

# Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod)

Emilie A. Geissinger, Robert S. Gregory, Benjamin J. Laurel, and Paul V.R. Snelgrove

**Abstract:** In subarctic Newfoundland, age-0 Atlantic cod (*Gadus morhua*) settle into coastal habitats in several summer–autumn pulses, resulting in broad length–frequency distributions before winter. Low winter temperatures and potential decreases in food availability pose challenges for young-of-year fish. To examine how size variation affects overwintering success under contrasting food scenarios, we conducted 114-day laboratory feeding trials at ambient overwinter sea temperatures, using demersal age-0 cod collected from Newman Sound, Newfoundland. We reared two size classes of juvenile cod under four daily ration levels (starvation, low, medium, high). We used Fulton’s *K* condition factor to interpret effects of food availability and fish size on survival over winter. We showed that small amounts of consumed food ( $<1\% \text{ BW} \cdot \text{day}^{-1}$ ) maximized winter growth and condition potential of juvenile cod in Newfoundland waters. With no food, survival of small cod dropped below 80% on Day 47, whereas survival of large juveniles remained  $>80\%$  until Day 74. Therefore, we expect higher survival of earlier settlers and increased size-selective mortality in age-0 cod during either unproductive or protracted winters, when food abundance is often low.

**Résumé :** Dans les régions subarctiques de Terre-Neuve, des morues (*Gadus morhua*) de moins d’un an s’établissent dans des habitats côtiers en plusieurs vagues durant l’été et l’automne, ce qui produit des distributions étalées de la fréquence des longueurs avant l’hiver. Les basses températures hivernales et des diminutions potentielles de la disponibilité de nourriture présentent des défis pour les jeunes de l’année. Afin d’examiner l’incidence des variations de la taille sur la survie hivernale pour différents scénarios de disponibilité de nourriture, nous avons mené des essais d’alimentation en laboratoire sur 114 jours aux températures de la mer hivernales ambiantes, en utilisant des morues démersales de moins d’un an prélevées dans la baie de Newman, à Terre-Neuve. Nous avons élevé des morues juvéniles de deux classes de taille en leur donnant l’une ou l’autre de quatre rations quotidiennes différentes (privation, faible, moyenne et grande). Nous avons utilisé le facteur d’embonpoint de Fulton, *K*, pour interpréter les effets de la disponibilité de nourriture et de la taille des poissons sur la survie hivernale. Nous avons démontré que de petites quantités de nourriture consommée ( $<1\% \text{ MC} \cdot \text{jour}^{-1}$ ) maximisent la croissance hivernale et l’embonpoint potentiel de morues juvéniles dans les eaux terre-neuviennes. En l’absence de nourriture, le taux de survie des petites morues est passé sous les 80 % au 47<sup>e</sup> jour, alors que celui des grosses morues est demeuré supérieur à 80 % jusqu’au 74<sup>e</sup> jour. Nous nous attendons donc à des taux de survie plus élevés pour les morues établies plus tôt et à une augmentation de la mortalité sélective selon la taille chez les morues de moins d’un an durant des hivers longs ou non productifs, quand l’abondance de nourriture est souvent faible. [Traduit par la Rédaction]

## Introduction

Juvenile fish experience high natural mortality in their first year of life (Sogard 1997; Kristiansen et al. 2000). Despite multiple studies of mortality in juvenile Atlantic cod (*Gadus morhua*) during the summer and fall seasons (Lindholm et al. 1999; Laurel et al. 2003; Bogstad et al. 2016) and several studies on population dynamics over winter (Goddard et al. 1992; Dutil and Lambert 2000; Björnsson and Steinarsson 2002), many aspects of overwinter survival remain unknown. In polar and temperate latitudes, low temperatures and potential decreases in food availability in winter pose challenges for young-of-year fish (Foy and Paul 1999). Most information on overwinter dynamics in fish comes from freshwater systems with a particular focus on salmonids and centrarchids (e.g., Post and Evans 1989; Pangle et al. 2004; Mogensen and Post 2012). While these

studies provide a theoretical framework to examine overwintering processes in other species (e.g., size-dependent survival), marine systems require additional considerations given differences in cooling characteristics of the water column, scale (e.g., migration potential), and osmoregulatory stress (Hurst 2007).

Current bioenergetic models to determine growth rates for fish often focus on spring, summer, and fall dynamics (Peck et al. 2003; Mogensen and Post 2012). However, subzero temperatures, size limitations, and food limitations expose juvenile fishes to different stressors and metabolic effects over winter. General bioenergetic models generally lack parameters to assess overwinter dynamics, particularly given major knowledge gaps on survival and cold-water physiology of fish at subarctic temperatures. During winter, juvenile fish must cope with direct, indirect, and interactive effects of temperature decline with other environmental variables.

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Although temperature determines the underlying rate of energy store depletion (Pangle et al. 2004; Huss et al. 2008; Copeman et al. 2017), extreme low temperatures can also cause acute thermal stress (Hurst 2007), related to osmoregulatory function (Lankford and Targett 2001) or freezing. Juvenile fish also experience size-dependent effects, with higher metabolic rates in smaller individuals (Werner and Gilliam 1984; Byström et al. 2006) and reduced capacity for lipid storage prior to winter (Huss et al. 2008). The large ratio of gill surface area to body mass in small individuals may also increase juvenile vulnerability (Oikawa and Itazawa 1985). However, superior acclimation capabilities in smaller individuals, such as more antifreeze proteins, than larger individuals (Fletcher et al. 1987; Goddard et al. 1992) may help offset these risks.

Growth plays a large role in survivorship for young-of-year fish, both preceding and during winter. The faster and more efficiently a juvenile grows, the more likely it can evade or exceed the prey size preference of a given predator (Sogard 1997; Kristiansen et al. 2000). In addition to size-at-age when entering winter, food availability during the winter months also limits fish growth and (presumably) survival. Higher lipid stores increase the likelihood that fish will survive over winter (Henderson et al. 1988). Condition indices, which researchers routinely use to indicate general fitness and energy storage, offer a means to evaluate these fat stores; they also offer a useful method to determine cod energy reserves (Bolger and Connolly 1989; Grant and Brown 1999). Cod store lipids in their liver and protein in their muscles, complicating measurement of condition in this species compared with fishes that store both lipid and protein in muscle tissue (Lambert and Dutil 1997). Favourable condition prior to winter allows cod to metabolize large amounts of energy reserves and body tissues to cope with limited food availability (Black and Love 1986), whereas fish in low condition may die of starvation over winter (Dutil and Lambert 2000). In freshwater systems, cold temperatures disproportionately impact smaller fish within a cohort because smaller fish begin winter with lower energy reserves and greater susceptibility to resource-limited environments (Post and Evans 1989; Thompson et al. 1991; Byström et al. 2006). For this reason, postwinter condition of individual freshwater fishes depends primarily on their size prior to winter. However, there is poor understanding of this relationship in marine ecosystems.

The once abundant northern population of Atlantic cod declined dramatically in the 1980s and was ultimately placed under a fisheries moratorium in 1992 (Taggart et al. 1994), which remains in place today (DFO 2019). Noting its lack of recovery, research on early life stages of cod may provide important information on critical periods and survival bottlenecks. Atlantic cod in Newfoundland settle from pelagic to demersal habitat in several pulses through the summer and fall (Methven and Bajdik 1994; Grant and Brown 1998a; Ings et al. 2008). A range in settlement times during this period results in multiple size classes for age-0 Atlantic cod entering winter, creating a size-structured population from fall to spring. In size-structured populations, individual growth and mortality rates play a central role in determining population trajectories (Werner and Gilliam 1984). More pronounced size-structured survival may characterize long, cold winters, with temperatures ranging from 2.1 to as low as  $-1.3^{\circ}\text{C}$  in coastal Newfoundland (R.S. Gregory, unpublished data). Although numerous studies demonstrate that temperature and food availability limit growth rates through winter for a variety of life stages (Krohn et al. 1997; Grant and Brown 1999; Otterlei et al. 1999), no research has examined how variable size impacts the survival potential of age-0 cod entering their first winter, which potentially determines year class abundance.

Our study assesses the effect of size and food availability on growth, condition, and survival of age-0 demersal Atlantic cod in ambient coastal seawater conditions from January to April ( $-0.8$  to  $2.7^{\circ}\text{C}$ ). We hypothesized that larger juvenile cod would survive

longer and remain in better condition than smaller fish, but ration would have little impact on vital rates at such low regional temperatures. Collectively, these experiments allow us to assess the role of size and food availability in overwinter survival in age-0 cod in coastal Newfoundland.

## Methods

### Study sites and sampling method

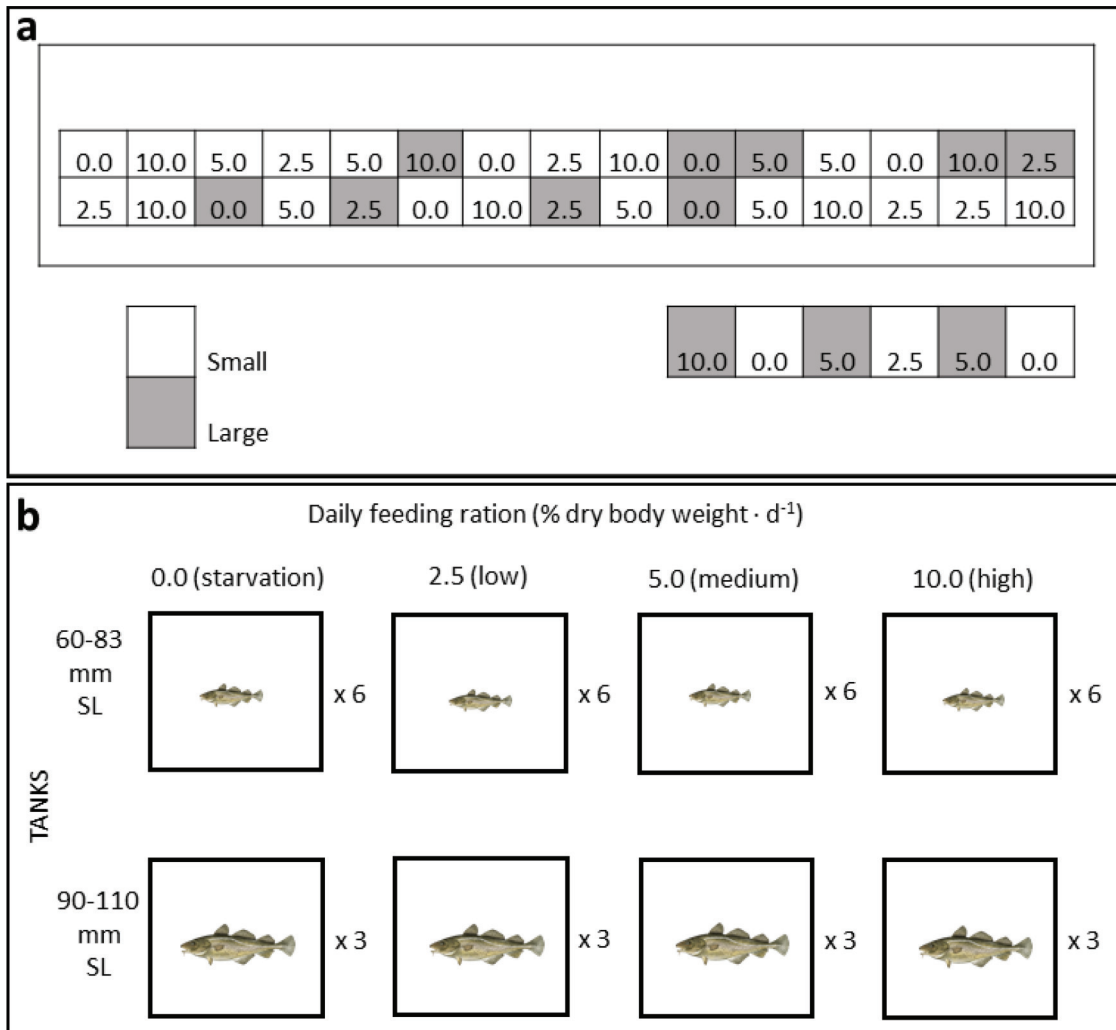
We collected 530 age-0 Atlantic cod from Newman Sound, Terra Nova National Park, Newfoundland ( $48.58^{\circ}\text{N}$ ,  $53.91^{\circ}\text{W}$ ) in November 2016 using a demersal seine net 25 m long, with 19 mm mesh, deployed 55 m from shore using a small boat and retrieved by two individuals standing 16 m apart on shore. The seine samples  $\sim 880\text{ m}^2$  of habitat from the seabed to 2 m into the water column with a capture efficiency of 95% (Gotceitas et al. 1997). Fish were then transported to the Ocean Sciences Centre in Logy Bay within 6 h for acclimation and experimental work.

### Experimental design

We divided age-0 Atlantic cod into small (60–83 mm standard length, SL) and large (90–110 mm SL) size classes and subdivided size classes across four feeding treatments (starvation, low food, medium food, high food). Based on relative body weight (BW), we anticipated  $<1\% \text{ BW}\cdot\text{day}^{-1}$  food consumption in all feeding treatments (Gotceitas et al. 1999), which is generally difficult to control in fish groups with potentially high competition for food (Karplus et al. 2000). Therefore, we spread food for each feeding treatment across the tanks' surface daily, in a single pass, to minimize competition and ensure all fish had access to some food in the water column. Therefore, feeding rations ( $\% \text{ BW}\cdot\text{day}^{-1}$ ) were set higher than target levels (0.0% starvation; 2.5% low; 5% medium; 10% high) based on dry mass conversion. This method increased the amount of uneaten food that remained on the bottom, which following removal and remeasurement (described below) yielded actual feeding treatments less than  $1\% \text{ BW}\cdot\text{day}^{-1}$  (Geissinger et al. 2020). Atlantic cod were fed freeze-dried krill (*Euphausia superba*) from JEHMCO Aquatic Breeder Supplies, Inc. (55% protein, 26% fat, 0.81% total carbohydrates,  $461\text{ kcal}\cdot 100\text{ g}^{-1}$ ). We configured thirty-six 100 L rectangular tanks ( $65\text{ cm} \times 42\text{ cm} \times 38\text{ cm}$ ), filled to a depth of 33.7 cm with ambient flow-through water system from a deep-water marine source at Ocean Sciences Centre of Memorial University of Newfoundland, at a mean flow rate of  $33\text{ mL}\cdot\text{s}^{-1}$ . We randomly assigned treatment, fish size, and ration to tanks filled with seawater filtered through a  $500\text{ }\mu\text{m}$  filter bag and maintained at ambient outside seawater temperature, which we measured twice daily (morning and evening). A total of 12 tanks with the large size class included three replicates of each feeding treatment level, and 24 tanks with the small size class included six replicates of each feeding treatment level (Fig. 1). Nine fish were assigned to each tank and acclimated and fed ad libitum for a 20-day acclimation period. Because we could not track individual fish throughout the study, each tank represented an individual measurement for growth and condition, with all measurements averaged within each tank. Ambient water temperature was  $3.0^{\circ}\text{C}$  at the start of acclimation, declining to  $2.2^{\circ}\text{C}$  by the initiation of our experiment. At Day 0, we euthanized 40 fish within each size class range from the holding tanks (18 small, 22 large) with tricaine methanesulfonate (MS-222) to evaluate condition at the start of our experiment. We maintained tanks at ambient photoperiods, and water temperature was measured twice daily in each tank throughout our experiment. Salinity was stable at 32‰. The experiment began on 31 December 2016; we were compelled to terminate our experiment on 24 April 2017 under the terms of our animal care protocol.

We dried and weighed unconsumed food collected in each tank daily after the 90 min feeding period. Once a month, experimental animals were anaesthetized in  $30\text{ mg}\cdot\text{L}^{-1}$  MS-222 and then

**Fig. 1.** Conceptual diagram of experimental design. The top panel (a) represents the tank layout with size class and ration level (percent dry body weight). The bottom panel (b) shows experimental design with treatment levels and sample size. Each square represents a tank, with nine fish per tank at the start of the study. The size range represents the standard length (SL) of fish at the start of the study, with the small size class shown on top and large size class shown on bottom. Study began on 31 December 2016 with  $36 \times 9$  cod and ended on 24 April 2017 with a total of 168 cod.



measured to determine length ( $\pm 1$  mm SL) and wet weight ( $\pm 0.01$  g; excess water was gently blotted away through a fine-meshed net) to adjust feeding ration and assess growth through the experiment.

Cod were checked twice daily for survival and health. Using  $100 \text{ mg} \cdot \text{L}^{-1}$  of MS-222, we euthanized fish that lost equilibrium and did not react to mechanical prodding. We euthanized all surviving fish at the conclusion of our experiment on 24 April 2017. Length and weight were determined on these remaining fish as described above. After dissecting and weighing the liver of each fish, we also measured eviscerated wet weight and stored liver and eviscerated bodies at  $-20^\circ\text{C}$  prior to drying the body and liver for 48 and 24 h, respectively, at  $65^\circ\text{C}$  (Lantry and O’Gorman 2007); we determined dry weight on these individuals. All experiments undertaken during our investigation were conducted under Memorial University of Newfoundland Animal Care Protocol No. 2016-02-RG.

**Data analysis and statistical methods**

Fulton’s condition factor,  $K_{\text{WET}}$ , for wet weight was calculated as follows (Fulton 1904):

$$(1) \quad K_{\text{WET}} = 100 \cdot (W_{\text{WET}} \cdot L^{-3})$$

where  $W_{\text{WET}}$  was total wet weight (g) and  $L$  was standard length (SL, cm).  $K_{\text{WET}}$  was calculated monthly for live fish. We calculated dry weight condition factor,  $K_{\text{DRY}}$ , at the end of the study, as follows (Grant and Brown 1999):

$$(2) \quad K_{\text{DRY}} = 1000 \cdot (W_{\text{DRY}} \cdot L^{-3})$$

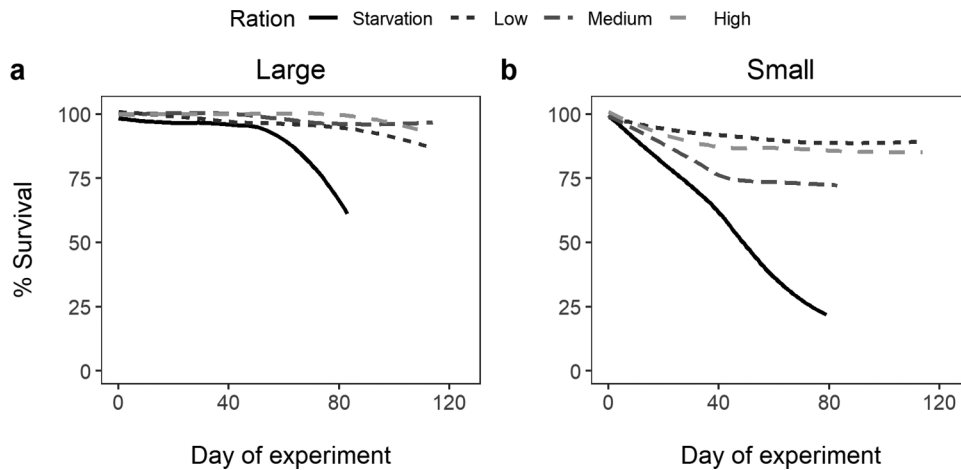
where  $W_{\text{DRY}}$  was eviscerated dry weight. Loss of lipids and proteins can result in an increase of water content (Love 1970; Grant and Brown 1999); therefore, we considered dry weight more reliable than wet weight for condition measurements. We calculated hepatosomatic index (HSI) as follows (Lambert and Dutil 1997):

$$(3) \quad \text{HSI} = 1000 \cdot (LW_{\text{DRY}} \cdot W_{\text{DRY}}^{-1})$$

where  $LW_{\text{DRY}}$  was dry liver weight (g).

We used juvenile fish sampled from the beginning of the experiment to calculate the change in  $K_{\text{DRY}}$  ( $\Delta K_{\text{DRY}}$ ) and HSI ( $\Delta \text{HSI}$ ) from Day 0 to termination by subtracting the final  $K_{\text{DRY}}$  and HSI from the mean initial  $K_{\text{DRY}}$  and initial HSI (see online

**Fig. 2.** Percent survival of (a) large (90–110 mm SL) and (b) small (60–83 mm SL) juvenile Atlantic cod (*Gadus morhua*) under four feeding rations (starvation (0.0%), low (2.5%), medium (5.0%), and high (10% dry body weight);  $n = 24$  small size class tanks, 12 large size class tanks), with nine fish per tank.



Supplementary data, Figs. S1–S2<sup>1</sup>). We calculated specific growth rate for weight ( $SGR_W$ ) according to the formula from Hawkins et al. (1985) as

$$(4) \quad SGR_W = (\ln W_{WET2} - \ln W_{WET1}) \cdot (t_i - t_{i-30})^{-1} \cdot 100$$

with  $W_{WET2}$  and  $W_{WET1}$  as total wet weights at times  $t_i$  and  $t_{i-30}$ . Fish were weighed and measured at 30-day intervals. We also calculated SGR for length ( $SGR_L$ ) with length in place of weight.

We calculated a conversion factor for total remaining feed, accounting for water absorption. We ran trials with a known amount of food placed in each tank with no fish and dried and then reweighed the residual food after the feeding period. The conversion factor was calculated as

$$(5) \quad CF = W_f \cdot W_i^{-1}$$

where CF denoted conversion factor, and  $W_f$  was final weight of food after tank removal, and  $W_i$  the initial weight of food before our treatments. This procedure yielded a conversion factor of 1.09. We therefore calculated daily total food consumption (g) as

$$(6) \quad C = TF - (1.09 \cdot RF)$$

where TF was weight of total food (g) provided, and RF was weight of remaining food (g). Feeding rate (F) was calculated as follows (Imsland et al. 2006):

$$(7) \quad F = 100 \cdot C \cdot [(W_{WET1} + W_{WET2})^{-1} \cdot 2] \cdot (t_i - t_{i-30})^{-1}$$

where  $W_{WET1}$  and  $W_{WET2}$  were total wet fish weight (g) on days  $t_{i-30}$  and  $t_i$ , respectively, at 30-day intervals. Feeding conversion efficiency (FCE) was calculated as follows (Imsland et al. 2006):

$$(8) \quad FCE = (W_{WET2} - W_{WET1}) \cdot C^{-1}$$

We used the R statistical programming language (R Core Team 2019) for all our statistical procedures and set  $\alpha = 0.05$ . We compared survival among treatments using the Kaplan–Meier estimator with the {survival} package (Therneau 2015; Moore 2016). We reported survival statistics including 95% confidence intervals (CIs). We used Pearson’s product-moment correlation to determine the relationship between day of death and SL for all

mortalities. Correlation analyses were conducted on small, large, and combined size classes.

We analyzed live condition ( $K_{WET}$ ) using a linear mixed effect model with the {lme4} package (Bates et al. 2015).  $K_{WET}$  was the response variable, with ration (categorical), size (categorical), day of experiment (covariate), and tank (random effect) as the explanatory variables. We analyzed  $\Delta K_{DRY}$  using a general linear model with Gaussian error distribution. We calculated the mortality endpoint as the mean  $K_{WET}$  at time of death, using a general linear model with  $K_{WET}$  as the response variable and day of experiment as the explanatory variable. We analyzed final condition using  $\Delta K_{DRY}$  as the response variable; explanatory variables included ration (categorical), size (categorical), and day of experiment (covariate). We treated tanks as replicates. We analyzed  $\Delta HSI$  with the same model format. We report all condition values with standard error (SE).

We analyzed  $SGR_W$  and  $SGR_L$  using a linear mixed effect model with the {lme4} package (Bates et al. 2015) with ration (categorical), size (categorical), day of experiment (covariate), and tank (random effect) as explanatory variables. Feeding rate and feed conversion efficiency (FCE) were analyzed using a general linear model with Gaussian error distribution. The explanatory variables for both models were ration (categorical), size (categorical), and temperature (covariate). Statistical models excluded non-significant interactions ( $\alpha > 0.05$ ). We have reported all growth values with standard error. Data calculations and visualizations were completed with {tidyverse} (Wickham 2017). The associated data are available on Dataverse (Geissinger et al. 2020). The associated statistical analysis outputs can be found in the online Supplementary data (Tables S1–S7<sup>1</sup>).

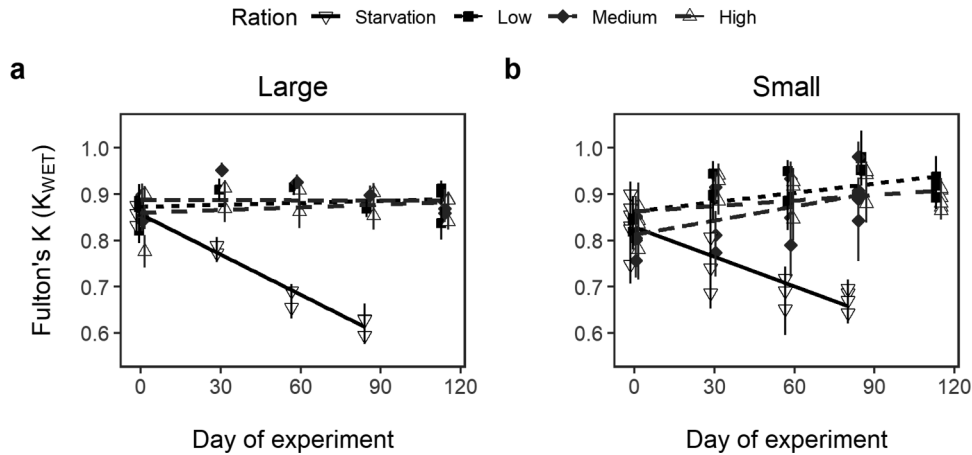
## Results

### Survival

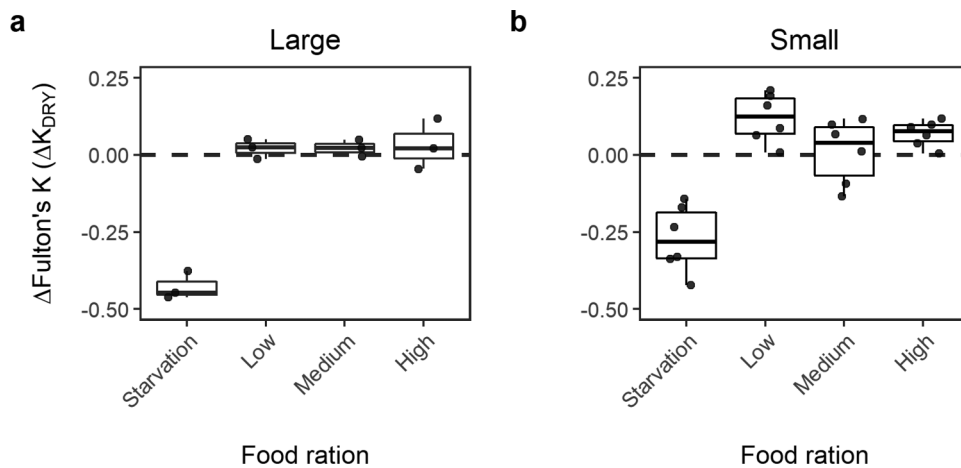
Survival of large cod across all rations was greater than for small cod through the duration of the experiment, with large cod averaging 94.6% (CI: 94.1%, 95.1%,  $n = 192$ ) survival at Day 80 in contrast with a mean of 67.4% (CI: 66.7%, 68.1%,  $n = 266$ ) for small cod. Starvation resulted in the lowest survival for both large and small size classes, with consistently high survival in low (2.5% BW·day<sup>-1</sup>), medium (5.0% BW·day<sup>-1</sup>), and high (10.0% BW·day<sup>-1</sup>) rations (Fig. 2). Reduced survival (58.2%, CI: 56.7%, 59.7%,  $n = 38$ ) in small cod under starvation at Day 60 contrasted high survival (93.9%, CI: 92.9%,

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-0142>.

**Fig. 3.** Fulton's condition factor  $K$  ( $K_{WET}$ ) of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation (0.0%), low (2.5%), medium (5.0%), and high (10% dry body weight)) during 30-day intervals ( $n = 24$  small size class tanks, 12 large size class tanks). Vertical error bars represent  $\pm$ SE.  $K_{WET}$  between size groups did not differ significantly (ANODEV,  $\chi^2 = 3.71$ ,  $p = 0.054$ ).  $K_{WET}$  under starvation differed significantly among low, medium, and high rations (ANODEV,  $\chi^2 = 3206.03$ ,  $p < 0.05$ ).



**Fig. 4.** Change in Fulton's condition factor  $K$  ( $\Delta K_{DRY}$ ) of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation (0.0%), low (2.5%), medium (5.0%), and high (10% dry body weight));  $n = 24$  small size class tanks, 12 large size class tanks). The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Individual points represent  $\Delta K_{DRY}$  values by tank.  $\Delta K_{DRY}$  in starvation treatment differed significantly among low, medium, and high rations (ANOVA,  $F = 49.56$ ,  $p < 0.05$ ), and size significantly affected  $\Delta K_{DRY}$  (ANOVA,  $F = 5.94$ ,  $p = 0.02$ ).



95.0%,  $n = 50$ ) in large cod under starvation. Small cod in the starvation treatment declined steadily throughout the study, in contrast with high survival in large cod until Day 64. Day of death did not correlate with SL for the small size class ( $r = 0.16$ ,  $p = 0.18$ ,  $df = 69$ ) or the large size class ( $r = 0.044$ ,  $p = 0.87$ ,  $df = 13$ ). For the study population as a whole, a significant correlation ( $r = 0.52$ ,  $p < 0.001$ ,  $df = 84$ ) between day of death during the experiment and length suggested size-dependent survival between the large and small size classes, with the small size class largely driving the relationship.

**Condition**

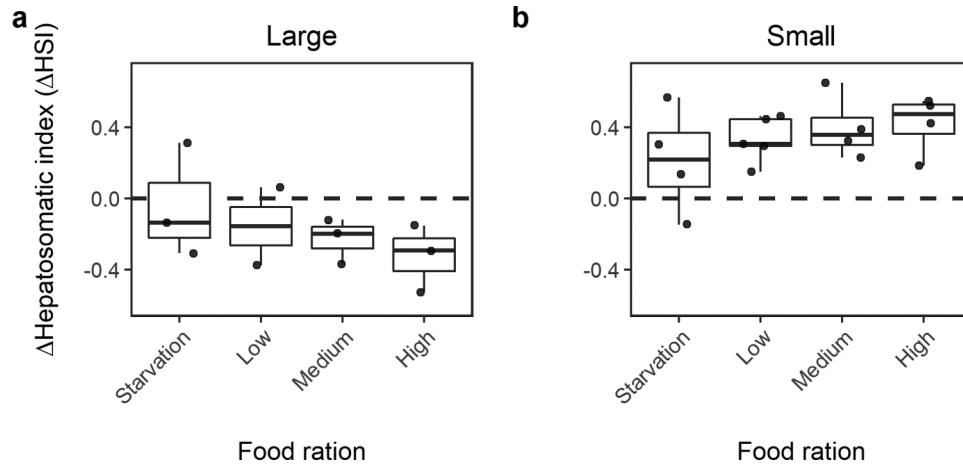
Condition ( $K_{WET}$ ) decreased significantly through the duration of our starvation trials for small and large cod relative to the other rations (ANODEV,  $\chi^2 = 167.89$ ,  $p < 0.05$ ,  $df = 3$ , 26); size had an interactive effect with duration of study (ANODEV,  $\chi^2 = 13.70$ ,  $p < 0.05$ ,  $df = 1$ , 26).  $K_{WET}$  in the small size class decreased from  $0.83 \pm 0.02$  on Day 0 to  $0.67 \pm 0.01$  on Day 80 (Fig. 3a), and in the

large size class  $K_{WET}$  decreased from  $0.86 \pm 0.01$  to  $0.62 \pm 0.01$  on Day 84 (Fig. 3b).  $K_{WET}$  changed over time in our starvation trials:  $K_{WET} = 0.839 - 0.002t$ , where  $t$  was Day and 0.839 was the starting condition. For the low, medium, and high rations, in both the small and large size classes,  $K_{WET}$  remained effectively constant (Fig. 2). Small juvenile cod reached a mortality endpoint at  $K_{WET} = 0.608 (\pm 0.021)$ ; large juvenile cod reached this endpoint at  $K_{WET} = 0.589 (\pm 0.016)$ . Small juvenile cod reached a lethal condition after 115.5 days, and large juvenile cod reached lethal condition after 125 days.

Change in dry weight condition ( $\Delta K_{DRY}$ ) was larger in fish fed the low, medium, and high rations than in fish from the starvation treatment (ANOVA,  $F = 9.56$ ,  $p < 0.05$ ,  $df = 3$ , 31; Fig. 4), and size class also affected  $\Delta K_{DRY}$ , with a larger difference in condition for small fish than large fish (ANOVA,  $F = 5.94$ ,  $p = 0.02$ ,  $df = 1$ , 31; Fig. 4). The  $\Delta K_{DRY} = -0.27 \pm 0.04$  in small cod under starvation contrasted  $\Delta K_{DRY}$  of  $-0.43 \pm 0.03$  in larger cod. Increasing ration beyond the lowest level (2.5%) had no further positive impact

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**Fig. 5.** Mean change in hepatosomatic index ( $\Delta$ HSI) by tank of (a) large and (b) small juvenile Atlantic cod under four feeding rations (starvation (0.0%), low (2.5%), medium (5.0%), and high (10% dry body weight);  $n = 24$  small size class tanks, 12 large size class tanks). The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Individual points represent  $\Delta$ HSI values by tank. Size (ANOVA,  $F = 37.42$ ,  $p < 0.05$ ) significantly influenced  $\Delta$ HSI.



on condition. The  $\Delta K_{\text{DRY}} = 0.02 \pm 0.02$  for low and medium rations was similar to  $\Delta K_{\text{DRY}} = 0.03 \pm 0.05$  for the high ration (Fig. 4).

Size class strongly affected  $\Delta$ HSI (ANOVA,  $F = 37.42$ ,  $p < 0.05$ ,  $df = 1, 23$ ; Supplementary Table S3<sup>1</sup>). The  $\Delta$ HSI in large cod decreased by 0.53 from small cod. Ration did not significantly affect  $\Delta$ HSI (ANOVA,  $F = 0.02$ ,  $p = 0.99$ ,  $df = 3, 23$ ), varying less than 0.03 in all rations relative to the starvation treatment. Although the effect was not statistically significant, the data trend suggested that positive  $\Delta$ HSI in small cod increased with increase in ration (Fig. 5a), whereas  $\Delta$ HSI in large cod decreased with increase in ration (Fig. 5b).

### Growth

Size class had no effect on  $\text{SGR}_W$  (ANODEV,  $\chi^2 = 0.27$ ,  $p = 0.606$ ,  $df = 1, 51$ ) or on  $\text{SGR}_L$  (ANODEV,  $\chi^2 = 3.37$ ,  $p = 0.066$ ,  $df = 1, 51$ ). We observed decreased weight in the starvation treatment with an  $\text{SGR}_W$  of  $-0.249\% \pm 0.059\% \text{ g}\cdot\text{day}^{-1}$  (Fig. 6a).  $\text{SGR}_L$  increased slightly for length ( $0.039\% \pm 0.013\% \text{ mm}\cdot\text{day}^{-1}$ ), but this increase likely reflects size-selective mortality in tanks (Table 1; Fig. 6b). Weight increased in all other rations (ANODEV,  $\chi^2 = 277.89$ ,  $p < 0.05$ ,  $df = 3, 51$ ), as did length (ANODEV,  $\chi^2 = 42.78$ ,  $p < 0.05$ ,  $df = 3, 51$ ), but did not differ significantly among treatments.  $\text{SGR}_W$  was identical for the low ration ( $0.45\% \pm 0.02\% \text{ g}\cdot\text{day}^{-1}$ ), and the medium ration ( $0.45\% \pm 0.04\% \text{ g}\cdot\text{day}^{-1}$ ), in contrast with the high ration ( $0.38\% \pm 0.01\% \text{ g}\cdot\text{day}^{-1}$ ) (Fig. 6a).  $\text{SGR}_L$  was also identical for the low ration ( $0.11\% \pm 0.01\% \text{ mm}\cdot\text{day}^{-1}$ ) and medium ration ( $0.11\% \pm 0.02\% \text{ mm}\cdot\text{day}^{-1}$ ), similar to the high ration ( $0.10\% \pm 0.01\% \text{ mm}\cdot\text{day}^{-1}$ ) (Fig. 6b).

### Feeding and conversion efficiency

Feeding rates had ranges of  $0.19\%$ – $0.45\% \text{ BW}\cdot\text{day}^{-1}$  in the low ration,  $0.24\%$ – $0.55\% \text{ BW}\cdot\text{day}^{-1}$  in the medium ration, and  $0.28\%$ – $0.61\% \text{ BW}\cdot\text{day}^{-1}$  in the high ration. Size did not influence feeding rate (ANOVA,  $F = 0.91$ ,  $p = 0.34$ ,  $df = 1, 97$ ), but feeding rate increased with increasing feeding ration (ANOVA,  $F = 11.51$ ,  $p < 0.05$ ,  $df = 2, 97$ ). The feeding rate of fish in the high ration treatment was  $\sim 0.04\% \text{ BW}\cdot\text{day}^{-1}$  higher than fish observed in the medium and low ration treatments. Fish in the medium and low ration treatments did not differ significantly in their feeding rate (Fig. 7). Feeding rate decreased significantly at lower ambient temperatures (ANOVA,  $F = 279.20$ ,  $p < 0.05$ ,  $df = 1, 97$ ; Fig. 7). Temperature ranged from  $-0.7$  to  $2.5\text{ }^\circ\text{C}$  (Fig. 8), with the lowest temperature on

Day 95 (4 April 2017) when pack ice moved into the bay, as is typical in the spring.

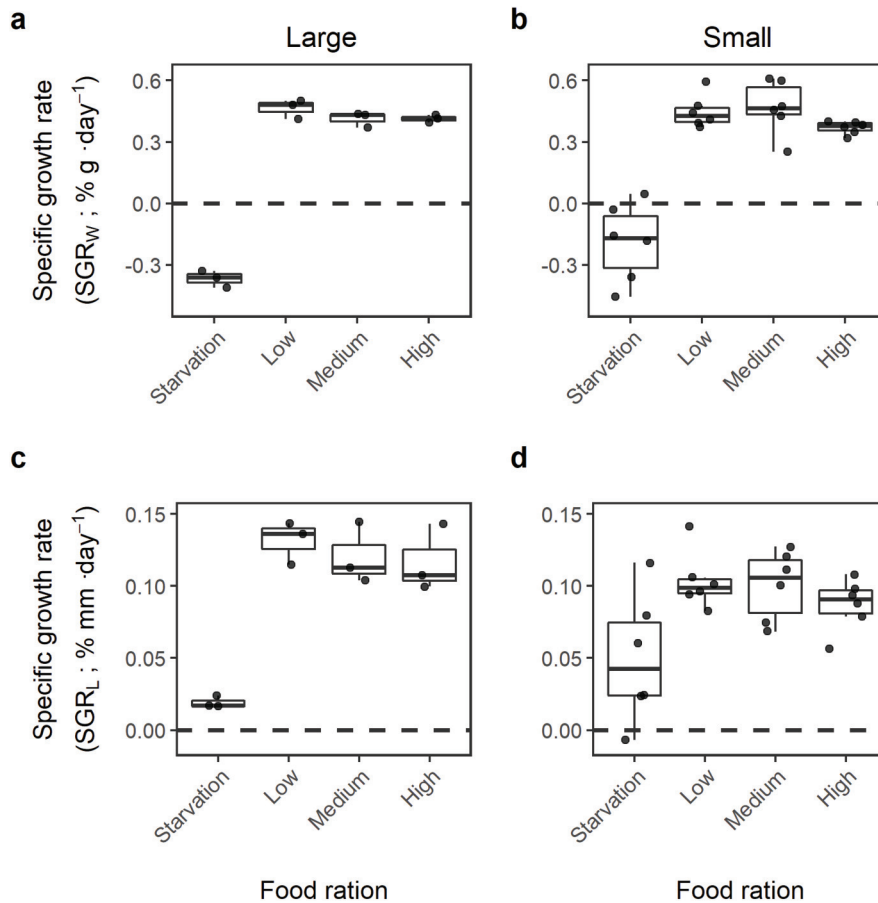
Across all rations, significantly higher FCE characterized large cod compared with small cod (ANOVA,  $F = 7.15$ ,  $p < 0.05$ ,  $df = 1, 109$ ), with the small size FCE decreasing by  $0.29 (\pm 0.11)$  relative to the large size fish. FCE changed with ration (ANOVA,  $F = 4.48$ ,  $p = 0.01$ ,  $df = 2, 109$ ; Fig. 9). The medium ration had a  $0.37 (\pm 0.13)$  decrease in FCE relative to the low ration, and the large ration had a  $0.27 (\pm 0.12)$  decrease in FCE relative to the low ration. Ambient temperature had no significant effect on FCE (ANOVA,  $F = 3.44$ ,  $p = 0.066$ ,  $df = 1, 109$ ).

### Discussion

Our results did not support our initial hypothesis that food availability would significantly impact growth, condition, or survival of age-0 Atlantic cod overwintering in coastal Newfoundland. Rather, modest rations ( $0.2\%$ – $0.6\% \text{ dry body mass}\cdot\text{day}^{-1}$ ) positively affected condition, growth, and survival, but additional food levels produced no further significant improvement in these metrics. Improved survival, condition, growth, and feeding rate all point to the importance of food presence for overwinter growth and survival, especially in small juveniles. Overwinter starvation results in low energy reserves and potential death in winter durations typical of north temperate and subarctic marine conditions.

Food availability in winter varies across regions. Zooplankton biomass decreases as winter temperatures decrease in Prince William Sound, Alaska (Foy and Paul 1999), whereas abundant food availability in areas of northern Norway over winter maintains or improves condition in sea trout (*Salmo trutta*; Rikardsen et al. 2006). Despite limited understanding of overwinter food availability in coastal Newfoundland, limited food availability could potentially occur during winter. We have sometimes observed low condition (Fulton's  $K < 0.60$ ; E.A. Geissinger, C.R. Bloom, R.S. Gregory, B.J. Laurel, and P.V.R. Snelgrove, unpublished data.) in wild age-1 Atlantic cod collected after winter, similar to fish sampled from starvation treatments in this study. Grant and Brown (1998b) observed a shift in diet from autumn to early winter, with age-0 cod diet dominated by small Crustacea zooplankton in the autumn, shifting to small copepods (e.g., *Pseudocalanus* spp., *Acartia* spp.) in November and December, and both ration size and size of zooplankton declined through December, possibly associated with decreased temperature (Grant and Brown 1998b). Nonetheless, diet,

**Fig. 6.** Specific growth rate of weight ( $SGR_W$ ) for (a) large and (b) small juvenile Atlantic cod and specific growth rate of length ( $SGR_L$ ) for (c) large and (d) small juvenile Atlantic cod under four feeding rations (starvation (0.0%), low (2.5%), medium (5.0%), and high (10% dry body weight);  $n = 24$  small size class tanks, 12 large size class tanks). The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Individual points represent  $SGR$  values by tank. Size did not significantly affect  $SGR_W$  (a, b; ANODEV,  $\chi^2 = 0.27$ ,  $p = 0.61$ ) or  $SGR_L$  (c, d; ANODEV,  $\chi^2 = 3.37$ ,  $p = 0.07$ ). The starvation treatment differed statistically among low, medium, and high rations for  $SGR_W$  (a, b; ANODEV,  $\chi^2 = 277.89$ ,  $p < 0.05$ ) and  $SGR_L$  (c, d; ANODEV,  $\chi^2 = 42.78$ ,  $p < 0.05$ ).



**Table 1.** Size-selective mortality of cod in starvation treatment.

Size class	Time interval (days)	SL cod mortalities (mm; mean $\pm$ SE (n))	SL live cod (mm; mean $\pm$ SE (n))
Small	0–31	70.60 $\pm$ 1.22 (16)	78.03 $\pm$ 0.89 (38)
	32–59	76.20 $\pm$ 1.30 (18)	79.43 $\pm$ 1.16 (20)
	60–80	78.90 $\pm$ 1.39 (7)	80.15 $\pm$ 0.87 (13)
Large	0–31	108.00 (1)	104.54 $\pm$ 0.63 (26)
	32–59	99.00 (1)	105.50 $\pm$ 0.68 (25)
	60–84	103.00 $\pm$ 0.43 (7)	106.06 $\pm$ 0.87 (18)

Note: Standard length (SL) of mortalities was measured throughout the 30-day time interval. SL of live cod was measured on the last day of each time interval.

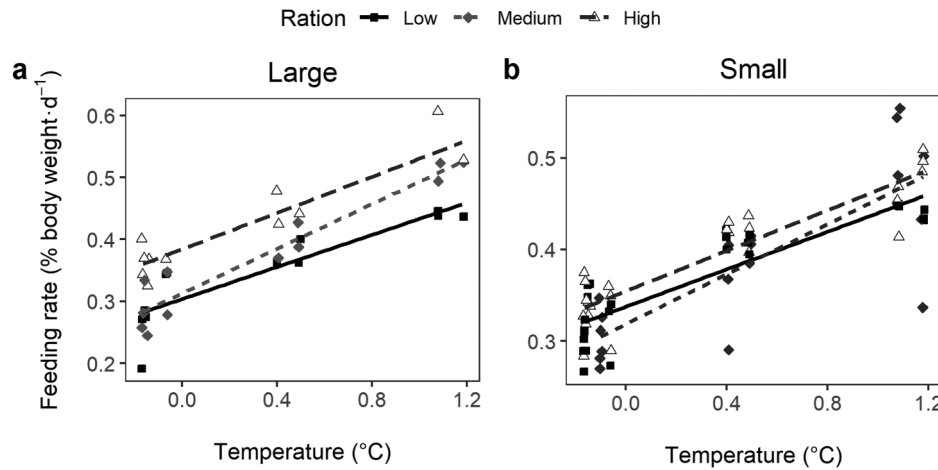
prey availability, and food consumption for age-0 cod after December is poorly understood as temperatures decrease and fish move into deeper water (Methven and Bajdik 1994).

Previous studies in fresh water emphasize the importance of size for overwinter survival (Post and Evans 1989; Huss et al. 2008), which our study confirms for a marine environment. Small fish in our study starved to death faster than large fish. Although both size groups reached a critical point (necessitating ethical termination of our trials), we observed much lower mortality of large cod in the starvation treatment (0.55·day<sup>-1</sup>) than

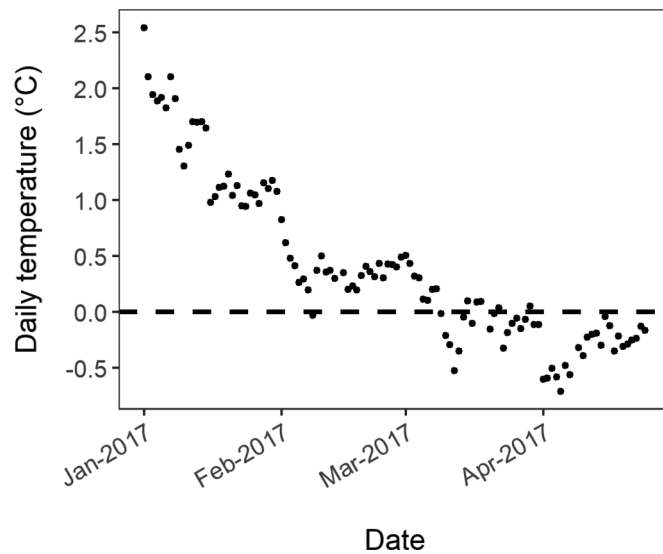
in small cod (2.21·day<sup>-1</sup>). Our results show that juvenile cod risk starving to death over winter, and larger cod entering winter have a greater chance of surviving longer than smaller cod. Low energy reserves can also increase susceptibility to predator attack and capture because of energy depletion (Jonas and Wahl 1998). Although large juveniles in our study also depleted their energy reserves, they reached a critical point later than small cod (Day 78 compared with Day 54), showing that larger fish have a survival advantage during longer winters. The condition endpoints and loss of Fulton's *K* over time provide an overwinter mortality predictor for juvenile Atlantic cod, which could be a useful tool for fisheries management. For example, assuming no access to food during winter, survival probabilities of individual fish sampled prior to or during winter could be estimated based on size, starting condition, and estimated duration of winter.

High mortality of small juveniles in our study relates to depletion of energy reserves (Huss et al. 2008). Cold-water marine juvenile fish often accumulate lipids during late summer and autumn to store excess energy for the overwinter period (Copeman et al. 2017). These fat reserves play a critical role in low-food situations. Young-of-year sand smelt (*Atherina boyeri*) accumulate fat reserves from September to November, with larger smelt building up more fat reserves than small individuals (Henderson et al. 1988). Previous work in Newfoundland, however, showed that juvenile Atlantic

**Fig. 7.** Feeding rate of (a) large (b) small juvenile Atlantic cod and mean temperature during 30-day intervals under low (2.5%), medium (5.0%), and high (10% dry body weight) rations. We calculated food consumption by tank ( $n = 24$  small size class tanks, 12 large size class tanks) averaging across 30-day intervals. Feeding ration significantly affected feeding rate (ANOVA,  $F = 11.51$ ,  $p < 0.05$ ), but size did not (ANOVA,  $F = 0.91$ ,  $p = 0.34$ ). Temperature strongly affected feeding rate (ANOVA,  $F = 279.20$ ,  $p < 0.05$ ).



**Fig. 8.** Mean daily temperatures of experimental tanks ( $n = 36$ ) from 31 December 2016 to 24 April 2017. Tanks were 100 L with ambient flow-through water system from a deep-water source at Ocean Sciences Centre of Memorial University of Newfoundland, at a mean flow rate of  $33 \text{ mL}\cdot\text{s}^{-1}$ .



cod do not increase condition or relative amounts of lipids during late summer and early fall, but size nonetheless influences lipid amounts in young-of-year cod, with higher total lipids in smaller juveniles compared with larger juveniles (Copeman et al. 2008). The higher total lipids in small juveniles, therefore, could potentially help them endure winter. However, for small juveniles to maintain condition throughout winter, food must be present in the system. Our results differ from freshwater systems where large and small lake herring (*Coregonus artedii*) declined in condition in fed and starved feeding treatments, with the largest decline in starved treatments (Pangle et al. 2004). In contrast, our results showed that juvenile Atlantic cod maintain condition with varying levels of food, so that rations above 2.5% dry body mass·day<sup>-1</sup> did not improve condition or growth. However, at starvation levels, condition decreased significantly for both small and large groups.

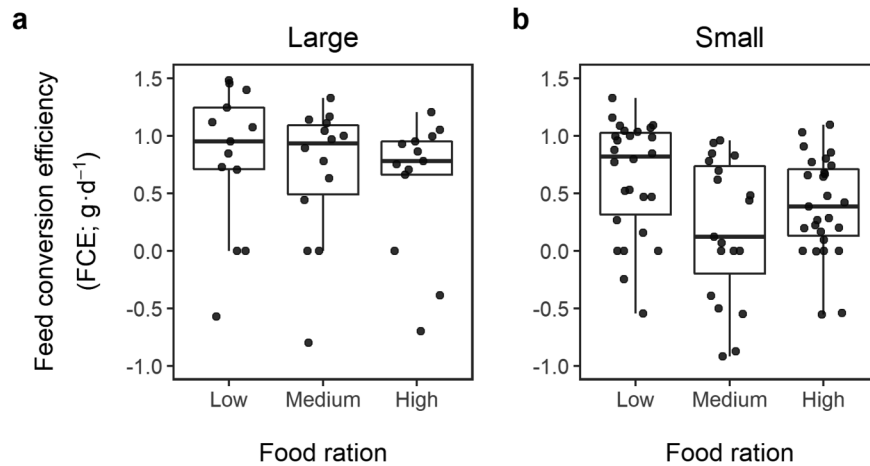
Although survival time differed between small and large size classes at the starvation level, condition did not differ between the two size classes. Our results are in line with an overwinter study on young-of-year Arctic char (*Salvelinus alpinus*) that reported differences in survival time between size classes, with larger char surviving longer than small char, but with no difference in lipid mass between the two size groups (Byström et al. 2006). Young-of-year fish are known to use stored energy reserves through the winter (Post and Evans 1989; Hurst and Conover 2003; Finstad et al. 2004) and as shown in our study, where highest mortality and poorest condition factor occurred in our starvation treatment, risk significant energy loss throughout winter.

Small juveniles experienced depleted condition and high mortality in the absence of food, indicating these fish are highly reliant on ample prewinter stored energy. However, in the presence of food, it is unclear whether juveniles use stored energy, because both large and small juvenile cod maintained their condition, regardless of how much food was available. Unexpectedly, more food did not translate into increased condition or growth. Potential causes could be either limited uptake or energetic cost to digest the additional food, therefore negating energy gain. Food consumption ranged from 0.2%–0.6% dry body mass·day<sup>-1</sup>, which was less than our supplied ration. However, cod consumed higher amounts of food when provided larger rations, indicating that limited uptake may not have maintained condition and growth. Alternatively, cod may have higher energetic costs associated with digesting food, as seen with decreased FCE with increased ration.

The trend in  $\Delta\text{HSI}$  differed from that in Fulton's  $K$  ( $\Delta K_{\text{DRY}}$ ). Small cod maintained HSI under starvation conditions and increased HSI with increased food ration. However, large juveniles depleted HSI as food availability increased. These two trends may represent two alternative strategies for age-0 fishes: energy storage and somatic growth. Potentially, limited capacity to draw on lipid stores in small juvenile livers for the duration of winter may contrast with large juveniles that continue to draw from liver lipid stores over the course of winter (Hemre et al. 1993). Despite higher HSI in large compared with small age-0 cod at the start of our study, cod in our overwinter experiment showed a strategy opposite that reported for freshwater ecosystems (Post and Parkinson 2001), with large cod investing in somatic growth, whereas small cod invested in energy storage. Therefore, large juveniles may use liver energy stores while



**Fig. 9.** Feed conversion efficiency (FCE) of (a) large and (b) small juvenile Atlantic cod for low (2.5%), medium (5.0%), and high (10.0% dry body weight) rations. The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Individual points represent the value for each tank ( $n = 36$ ; 24 small size class tanks and 12 large size class tanks) averaged across 30-day intervals. Size (ANOVA,  $F = 7.15$ ,  $p < 0.05$ ) and ration (ANOVA,  $F = 4.48$ ,  $p < 0.05$ ) both significantly affected FCE.



investing in growth and body condition, whereas small juveniles invest energy into liver stores as resources become available.

Cod increased in both weight and length with the presence of food but invested more energy to increasing weight rather than length under feeding conditions. This pattern is consistent with an energy allocation strategy opposed to somatic growth (Mogensen and Post 2012). A previous study on growth and survival in age-0 Atlantic cod (Gotceitas et al. 1999) reported no difference in SGR at two feeding rations, 0.25% and 1.0% BW·day<sup>-1</sup> with temperatures ranging from -0.95 (±0.06) to 2.46 (±0.37) °C. In freshwater systems, age-0 largemouth bass (*Micropterus salmoides*) increased in weight when fed in warm winters but decreased in cold winters with a temperature low of ~1 °C (Fullerton et al. 2000). In contrast, juvenile cod in our study gained weight at low temperatures (-0.7 to 2.5 °C) when fed. Juvenile cod in coastal Newfoundland appear to allocate energy towards storage in the winter, in sharp contrast with allocation to size (length) in the summer and fall periods (Copeman et al. 2008). This switch likely represents shifting relative risk from size-dependent predation in smaller cod in summer (Sogard 1997; Linehan et al. 2001; Copeman et al. 2008) to increased starvation risk in winter.

The size-dependent survival, growth, and condition observed in our study link mechanistically to ontogenetic changes in metabolism, behavior, and conversion efficiencies observed in Atlantic silverside (*Menidia menidia*), Atlantic cod, and rainbow trout (*Oncorhynchus mykiss*) (Schultz and Conover 1999; Imsland et al. 2006; Mogensen and Post 2012). Other fish species, such as muskellunge (*Esox masquinongy*) show size-dependent trends related to winter temperatures (Chipps et al. 2000), but with large variation among species, including bluegill (*Lepomis macrochirus*), lake char (*Salvelinus namaycush*), and walleye (*Sander vitreus*) (Wohlschlag and Juliano 1959; William and Beamish 1990). In our study, juvenile cod feeding rate declined at temperatures below 0 °C. Low metabolic rates associated with temperature reduce food requirements, and by also reducing energetic activity (e.g., age-0 smelt, *Atherina boyeri*), fish may completely cease feeding during the winter (Henderson et al. 1988). In marine temperate systems, juvenile Atlantic cod and haddock (*Melanogrammus aeglefinus*) reduced food consumption by 80% when temperature decreased from 11 to 2 °C (Pérez-Casanova et al. 2009), and food consumption for juvenile Atlantic cod declined as temperature decreased from 8.3 to 0.6 °C (Brown et al. 1989). Higher food conversion efficiency in large cod compared with small cod, in our study, could result from size-dependent

differences in metabolic, biochemical, or behavioral activity (Kerr 1971). However, the negative relationship between food ration and conversion efficiency (as observed within the small fish of this study) typifies patterns observed in other fish species (e.g., tilapia (*Oreochromis niloticus*), turbot (*Scophthalmus maximus*), and rainbow trout; Wurtsbaugh and Davis 1977; Meyer-Burgdorff et al. 1989; Van Ham et al. 2003) that previous studies generally attributed to increased energy expenditure for digestion (i.e., specific dynamic action (SDA); Jobling 1981) or increased activity (Wurtsbaugh and Davis 1977). Because fish in our study showed no signs of increased activity, increased SDA from high feeding rates offers a likely mechanism to explain the decline in food conversion efficiency.

When even low levels of food are available (<1% BW·day<sup>-1</sup>), age-0 juvenile cod in Newfoundland should be able to continue to grow and maintain condition through the spring, irrespective of their size at the start of winter. Based on our experimental results and observations of prey items in the stomachs of juvenile cod in the early winter (Grant and Brown 1998b), we expect relatively low size-selective survival compared with other systems (Tsukamoto et al. 1989; Garvey et al. 1998; Byström et al. 2006), but that increased size-selective mortality in juvenile cod could become more important as winters become warmer and metabolically more stressful in scenarios with no food availability. Although largely nutrient-poor, many Newfoundland fjords experience pulses of high productivity when onshore wind events transport nutrient-rich water into the fjord (Syvitski et al. 1987; Ings et al. 2008). Therefore, characterizing both the timing and magnitude of food availability in overwintering habitats offers important future research directions regarding overwinter dynamics in juvenile Atlantic cod.

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