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Original Article

Effects of temperature and food availability on the survival and growth of larval Arctic cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*)

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Arctic cod (*Boreogadus saida*) is an ecologically significant species that is uniquely adapted to occupy ice edges, but warming and loss of sea ice are hypothesized to favour more facultative gadids, such as walleye pollock (*Gadus chalcogrammus*). To test this hypothesis, we experimentally measured the growth and survival of Arctic cod and walleye pollock at two larval stages across a range of temperature and food conditions in the laboratory. Results indicated early and late-stage Arctic cod larvae have a competitive growth and survival advantage over walleye pollock at low temperatures. However, these advantages are lost under warmer, food-productive conditions where walleye pollock larvae survived and experienced accelerated growth rates. Growth models developed from this study emphasize the need to account for both species- and stage-specific differences in the thermal response of closely related marine fish larvae. More broadly, these new vital rate data provide a mechanistic framework to forecast spatial-temporal shifts of gadids at the Arctic-boreal interface resulting from climatic warming and altered productivity regimes.

Keywords: biogeography, climate change, match-mismatch, Polar cod, thermal sensitivity

Introduction

In polar regions, mean near-surface temperatures are predicted to warm at rates exceeding global climate change averages (Serreze and Barry, 2011; IPCC, 2013) resulting in drastic impacts to regional ocean conditions. In the Chukchi Sea, August sea surface temperatures are warming at a rate of about + 0.5°C per decade (Richter-Menge *et al.*, 2016) in combination with declining seasonal and perennial sea ice cover (Comiso *et al.*, 2008; Moore and Stabeno, 2015; Frey *et al.*, 2015). The resultant rapid ecosystem-level change in the Arctic marine environment (Hoegh-Guldberg and Bruno, 2010) is predicted to result in accelerated rates of species turnover and severe changes in marine biodiversity (Cheung *et al.*, 2009; Fossheim *et al.*, 2015).

Sea ice extent and seawater temperatures in the polar marine ecosystems are closely tied and together influence processes related to food web dynamics, species physiology, and biogeochemical cycling (Doney *et al.*, 2012). By the mid- to late- twenty-first century, forecasted changes in sea ice thickness and extent may result in an ice-free Arctic in the summer months (Holland *et al.*, 2010; Moore and Stabeno, 2015). Altered timing of sea ice break up has the potential to change the primary productivity regime in the region to the extent that a mismatch occurs between the production of high-quality food

and key Arctic grazers (Søreide *et al.*, 2010; Leu *et al.*, 2011). The indirect effects of temperature through changes in food supply and timing have been shown to be important in determining Atlantic cod recruitment in the North Sea (Beaugrand and Kirby, 2010). Thus, it is likely that bottom-up changes in trophic interactions will influence the success of key Arctic species at all levels of the marine food web (Søreide *et al.*, 2010). However, a mechanistic understanding of these changes remains challenging due to the complex mosaic of direct (i.e. temperature) and indirect (i.e. changes in prey phenology) impacts that result from a rapidly changing climate (Smetacek and Nicol, 2005).

The Alaskan Arctic region includes the US waters of the Chukchi and Beaufort Seas north of the Bering Strait (NPFMC, 2009). Arctic cod (*Boreogadus saida*) is an ecologically important species throughout this region, where it plays a critical mid-trophic role in channelling energy from plankton to upper trophic levels such as marine mammals, seabirds, and other fish (Craig *et al.*, 1982; Bluhm and Gradinger, 2008; Logerwell *et al.*, 2015). Arctic cod often associate with ice edges which may offer both predator refuge and feeding habitat in the form of ice-associated phytoplankton blooms. However, forecasted shrinkage of sea ice habitat could facilitate invasions by more generalist boreal fish species, such as walleye pollock (*Gadus chalcogrammus*), from the North Pacific (Barber *et al.*, 2009; Rand and Logerwell, 2011; Fossheim *et al.*, 2015). Walleye pollock occupies a similar ecologically important role in the Bering Sea and Gulf of Alaska, but because of their high commercial value, their life history and biology is comparatively much better understood than Arctic cod. This is particularly evident during the early life history, as sea ice makes it logistically challenging to conduct field work (e.g. Bouchard and Fortier, 2008, 2011; Falardeau *et al.* 2014) and live-animal experiments in the laboratory (e.g. Sakurai *et al.*, 1998, Graham and Hop, 1995; Laurel *et al.*, 2018). In contrast, the early life history of walleye pollock has been the focus of multiple laboratory studies examining the effects of temperature on egg and larval development and survival (e.g. Bacheler *et al.* 2010; Duffy-Anderson *et al.*, 2016). The absence of comparative biological data on early life stages makes it difficult to determine whether and when poleward shifts of marine fish species might result from climate change (Christiansen *et al.*, 2014).

In marine environments, relatively small changes in temperature and food availability can influence the growth, development, and survival of fish (Peck *et al.*, 2004; Pörtner and Peck, 2010). As poikilotherms, a number of critical physiological processes in fish are regulated by the temperature of the surrounding water. Typically, high latitude fish are characterized by a narrower thermal tolerance range (i.e. stenothermic) than those inhabiting mid-latitudes where wider seasonal fluctuations are common (Pörtner and Peck, 2010). In polar environments, summers are short and subzero temperatures persist during the prolonged winter spawning season (Bouchard and Fortier, 2011). Furthermore, thermal sensitivity in terms of growth and food conversion can vary considerably with ontogenetic stage (Björnsson *et al.* 2001). This is particularly important for fish at critical early life stages when predation, starvation, advective loss, and other external stressors enhance mortality risks (Zhao *et al.*, 2001; Houde, 2008). First-feeding and early life stage cod larvae are likely more sensitive to variable temperatures than later stage larvae and early juveniles due to developmental limitations and low energy storage capacity (Pörtner and Farrell, 2008; Fouzai *et al.*, 2015). These variations in thermal tolerance can be significant at the individual, population, and ecosystem level as different thermal tolerance windows may result in changes in species distributions (Pörtner and Farrell, 2008).

The "Stage-Duration" hypothesis postulates that rapid growth allows larvae to reach a larger size where risk of mortality is reduced and survival to recruitment is improved (Miller *et al.*, 1988; Houde, 2008). However, efforts to assess growth and survival potential in fish rely upon a strong understanding of species-specific environmental tolerances and food requirements (Jobling, 1988). Prey availability and temperature are arguably the most important factors affecting larval growth and early size-at-age (Otterlei *et al.*, 1999). Growth and mortality, in turn, influence recruitment levels in marine fish (Houde, 2008). Therefore, by assessing the sensitivity of a species to environmental conditions affecting growth, it is possible to better understand their likelihood of survival and, thus, the factors dictating population success under a changing climate.

Currently, the growth and survival of larval Arctic cod under various temperature and productivity scenarios has not been investigated experimentally. In this study, we examine the effects of temperature and food availability on the growth and survival of larval Arctic cod and walleye pollock. Specifically, the objectives of this study were to (i) compare temperature-dependent growth and survival at two larval stages across a range of temperatures (−1 to 12°C), (ii) determine the interactive effects of temperature and food availability acting on the species- and stage-specific larval growth and survival, and (iii) develop temperature-dependent growth models for first-feeding and later stage Arctic cod and walleye pollock larvae.

Methods

Egg sources

Laboratory experiments utilized the Alaska Fisheries Science Center's gadid broodstock programme and facilities at the Hatfield Marine Science Center in Newport, OR, USA. Arctic cod broodstock were collected as juvenile fish [70- to 85-mm standard length (SL)] in early August of 2012 and 2013 using a fyke net in the nearshore of Prudhoe Bay, AK (Beaufort Sea, 70.383°N–148.552°W). Walleye pollock broodstock were sourced from juvenile walleye pollock (30- to 50-mm SL at capture) that were collected using light and lift nets in the nearshore of Puget Sound, WA (48.135°N–122.760°W) in late June of 2011, 2012, and 2013.

Fish were transported alive to the laboratory where they were weaned onto formulated foods and held under a 12:12-h light:dark photoperiod to mimic field conditions. All broodstock 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). Juveniles were reared for over 3 years in the laboratory until they became active spawners (age-3+ fish). Additional details on collection and husbandry of Arctic cod can be found in Laurel *et al.* (2016).

Experiments were conducted for first-feeding larvae and later stage pre-flexion larvae of both species. Laboratory experiments for both later stage species and for first-feeding walleye pollock took place in 2015, whereas the first-feeding Arctic cod experiment took place the following spring in 2016.

Egg incubation

A full detailed description of egg collection and incubation of Arctic cod and walleye pollock can be found in Laurel *et al.* (2018). Briefly, adult Arctic cod broodstock ($n = 27$) were held at 2°C and

non-lethally strip spawned in March of each year to produce a series of egg batches. Each egg batch consisted of a single female fertilized with milt from three males. Eggs batches were incubated between 1 and 2°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 a series of 400-l holding tanks maintained between 2 and 3°C until needed for experimentation. First-feeding larval experiments were sourced from a holding tank comprised of two batches spawned on the same day. Later stage feeding experiments were sourced from a holding tank comprised of three separate batches spawned across 2 successive days.

Walleye pollock eggs were collected from a tank of 32 adult broodstock held at 5°C from February to late April 2015. Unlike Arctic cod, pollock are difficult to strip spawn non-lethally, and were instead allowed to spawn naturally in the tank. Fertilized eggs were retained in an egg basket for 24 h to assess quality and then transferred across a series of 100-l stock tanks held at 5–6°C until they were needed for experiments. Although parentage was unknown, the high volume of eggs indicated that multiple females contributed to the egg batches used in both first-feeding and later stage feeding experiments.

General husbandry

Growth experiments were carried out in a series of 38-l glass aquaria covered externally with black plastic and supplied with flow-through, temperature-controlled seawater. Throughout larval experiments, tanks were held at a 12:12-h light:dark photoperiod. Light levels ranged from 1.4 to 2.7 μE m^{-2} s^{-1} 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 if necessary to account for fluctuations in ambient water temperature. Aeration was checked to ensure gentle bubbling beneath the outflow mesh in each tank. Flow rates were adjusted to 300 ml min^{-1} at the start of each experiment using a stopwatch and visually modified to within 270–330 ml min^{-1} each day. Tanks were siphoned daily to remove any mortalities along with excess food and debris. This process was conducted at least 2 h after feeding when visibility was sufficient and most of the live prey had already exited the tank (see below). Tanks were monitored daily and experiments continued for 3 weeks (for later stage experiments) or 5 weeks (for first-feeding experiments). However, if an individual tank approached 100% mortality, larvae were sampled to ensure that morphometric data was collected from each tank. Due to differential mortality, experimental duration varied slightly among tanks (3–5 weeks for first-feeding experiments, 2–3 weeks for later stage experiments).

Live food preparation

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". The addition of green water has been shown to alter the visual feeding environment and change light conditions in a manner that improves larval prey ingestion (Naas *et al.*, 1996). 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 harvested and enriched twice daily in conical tanks to produce two batches for morning and afternoon larval fish feedings. The daytime and overnight batches were enriched for 5 and 16 h, respectively, with Algamac 3050 (0.3 g per million rotifers; Aquafauna, Hawthorne, CA, USA) and RotiGrow Plus (daytime: 0.5 ml per million rotifers, overnight: 1.0 mL per million rotifers; Reed Mariculture, Campbell, CA, USA). Algamac was chosen as a suitable enrichment because it contains a high proportion of long-chained fatty acids which are important for North Pacific larval fish (Copeman and Laurel, 2010). Enrichment tanks were drained overnight through a 53 μm sieve, rinsed with seawater, and resuspended in cooler (5°C) seawater prior to feeding. Enriched rotifers were counted daily for quality control and prey counts. First-feeding larvae in high food ration treatments were supplied enriched rotifers 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.

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. Enriched brine shrimp were drained through nylon mesh and rinsed before being resuspended in seawater. Harvested brine shrimp were counted to determine accurate prey counts for larvae and for quality control. Later stage larvae in high food ration treatments were supplied enriched brine shrimp 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. Low food ration tanks still received green water 2× daily despite not receiving prey in the afternoon.

Tanks were clear of all live prey after ~2 h of each feeding, indicating all prey were either consumed and/or flowed out of the tank between feedings. This ensured that prey quality did not deteriorate over the course of the experiment and larvae were feeding on newly enriched prey.

Experimental design

A summary of experimental temperatures, food rations, and tank replications for all larval experiments is provided in Table 1.

Arctic cod larval experiments

For first-feeding experiments, yolk-sac Arctic cod larvae (mean 5.9-mm SL) were transferred into 1-l beakers to acclimate to each temperature treatment in April 2016 at ~90% hatch level. Once larvae were within 0.5°C of their target temperature, larvae were gently poured into their corresponding aquaria. First-feeding Arctic cod experiments utilized 12 aquaria for high food ration treatments (−1, 2, 5, and 9°C; $n = 3$ replicate tanks/temperature) and 6 for low food ration treatments (2 and 5°C; $n = 3$ replicate tanks/temperature) with larvae stocked at a density of 450 individuals per tank. The first-feeding Arctic cod experiment continued for 35 days, with the exception of the 9°C tanks which were sampled at 21 days and reached 100% mortality prior to 5 weeks.

For the later stage experiment, Arctic cod larvae remained in stock tanks where they were "pulse fed" enriched rotifers (*Brachionus* sp.) twice daily at a density of 5 prey ml^{-1}. Several weeks prior to the start of later stage experiments, larvae began receiving enriched brine shrimp (*Artemia* sp.) at a prey density of 2 prey ml^{-1} in addition to rotifers. Before later stage experiments began, larval gut content was visually examined to ensure that *Artemia* sp. were being consumed. Later stage larvae were in a stage of pre-flexion prior to the experiment.

The later stage Arctic cod experiment began in June 2015 (78 dph) when larvae from the 400-l holding tanks achieved a

Table 1. Experimental design (treatment temperatures, food ration, and replicate tanks) at the start of first-feeding and later stage Arctic cod and walleye pollock larval growth experiments.

Ontogenetic stage	Species	Temperature (°C)	Food ration[a] (HF: high food; LF: low food)	No. of replicate tanks
First-feeding	Arctic Cod	−1	HF: Enriched *Brachionus* sp;	3
		2		3
		5	5 prey ml^{-1}; twice daily	3
		9		3
		2	LF: Enriched *Brachionus* sp;	3
		5	0.5 prey ml^{-1}; twice daily	3
	Walleye Pollock	0	HF: Enriched *Brachionus* sp;	3
		2		3
		5	5 prey ml^{-1}; twice daily	3
		12		3
		2	LF: Enriched *Brachionus* sp;	3
		5	0.5 prey ml^{-1}; twice daily	3
Later stage	Arctic Cod	0	HF: Enriched *Artemia* sp;	4
		2		3
		5	2 prey ml^{-1}; twice daily	3
		7		4
		9		1
		2	LF: Enriched *Artemia* sp;	3
		5	0.5 prey ml^{-1}; once daily	3
	Walleye Pollock	0	HF: Enriched *Artemia* sp;	3
		2		3
		5	2 prey ml^{-1}; twice daily	3
		9		3
		12		3
		2	LF: Enriched *Artemia* sp;	3
		5	0.5 prey ml^{-1}; once daily	3
		9		3

[a]Food rations were manipulated only at intermediate temperatures, 2 and 5°C.

mean SL of 11.3 mm. Later stage experiments used 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) with larvae stocked at a density of ∼100 individuals per tank. 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). The later stage Arctic cod experiment continued for 19–20 days, with the exception of the added tanks which were sampled at the same time (14–15 days total) and one 7°C tank which was sampled at 16 days at it approached 100% mortality.

Walleye pollock larval experiments

In April 2015, first-feeding walleye pollock larvae (mean 4.7-mm SL) were transferred and slowly acclimated (as described above for Arctic cod) 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) with larvae stocked at a density of 450 individuals per tank. The first-feeding walleye pollock experiment continued for 35 days, with the exception of one 12°C tank which was sampled at 21 days and reached 100% mortality prior to 5 weeks.

Walleye pollock larvae used in the later stage experiment remained in stock tanks until July 2015 (84 dph) when they reached a larger length (mean 8.6-mm SL) and were exclusively weaned onto *Artemia* sp., similar to later stage Arctic cod. Prior to experiments, later stage walleye pollock were in a stage of pre-flexion. Later stage walleye pollock larvae were transferred following the same methods 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). The later stage walleye pollock experiment continued for 26 days, with the exception of the 0 and 12°C tanks which were sampled at 12–13 days and the 9°C high food ration tanks which were sampled at 13–19 days as they approached 100% mortality.

Data collection and analysis

Survival was estimated differently for first-feeding and later stage larval experiments. Due to the small size and rapid decay of first-feeding larvae, survival estimates based on daily mortality counts were only possible for later stage larvae. As such, later stage larval mortality was assessed daily to quantify cumulative percent mortality for each species under different treatments. From these measurements, a daily mortality schedule was produced for each species based on the mean daily cumulative percent mortality at each temperature. Additionally, for the purpose of statistical analyses, each tank was assigned a time to 50% cumulative mortality (D_{50}) which was determined as the first day of the experiments where cumulative mortality was at or above 50%. Two of the Arctic cod tanks were assigned a D_{50} equal to the last day of the experiment despite ∼55% of the larvae surviving the entire experimental period.

For first-feeding larvae, survival was estimated from counts of remaining larvae at the end of the experiment. For consistency, this method of estimating survival was also used for later stage

larvae to complement cumulative mortality estimates. To account for slight differences in experimental duration among tanks, a survival fraction representing the fraction of larvae surviving on a daily basis was computed. In this study, the survival fraction, *S*, was calculated for each tank according to the following equation:

$$S = e^{-M}$$

In this equation, M is the daily mortality rate (day^{-1}) derived from the exponential mortality model and calculated as:

$$M = (\ln N_0 - \ln N_t)/t$$

when N_0 is the initial number of larvae stocked, N_t is the number of larvae that survived to the end of the experiment, and t is the experiment duration in days. In instances when no larvae survived (two tanks at 12°C), calculation of the survival fraction was based on a single larvae surviving the duration of the experiment.

Larvae from each tank were randomly sampled from throughout the water column for morphometric measurements (i.e. dry mass, SL, and body depth) at the start, middle, and end of each experiment. Larvae were anaesthetized with MS-222 (50 g l^{-1}) and individual images were taken under calibrated magnification using a digital camera attached to a stereo microscope. Measurements for each fish were obtained from digital images using ImagePro software (Media Cybernetics, Bethesda, MD, USA). SL was determined as the length (mm) from the tip of the snout to the end of the notochord. Body depth was the width (mm) of the larvae posterior to the anus not including the fin-fold. Fish were then rinsed with a 3% ammonium formate solution to remove excess salts and placed on pre-weighed aluminium foil squares. Foils squares were then folded securely and placed in labelled slots on a baking sheet in a drying oven. Samples were dried at 55°C for a minimum of 48 h before determination of dry mass with a microbalance (Sartorius R16OP) to the nearest 1.0 μg.

Specific growth rate (*SGR*), (% mass day^{-1}) was calculated under different temperature-food ration treatments according to the following equation:

$$\mathrm{SGR} = 100(e^{g} - 1)$$

In this equation, g is the instantaneous growth coefficient calculated as:

$$g = (lnW_t - lnW_0)/t$$

where W_t is the final mean dry mass, W_0 is the initial mean dry mass, and t is the number of days between measurements.

All growth and survival analyses were performed using RStudio statistical software (ver. 0.99.491, RStudio, Inc., Boston, MA, USA). Survival (either *S* or D_{50}) for each high food ration tank was analysed using a series of two-way analysis of variances (ANOVAs) examining the effects of temperature by species or ontogenetic stage. To account for the interactive effects of temperature and food availability, a three-way ANOVA was used to test for statistical differences in survival between species, temperature, and food ration at 2 and 5°C. An additional three-way ANOVA was used to consider the effects of stage, temperature, and food ration on survival at these intermediate temperatures. Data were examined for normality and homogeneity of variance to satisfy the assumptions of the ANOVA. A significance level of $\alpha = 0.05$ was used in all analyses.

Statistical differences in growth under high food ration treatments were determined using a two-way ANOVA to examine the effects of species and temperature, and also to examine the effects of ontogenetic stage and temperature. Analysis was conducted on tank replicates (average *SGR*/tank). Three-way ANOVAs were used to test for statistical differences in growth between species, temperature (2 and 5°C only), and food ration within each ontogenetic stage. Additional three-way ANOVAs were also used to assess the effect of ontogenetic stage, temperature (2 and 5°C only), and food ration on growth within species.

A temperature-dependent growth model based on mean *SGR* for tank replicates was developed for the high food ration treatments. This model followed the form below:

$$\mathrm{SGR} = \beta_0 + \beta_1 T + \beta_2 T^2 + I_s\beta_3 + I_s\beta_4 T + I_s\beta_5 T^2$$

where the *SGR* is the response variable, temperature (T) and temperature-squared (T^2) are explanatory variables, and species or stage (I_s) is an indicator variable. The Akaike Information Criterion (AIC) was used to determine whether species-specific models of temperature-dependent growth were justified at each ontogenetic stage. That is, species-specific models were used when AIC values were lower than the simplified model that excluded the I_s indicator variable and therefore assumed no difference in growth between the two species. Similarly, stage-specific models were used when AIC values were lower than the simplified model excluding the I_s indicator variable which assumed no difference in growth between first-feeding and later larval stages.

Following AIC, best-fit regression models (up to two parameters) were used to describe temperature-dependent growth relationships for each species and/or ontogenetic stage. To minimize the impact of size-selective mortality, any treatments experiencing > 80% mortality within the first week of experiments were not used in growth analysis or development of these explanatory growth models.

Results

Temperature effects on survival and growth

The size-at-age (based on SL) of first-feeding and later stage Arctic cod and walleye pollock in high food ration treatments over the course of laboratory experiments is shown in Figure 1. The survival fraction ranged from 0.80–0.97 for Arctic cod and 0.77–0.94 for walleye pollock in high food ration experiments. Although first-feeding Arctic cod were reared across a cooler temperature range (−1 to 9°C) than walleye pollock (0–12°C), survival was lowest in the high temperature treatment for both species (Figure 2a and b; two-way ANOVA; $F_{1,\ 18} = 10.581$, $p = 0.004$). Similar patterns were observed at later stages, with highest survival of both species observed at 2°C (Figure 2c and d). However, unlike first-feeding larvae, there was significantly higher survival of Arctic cod than walleye pollock at comparable temperatures during the later stage (two-way ANOVA, $F_{1,\ 26} = 14.688$, $p < 0.001$).

The impacts of temperature and ontogenetic stage on the survival fraction of each species differed. In Arctic cod, higher temperatures negatively impacted survival for both ontogenetic stages (two-way ANOVA; $F_{1,\ 21} = 13.989$, $p = 0.001$). However, in walleye pollock the survival impacts varied with ontogenetic stage ($F_{1,\ 23} = 12.589$, $p = 0.002$), driven by lower observed survival at the later stage than the first-feeding stage (Figure 2). The effects

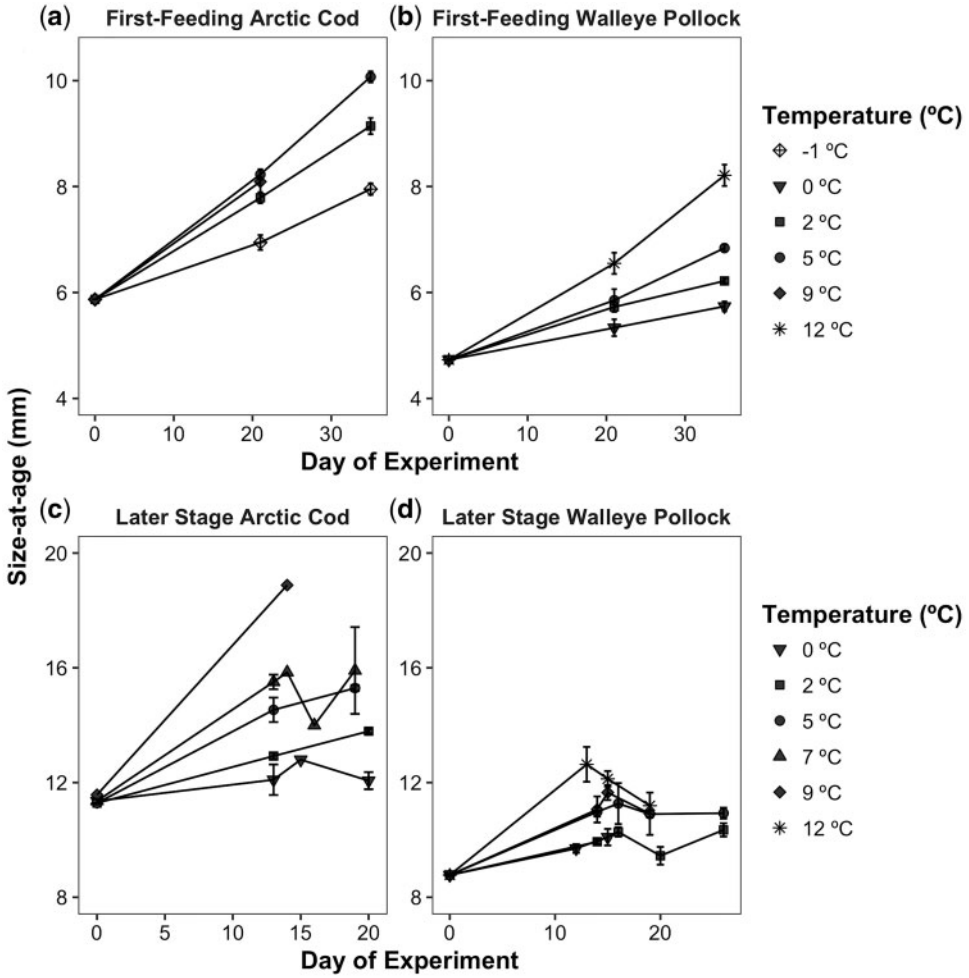

Figure 1. Size-at-age based on SL (mm) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae in high food ration treatments over the course of laboratory experiments. Data are treatment means ±1 s.e. (n = 1–4 replicate tanks/treatment).

of temperature on survival in walleye pollock was not statistically significant ($p = 0.094$), although there was very low survival of late-stage larvae observed in the lowest temperature treatment

For reasons indicated in the "Methods: Section, cumulative percent mortality was only quantified for later stage species (Figure 3). However, time to 50% cumulative mortality (D_{50}) did not vary between species ($F_{1,26} = 0.055$, $p = 0.817$) and temperature treatments ($F_{1,26} = 0.006$, $p = 0.937$) or in the interaction term of the model ($F_{1,26} = 2.726$, $p = 0.111$). Despite not being significant, there were some notable differences in temperature-dependent survival between the two species. Later stage Arctic cod larvae at 9°C rapidly reached 50% cumulative mortality after one day, compared with a mean D_{50} of ≥ 8 days for all other temperature treatments receiving high food (Figure 4a). Conversely, later stage walleye pollock reached 50% cumulative mortality at 0°C after 2 days, whereas D_{50} among the remaining high food ration treatments was $\geq$ 10 days (Figure 4b).

The *SGR* of larvae generally increased with temperature for each species within each ontogenetic stage. However, first-feeding Arctic cod larvae achieved maximum growth at 5°C whereas first-feeding pollock grew progressively faster with temperature to 12°C (Figure 5a and b). This pattern was reflected statistically by way of a significant interaction in the "species*temperature" term of the model of first-feeding larvae ($F_{1,19} = 21.634$, $p < 0.001$). Conversely, a significant interaction was not detected for later stage larvae, although Arctic cod larvae grew faster than walleye pollock across overlapping temperature treatments ($F_{1,22} = 6.153$, $p = 0.021$; Figure 5c and d).

Additional two-way ANOVAs were conducted by species to determine the effects of ontogenetic stage and temperature on growth. A significant interaction between stage and temperature was found for both Arctic cod ($F_{1,21} = 35.513$, $p < 0.001$) and walleye pollock ($F_{1,20} = 4.802$, $p = 0.040$). This interaction was driven by increased temperature-dependent growth in later stage larvae of both species.

Interaction of temperature and food availability

The interactive effects of temperature and food ration were assessed at intermediate temperatures (2 and 5°C) where food rations were manipulated. The size-at-age of first-feeding and later stage Arctic cod and walleye pollock in these treatments over the course of laboratory experiments is shown in Figure 6.

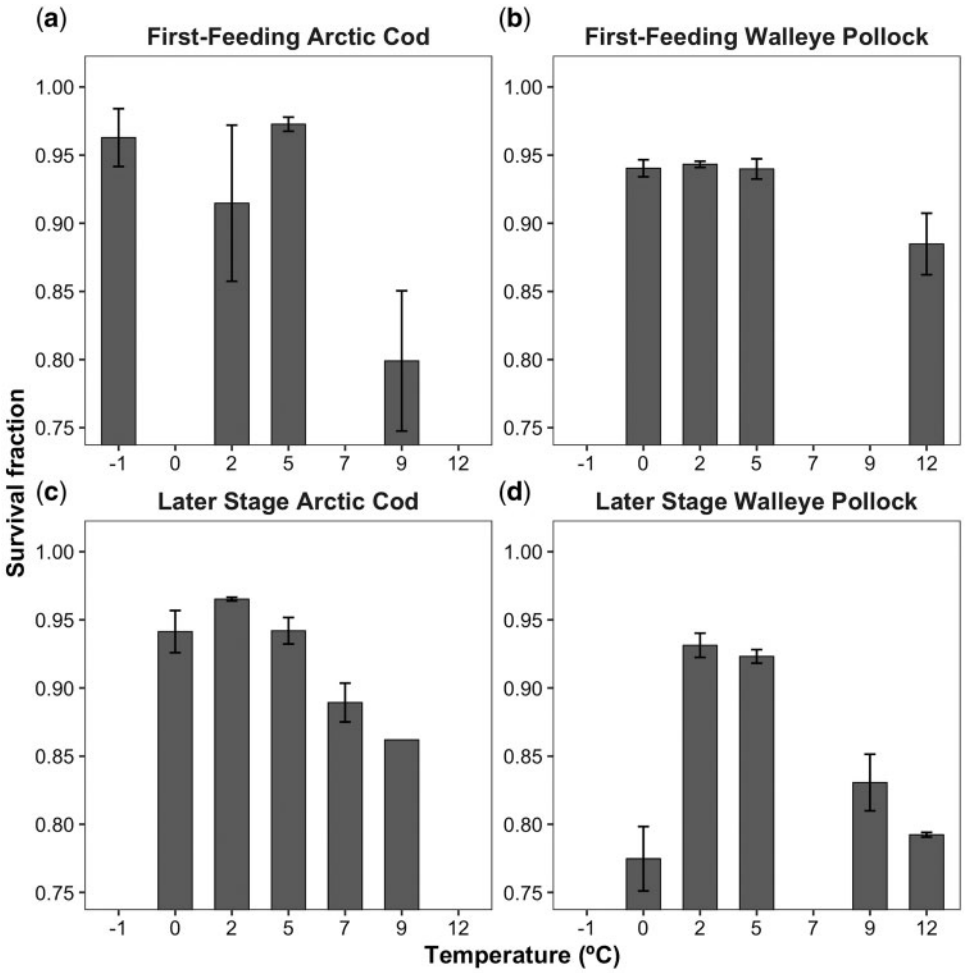

Figure 2. The survival fraction, or the fraction of larvae surviving on a daily basis, for (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock receiving high food rations. Data represent treatment means ±1 s.e. (n = 3 replicate tanks/treatment, except for first-feeding Arctic cod at 2 and 9°C where n = 2 and later stage Arctic cod at 0, 7, and 9°C where n = 4, 4, and 1, respectively).

For first-feeding larvae, there was a significant interaction between the effects of species, temperature, and food ration explaining survival (three-way ANOVA; $F_{1,15} = 5.855$, $p = 0.029$; Figure 7a and b). To better understand the nature of this interaction, species were analysed separately using two-way ANOVAs with temperature and food ration as independent variables. The effects of temperature and food ration on the survival fraction of first-feeding Arctic cod were not significant, although the interaction was close to the statistical alpha ($F_{1,7} = 4.750$, $p = 0.066$). The near-significant interaction term was due to a more positive effect of food on survival within the warmer of the two temperature treatments (Figure 7a). There was also no significant interaction between temperature and food ration for first-feeding walleye pollock, but there was higher survival among high food ration treatments than those receiving low food at both 2 and 5°C ($F_{1,8} = 6.738$, $p = 0.032$; Figure 7b).

For later stage larvae, there was a significant interaction between temperature and food ration ($F_{1,16} = 6.091$, $p = 0.025$) as well as a significant species effect ($F_{1,16} = 10.838$, $p = 0.005$) (Figure 7c and d). These statistical effects were due to higher survival in later stage Arctic cod compared to later stage walleye pollock larvae, and higher survival in low food ration tanks than high food ration tanks at 5°C for both species.

Additional three-way ANOVAs were conducted for each species to determine the effects of ontogenetic stage, temperature, and food ration on survival. A significant three-way interaction was detected for Arctic cod ($F_{1,15} = 7.117$, $p = 0.018$), driven by observations that first-feeding Arctic cod larvae underwent more mortality under low food, warm conditions (5°C) but were relatively insensitive to such changes as later stage larvae (Figure 7a and c). In contrast, the negative effects of low food availability were not exacerbated at higher temperature in walleye pollock larvae (Figure 7b and d). However, first-feeding walleye pollock larvae were more food sensitive than later stage larvae, indicated by a significant interaction between ontogenetic stage and food ration (three-way ANOVA; $F_{1,16} = 12.014$, $p = 0.003$).

The cumulative percent mortality of larvae receiving high and low food rations at 2 and 5°C spanning the duration of later stage laboratory experiments is shown in Figure 8. The time to 50% mortality (D_{50}) was not significantly different between species ($F_{1,16} = 1.200$, $p = 0.290$), among temperatures ($F_{1,16} = 0.048$, $p = 0.829$), or across food rations ($F_{1,16} = 1.614$, $p = 0.222$) by

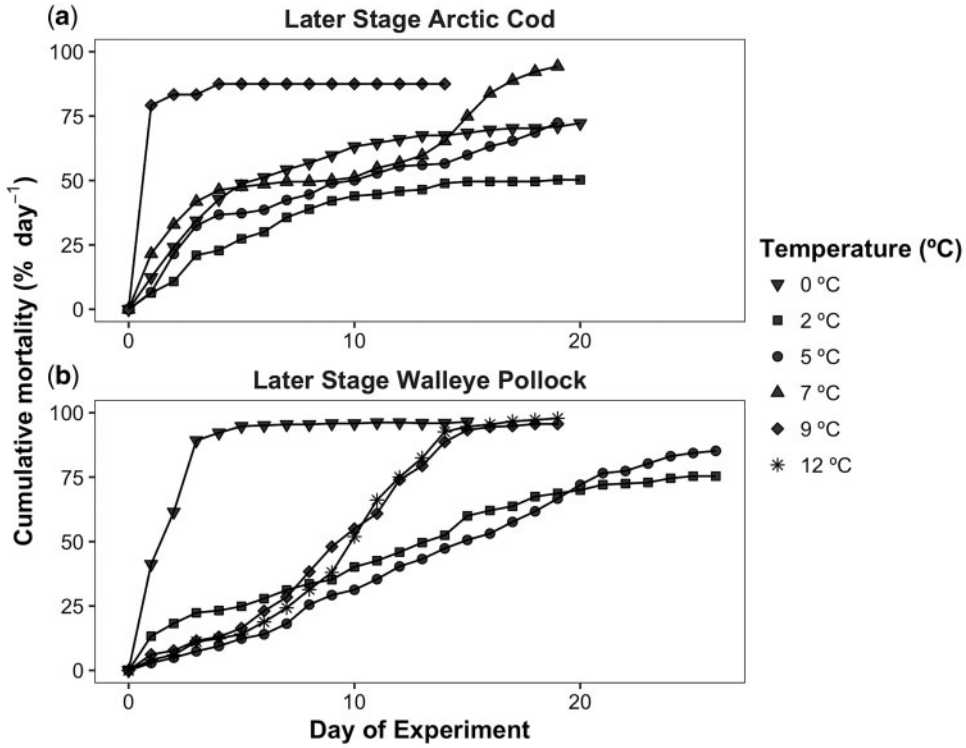

Figure 3. Daily mortality schedule based on the cumulative percent mortality (% day^{-1}) of (a) later stage Arctic cod and (b) later stage walleye pollock receiving high food rations over the duration of laboratory experiments. Data represent treatment mean cumulative mortality based on daily tank mortality counts ($n = 3$ replicate tanks/treatment except for Arctic cod at 0, 7, and 9°C where $n = 4$, 4, and 1, respectively).

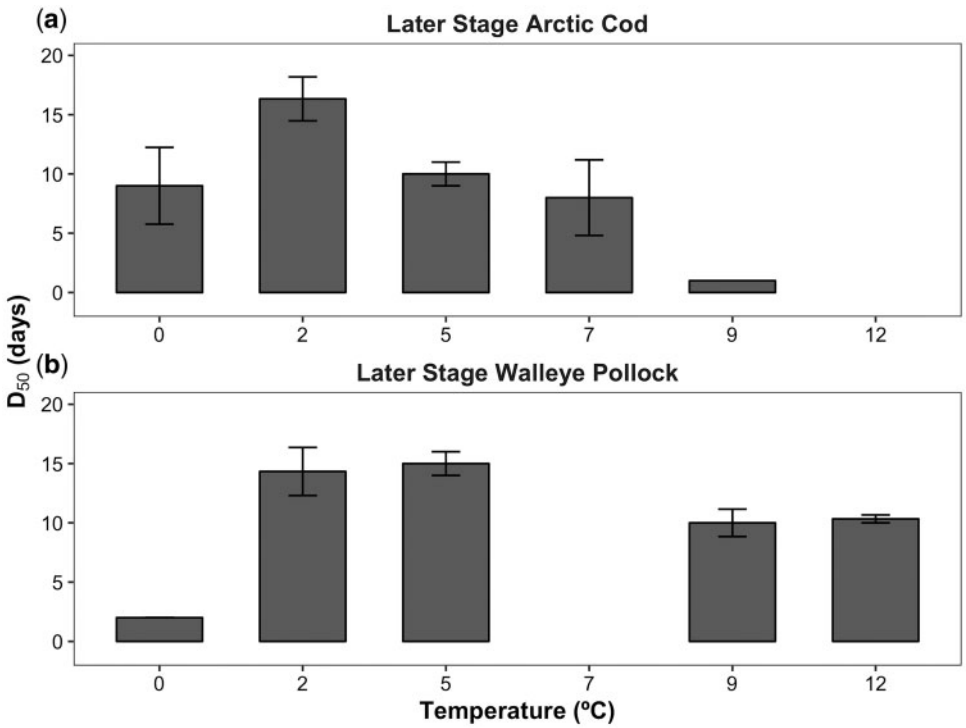

Figure 4. Time to 50% mortality (D_{50}) in days for (a) later stage Arctic cod and (b) later stage walleye pollock. Data represent treatment means ±1 s.e. based on D_{50} values derived from daily tank mortality counts ($n = 3$ replicate tanks/treatment except for Arctic cod at 0, 7, and 9°C where $n = 4$, 4, and 1, respectively).

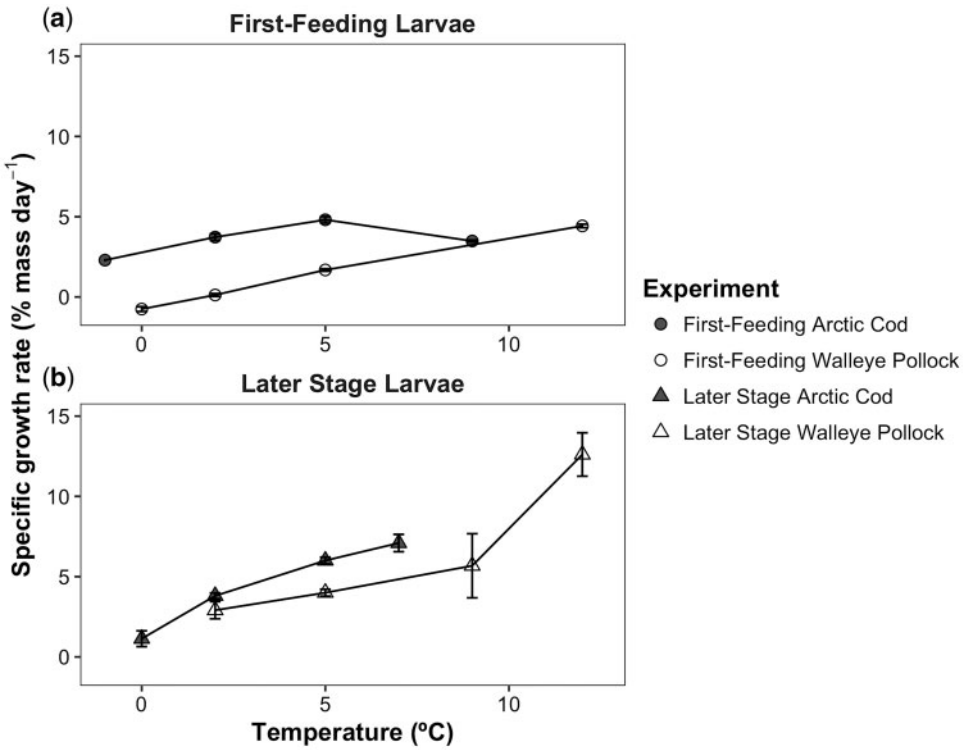

Figure 5. *SGRs* (% mass day^{-1}) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae receiving high food rations. Data are treatment means ±1 s.e. ($n = 3$ replicate tanks/treatment, except for first-feeding Arctic cod at 9°C where $n = 2$ and later stage Arctic cod at 0 and 7°C where $n = 4$). Later stage Arctic cod 9°C data and later stage walleye pollock 0°C data were not used in growth analysis as these treatments experienced > 80% mortality within the first week of experiments.

way of the (three-way ANOVA) (Figure 9). The lack of significance was likely due to high error resulting from variability between tanks. However, a graphical trend was present demonstrating that tanks receiving high food rations took longer to reach 50% mortality than tanks receiving low food rations in most instances (Figure 8).

A significant interaction between species and temperature ($F_{1,\ 16} = 11.426$, $p = 0.004$) and species and food ration ($F_{1,\ 16} = 24.518$, $p < 0.001$) on the *SGR* of first-feeding larvae at intermediate temperatures was detected (three-way ANOVA) (Figure 10a and b). First-feeding Arctic cod were more sensitive to food ration, whereas first-feeding walleye pollock were more sensitive to temperature. Similarly, for later stage larvae, there was a significant interaction between species and temperature ($F_{1,\ 16} = 12.300$, $p = 0.003$) on the larval growth rate at 2 and 5°C (Figure 10c and d), but unlike first-feeding larvae, later stage Arctic cod were more sensitive to temperature than later stage walleye pollock. Growth in the high food ration tanks was also higher than low ration treatments as indicated by significant single term effect of 'food ration' in the model ($F_{1,\ 16} = 9.530$, $p = 0.007$).

Last, a three-way ANOVA between ontogenetic stage, temperature, and food ration revealed a significant interaction between stage and temperature ($F_{1,\ 16} = 13.900$, $p = 0.002$) on the *SGR* of Arctic cod larvae (Figure 10a and c). The effect of temperature on growth was stronger for later stage Arctic cod than for first-feeding larvae. Similarly, a stage-temperature interaction ($F_{1,\ 16} = 9.233$, $p = 0.008$) was statistically supported for walleye pollock, but unlike Arctic cod, the effect of temperature on growth was stronger for first-feeding walleye pollock than for later stage walleye pollock (Figure 10b and d). Additionally, food ration was found to be significant for Arctic cod ($F_{1,\ 16} = 52.135$, $p < 0.001$), and just above the statistical alpha for walleye pollock ($F_{1,\ 16} = 4.343$, $p = 0.054$).

Temperature-dependent growth models

Based on AIC criteria, temperature-dependent growth models were developed separately for each species at each ontogenetic stage. For first-feeding larvae AIC values improved from 93.79 to 4.92 by including a species term in the model. At later stages, AIC scores modestly improved from 112.16 to 105.40 by including the species. Similarly, the growth model for Arctic cod and walleye pollock improved with the inclusion of an ontogenetic term to a model that pooled data across ontogenetic stages (Arctic cod, AIC = 54.77 vs. 77.05; walleye pollock, AIC =96.99 vs. 119.54; See Table 2)

The growth models for first-feeding larvae indicated significantly higher growth by Arctic cod at modelled temperatures < 8.8°C, relative to walleye pollock (Figure 11a). Although Arctic cod were not reared at temperatures > 9°C, model extrapolation indicated walleye pollock growth surpassed Arctic cod at temperatures > 8.8°C. Arctic cod had approximately three times more growth than walleye pollock at temperatures between 0 and 5°C. Furthermore, Arctic cod achieved maximum growth at 5.2°C, while walleye pollock achieved maximum growth at 10.6°C.

Later stage Arctic cod had higher growth than later stage walleye pollock across experimental temperatures from 2.2 to 6.7°C

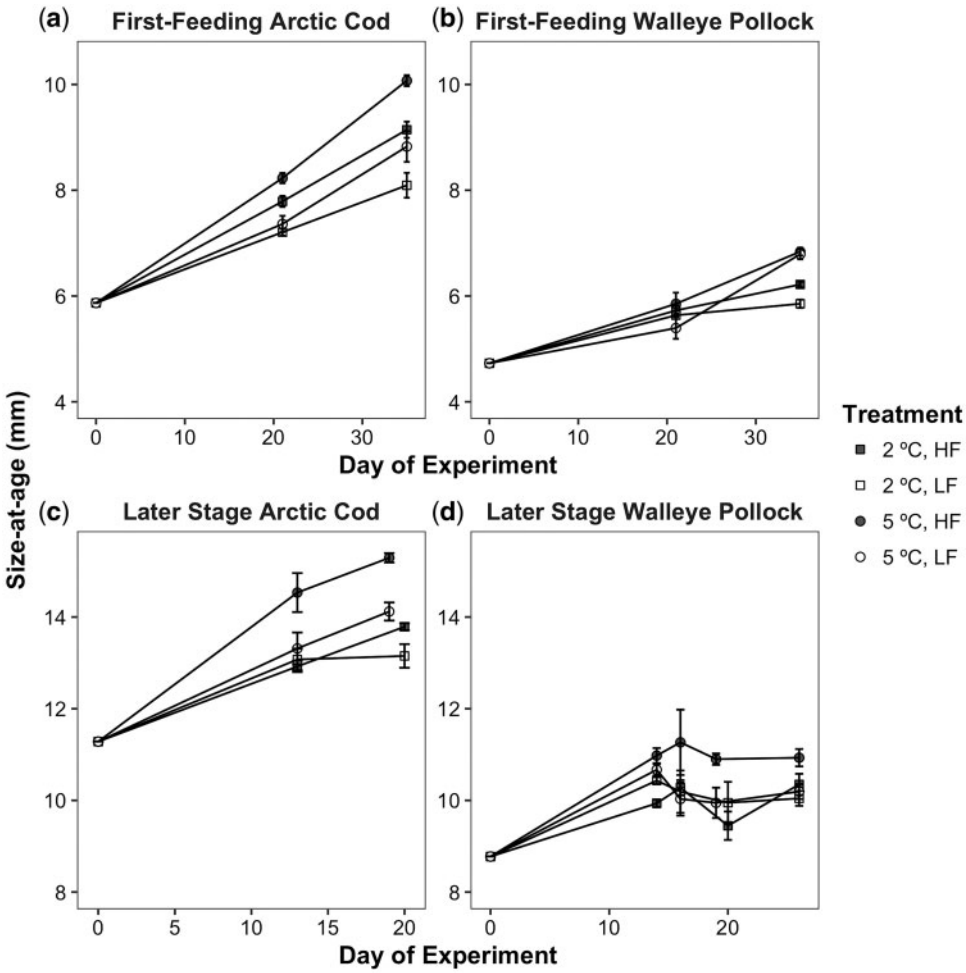

Figure 6. Size-at-age based on SL (mm) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock receiving high and low food rations at intermediate temperature (2 and 5°C) over the duration of laboratory experiments. Data are treatment means ± 1 s.e. ($n = 3$ replicate tanks/treatment).

(Figure 11b). Extrapolated model growth suggests that walleye pollock had a growth advantage over Arctic cod at temperatures > 9.0°C. Within the observed temperature treatments, Arctic cod and walleye pollock achieved maximum growth at 6.7 and 11.2°C, respectively.

Ontogenetic differences in growth were also observed within each species. First-feeding Arctic cod had higher growth from 0 to 2.3°C, but were surpassed by later stage larvae at temperatures > 2.3°C (Figure 11c). First-feeding Arctic cod experienced maximum growth at 5.2°C, while later stage Arctic cod had highest growth at a slightly higher temperature, 6.7°C. Later stage walleye pollock maintained a growth advantage over first-feeding walleye pollock across all modelled temperatures (Figure 11d). Both first-feeding and later stage walleye pollock achieved maximum growth at the upper end of the modelled temperature range (10.6 and 11.2°C, respectively). However, first-feeding walleye pollock growth increased at a relatively linear rate across the temperature range, whereas later stage walleye pollock growth appeared to have an exponential increase in growth at towards higher temperatures.

Discussion

This study is the first laboratory investigation of larval growth for feeding stages of Arctic cod and provided new growth and survival data for walleye pollock over a broader thermal range. Results indicated there was: (i) variable growth and survival responses by Arctic cod and walleye pollock with temperature, and (ii) stage-specific and species-specific differences in larval sensitivity to temperatures and food availability. Together, these data suggest common environmental conditions will impact these species differently, but need to be considered regionally within the ontogenetic stage of each species separately. These results are contextualized with other field and lab studies to determine how Arctic cod and walleye pollock may differentially respond to environmental variability resulting from climate change.

Temperature-dependent survival and growth

Species-specific differences in temperature-dependent survival were evident, as Arctic cod generally had higher survival than walleye pollock at lower temperatures (<7°C). At later stages,

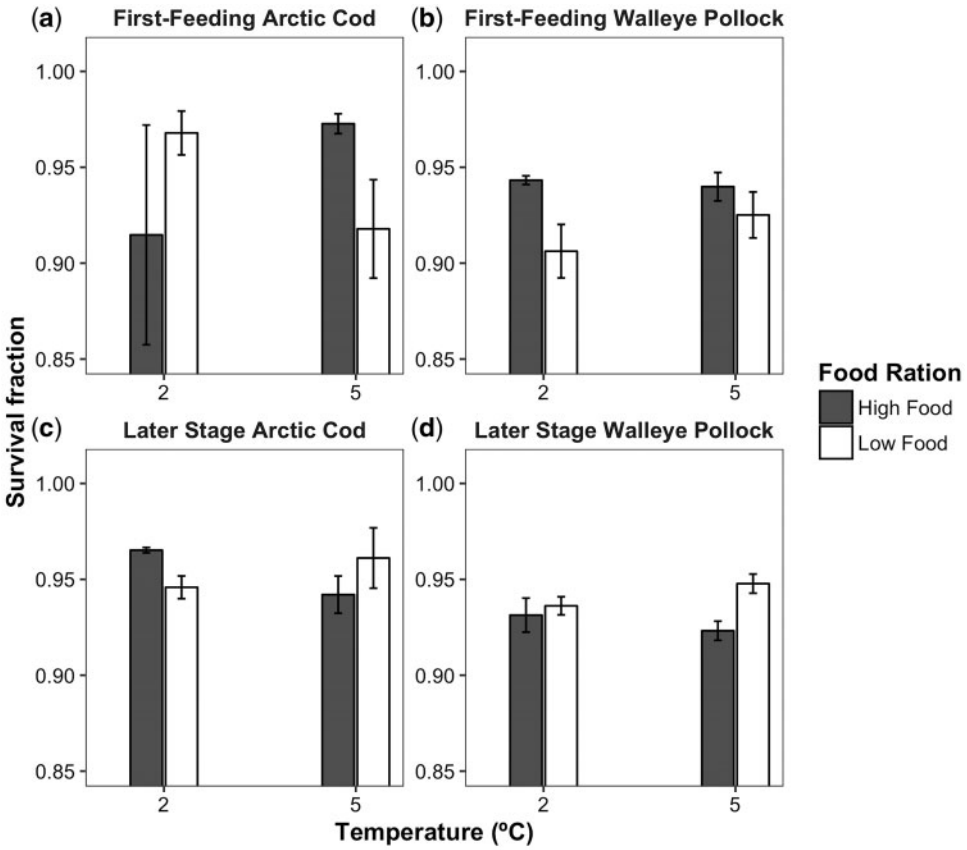

Figure 7. The survival fraction of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae. Data represent treatment means ±1 s.e. ($n = 3$ replicate tanks/treatment except for first-feeding Arctic cod receiving high food rations at 2°C where $n = 2$).

both species appeared to have increased survival at slightly warmer temperatures (highest survival at 2°C), possibly reflecting late-spring conditions during or shortly after ice-melt. However, walleye pollock larvae were clearly more tolerant of warm temperatures than Arctic cod at both stages. In addition, Arctic cod mortality occurred rapidly at 9°C (>80% in 2 days), suggesting that Arctic cod are highly sensitive to even short term increases in temperature.

Temperature-dependent growth rates were also different between species, and these growth differences further changed with ontogeny. Larval Arctic cod maintained a growth advantage over walleye pollock at low temperatures, but were surpassed at ∼ 9°C during both larval stages. Within this range, maximum growth was achieved by Arctic cod at 5–7°C and by walleye pollock at 12°C. This thermal range was similar to laboratory work on juvenile gadids, which report maximum growth at 7°C for age-1 Arctic cod and 13°C for age-0 walleye pollock (Laurel *et al.*, 2016). Laboratory findings by Kunz *et al.* (2016) also reported highest growth rates for age-2 Arctic cod were observed at 6°C, with decreased survival growth observed at 8°C. However, temperature-dependent growth patterns within the larval period shifted between the first-feeding and later feeding stages. For both species, later stage larvae had higher growth at temperatures >2°C and were more growth sensitive to temperature overall than first-feeding larvae. Although the growth rates of fish typically decline with body size and age (Jobling, 1988; Björnsson *et al.*, 2007), growth rates typically increase through the larval stage (Campana, 1990; Baumann *et al.*, 2006; Otterlei *et al.*, 1999). It has been suggested that this increase in growth with size may be due to improved foraging ability with development at the larval stage (Pepin, 1991). First-feeding larvae also begin exogenous feeding before exhaustion of the yolk sac (Hunter, 1981) when the digestive system is not fully functional and enzyme activity levels remain relatively low (Kolkovski, 2001).

These differences in temperature-dependent survival and growth broadly reflect the current distributions of these species in Alaskan waters. Arctic cod are principally restricted to the Chukchi and Beaufort Seas where offshore bottom temperatures seldom exceed 4°C in summer months (Sigler *et al.*, 2011) . Summer surface temperatures vary along an inshore-offshore gradient, ranging from 0 to 2°C in offshore habitats (Crawford *et al.*, 2012) to >14°C in the nearshore (Craig *et al.*, 1982). In the Beaufort Sea, Arctic cod are commonly found shoaling near thermal-salinity fronts separating these surface water masses (Moulton and Tarbox, 1987). Further offshore, Arctic cod are either found in the near-surface waters or deeper, Atlantic-sourced water layer where temperatures range from 0 to 6°C (De Robertis *et al.*, 2017). Although juvenile Arctic cod avoid the coldest intermediate depth waters (<0°C) originating from the Pacific (Crawford *et al.*, 2012), larvae are typically hatching and feeding

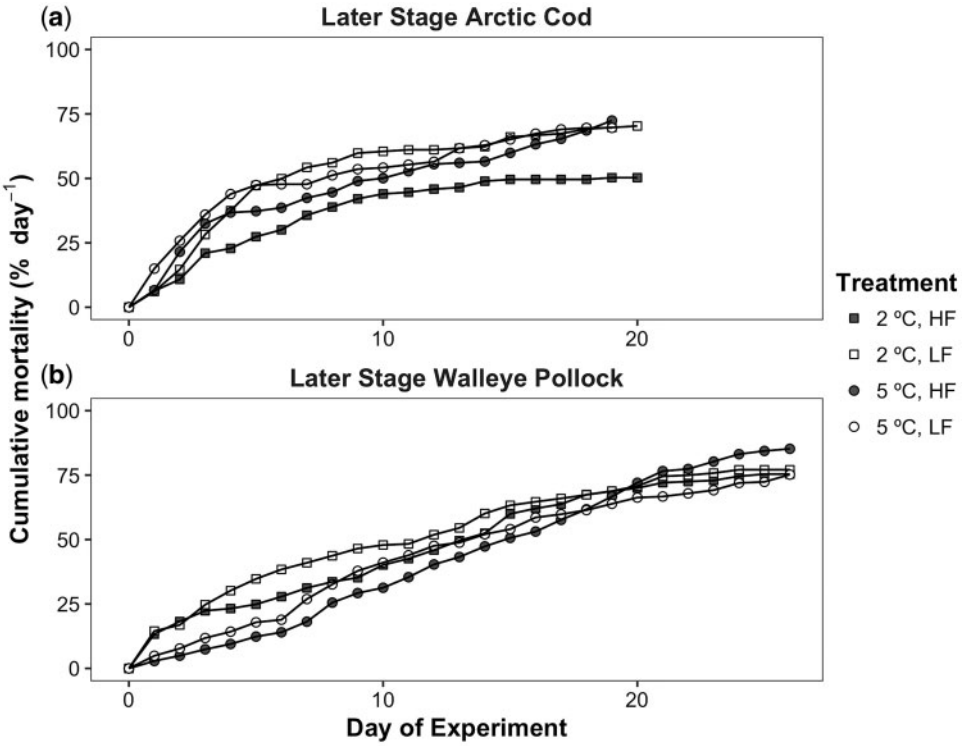

Figure 8. Daily mortality schedule based on the cumulative percent mortality (% day^{-1}) of (a) later stage Arctic cod and (b) later stage walleye pollock receiving high and low food rations at 2 and 5°C over the duration of laboratory experiments. Data represent treatment mean cumulative mortality based on daily tank mortality counts ($n = 3$ replicate tanks/treatment).

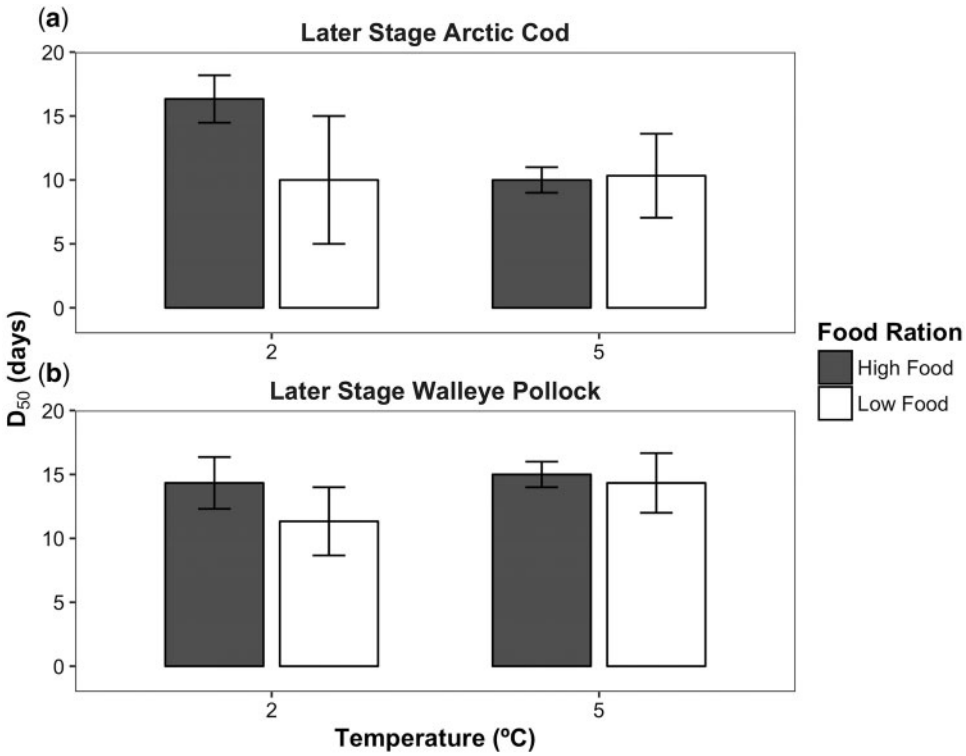

Figure 9. Time to 50% mortality (D_{50}) in days for (a) later stage Arctic cod and (b) later stage walleye pollock receiving high and low food rations at 2 and 5°C. Data represent treatment means ±1 s.e. based on D_{50} values derived from daily tank mortality counts ($n = 3$ replicate tanks/treatment).

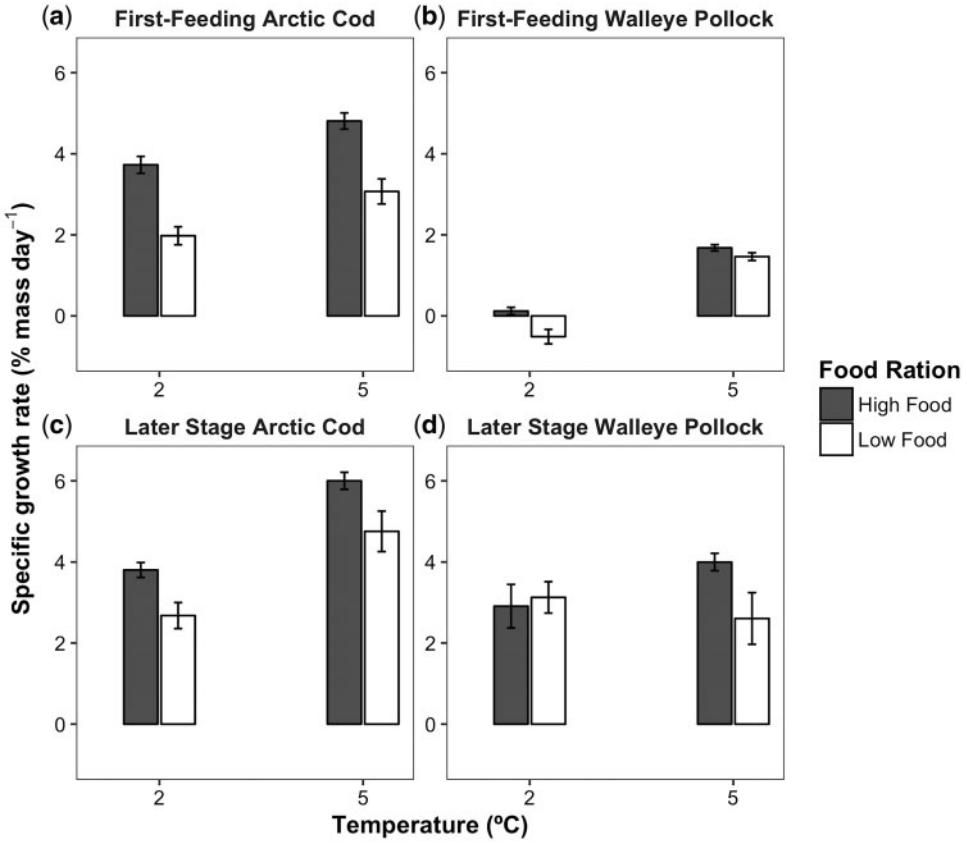

Figure 10. *SGRs* (% mass day^{-1}) of (a) first-feeding Arctic cod, (b) first-feeding walleye pollock, (c) later stage Arctic cod, and (d) later stage walleye pollock larvae receiving high and low food rations at 2 and 5°C. Data are treatment means ±1 s.e. ($n = 3$ replicate tanks/treatment).

Table 2. Parameter estimates for temperature-dependent growth models for Arctic cod (AC) and walleye pollock (WP) under high food ration treatments.

					Parameter estimates		
Ontogenetic stage	**Species**	***T* (°C)**	***SGR* (% mass day^{-1})**	**Model**	**Y_0 mean ± s.e.**	**α mean ± s.e.**	**β mean ± s.e.**
First-feeding	AC	−0.1	2.294	$SGR = Y_o + \alpha T + \beta T^2$	2.349 ± 0.120	0.939 ± 0.072	−0.090 ± 0.008
		1.9	3.727				
		4.8	4.809				
		9.0	3.486				
	WP	0.6	−0.755	$SGR = Y_o + \alpha T + \beta T^2$	−1.141 ± 0.317	0.599 ± 0.178	−0.007 ± 0.018
		2.3	0.122				
		4.9	1.682				
		10.6	4.424				
Later stage	AC	0.0	1.133	$SGR = Y_o + \alpha T + \beta T^2$	1.140 ± 0.775	1.450 ± 0.594	−0.083 ± 0.085
		2.2	3.803				
		4.4	6.003				
		6.7	7.094				
	WP	2.2	2.909	$SGR = ae^{(\beta T)}$	na	−1.352 ±0.586	0.194 ± 0.042
		4.7	3.998				
		8.6	5.678				
		11.2	12.609				

Mean treatment *SGR* values are based on replicate tanks ($n = 3$ except for first-feeding Arctic cod at ~9°C where $n = 2$ and later stage Arctic cod at 0 and 7°C where $n = 4$) for each species at each temperature. See "Methods" section for additional details on model selection criteria.

under extremely cold, unstratified conditions in spring following ice break-up (−1.8 to 0°C), possibly as a means extending the duration of the first summer growth period to achieve sufficient pre-winter size (Bouchard and Fortier, 2011). The results from this study confirm that Arctic cod larvae can indeed successfully grow and maintain high survival at 0°C well into the late larval stages.

In contrast, walleye pollock occupy a more diverse range of thermal habitats along a very broad latitudinal range extending

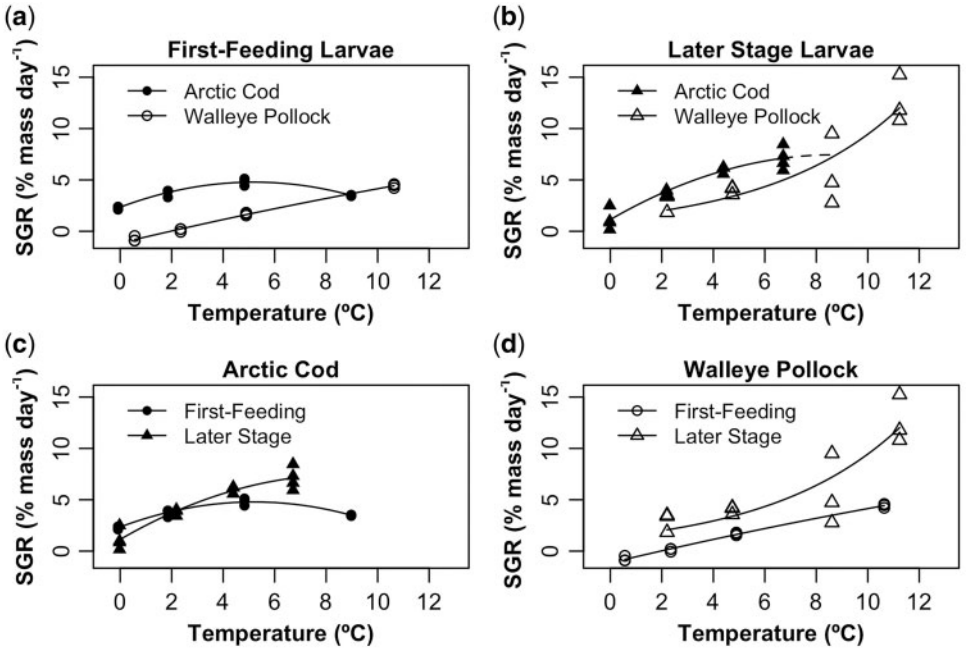

Figure 11. Explanatory models of SGRs; % mass day^{-1}) for each species and ontogenetic stage. Top panels (a) and (b) compare species by ontogenetic stages whereas bottom panels (c) and (d) compare ontogenetic stages by species. All growth rates are based on larvae receiving high food rations. Data are tank means ($n = 3$ replicate tanks/treatment, except for first-feeding Arctic cod at 9°C where $n = 2$ and later stage Arctic cod at 0 and 7°C where $n = 4$). Later stage Arctic cod at 9°C and later stage walleye pollock at 0°C were not used in developing growth models due to high mortality (>80%) within the first week of experiments. The dashed line in the later stage Arctic cod model represents extrapolation of the model beyond the experimental temperature range. See "Methods" section and Table 2 for additional details on model selection criteria and parameters.

from the Puget Sound to the Northern Bering Sea (e.g. Bailey *et al.*, 1999). Eggs and larvae can be exposed to spring temperatures <0°C in the Bering Sea (Blood, 2002), and eggs develop and hatch successfully at temperatures between −1.0 and 12°C without experiencing significant malformations or mortality (Blood, 2002; Laurel *et al.*, 2018). Although persistent, cold bottom water (<2°C) on the Bering Sea continental shelf (i.e. "cold pool") may restrict poleward shifts in adult distribution and spawning activity (Mueter and Litzow, 2008), some portion of eggs are likely advecting into the cold pool (Blood, 2002). Age-0 juvenile stages of pollock are occasionally found in the Chukchi Sea (Logerwell *et al.*, 2015), and although the thermal histories of these walleye pollock are unknown, the observations suggest larvae can indeed successfully develop and feed under some Arctic conditions. However, our laboratory data suggest feeding stages of walleye pollock larvae would undergo high rates of temperature-dependent mortality if spring-early summer conditions remained <2°C into the later larval stages. In the Bering Sea, feeding stage larvae are most associated with higher summer temperatures, more so than feeding conditions and other environmental parameters (Smart *et al.*, 2012). The same study also noted that the temperature-relationships are stage-specific for walleye pollock larvae, with early stages associated with lower temperature and late stages associated with higher temperatures (Smart *et al.*, 2012). These patterns support the observed shift in survival and growth we observed in later stage walleye pollock exposed to higher temperatures, and further emphasize the importance of including ontogeny in predictions of environmental response of marine fish larvae.

Interaction of temperature and food availability

Complex interactions of sea ice decline are linked to variable productivity (Arrigo and van Dijken, 2011) and will likely impact larval fish survival, growth, feeding, and condition (Thanassekos and Fortier, 2012; Kristiansen *et al.*, 2014). Although we did not fully parameterize growth and survival across a continuous range of temperature-feeding scenarios, this study provided an indication of the relative impact of "match-mismatch" scenarios (Cushing, 1990) for these two species under cold or warm conditions in the spring (first-feeding stages) and early summer (late-feeding stages).

In terms of survival, first-feeding walleye pollock exhibited sensitivity to food availability at both 2 and 5°C, while Arctic cod were not significantly impacted. Survival responses to the food environment at this stage are likely the result of species differences in size-at-hatch and corresponding foraging capabilities. At hatch, Arctic cod are substantially larger than walleye pollock (~6.2 vs. 4.5 mm, respectively) and have 3–6× more yolk reserves (Laurel *et al.*, 2018). These characteristics likely lower the risk to prey mismatch and may contribute to the higher food sensitivity of walleye pollock compared with Arctic cod observed in this study.

At the later larval stage, it was unexpected to find that both species experienced higher survival under low food conditions in the 5°C treatment. An examination of the mortality schedule for these treatments indicated that the larvae in the low food ration treatments experienced higher mortality than larvae in the high food ration treatments at the early onset of the experiment. This suggests there was an immediate negative impact of low food

conditions on these larvae. The high larval mortality measured in the high food treatments was observed at the end of the experiment, possibly because these larvae were growing faster and approaching the onset of flexion. Ultimately, physiological and morphological changes during larval fish development improve feeding and growth efficiency, but metamorphic changes are considered to be energy-demanding processes which may interfere with growth and survival when feeding ability is compromised during developmental changes (Geffen *et al.*, 2007). It has been shown that the onset of flexion and metamorphosis is generally size-dependent but can also be influenced by both environmental and nutritional factors (Falk-Petersen, 2005). Therefore, larvae in the high food ration tanks may have experienced a size- or growth-dependent critical period near the end of the experiment.

Growth sensitivity to temperature and food also shifted with ontogeny. At the first-feeding larval stage, Arctic cod growth was more sensitive to food availability, while walleye pollock were more temperature sensitive. An assessment of growth rates across ontogenetic stages revealed that the temperature sensitivity of Arctic cod increased with age, while it decreased for walleye pollock. Other studies of larval Arctic cod have demonstrated the highly variable nature of the relative impacts of temperature and prey availability on growth. For example, prey density has been shown to limit the feeding success (and subsequent growth) of Arctic cod larvae in Hudson Bay (Fortier *et al.*, 1996), yet contradictory findings from the Northeast Water polynya indicate that larval Arctic cod feeding success is largely determined by temperature with little to no impact of prey density on the feeding success of larvae of all sizes (Michaud *et al.*, 1996).

Impacts of climate change

The results of this study provide a clear indication that temperature is a key factor determining growth and survival rates in larval Arctic cod and walleye pollock. Laboratory-derived growth rates are increasingly being used to understand the mechanisms impacting growth rates of fish in the wild (Folkvord, 2005), therefore we anticipate the growth models presented here will provide some information on how these species will respond to ocean warming. These data are also important in the development of Individual Based Models (IBMs) incorporating biophysical transport models (e.g. Petrik *et al.*, 2016) and bioclimate envelope models (e.g. Pearson and Dawson, 2003) used to define current and future biogeographies, as well as, better understand the potential for acclimatization of these species to changing conditions (Pörtner and Farrell, 2008). It is important to recognize that the offspring from this study are sources from broodstock that were grown and matured in the laboratory under environmental conditions that differed from natural conditions. The influence of maternal experience on the thermal reaction norms of the embryos studied in this experiment are unknown. Therefore, the derived parameters on growth and survival derived from this study will remain uncertain in the absence of knowing maternal effects on offspring phenotypes.

Our results clearly emphasize the need to consider both the species-specific and within species, ontogenetic thermal reaction norms of growth and survival, as marine species from different regions will be exposed to seasonally dynamic changes in ocean temperatures throughout their life history. Distinct temperature-dependent growth models have been used to describe juvenile gadid growth in laboratory experiments (Laurel *et al.*, 2016), but it is clear from this study that stage-specific growth models will be required for larvae during the winter-spring transition in the Arctic. It is also notable that stage-specific models were required for both species across a relatively short developmental period from first-feeding to later larval stages (2–3 months). These shifts in temperature-dependent growth within and between species also change the thermal "tipping-points" where one species has a growth advantage over the other. For example, juvenile growth models indicate that Arctic cod have a growth advantage at low temperatures, but are surpassed by walleye pollock at temperature >2.5°C (Laurel *et al.*, 2016). In contrast, at the larval stage, Arctic cod maintained a growth advantage over a wider range of temperatures, up to 6.7°C without notable changes in observed mortality.

Ultimately, changes in extreme temperatures, rather than mean temperatures, may be critical for a species' persistence in a region (Stachowicz *et al.*, 2002). The low survival and reduced growth potential relative to walleye pollock at 9°C in the laboratory demonstrates that late hatching Arctic cod may experience reduced survival under extreme summer conditions in some areas. The thermal range under which larval Arctic cod can survive, despite being even narrower than the juvenile stage, may still be broad enough to survive or even benefit from further spring warming and early ice breakup in the Chukchi and Beaufort Sea. Long-term scenarios depend on whether ice coverage and cold temperatures in the North Bering and Chukchi Seas will continue to serve as a barrier preventing spawning activity of walleye pollock from advancing poleward.

Conclusions

In conclusion, Arctic cod were able to maximize growth and survival at lower temperatures than walleye pollock larvae. Rising temperatures and altered productivity regimes associated with climate change in the Arctic have the potential to constrain the habitat available to Arctic cod and, thus, dramatically decrease its competitive strength relative to North Pacific gadid species, like walleye pollock. Temperature-dependent growth models developed in this study emphasize the need to consider species- and stage-specific differences in the growth during the larval period. Furthermore, significant impacts to the growth and survival of Alaskan gadids from continued warming in the Arctic have implications for recruitment and population success of these species and those that prey upon them. Knowledge of the habitat requirements of these ecologically important species is essential for effective resource management, and is key to understanding the broad implications of global change.

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References

Arrigo, K. R., and van Dijken, G. L. 2011. Secular trends in Arctic Ocean net primary production. Journal of Geophysical Research: Oceans, 116: C09011.

Bacheler, N. M., Ciannelli, L., Bailey, K. M., and Duffy-Anderson, J. T. 2010. Spatial and temporal patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering Sea inferred from egg and larval distributions. Fisheries Oceanography, 19: 107–120.

Bailey, K. M., Quinn, T. J., Bentzen, P., and Grant, W. S. 1999. Population structure and dynamics of walleye pollock, Theragra chalcogramma. Advances in Marine Biology, 37: 179–255.

Barber, D. G., Lukovich, J. V., Keogak, J., Baryluk, S., Fortier, L., and Henry, G. H. R. 2009. The changing climate of the Arctic. Arctic, 61: 7–26.

Baumann, H., Grohsler, T., Kornilovs, G., Makarchouk, A., Feldmann, V., and Temming, A. 2006. Temperature-induced regional and temporal growth differences in Baltic young-of-the-year sprat Sprattus sprattus. Marine Ecology Progress Series, 319: 311–311.

Beaugrand, G., and Kirby, R. R. 2010. Climate, plankton and cod. Global Change Biology, 16: 1268–1280.

Björnsson, B., Steinarsson, A., and Oddgeirsson, M. 2001. Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES Journal of Marine Science, 58: 29–38.

Björnsson, B., Steinarsson, A., and Árnason, T. 2007. Growth model for Atlantic cod (*Gadus morhua*): effects of temperature and body weight on growth rate. Aquaculture, 271: 216–226.

Blood, D. M. 2002. Low-temperature incubation of walleye pollock (*Theragra chalcogramma*) eggs from the southeast Bering Sea shelf and Shelikof Strait, Gulf of Alaska. Deep-Sea Research II, 49: 6095–6108.

Bluhm, B. A., and Gradinger, R. 2008. Regional variability in food availability for Arctic marine mammals. Ecological Applications, 18: S77–S96.

Bouchard, C., and Fortier, L. 2008. Effects of polynyas on the hatching season, early growth and survival of polar cod *Boreogadus saida* in the Laptev Sea. Marine Ecology Progress Series, 355: 247–256.

Bouchard, C., and Fortier, L. 2011. Circum-arctic comparison of the hatching season of polar cod *Boreogadus saida*: a test of the freshwater winter refuge hypothesis. Progress in Oceanography, 90: 105–116.

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries Aquatic Sciences, 47: 2219–2227.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries, 10: 235–251.

Christiansen, J. S., Mecklenburg, C. W., and Karamushko, O. V. 2014. Arctic marine fishes and their fisheries in light of global change. Global Change Biology, 20: 352–359.

Comiso, J. C., Parkinson, C. L., Gersten, R., and Stock, L. 2008. Accelerated decline in the Arctic sea ice cover. Geophysical Research Letters, 35: L01703.

Copeman, L. A., and Laurel, B. J. 2010. Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Marine Ecology Progress Series, 412: 259–272.

Copeman, L. A., Laurel, B. J., and Parrish, C. C. 2013. Effect of temperature and tissue type on fatty acid signatures of two species of North Pacific juvenile gadids: a laboratory feeding study. Journal of Experimental Marine Biology and Ecology, 448: 188–196.

Craig, P. C., Griffiths, W. B., Haldorson, L., and McElderry, H. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 39: 395–406.

Crawford, R. E., Vagle, S., and Carmack, E. C. 2012. Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. Polar Biology, 35: 179–190.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology, 26: 249–293.

De Robertis, A., Taylor, K., Wilson, C. D., and Farley, E. V. 2017. Abundance and distribution of Arctic cod (*Boreogadus saida*) and other pelagic fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas. Deep Sea Research Part II: Topical Studies in Oceanography, 135: 51–65.

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H. M. *et al.* 2012. Climate change impacts on marine ecosystems. Annual Review of Marine Science, 4: 11–37.

Duffy-Anderson, J. T., Barbeaux, S. J., Farley, E., Heintz, R., Horne, J. K., Parker-Stetter, S. L., Petrik, C. *et al.* 2016. The critical first year of life of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea: implications for recruitment and future research. Deep-Sea Research Part II-Topical Studies in Oceanography, 134: 283–301.

Falk-Petersen, I. B. 2005. Comparative organ differentiation during early life stages of marine fish. Fish and Shellfish Immunology, 19: 397–412.

Falardeau, M., Robert, D., and Fortier, L. 2014. Could the planktonic stages of polar cod and Pacific sand lance compete for food in the warming Beaufort Sea? ICES Journal of Marine Science, 71: 1956–1965.

Folkvord, A. 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1037–1052.

Fortier, L., Gilbert, M., Ponton, D., Ingram, R. G., Robineau, B., and Legendre, L. 1996. Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). III. Feeding success of marine fish larvae. Journal of Marine Systems, 7: 251–265.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change, 5: 673–677.

Fouzai, N., Opdal, A. F., Jørgensen, C., and Fiksen, Ø. 2015. Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients. Marine Ecology Progress Series, 529: 199–212.

Frey, K. E., Moore, G. W. K., Cooper, L. W., and Grebmeier, J. M. 2015. Divergent patterns of recent sea ice cover across the Bering, Chukchi, and Beaufort Seas of the Pacific Arctic Region. Progress in Oceanography, 136: 32–49.

Geffen, A. J., van der Veer, H. W., and Nash, R. D. M. 2007. The cost of metamorphosis in flatfishes. Journal of Sea Research, 58: 35–45.

Graham, M., and Hop, H. 1995. Aspects of reproduction and larval biology of Arctic cod (*Boreogadus saida*). Arctic, 48: 130–135.

Hoegh-Guldberg, O., and Bruno, J. F. 2010. The impact of climate change on the world's marine ecosystems. Science, 328: 1523–1528.

Holland, M. M., Serreze, M. C., and Stroeve, J. 2010. The sea ice mass budget of the Arctic and its future change as simulated by coupled climate models. Climate Dynamics, 34: 185–200.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science, 41: 53–70.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. *In* Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries, pp. 34–77. Ed. by R. Lasker. University of Washington Press, Seattle, WA, USA. 131 pp.

IPCC. 2013. Long-term Climate Change: Projections, Commitments and Irreversibility. *In* Climate Change 2013: The Physical Science Basis. IPCC Working Group I Contribution to AR5, Cambridge University Press, Cambridge, UK and New York, NY, USA. 107 pp.

Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. Aquaculture, 70: 1–19.

Kolkovski, S. 2001. Digestive enzymes in fish larvae and juveniles—implications and applications to formulated diets. Aquaculture, 200: 181–201.

Kristiansen, T., Stock, C., Drinkwater, K. F., and Curchitser, E. N. 2014. Mechanistic insights into the effects of climate change on larval cod. Global Change Biology, 20: 1559–1584.

Kunz, K. L., Frickenhaus, S., Hardenberg, S., Johansen, T., Leo, E., Pörtner, H.-O., Schmidt, M. *et al.* 2016. New encounters in Arctic waters: a comparison of metabolism and performance of polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) under ocean acidification and warming. Polar Biology, 39: 1137–1153.

Laurel, B. J., Spencer, M., Iseri, P., and Copeman, L. A. 2016. Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biology, 39: 1127–1135.

Laurel, B. J., Copeman, L. A., Spencer, M., and Iseri, P. 2018. Comparative effects of temperature on rates of development and survival of eggs and yolk-sac larvae of Arctic cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*). ICES Journal of Marine Science, 75: 2403–2412.

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S., and Berge, J. 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Progress in Oceanography, 90: 18–32.

Logerwell, E., Busby, M., Carothers, C., Cotton, S., Duffy-Anderson, J., Farley, E., Goddard, P. *et al.* 2015. Fish communities across a spectrum of habitats in the western Beaufort Sea and Chukchi Sea. Progress in Oceanography, 136: 115–132.

Michaud, J., Fortier, L., Rowe, P., and Ramseier, R. 1996. Feeding success and survivorship of Arctic cod larvae, *Boreogadus saida*, in the Northeast Water polynya (Greenland Sea). Fisheries Oceanography, 5: 120–135.

Miller, T. J., Crowder, L. B., Rice, J. A., and Marschall, E. A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1657–1670.

Moore, S. E., and Stabeno, P. J. 2015. Synthesis of Arctic Research (SOAR) in marine ecosystems of the Pacific Arctic. Progress in Oceanography, 136: 1–11.

Moulton, L. L., and Tarbox, K. E. 1987. Analysis of Arctic cod movements in the Beaufort Sea nearshore region, 1978-79. Arctic, 40: 43–49.

Mueter, F. J., and Litzow, M. A. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecological Applications, 18: 309–320.

Naas, K., Huse, I., and Iglesias, J. 1996. Illumination in first feeding tanks for marine fish larvae. Aquacultural Engineering, 15: 291–300.

NPFMC. 2009. Fishery Management Plan for Fish Resources of the Arctic Management Area. Anchorage, AK.

Otterlei, E., Nyhammer, G., Folkvord, A., and Stefansson, S. O. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2099–2111.

Pearson, R. G., and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12: 361–371.

Peck, L. S., Webb, K. E., and Bailey, D. M. 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. Functional Ecology, 18: 625–630.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences, 48: 503–518.

Petrik, C. M., Duffy-Anderson, J. T., Castruccio, F., Curchitser, E. N., Danielson, S. L., Hedstrom, K., and Mueter, F. 2016. Modelled connectivity between walleye pollock (*Gadus chalcogrammus*) spawning and age-0 nursery areas in warm and cold years with implications for juvenile survival. ICES Journal of Marine Science, 73: 1890–1900.

Pörtner, H. O., and Farrell, A. P. 2008. Physiology and climate change. Science, 322: 690–692.

Pörtner, H. O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology, 77: 1745–1779.

Rand, K. M., and Logerwell, E. A. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biology, 34: 475–488.

Richter-Menge, J., Overland, J. E., and Mathis, J. T. (Eds). 2016. Arctic Report Card 2016. NOAA Arctic Program. www.arctic.noaa.gov/Report-Card

Sakurai, Y., Ishii, K., Nakatani, T., Yamaguchi, H., Anma, G., and Jin, M. 1998. 15 Reproductive characteristics and effects of temperature and salinity on the development and survival of eggs and larvae of Arctic cod (Boreogadus saida). Memoirs of the Faulty of Fisheries Hokkaido University, 45: 77–89.

Serreze, M. C., and Barry, R. G. 2011. Processes and impacts of Arctic amplification: a research synthesis. Global and Planetary Change, 77: 85–96.

Sigler, M., Renner, M., Danielson, S., Eisner, L., Lauth, R., Kuletz, K., Logerwell, E. *et al.* 2011. Fluxes, fins, and feathers: relationships among the Bering, Chukchi, and Beaufort Seas in a time of climate change. Oceanography, 24: 250–265.

Smart, T. I., Duffy-Anderson, J. T., Horne, J. K., Farley, E. V., Wilson, C. D., and Napp, J. M. 2012. Influence of environment on walleye pollock eggs, larvae, and juveniles in the southeastern Bering Sea. Deep-Sea Research Part II-Topical Studies in Oceanography, 65-70: 196–207.

Smetacek, V., and Nicol, S. 2005. Polar ocean ecosystems in a changing world. Nature, 437: 362–368.

Søreide, J. E., Leu, E., Berge, J., Graeve, M., and Falk-Petersen, S. 2010. Timing of blooms, algal food quality and Calanus glacialis reproduction and growth in a changing Arctic. Global Change Biology, 16: 3154–3163.

Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., and Osman, R. W. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America, 99: 15497–15500.

Thanassekos, S., and Fortier, L. 2012. An Individual Based Model of Arctic cod (*Boreogadus saida*) early life in Arctic polynyas: i. Simulated growth in relation to hatch date in the Northeast Water (Greenland Sea) and the North Water (Baffin Bay). Journal of Marine Systems, 93: 25–38.

Zhao, Y., Chen, Y., and Brown, J. A. 2001. Impacts of egg and larval size on survival and growth of Atlantic cod under different feeding conditions. Journal of Fish Biology, 59: 569–581.

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