthorne, CA, USA) and Roti Grow Plus (daytime: 0.5 ml per million rotifers, overnight: 1.0 ml per million rotifers; Reed Mariculture, Campbell, CA, USA). Algamac was selected as a suitable enrichment because it contains a high proportion of long-chained fatty acids which are essential for North Pacific larval fish (Copeman and Laurel, 2010). Decapsulated brine shrimp were hatched for 24 h in hatching cones at 26–27°C before being enriched with Selco S.Presso (7.5 g per 15 l seawater; INVE Aquaculture, Nonthaburi, Thailand) for an additional 24 h. Both rotifers and brine shrimp were counted daily for quality control and to determine accurate prey counts.

Prior to each feeding, Nanno 3600 algae paste (Reed Mariculture, Campbell, CA, USA) diluted with 2°C seawater was added to each tank to provide "green water" as a means of improving larval prey ingestion (Naas *et al.*, 1996). First-feeding larvae in high food ration treatments were fed twice daily at prey densities of 5 prey ml^{-1}, while low food ration treatments received prey densities of 0.5 prey ml^{-1} twice daily. Later stage larvae in high food ration treatments were fed twice daily at prey densities of 2 prey ml^{-1} and low food ration treatments received prey densities of 0.5 prey ml^{-1} once daily. All treatments received green water, including low food ration tanks that were not receiving prey in the afternoon. Tanks were clear of all live prey after ∼2 h following each feeding, indicating that all prey were either consumed or flowed out of the tank between feedings. This ensured that larvae were feeding on newly enriched prey and that prey quality did not deteriorate over the duration of the experiments.

Throughout larval experiments, tanks were held at a 12:12-h light:dark photoperiod, with light levels ranging from 1.4 to 2.7 $\mu E/m^2sec$ at the surface of the water in the centre of each tank. Maintenance of tank temperatures, aeration, and flow rates was completed daily. Temperature was recorded in the morning and adjusted to within 0.5°C of the target temperature to account for fluctuations in ambient water temperature. Aeration was monitored to maintain gentle bubbling beneath the outflow mesh in each tank and flow rates were adjusted to within 270–330 ml min^{-1} each day. Tanks were siphoned daily, at least 2 h after feeding, to remove any mortalities along with excess food and debris. Due to differential mortality, experimental duration varied slightly among tanks (3–5 weeks for first-feeding experiments, 2–3 weeks for later stage experiments)

Morphometric analyses

Larvae from each tank were randomly sampled from throughout the water column for morphometric measurements (i.e., DWT, standard length [SL], BD) at the start and end of each experiment (12–35 days) as described in Koenker *et al.* (this issue). The number of individual larvae sampled varied based on mortality among tanks and throughout experiments. For first-feeding Arctic cod, one to five samples per tank containing 1 individual were used for end of experiment measurements (except for one tank at 9°C which was sampled at 3 weeks, rather than 5 weeks, due to mortality and contained five individuals). For first-feeding walleye pollock, 1 sample per tank containing 5–10 individuals was used for final measurements. For later stage experiments, 2–5 samples per tank containing one individual were used. Later stage BD:SL ratio analyses (Figures 2 and 6) also contain morphometric measurements for individuals used in lipid analyses outlined below.

SL was determined as the length (mm) from the tip of the snout to the end of the notochord. BD was the width (mm) of the larvae just posterior to the anus not including the fin-fold.

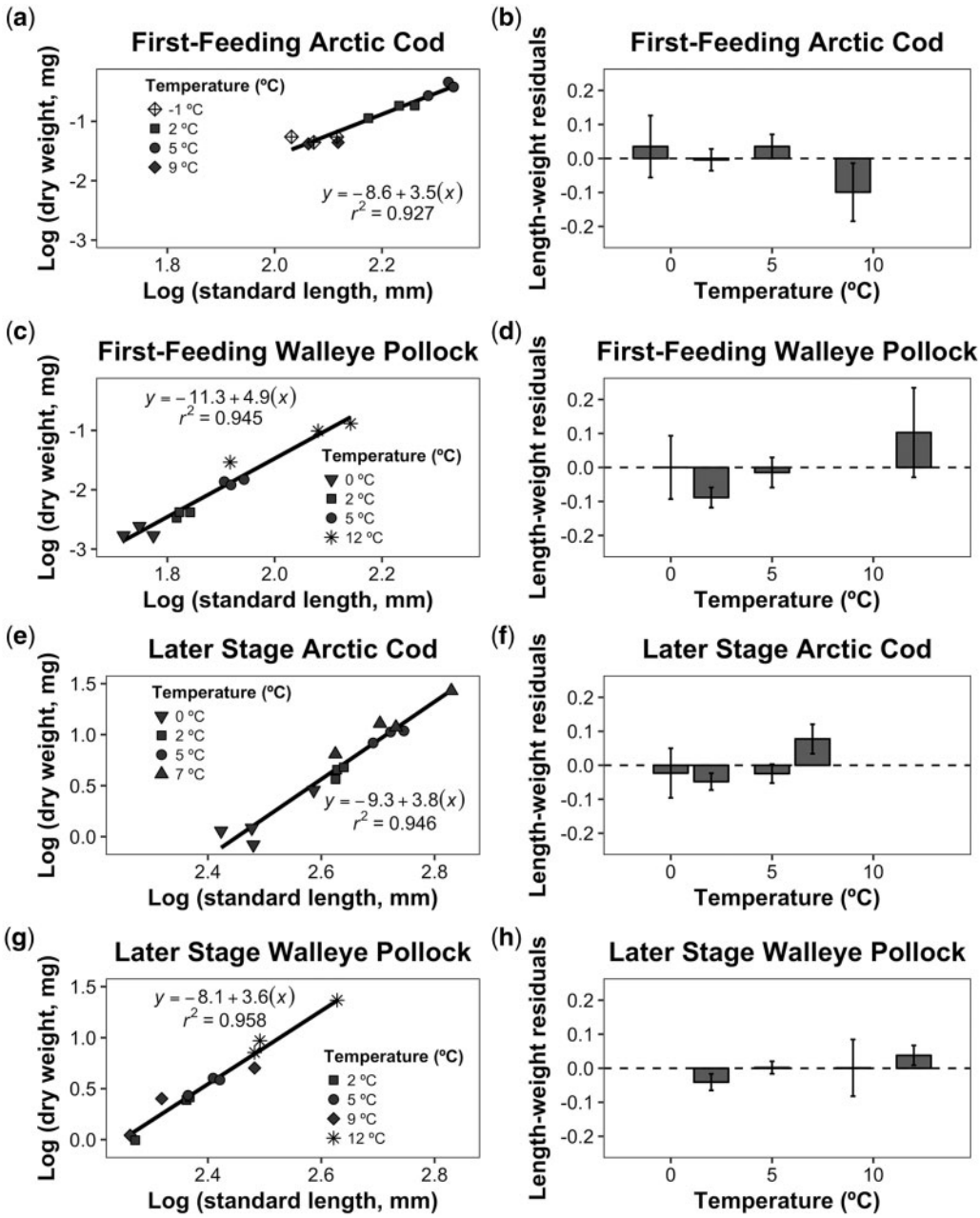

Figure 1. Linear relationships between log-transformed length (SL, mm) and log-transformed DWT (mg) of (a) first-feeding Arctic cod, (c) first-feeding walleye pollock, (e) later stage Arctic cod, and (g) later stage walleye pollock larvae and the residuals of this relationship for (b) first-feeding Arctic cod, (d) first-feeding walleye pollock, (f) later stage Arctic cod, and (h) later stage walleye pollock larvae in high food ration treatments at the end of laboratory experiments. Linear regression was fitted to mean tank data. Length–weight residuals were computed for each tank and plotted as treatment means ± 1 SE (n = 2–4 replicate tanks/treatment).

Length–weight residuals were obtained from the relationship between the natural log-transformed post-treatment mean SL (in mm) and mean DWT (in mg) for each tank in a single experiment. These length–weight residuals, at the tank level of observation, served as a morphometric condition index. Additionally, the ratio of BD:SL was computed for all larvae and applied as a measure of condition. BD represents the muscular tissue stored energy which is consumed by larvae after exhaustion of lipid reserves (Diaz *et al.*, 2013). As such, larvae with a higher BD:SL were considered to be in better condition.

Lipid extraction and analysis

Additional larvae were sampled at the end of the experiments and used for total lipid and lipid class analyses. The number of individual larvae sampled was adjusted to obtain sufficient mass for lipid analyses (mean ∼200 µg total lipids per sample). For first-feeding Arctic cod, two pools of ten individuals per tank were sampled. For first-feeding walleye pollock, lipids per individual were limiting so all remaining larvae in each tank were pooled to produce one sample per tank (n = 7–52 individuals). For later stage experiments of both species, two to three samples per tank

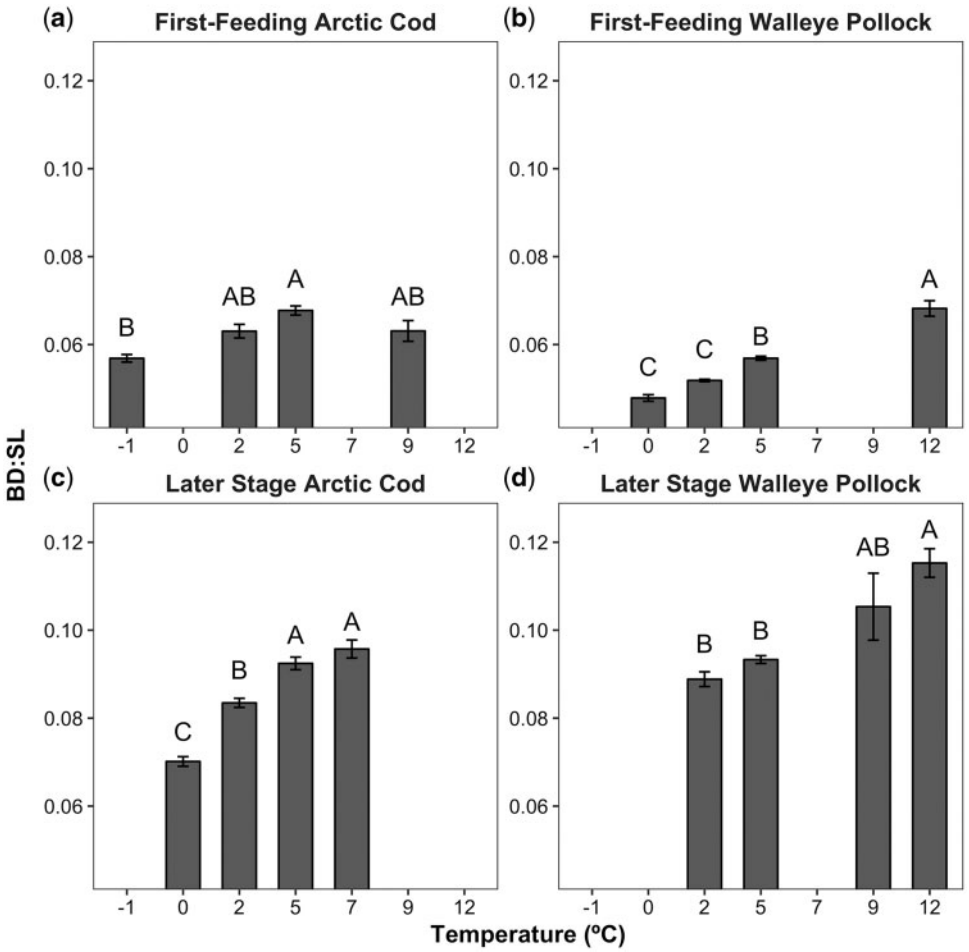

Figure 2. BD:SL ratio of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae in high food ration treatments at the end of laboratory experiments. Data are treatment means ± 1 s.e. ($n = 2$–4 replicate tanks per treatment). Different letters indicate significant differences according to Tukey's pairwise comparisons.

of 1 individual were used. Lipid samples were stored at −25°C in 2 ml of chloroform under nitrogen and sealed with Teflon tape for <3 months prior to lipid extraction.

Lipids were extracted in chloroform and methanol according to Parrish (1987) using a modified Folch procedure (Folch *et al.*, 1957). Thin layer chromatography with flame ionization detection with a MARK V Iatroscan (Iatron Laboratories, Tokyo, Japan) was used to classify and quantify total lipids and lipid classes using a procedure described by Lu *et al.* (2008) and modified by Copeman *et al.* (2016). Silica-coated Chromarods were spotted in duplicate with lipid extracts and a three-stage development system was employed for lipid class separation. The first separation involved a 90-s development in a chloroform:methanol:cholo-form-extracted water solution (150:120:30) to move polar lipids off the origin. The second separation involved a 48-min development in a hexane:diethyl ether:formic acid solution (99:1:0.05) and the final separation consisted of a 38-min development in a hexane:diethyl ether:formic acid solution (80:20:0.1). Following each separation, the rods were dried for 5 min and conditioned at constant humidity (~32%) for an additional 5 min.

After the final development, the Chromarods were scanned using PeakSimple software (ver. 3.67, SRI Inc.) and the signal (detected in mV) was quantified using lipid standards as described in Copeman *et al.* (2016). The resulting chromatograms were integrated to quantify absolute amounts of four lipid classes: TAGs, free fatty acids (FFA), sterols, and polar lipids. Lipid class values were taken as the average of duplicate runs for each lipid sample. For statistical analyses, tank means were used ($n = 1$–3 samples per tank as described above).

Data analysis

Primary growth and condition analyses were performed using RStudio statistical software (ver. 0.99.491, RStudio, Inc., Boston, MA, USA) using a significance level of $\alpha = 0.05$. Tukey's pairwise comparisons were performed using Minitab 17 statistical software (Minitab, Inc., State College, PA, USA) using a significance level of $\alpha = 0.05$. Later stage Arctic cod at 9°C and later stage walleye pollock at 0°C were removed from condition analyses to account for size-selective mortality in treatments that experienced > 80% mortality within the first week of experiments (see Koenker *et al.*, (this issue) for mortality details).

Statistical tests were performed to assess the impacts of species, temperature, and food ration on larval condition and lipid storage within each ontogenetic stage. The effects of ontogeny within

Table 1. Total lipid content (μg lipid mg^{-1} DWT) and lipid class composition of first-feeding and later stage Arctic cod and walleye pollock larvae under different temperature-food ration scenarios.

Ontogenetic stage	Species	Temp (°C)	Food Ration	*n*	TL (μg mg^{-1})	TAG (%)	FFA (%)	ST (%)	PL (%)
First-feeding	Arctic Cod	−1	High	3	60.2 ± 3.1	3.1 ± 0.5	0.5 ± 0.1	7.4 ± 0.7	89.0 ± 0.7
		2	High	2	90.9 ± 0.7	4.4 ± 0.0	0.4 ± 0.0	9.8 ± 0.6	85.4 ± 0.6
		2	Low	3	85.5 ± 9.0	1.4 ± 0.3	0.5 ± 0.1	10.6 ± 0.8	87.4 ± 0.8
		5	High	3	94.9 ± 5.1	4.4 ± 0.8	0.3 ± 0.1	10.8 ± 0.6	84.2 ± 1.4
		5	Low	2	101.4 ± 6.7	2.9 ± 0.3	0.3 ± 0.0	10.8 ± 0.3	86.0 ± 0.6
	Walleye Pollock	0	High	3	59.8 ± 4.8	1.3 ± 0.0	0.7 ± 0.0	14.0 ± 0.4	84.0 ± 0.4
		2	High	3	55.3 ± 3.3	1.3 ± 0.2	0.7 ± 0.1	14.5 ± 0.7	83.5 ± 0.8
		2	Low	1	29.9 ± 0.0	0.0 ± 0.0	4.1 ± 0.0	27.0 ± 0.0	68.9 ± 0.0
		5	High	3	92.9 ± 9.4	3.7 ± 1.8	0.8 ± 0.3	12.2 ± 0.4	83.3 ± 2.6
		5	Low	3	54.9 ± 10.8	1.6 ± 0.3	0.5 ± 0.1	12.0 ± 0.4	86.0 ± 0.3
		12	High	2	74.4 ± 4.4	1.8 ± 0.2	0.4 ± 0.0	14.9 ± 1.5	82.6 ± 0.9
Later stage	Arctic Cod	0	High	4	102.6 ± 2.4	5.6 ± 0.3	0.7 ± 0.1	10.2 ± 0.3	83.5 ± 0.6
		2	High	3	104.9 ± 5.4	11.5 ± 0.5	0.7 ± 0.1	9.8 ± 0.6	78.0 ± 0.8
		2	Low	3	99.0 ± 7.1	6.3 ± 1.0	0.7 ± 0.1	12.3 ± 0.6	80.7 ± 0.7
		5	High	3	136.3 ± 5.0	19.0 ± 0.4	0.5 ± 0.1	10.9 ± 0.3	69.6 ± 0.7
		5	Low	3	108.7 ± 1.4	14.1 ± 1.1	0.6 ± 0.1	11.0 ± 0.2	74.3 ± 1.3
		7	High	4	138.1 ± 9.5	21.8 ± 2.1	0.5 ± 0.1	10.1 ± 0.4	67.6 ± 1.9
	Walleye pollock	0	High	2	75.7 ± 0.0	6.8 ± 2.6	1.4 ± 0.2	13.2 ± 1.2	78.3 ± 1.8
		2	High	3	113.1 ± 14.6	8.6 ± 1.2	0.9 ± 0.1	11.0 ± 0.6	79.5 ± 1.4
		2	Low	3	97.2 ± 4.7	5.6 ± 1.0	0.9 ± 0.2	11.2 ± 0.5	82.2 ± 0.9
		5	High	3	128.9 ± 5.9	14.7 ± 0.4	0.9 ± 0.1	11.1 ± 0.3	73.3 ± 0.7
		5	Low	3	88.6 ± 4.7	4.3 ± 0.7	1.0 ± 0.3	13.8 ± 0.8	80.9 ± 0.3
		9	High	3	126.0 ± 6.0	15.7 ± 2.0	0.6 ± 0.1	9.3 ± 0.5	74.4 ± 2.3
		9	Low	3	95.0 ± 5.6	4.3 ± 0.8	0.9 ± 0.2	12.6 ± 0.6	82.2 ± 0.8
		12	High	3	104.8 ± 4.6	11.8 ± 2.8	0.7 ± 0.1	9.8 ± 0.3	77.7 ± 2.7

TL, total lipid; TAG, triacylglycerols; FFA, free fatty acids; ST, sterols, PL, polar lipids. Arctic cod at both ontogenetic stages at 9°C are not included due to high mortality in treatment tanks. Data are treatment means ± 1 s.e. (n = 1–4 replicate tanks, depending on mortality).

each species were not statistically tested as nutritional condition has been shown to be highly dependent on developmental stage (Richard *et al.*, 1991), and thus, analysis across stages is not recommended. Furthermore, morphological and physiological changes during the early ontogeny of fish vary substantially within and among species (Pepin, 1995). Morphological condition indices are closely tied to species-specific allometric growth patterns and, so, this study considers temperature and food ration effects on morphological condition within a single species only. Lipid condition indices are less constrained by allometry, but still prone to species-specific lipid accumulation. Therefore, considerable care should be used when interpreting differences derived from the comparison of lipid condition across species in this study.

For high food ration treatments, one-way analysis of variance (ANOVA) was used to assess the effects of temperature on morphological condition (length–weight residuals and BD:SL) within each stage. Additionally, two-way ANOVAs were used to determine species and temperature effects on lipid condition (TAG:ST) and total lipid storage (per larval DWT) within each stage. At intermediate temperatures where food rations were manipulated, two-way ANOVAs were used to assess the effects of temperature and food ration on morphological condition. Three-way ANOVAs were used to examine the interactive effects of temperature, food ration, and species on lipid condition and storage at each larval stage. Data were examined for normality and homogeneity of variance to satisfy the assumptions of ANOVA. Posteriori tests (Tukey's pairwise comparisons) were performed to identify significant differences in morphometric (BD:SL) and lipid condition (TAG:ST, total lipids) with response to temperature within each experiment. For all statistical analyses, individual tanks were used as the level of observation and morphometric and lipid measurements taken at the end of laboratory experiments were used.

Results

Temperature effects on larval condition

Logarithmic transformation was performed to linearize the relationship between post-treatment SL and DWT of larval fish from each experiment (Figure 1a, c, e, and g). The relationships for each experiment were described by the linear regression equations for first-feeding Arctic cod, first-feeding walleye pollock, later stage Arctic cod, and later stage walleye pollock shown in Figure 1. At the first-feeding stage, one-way ANOVAs detected no significant effect of temperature on the morphometric condition (length–weight residuals) of Arctic cod ($F_{1,9} = 1.519$, $p = 0.249$; Figure 1b) or walleye pollock ($F_{1,10} = 1.767$, $p = 0.213$; Figure 1d). Similarly, at the later larval stage, temperature did not statistically affect the condition of Arctic cod ($F_{1,12} = 2.347$, $p = 0.152$; Figure 1f) or walleye pollock ($F_{1,10} = 1.439$, $p = 0.258$; Figure 1h). The standard error of length–weight residual values was high because of large variation between tank means, likely contributing to the non-significant ANOVA results.

The BD:SL ratio of gadid larvae under high food ration conditions generally increased across the experimental temperature range. For first-feeding Arctic cod, the effect of temperature on the BD:SL (one-way ANOVA; $F_{1,9} = 3.891$, $p = 0.080$) was not statistically significant (Figure 2a). For first-feeding walleye pollock, the BD:SL increased with temperature (from 0 to 12°C) as evidenced by a statistically significant temperature effect ($F_{1,10} = 289.38$, $p < 0.001$; Figure 2b). Similarly, a significant positive relationship between

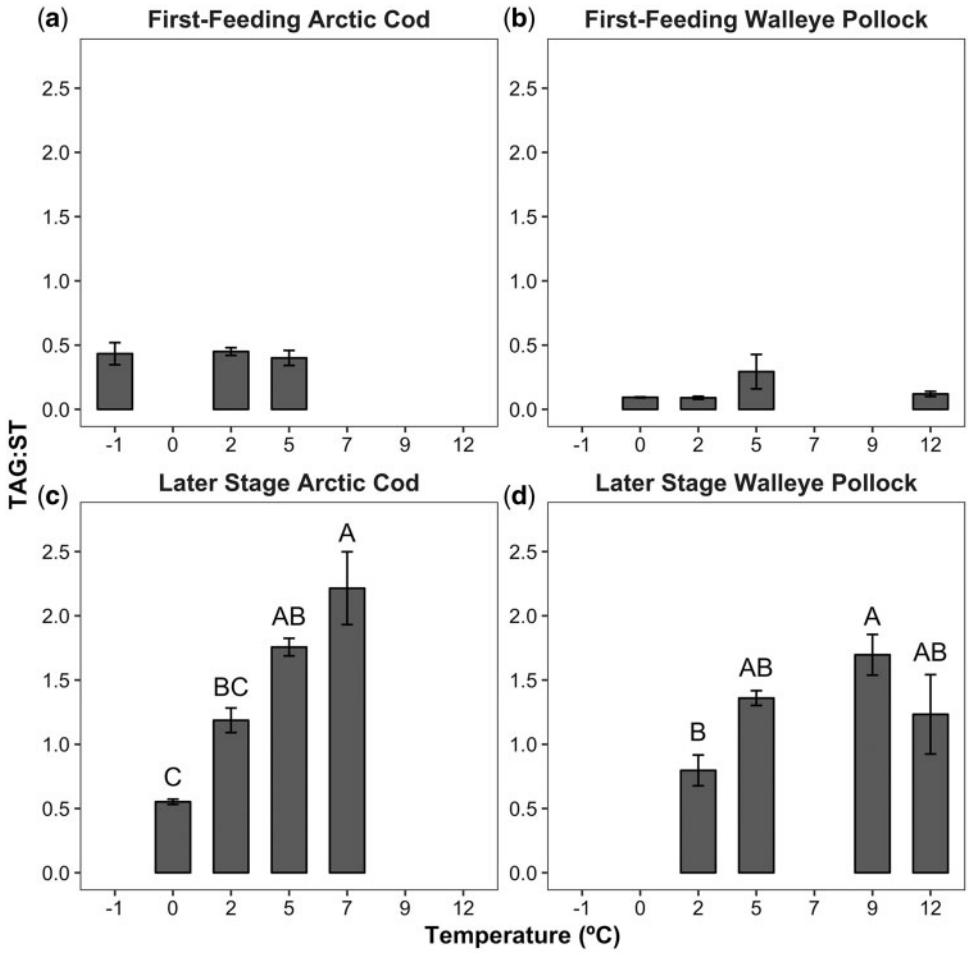

Figure 3. TAG:ST ratio of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae in high food ration treatments at the end of laboratory experiments. First-feeding Arctic cod lipid data at 9°C was not collected because not enough larvae remained at the end of experiments due to high mortality. Data are treatment means ± 1 s.e. ($n = 2$–4 replicate tanks per treatment). Different letters indicate significant differences according to Tukey's pairwise comparisons.

temperature and the BD:SL of both later stage Arctic cod ($F_{1,12} = 95.436$, $p < 0.001$) and walleye pollock ($F_{1,10} = 27.902$, $p < 0.001$) was statistically supported (Figure 2c and d).

Total lipid and proportional lipid class composition for larvae in all experiments are included in Table 1. Among high food ration treatments, the largest proportion of each sample was comprised of PL, with first-feeding larvae containing proportionally more PL (84.6%) than later stage larvae (75.8%). The opposite was true with the TAG proportion, which was lower in first-feeding larvae (2.9%) than later stage larvae (12.8%). Both FFA (first-feeding: 0.5%; later stage: 0.8%) and ST (first-feeding: 11.9%; later stage: 10.6%) proportions remained relatively constant between stages.

First-feeding Arctic cod were in higher lipid-based condition than first-feeding walleye pollock as evidenced by the significant effect of species (two-way ANOVA; $F_{1,15} = 20.256$, $p < 0.001$) on the TAG:ST of first-feeding larvae in high food ration treatments (Figure 3a and b). At this stage, temperature did not significantly impact the TAG: ST independently or as an interaction. At the later larval stage, a significant species–temperature interaction existed ($F_{1,22} = 17.548$, $p < 0.001$) such that Arctic cod were in better condition than walleye pollock at a given temperature and were also more sensitive to changes in temperature (Figure 3c and d).

Finally, the total body lipid storage (lipid per DWT, μg mg^{-1}) generally increased with temperature up to 5°C for first-feeding larvae as evidenced by a significant temperature effect on first-feeding larval total lipids (two-way ANOVA; $F_{1,15} = 7.785$, $p = 0.014$; Figure 4a and b). Later stage Arctic cod lipid storage also increased with temperature, while walleye pollock lipid storage reached a maximum at ∼5°C and then declined slightly resulting in a significant species–temperature interaction term ($F_{1,22} = 12.358$, $p = 0.002$; Figure 4c and d).

The temperatures of maximum condition observed for each experiment based on different morphometric and lipid indices are included in Table 2. According to these indices, condition was maximized at 2–5°C and 7°C for first-feeding and later stage Arctic cod, respectively. Walleye pollock larval

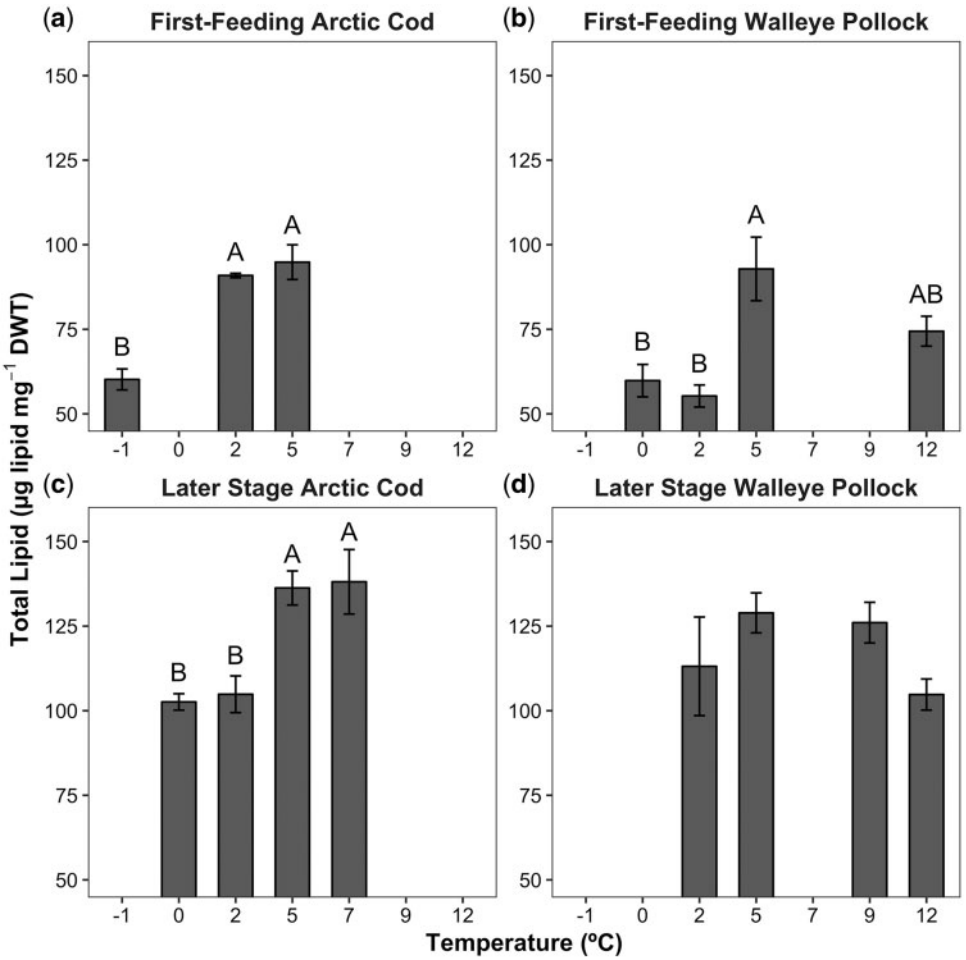

Figure 4. Total lipid (µg lipid mg^{-1} DWT) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae in high food ration treatments at the end of laboratory experiments. Data are treatment means ± 1 s.e. ($n = 2$–4 replicate tanks per treatment). Different letters indicate significant differences according to Tukey's pairwise comparisons.

Table 2. Temperatures of maximum condition observed for first-feeding and later stage Arctic cod and walleye pollock based on different morphometric and lipid condition indices.

Ontogenetic stage	Species	Condition index	Experimental temperature (°C)
First-Feeding	Arctic Cod	Length–weight residuals	5
		BD:SL	5
		TAG:ST	2
		Total lipid storage	5
	Walleye Pollock	Length–weight residuals	12
		BD:SL	12
		TAG:ST	5
		Total lipid storage	5
Later Stage	Arctic Cod	Length–weight residuals	7
		BD:SL	7
		TAG:ST	7
		Total lipid storage	7
	Walleye Pollock	Length–weight residuals	12
		BD:SL	12
		TAG:ST	9
		Total lipid storage	5

condition was maximized between 5 and 12°C at both ontogenetic stages.

The significant one-way ANOVA (temperature effects) and two-way ANOVA (temperature and food ration effects) results across high food ration treatments are summarized in Tables 3 and 4, respectively.

Temperature–prey interactive effects

The interactive effects of temperature and food ration were assessed at intermediate temperatures (2 and 5°C) where food rations were manipulated.

The logarithmic–transformed linear relationships between SL and DWT of larval fish at intermediate temperatures (2 and 5°C) and high and low food rations (Figure 5a, c, e, and g) were described by linear regression equations for first-feeding Arctic cod, first-feeding walleye pollock, later stage Arctic cod, and later stage walleye pollock. Analysis of morphometric condition (length–weight residuals) of first-feeding Arctic cod revealed no statistically significant independent or interactive effects of temperature and food ration (two-way ANOVA; Figure 5b).

Table 3. Summary of *p*-values from one-way ANOVAs assessing the effect of temperature on larval condition across high food ration treatments according to different morphometric condition indices.

Ontogenetic stage	Species	Length–weight residuals	BD:SL
First-feeding	Arctic cod	0.249	0.080
	Walleye pollock	0.213	**<0.001**
Later stage	Arctic cod	0.152	**<0.001**
	Walleye pollock	0.258	**<0.001**

Significant results ($\alpha = 0.05$) for each condition index are indicated in bold.

Table 4. Summary of p-values from two-way ANOVAs assessing the effects of temperature and species on larval condition across high food ration treatments according to different lipid condition indices.

Ontogenetic stage	Results	TAG:ST	Total lipid storage
First-feeding	Species	**< 0.001**	0.146
	Temperature	0.733	**0.014**
	Species*Temperature	0.577	0.128
Later stage	Species	0.293	0.707
	Temperature	**< 0.001**	0.066
	Species*Temperature	**< 0.001**	**0.002**

Significant results ($\alpha = 0.05$) for each condition index are indicated in bold.

Similarly, the effects of temperature and food ration were not significant for first-feeding walleye pollock (Figure 5d).

For first-feeding larvae, a significant effect of temperature on the BD:SL ratio was detected for both Arctic cod (two-way ANOVA; $F_{1,8} = 15.056$, $p = 0.005$; Figure 6a) and walleye pollock (two-way ANOVA; $F_{1,8} = 109.682$, $p < 0.001$; Figure 6b). The BD:SL was higher at 5°C than at 2°C for both first-feeding species. The effect of food ration on the BD:SL was significant for first-feeding Arctic cod ($F_{1,8} = 33.808$, $p < 0.001$), but not for walleye pollock ($F_{1,8} = 2.308$, $p = 0.167$). At both temperatures, Arctic cod larvae receiving high food rations were in better condition than those receiving low food rations. At the later larval stage, an independent food ration effect was detected for both Arctic cod ($F_{1,8} = 48.922$, $p < 0.001$; Figure 6c) and walleye pollock ($F_{1,8} = 22.205$, $p = 0.002$; Figure 6d). The BD:SL for both later stage species was higher under high food ration treatments than low food ration treatments. Unlike with first-feeding experiments, temperature sensitivity among later stage larvae varied with species. Temperature significantly affected the BD:SL of later stage Arctic cod ($F_{1,8} = 26.338$, $p < 0.001$), but not walleye pollock ($F_{1,8} = 1.189$, $p = 0.307$).

Total lipid and proportional lipid class composition for larvae in 2 and 5°C treatments (Table 1) followed the same patterns as those detailed above. The largest proportion of each sample was comprised of PL, with first-feeding larvae containing more PL (82.9%) than later stage larvae (77.3%) on average. Once again, the opposite was true with the TAG proportion, which was lower in first-feeding larvae (2.5%) than later larval stage (10.5%). Both FFA (first-feeding: 1.0%; later stage: 0.8%) and ST (first-feeding: 13.5%; later stage: 11.4%) proportions remained relatively constant between stages.

For first-feeding larvae, significant independent effects of species ($F_{1,12} = 9.492$, $p = 0.010$), temperature ($F_{1,12} = 5.010$, $p = 0.045$), and food ration ($F_{1,12} = 11.211$, $p = 0.006$) acting on the TAG:ST condition index was detected (three-way ANOVA; Figure 7a and b). Under the same experimental conditions (temperature and food ration), Arctic cod were in higher condition than walleye pollock at this stage. Additionally, nutritional condition of first-feeding larvae increased with temperature and with food ration. At the later larval stage, a significant three-way interaction between species, temperature, and food ration ($F_{1,16} = 13.178$, $p = 0.002$) on the TAG:ST was detected (Figure 7c and d). To further investigate this interaction, separate two-way ANOVAs considering temperature and food ration were conducted for each species. For later stage Arctic cod, the independent effects of temperature ($F_{1,8} = 59.370$, $p < 0.001$) and food ration ($F_{1,8} = 40.494$, $p < 0.001$) were statistically significant, but an interaction was not supported (Figure 7c). Larvae were in higher condition when receiving high food rations and in higher temperature treatments. Conversely, an interaction between temperature and food ration ($F_{1,8} = 17.243$, $p = 0.003$) was detected for later stage walleye pollock such that food sensitivity was significantly higher at 5°C than at 2°C (Figure 7d).

Furthermore, a three-way ANOVA revealed a significant interactive effect of species and food ration ($F_{1,12} = 8.120$, $p = 0.015$), in addition to an independent temperature effect ($F_{1,12} = 7.943$, $p = 0.016$), acting on the total body lipid storage of first-feeding larvae (Figure 8a and b). For both species, total lipid per DWT increased with temperature. Additionally, first-feeding walleye pollock lipid storage was more sensitive to changes in food ration than first-feeding Arctic cod. At the later larval stage, a temperature-food ration interaction ($F_{1,16} = 5.340$, $p = 0.035$) was demonstrated by increased food sensitivity at higher temperatures for both species (Figure 8c and d).

The significant two-way ANOVA (temperature and food ration effects) and three-way ANOVA (temperature, food ration, and species effects) results at intermediate temperatures (2 and 5°C) are summarized in Tables 5 and 6, respectively.

Discussion

Our understanding of gadid condition in response to environmental factors largely stems from studies of Atlantic cod, *Gadus morhua* (e.g. Neilson *et al.*, 1986; Suthers *et al.*, 1992; Lochmann *et al.*, 1995) making direct inferences to polar species unsuitable. Furthermore, while both morphological (e.g. Brodeur *et al.*, 2000; Laurel *et al.*, 2016) and lipid (e.g. Heintz *et al.*, 2013; Copeman *et al.*, 2017) indices have been used separately to assess the condition of early life stage gadids, this study is unique in that it employs the use of multiple indices simultaneously to assess the relative strength and sensitivity of each.

This study provides a direct examination of the morphometric and lipid condition of larval Arctic cod and walleye pollock under different temperature-food ration scenarios. Analyses from this study indicate that: (i) temperature directly impacts the larval condition of Arctic cod and walleye pollock, (ii) effects on larval condition (i.e. BD:SL, TAG:ST, and total lipid storage) vary with both temperature and food availability in a species-dependent manner, and (iii) morphometric and lipid indices should be used in combination, when possible, to sufficiently reflect changes in larval condition across temperature-food ration scenarios.

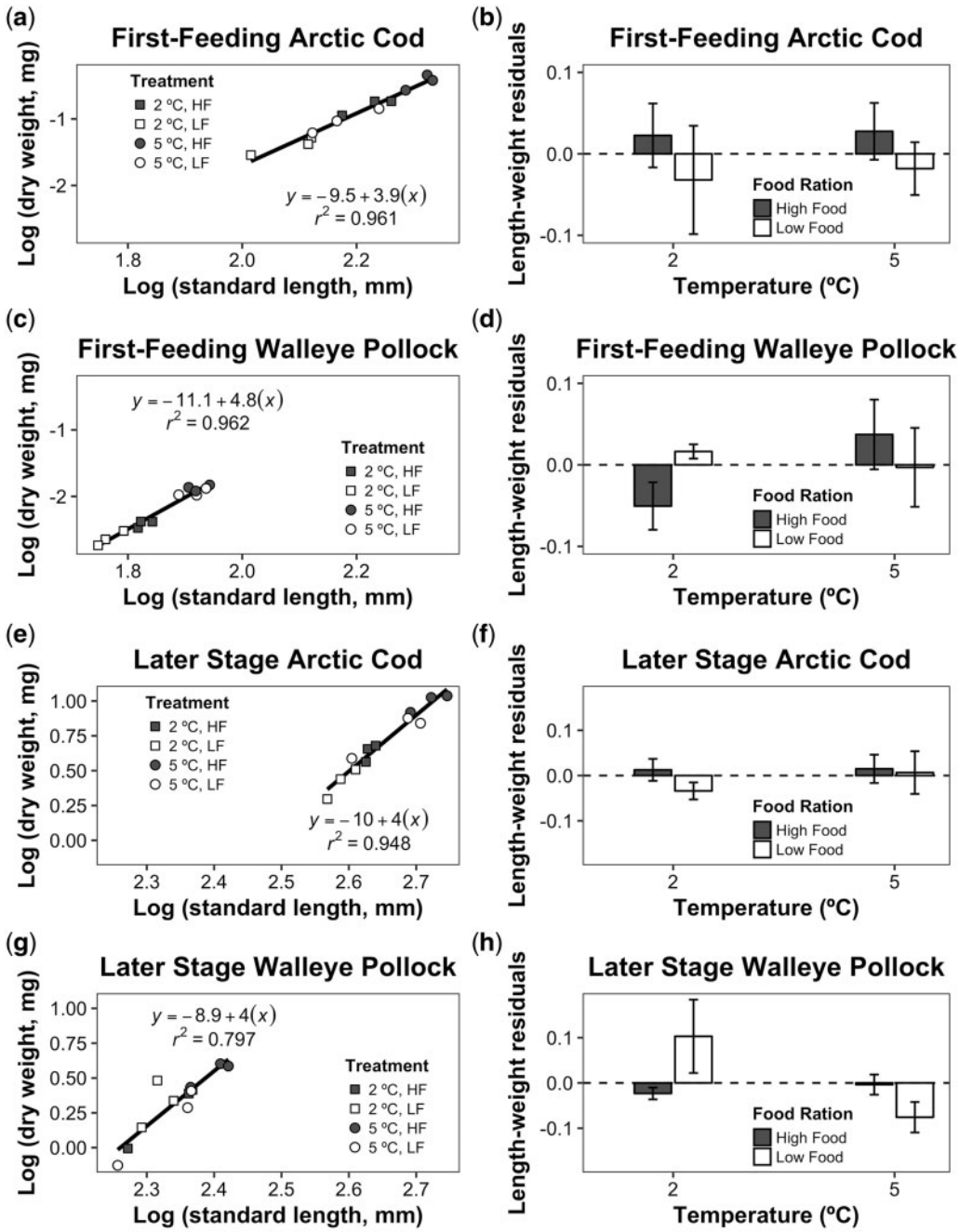

Figure 5. Linear relationships between log-transformed length (SL, mm) and log-transformed DWT (mg) of (a) first-feeding Arctic cod, (c) first-feeding walleye pollock, (e) later stage Arctic cod, and (g) later stage walleye pollock larvae and the residuals of this relationship for (b) first-feeding Arctic cod, (d) first-feeding walleye pollock, (f) later stage Arctic cod, and (h) later stage walleye pollock larvae in high and low food ration treatments at the end of laboratory experiments. Linear regressions were fitted to mean tank data. Length–weight residuals were computed for each tank and plotted as treatment means ± 1 s.e. ($n = 3$ replicate tanks/treatment).

Temperature effects on larval condition

Morphometric condition based on length–weight residuals was not statistically sensitive to temperature differences. This could be partially due to the high variability between replicate tanks, particularly at the more extreme temperatures. At these temperatures, variability between tanks may have exceeded variability between treatments to the extent that treatment differences were not detectable.

The BD:SL condition index generally increased with temperature in all experiments, except for first-feeding Arctic cod where condition was compromised at high temperatures. It has been suggested that at early life stages, fish growth in length precedes an increase in mass (Farbridge and Leatherland, 1987; Ferron and Leggett, 1994). As such, the fish at higher temperatures in this study were growing faster and had therefore likely begun to transition from lengthwise growth to an increase in BD and mass.

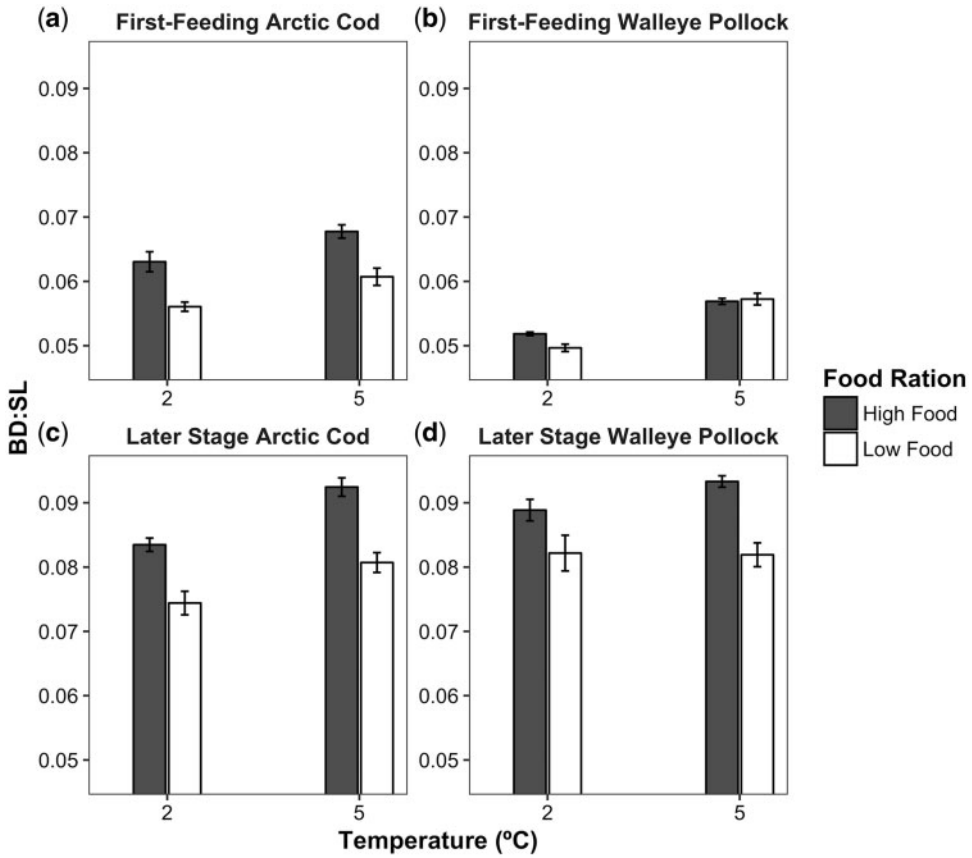

Figure 6. BD:SL of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae receiving high and low food rations at the end of laboratory experiments. Data are treatment means ± 1 s.e. ($n = 3$ replicate tanks per treatment).

Collectively, study metrics from Koenker *et al.* (this issue) and this work indicate that the overall well-being (manifested in terms of survival, growth, and condition) of first-feeding Arctic cod is reduced at 9°C.

First-feeding and later stage Arctic cod were in highest morphometric condition (length–weight residuals and BD:SL) at 5 and 7°C, respectively, which coincides with temperatures of maximum growth (Koenker *et al.*, this issue). In summer months, Arctic cod are commonly associated with thermal-salinity fronts ranging from 2 to 9°C in the nearshore Beaufort Sea (Moulton and Tarbox, 1987). This study indicates that these regions may provide optimal thermal habitat for larval Arctic cod, allowing for the maximization of growth and nutritional condition when food is abundant.

Though the TAG:ST condition of later larval stages of both species were highly sensitive to changes in temperature, it was surprising that first-feeding larval TAG: ST condition did not demonstrate a relationship with temperature despite a general increase in total lipid storage. This largely relates to the relative proportion of different lipid classes accumulated at different ontogenetic stages. The proportion of TAG in first-feeding larvae (2.9%) was substantially lower than in later stage larvae (12.8%). Instead, first-feeding larval lipid composition was made up of considerably more PL. The TAG:ST condition index is sensitive to changes in temperature at the later larval stage but it may be that it should not be employed with first-feeding larvae that are unable to accumulate sufficient TAG to contribute to the TAG:ST index.

Although the BD:SL condition index demonstrated a general increase in condition with temperature, the total lipid storage and later stage TAG:ST reveal unique temperature responses between species. As has been demonstrated for juvenile Arctic cod, the lipid storage of larval Arctic cod in this study increased with temperature over the range where individuals survived. In this case, lipid storage was highest at 5–7°C, with elevated mortality inhibiting lipid analyses above these temperatures. Walleye pollock lipid storage demonstrated a dome-shaped response to temperature with highest measured lipid storage at intermediate temperatures (5–9°C). This trend has been shown with boreal gadid species at the juvenile stage (Copeman *et al.*, 2017) highlighting the high sensitivity of lipid storage to environmental temperature, that was not evident from body mass measures alone.

Furthermore, according to the TAG:ST condition index, Arctic cod were in higher condition than walleye pollock at comparable temperatures. It has been suggested that increased lipid storage by juvenile Arctic cod, relative to boreal gadids, may indicate a life history strategy for prolonged overwintering (Copeman *et al.*, 2017) in environments where winter temperatures are <0°C (Bouchard and Fortier, 2011). The results of this study provide evidence that rapid lipid accumulation by Arctic cod can be observed in the early larval stages.

Based on these collective indices, maximum condition for Arctic cod was observed at 2–5°C for first-feeding larvae and at 7°C for later stage larvae. Summer observations from the field indicate a high abundance of larval Arctic cod in the northeastern

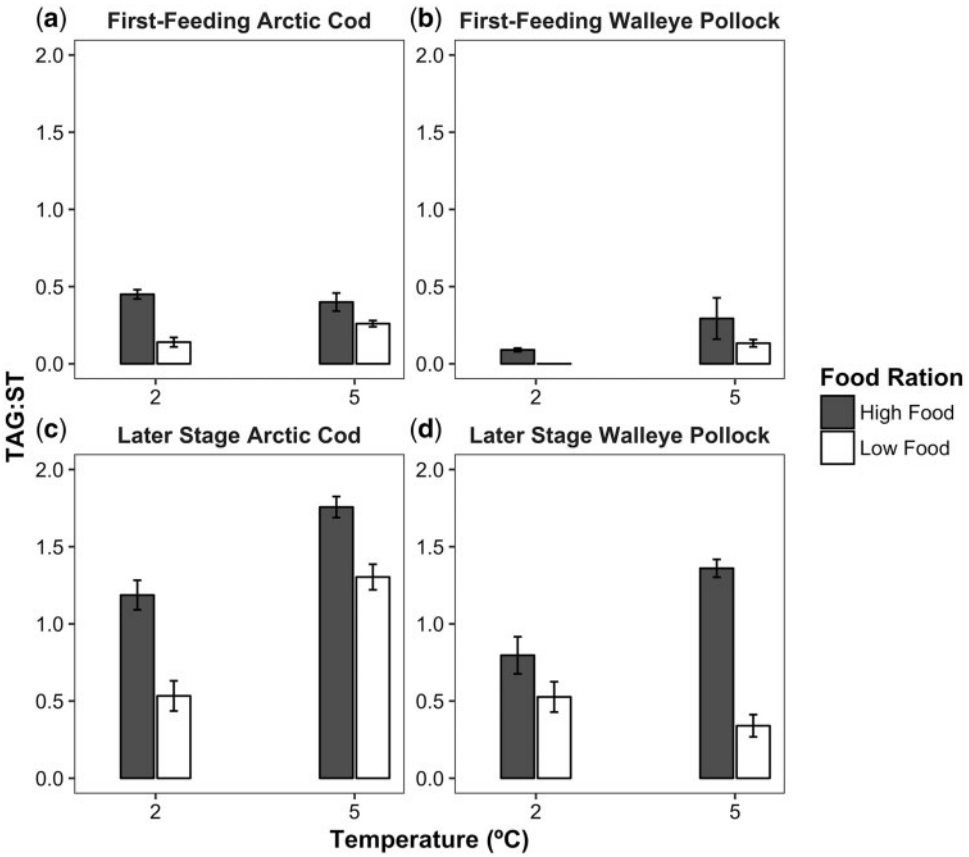

Figure 7. TAG:ST of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae receiving high and low food rations at the end of laboratory experiments. Data are treatment means ± 1 s.e. ($n = 2$–3 replicate tanks per treatment, except for firstfeeding walleye pollock at 2°C and low food ration where $n = 1$).

Chukchi Sea between 0.3 and 5.9°C, with a lower abundance found in the northern Bering Sea and southern Chuckchi Sea between 0.7 and 9.7°C (Kono *et al.*, 2016). This larval distribution pattern is in line with the temperatures of maximum condition reported in this study.

Interactive temperature-prey effects on condition

The residuals from the regression between log-transformed SL and log-transformed DWT can be interpreted as deviations from an average length–weight condition. This study demonstrates that the residuals of this relationship do not provide an adequate condition measure for assessing the impacts of food availability on larval fish species. Length–weight residuals did not detect a significant food ration effect for either species at any larval stage.

Relative to other morphometric variables, BD has been found to be particularly responsive to starvation (Ehrlich *et al.*, 1976; Diaz *et al.*, 2013). In addition to detecting temperature effects throughout most larval experiments, the BD:SL index detected food ration effects on first-feeding Arctic cod condition and both later stage species. First-feeding Arctic cod were more food sensitive than first-feeding walleye pollock, which was contrary to expectation. At hatch, Arctic cod are larger and contain higher yolk reserves that led to the expectation that Arctic cod would be less susceptible to starvation at the onset of feeding. However, it may be that the observed food effect was due to improved foraging and feeding ability of Arctic cod at hatch (relative to walleye pollock) which allowed those under high food ration treatments to take better advantage of the abundant food environment than their low food ration counterparts.

In first-feeding larvae across all high food ration treatments, the TAG:ST condition index did not indicate a significant relationship with temperature, though it proved to be sensitive to changes in both temperature and food availability at 2 and 5°C. At both stages, Arctic cod were in higher condition than walleye pollock and nutritional condition increased with temperature and food ration.

Higher sensitivity to changes in food quantity at 5°C than at 2°C was expected due to elevated metabolic rates at higher temperatures. This pattern was demonstrated by later stage Arctic cod and walleye pollock through one or more lipid condition metrics. Throughout the Arctic, declining sea ice is expected to alter the primary productivity regime, potentially resulting in a mismatch between key Arctic grazers and the production of high-quality food (Søreide *et al.*, 2010; Leu *et al.*, 2011). It has been hypothesized that inter-annual variability in ocean conditions and shifting circulation patterns on the Chukchi Sea shelf may alter the distribution of large energy-rich Arctic zooplankton species (e.g. *Calanus hyperboreus*, *Calanus glacialis*) and increase the contribution of Pacific copepods (e.g. *Neocalanus* sp.) to the diets of Arctic fish species (Pinchuk and Eisner, 2017). Under this scenario, warm temperatures combined with altered timing and availability of lipid-rich prey may interact to decrease the condition of the larval gadid assemblage.

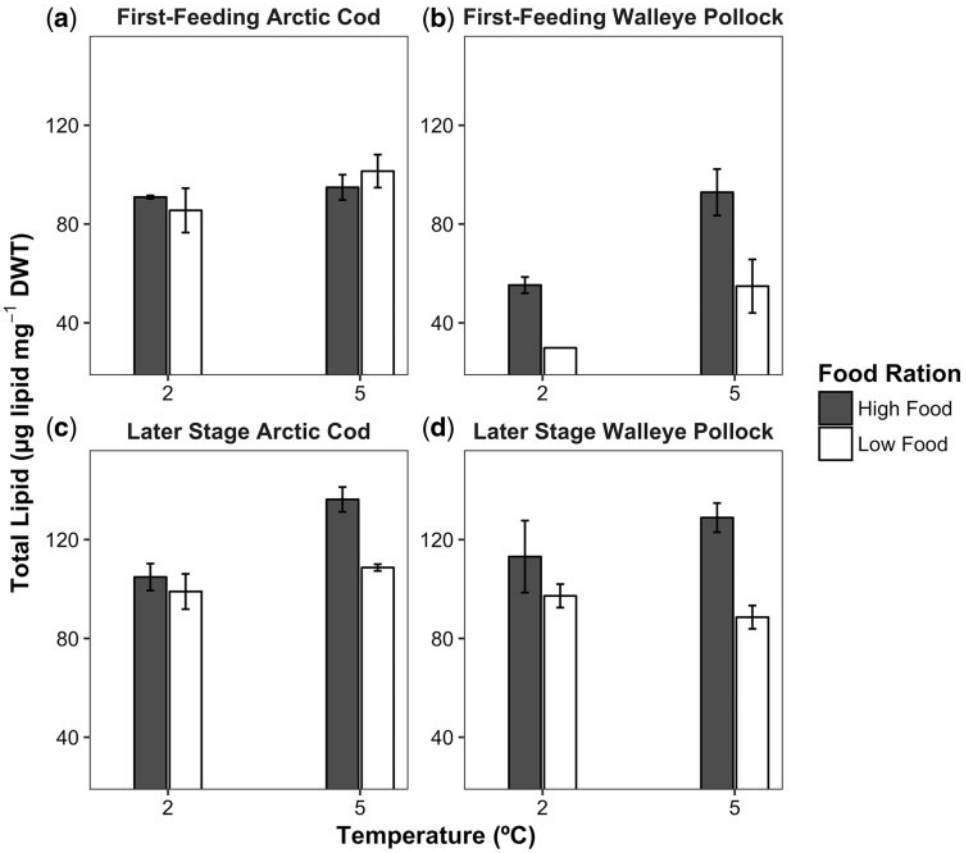

Figure 8. Total lipid (µg lipid mg^{-1} DWT) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae under high and low food rations at the end of laboratory experiments. Data are treatment means ± 1 s.e. (n = 2–3 replicate tanks per treatment, except for first-feeding walleye pollock at 2°C receiving a low food ration where n = 1).

Table 5. Summary of *p*-values from two-way ANOVAs assessing the effects of temperature and food ration on larval condition across high and low food ration treatments at intermediate temperatures (2 and 5°C) according to different morphometric condition indices.

Ontogenetic stage	Species	Results	Length–weight residuals	BD:SL
First-Feeding	Arctic Cod	Temperature	0.840	**0.005**
		Food Ration	0.301	**<0.001**
		Temperature*Food Ration	0.925	0.985
	Walleye Pollock	Temperature	0.366	**<0.001**
		Food Ration	0.719	0.167
		Temperature*Food Ration	0.172	0.068
Later Stage	Arctic Cod	Temperature	0.525	**<0.001**
		Food Ration	0.418	**<0.001**
		Temperature*Food Ration	0.567	0.395
	Walleye Pollock	Temperature	0.120	0.307
		Food Ration	0.571	**0.002**
		Temperature*Food Ration	0.062	0.254

Significant results (α = 0.05) for each condition index are indicated in bold.

Considerations for larval fish condition indices

A comparison of the morphometric and lipid condition indices used in this study, suggests that multiple indices should be utilized, if possible, to assess the sensitivity of larval cod species to environmental conditions. Previous work with juvenile fish (e.g. Gilliers *et al.*, 2004; Walther *et al.*, 2010; Stowell, 2016) has demonstrated the limitations of using a single index to fully explain the impacts of environmental conditions on fish condition.

Morphometric indices offer a logistic advantage, as they are often easier to obtain. However, the larval stage is characterised by rapid morphological changes (e.g. transition to exogenous feeding) (Neilson *et al.*, 1986) which can make it difficult to differentiate between developmental changes and those related to environmental conditions (Ferron and Leggett, 1994). Results from this study indicate that the BD:SL was a good morphometric indicator of condition as it effectively detected species-specific

Table 6. Summary of *p*-values from three-way ANOVAs assessing the effects of species, temperature, and food ration on larval condition across high and low food ration treatments at intermediate temperatures (2 and 5°C) according to different lipid condition indices.

Ontogenetic stage	Results	TAG:ST	Total lipid storage
First-Feeding	Species	**0.010**	**<0.001**
	Temperature	**0.045**	**0.016**
	Food Ration	**0.006**	**0.044**
	Species*Temperature	0.125	0.061
	Species*Food Ration	0.396	**0.015**
	Temperature*Food Ration	0.510	0.890
	Species*Temperature*Food Ration	0.289	0.348
Later Stage	Species	**< 0.001**	0.310
	Temperature	**<0.001**	**0.036**
	Food Ration	**<0.001**	**<0.001**
	Species*Temperature	**<0.001**	0.081
	Species*Food Ration	0.475	0.272
	Temperature*Food Ration	**0.026**	**0.035**
	Species*Temperature*Food Ration	**0.002**[a]	0.981

Significant results ($\alpha = 0.05$) for each condition index are indicated in bold.
[a]Additional separate two-way ANOVAs (temp and food ration) for each later stage species revealed significant temperature ($p < 0.001$) and food ration ($p < 0.001$) effects on Arctic cod condition and a significant temperature*food ration interaction ($p = 0.003$) acting on walleye pollock condition.

responses to temperature and food availability at both larval stages.

It has been suggested that lipid indices are more responsive to short-term change (Lochmann *et al.*, 1995) and to physiological stress in some cases (Copeman *et al.*, 2008). In this study, lipid indices were highly sensitive to species-dependent responses to changes in temperature and food availability at the later larval stage. However, it was found that first-feeding larvae were not yet feeding at a sufficient level to accumulate TAG and, therefore, the TAG: ST condition index was not suitable. Though first-feeding larvae did not appear to accumulate TAG, total lipid storage at this stage was sensitive to changes in temperature and food availability.

Conclusions

This study suggests that the nutritional condition of larval gadids is highly sensitive to changes in temperature and food availability, and that larval condition is highly variable between species. In the Canadian High Arctic, it has been hypothesized that ongoing warming in the short term will increase recruitment of age-0 Arctic cod in the presence of adequate prey availability (Bouchard *et al.*, 2017). However, in regions like the Chukchi Sea, where ocean warming is most pronounced, rising temperatures may interact with reduced availability of lipid-rich prey to decrease the condition of larval gadids. Species-specific impacts to the lipid storage and condition of larval gadids associated with climate change will influence the quality of the forage fish assemblage in the Arctic. These species play a critical role in influencing energy transfer to upper trophic levels and changes in their lipid storage and condition will likely be recognized throughout the lipid-rich Arctic marine food web.

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