



# Condition, size, and winter duration affect winter survival probability of juvenile Atlantic cod *Gadus morhua* in a coastal subarctic ecosystem

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**ABSTRACT:** Juvenile Atlantic cod *Gadus morhua* in coastal Newfoundland, Canada, settle in nearshore habitats in 3–6 pulsed events each year, from mid-summer to early winter, creating a broad size range of age-0 fish within each year-class, with potentially different survival trajectories entering their first winter. We hypothesized that early-arriving pulses, high autumn body condition, and low winter severity would contribute to high first-winter survival of age-0 cod. To test these hypotheses, we examined juvenile cod catch data, archived samples, and winter temperature records to determine the impact of winter duration, body condition, and settlement time on winter survival from 2001 to 2019. Settlement pulse, pre-winter condition, and winter duration had an interactive effect on survival. Fish condition did not vary across pulses within a given year-class, but we observed improved winter survival during long winters when body condition was high, with highest survival among the larger, early-arriving pulses of fish. Late-arriving pulses of fish were small-sized before winter onset, but these pulses unexpectedly survived better than pulses settling earlier in the season during short winters when body condition was high. However, all settlement pulses had a survival advantage when settlement occurred earlier on average (associated with warmer autumns), suggesting that increased growth and size within a pulse can also contribute to overwintering success. Our findings challenge some assumptions of overwintering ecology (e.g. 'bigger is better', low temperature stress) but illustrate the importance of cohort effects for overwintering survival in a sub-arctic marine ecosystem in a changing climate.

**KEY WORDS:** Settlement · Recruitment · Juvenile fish · *Gadus morhua* · Survival · Winter · Condition · Size structure

## 1. INTRODUCTION

Recruitment dynamics play an important role in fisheries management, and previous studies have hypothesized that in marine fishes, recruitment patterns are largely set in the larval stage (Hjort 1926, Bannister et al. 1974, Oeberst et al. 2009). Many challenges constrain efforts to determine biological and

physical drivers that predict cohort strength from data collected at the earliest life stages; yet interactions between biological and physical drivers demonstrate the importance of evaluating survival across multiple early-life stages (Ottersen & Loeng 2000, Ottersen et al. 2014). Pre-recruit abundances and cohort strength vary across species, time, and populations, and older pre-recruits (age-0 juveniles)

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can provide an early indication of adult recruitment for fisheries management (Stige et al. 2013). Juvenile abundance has been linked to cohort strength in several fish species (Atlantic salmon *Salmo salar*, Niemelä et al. 2005; haddock *Melanogrammus aeglefinus*, Stige et al. 2019; Atlantic cod *Gadus morhua*, Lunzmann-Cooke et al. 2021), demonstrating the importance of juvenile abundance as an indicator of future population status in marine fish species. However, age-0 juvenile recruitment signals may 'disappear' in sub-arctic/arctic fish populations by way of high overwintering mortality (Laurel et al. 2017), indicating the need to account for regional environmental and biological factors later in the juvenile phase (Churchill et al. 2011, Stige et al. 2013).

Individual size among juveniles strongly influences overwintering survival in lakes (Post & Evans 1989), with increased survival in larger compared to smaller individuals (Byström et al. 2006, Huss et al. 2008). Differences in survival may be size-dependent, reflecting higher weight-specific standard metabolic rates and lower energy storage in smaller individuals, leading to depleted energy reserves throughout winter (Paloheimo & Dickie 1966, Shuter & Post 1990, Lankford & Targett 2001). However, winter energy depletion may be less of a concern in arctic regions where fish both feed and maintain body condition throughout winter, even with only modest food availability (Brown et al. 1989, Geissinger et al. 2021). However, in the complete absence of food, high overwintering mortality likely occurs across a range of winter environmental conditions, with smaller juveniles more susceptible to earlier starvation than larger conspecifics (Post & Evans 1989, Geissinger et al. 2021).

Pre-winter size variation within an age-0 juvenile cohort can occur by way of a number of mechanisms, including spawning timing (Conover et al. 2003), selective mortality (Sogard 1997), and growth (Dolan et al. 2021), and can become magnified in demersal species when pelagic–demersal transitions ('settlement') are not synchronized in time and space. Multiple settlement 'pulses' occur in numerous flatfish species (e.g. winter flounder *Pseudopleuronectes americanus*, Sogard & Able 1992; European plaice *Pleuronectes platessa*, Geffen et al. 2011), when flatfish metamorphose and settle to the benthos, which in turn affects post-settlement growth and mortality rates (Geffen et al. 2011). Atlantic cod in Newfoundland may be the most extreme example, where as many as 6 settlement pulses occur throughout the summer and into the late autumn (Methven & Bajdik 1994, Grant & Brown 1998, Gregory et al. 2019). These settlement pulses are likely the result of pro-

tracted spawning and/or distinct spawning groups (Horne et al. 2016) and are associated with onshore wind events, occurring within 3 d of juvenile fish arriving to the nearshore (Ings et al. 2008). Settlement pulses in Atlantic cod produce distinct size classes (Methven & Bajdik 1994, Ings et al. 2008), which can be identified with length-frequency histograms and mixture distribution models (Macdonald & Pitcher 1979, Rogers et al. 2011, Dolan et al. 2021). This pattern contrasts plaice, which settle in 2 to 3 pulses associated with spring tides (Geffen et al. 2011), and winter flounder, which settle in only 2 pulses associated with spawning within estuaries (Pearcy 1962, Dolan et al. 2021).

The absence of winter field observations has limited our understanding of overwintering dynamics in marine fish. However, snapshots in autumn and spring provide an opportunity to study winter ecology based on the demographics of the population during these 2 time periods. To determine the influence of cohort demographics on first-winter survival of Newfoundland (Canada) coastal cod, we used data and archived samples from a long-term monitoring program where settlement pulses of juvenile cod were annually tracked from July to the following spring from 2001 to 2018 (Gregory et al. 2019). In addition to settlement timing, we considered associations of winter duration, fish condition (pre-winter), and size class (represented by settlement pulse) on winter survival within each year. We hypothesized: ( $H_1$ ) higher survival in age-0 Atlantic cod that settle in early pulses than in late pulses, ( $H_2$ ) long, cold winters, defined by the number of days below 1°C, decrease survival of the smallest size class of age-0 Atlantic cod entering winter, and ( $H_3$ ) higher survivorship characterizes age-0 cod with high body condition entering long, cold winters compared to age-0 cod with low body condition.

## 2. MATERIALS AND METHODS

### 2.1. Study site, fish sampling, and water temperature

Newman Sound is a fjord of Bonavista Bay, Newfoundland, Canada, located adjacent to Terra Nova National Park. We used a seine net to capture juvenile fishes at 12 shore sites in Newman Sound (Fig. 1) every 2 wk from July to November, and once during May, from 2001 to 2019. The seine net was 25 m long and 2 m high, consisting of 9 mm stretched mesh.

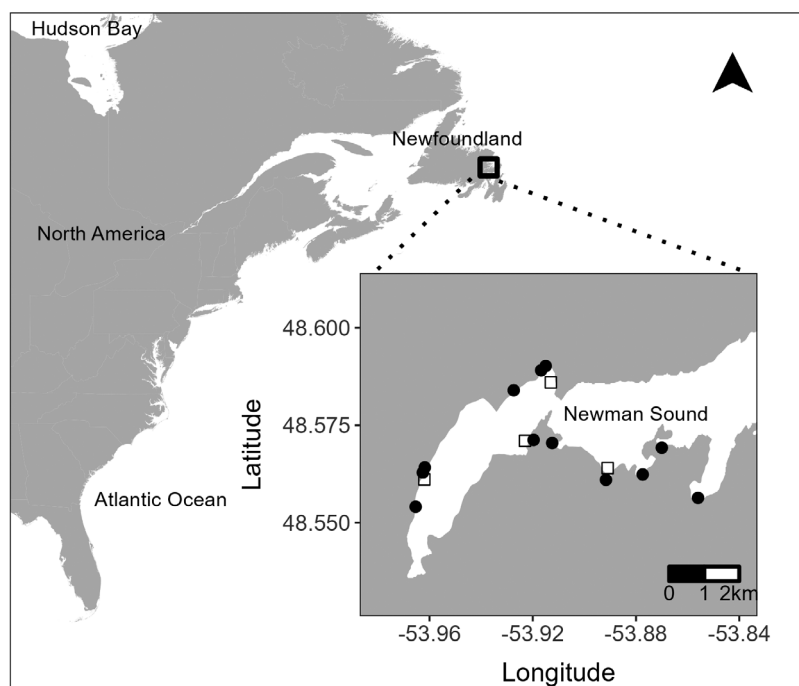


Fig. 1. Sampling sites (black dots;  $n = 12$ ) in Newman Sound, Newfoundland, Canada. Juvenile Atlantic cod *Gadus morhua* were sampled by a boat-deployed beach seine from 2001 to 2019 during May and July to November. Open squares represent locations of Minilog-T-II thermographs (<sup>TM</sup>Vemco), placed 25 cm above the ocean floor at an approximate water depth of 3 m

The net was deployed 55 m from shore from a small open boat and retrieved by 2 individuals standing 16 m apart. The seine samples approximately 880 m<sup>2</sup> of seabed habitat from the seabed to 2 m into the water column with a capture efficiency of approximately 95 % (Gotceitas et al. 1997). Age-0 and age-1 Atlantic cod were captured, counted, measured (to the nearest mm standard length, SL, from the tip of the snout to the end of the caudal peduncle), and returned live to the site of capture. Age-0 cod do not settle in the coastal zone until July or August and can be easily distinguished from age-1 juveniles sampled in May and July; sampling every 2 wk from July to early December enabled us to differentiate newly settled age-0 juveniles from age-1 juveniles (e.g. Gregory et al. 2019). A maximum of 10 Atlantic cod were haphazardly collected, euthanized, and preserved in 4 % formalin in seawater during each sampling trip; individuals were then transferred to 95 % ethanol within 48 h for long-term storage.

All preserved fish were blotted dry, weighed to  $\pm 0.01$  g, and measured to  $\pm 1$  mm SL. Fulton's condition factor,  $K$ , was calculated as:

$$K = 100 \times (W \times L^{-3}) \quad (1)$$

where  $W$  is weight (g) and  $L$  is standard length (cm SL; Fulton 1904). Fulton's  $K$  is an imprecise measure of energy but can serve as a relative measure of fish condition (Lambert & Dutil 1997, Grant & Brown 1999).

We obtained hourly temperature using Minilog-T-II thermographs (<sup>TM</sup>Vemco) placed in 4 locations in Newman Sound at 25 cm above the ocean floor at a water depth of approximately 3 m; these data are expressed as mean daily temperature. We defined start of winter for each year as the date when daily mean temperature fell below 1°C, and end of winter as the date when daily mean temperature exceeded 1°C, for at least 3 consecutive days. We calculated average winter temperature and standard deviation for the periods between start and end dates of winter each year, and length of winter as the number of days during the winter period with mean daily temperatures below 1°C.

## 2.2. Statistical analysis

Previous studies have identified pulse structure for age-0 Atlantic cod in Newman Sound, Newfoundland (Grant & Brown 1998, Ings et al. 2008), and across other species (Geffen et al. 2011, Dolan et al. 2021). We used finite mixture distribution models (Macdonald & Du 2018) to determine the size-class distributions for each sampling period and assigned the pulses using mixture model output in conjunction with growth trajectories over the course of the season (Gregory et al. 2019, see the Supplement at [www.int-res.com/articles/suppl/m711p047\\_supp.pdf](http://www.int-res.com/articles/suppl/m711p047_supp.pdf)). This process allowed us to assign settlement pulses for age-0 in autumn and again for age-1 in the following spring. Distinct size classes carry through the winter from age-0 to age-1 cod (Geissinger et al. 2022) and have been validated through otolith analysis from 2016 to 2017, with otoliths showing limited growth during winter (E. A. Geissinger unpubl. data). Settlement date was estimated by regressing daily modal length against day of year and daily temperature (°C) to account for temperature-dependent growth and back-calculated to the date using an initial settlement size of 39 mm SL (Ings et al. 2008). We further

standardized settlement time by calculating the mean settlement time for each pulse from 2001 to 2018 and subtracting annual settlement time for each pulse from the mean value.

We calculated fish abundance as mean number of age-0 juvenile Atlantic cod caught per seine haul for each sampling period across all 12 sampling sites, and then grouped them by settlement pulse. We selected October as our pre-winter sampling period for each year because it represents a reliable abundance estimate before juveniles move to deeper water. Similarly, we selected July of the following year as the post-winter sampling period because July represents a reliable post-winter estimate of abundance when nearshore waters are cool, and age-1 fish are available to the seine (R. S. Gregory unpubl. data). We present summary statistics on the first 4 pulses. We excluded individuals settling after October (Pulse 4) from statistical analyses because of limited archived samples in October. Pre-winter and post-winter abundances were used to calculate estimated winter survival. Sampling constraints and availability of fish in the sampling zone limited sampling to periods approximately 9 mo apart. Juvenile fish become less abundant in November when temperatures drop rapidly (Methven & Bajdik 1994), therefore limiting our ability to draw inferences on abundance estimates past October. Winter ( $<1^{\circ}\text{C}$ ) ranges from 2 to 6 mo, with the earliest start date in mid-December, and latest end date in mid-June.

We evaluated survival probability with pre-winter and post-winter fish abundance (mean catch haul $^{-1}$ ) by cohort (i.e. year-class) for 18 cohorts from 2001 to 2018. Explanatory variables included: settlement pulse (Pulse 1, Pulse 2, and Pulse 3), settlement anomaly, mean pre-winter condition, and the length of winter. Analysis of survival probability (post-winter abundance/pre-winter abundance) used a generalized linear model with a binomial error distribution and logit link. We assessed the model fit using visual residual diagnostics along with residual and null deviance. Analysis of deviance (ANODEV) was used to evaluate the significance of explanatory variables. We considered interactive effects between all explanatory variables and removed them from the model when  $\alpha > 0.05$  to increase our degrees of freedom and improve biological interpretation. We calculated effect size of explanatory variables using survival odds:

$$\text{Odds} = e^{\beta_i} \quad (2)$$

with  $\beta_i$  as the coefficient estimate with the logit link. Survival odds are expressed as the odds ratio (OR).

Calculations of predictor effects for generalized linear models used the 'effects' package version 4.2-2 in R (Fox 2003, Fox & Hong 2009, Fox & Weisberg 2018, 2019).

We investigated relationships between explanatory variables in subsequent models to separate interactive effects and identify underlying relationships between variables and categorized subsequent models by winter duration, settlement timing, and condition. Response and explanatory variables with model structure for each analysis are provided in Table 1. We evaluated model fit through visual inspection of residual diagnostic plots. Gaussian error distribution was initially used for each model, with more appropriate distributions selected, as needed, based on diagnostics. We classified a subset of data into 2 categories to assess winter duration and investigate the interactive effect between winter duration, pulse, and condition. Winters with  $\leq 90$  d below  $1^{\circ}\text{C}$  were classified as 'short', and winters with  $\geq 120$  d below  $1^{\circ}\text{C}$  were classified as 'long'.

We conducted all computations and statistical models using the R statistical programming language (version 4.2, R Core Team 2022), with additional functions from the 'car' package (Fox & Weisberg 2019). All data organization and data visualization were conducted in R using 'tidyverse' version 1.3.2 (Wickham et al. 2019). We report summary statistics as the mean  $\pm$  SD and provide model parameter estimates with 95 % confidence intervals.

### 3. RESULTS

#### 3.1. Data summary

Table 2 provides estimated settlement time and recorded October size for Pulse 1 through Pulse 4. Average settlement time between settlement pulses each year was  $4.9 \pm 1.4$  wk. The shortest interval between settlement pulses was 2 wk (between Pulse 1 and Pulse 2 in 2017), and the longest interval between settlement pulses was 8 wk (between Pulse 1 and Pulse 2 in 2006; Pulse 2 and Pulse 3 in 2007). Settlement week anomalies showed that Pulse 1 often settled later than average, whereas Pulse 2 settled earlier than average. Pulse 3 had an equal rate of early and late settlement, and Pulse 4 settled earlier more often (Fig. 2).

Condition ( $K$ ) for Pulses 1, 2, and 3 entering winter ranged from 0.51 to 1.1 (Fig. 3a). Pre-winter Fulton's  $K$  varied significantly by cohort ( $\chi^2 = 385.1$ ;  $\text{df} = 16$ , 492;  $p < 0.0001$ ) but did not vary among pulses ( $p > 0.05$ ).

Table 1. Generalized linear models used for all analyses. Models are divided by section in the Results. Error distributions are presented as probability models. Gaussian distribution includes  $\mu$  (distribution of residuals around the fitted model) and  $\sigma$  (standard deviation of the sampled population). Gamma distribution includes  $k$  (shape parameter) and  $\Theta$  (scale parameter). Binomial distribution includes  $N$  (number of juveniles) and  $\pi$  (binomial proportion). Link functions are listed for each respective model, and the structural model is included in the form of  $\eta = \Sigma \beta_i X_i$ . Explanatory variables include the following terms:  $X_0$  = cohort;  $X_1$  = pulse;  $X_2$  = settlement anomaly;  $X_3$  = pre-winter condition;  $X_4$  = days below 1°C (scaled);  $X_5$  = mean autumn temperature;  $X_6$  = mean autumn standard length (mm).  $K$ : Fulton's condition factor

Section	Distribution	Link function	Structural model
3.1	Pre-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_0 X_0 + \beta_1 X_1$
	Post-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_0 X_0 + \beta_1 X_1$
3.2	Post-winter count/pre-winter count $\sim \text{Binomial}(N, \pi)$	$\pi / (1 - \pi) = e^\eta$	$\eta = \beta + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$ $+ \beta_4 X_4 + \beta_{1.3} X_1 \times X_3 + \beta_{1.4} X_1 \times X_4$ $+ \beta_{3.4} X_3 \times X_4 + \beta_{1.3.4} X_1 \times X_3 \times X_4$
3.3	Post-winter count/pre-winter count $\sim \text{Binomial}(N, \pi)$	$\pi / (1 - \pi) = e^\eta$	$\eta = \beta + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$
3.4	Autumn standard length $\sim \text{Normal}(\mu, \sigma)$	Identity	$\mu = \beta + \beta_2 X_2 + (1 \mid \beta_1 X_1)$
	Settlement Anomaly $\sim \text{Normal}(\mu, \sigma)$	Identity	$\mu = \beta + \beta_5 X_5$
3.5	Pre-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_1 X_1$
	Pre-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_2 X_2$
	Pre-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_5 X_5$
	Pre-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_6 X_6$
	Post-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_3 X_3$
	Post-winter $K \sim \text{Gamma}(k, \Theta)$	Identity	$\mu = \beta + \beta_1 X_1 + \beta_2 X_2 + \beta_4 X_4$

Table 2. Earliest and latest settlement week estimated between 2001 and 2018 for age-0 juvenile *Gadus morhua*. Mean settlement week ( $\pm$ SD) is the average settlement time across the time series within each pulse group. Size range (mm standard length) includes the full range of sizes for all years and mean standard length ( $\pm$ SD) recorded in October for each pulse group throughout the entire time series

Pulse	Settlement week		Mean	Size range	
	Earliest	Latest		Full range	Mean length
1	Week 27 (early July 2006)	Week 34 (late August 2002)	$31.4 \pm 1.5$	42–121	$76.6 \pm 10.0$
2	Week 33 (mid-August 2008)	Week 40 (early October 2002)	$36.1 \pm 1.7$	33–91	$59.3 \pm 7.4$
3	Week 36 (early September 2008)	Week 46 (mid-November 2002)	$41.2 \pm 2.6$	24–70	$47.6 \pm 7.9$
4	Week 40 (early October 2008)	Week 49 (early December 2010)	$44.3 \pm 2.5$	24–56	$39.4 \pm 9.8$

Pre-winter  $K$  for all sampled juveniles across the entire time series averaged  $0.71 \pm 0.08$ . Mean Fulton's  $K$  was lowest in the 2017 cohort ( $0.59 \pm 0.06$ ) and highest in the 2012 cohort ( $0.84 \pm 0.08$ ).

Condition for Pulses 2, 3, and 4 after winter ranged from 0.48 to 1.0 (Fig. 3b). Post-winter Fulton's  $K$  varied significantly by cohort ( $\chi^2 = 122.2$ ;  $df = 15$ , 270;  $p < 0.0001$ ) but did not vary among pulses ( $p > 0.05$ ). Post-winter  $K$  for all sampled juveniles across the entire time-series averaged  $0.70 \pm 0.09$ , with the lowest mean Fulton's  $K$  ( $0.62 \pm 0.05$ ) for the 2005 cohort and highest mean Fulton's  $K$  ( $0.85 \pm 0.05$ ) for the 2016 cohort.

The 2007 cohort experienced the longest winter duration, i.e. 131 d ( $\sim 4$  mo), with an average winter temperature of  $-0.15 \pm 0.56^\circ\text{C}$ , whereas the 2010 cohort experienced the shortest winter of 64 d ( $\sim 2$  mo), with an average winter mean temperature of  $0.47 \pm$

$0.36^\circ\text{C}$ . The 2010 cohort also experienced the mildest winter among all years in this study, whereas the 2015 cohort experienced the coldest, with a mean temperature of  $-0.44 \pm 0.39^\circ\text{C}$  and 110 d below  $1^\circ\text{C}$  (Fig. 4).

### 3.2. Model results

The full model, which included Pulse 1, Pulse 2, and Pulse 3, had a null deviance of 215.9 on 42 degrees of freedom and a residual deviance of 77.4 on 30 degrees of freedom; the full model explained a significant amount of variance relative to the null model ( $\chi^2 = 138.6$ ;  $df = 12$ ;  $p < 0.001$ ). We detected a 3-way significant interaction ( $p = 0.021$ ) among pulse, pre-winter  $K$ , and winter duration (ANODEV; Table 3).



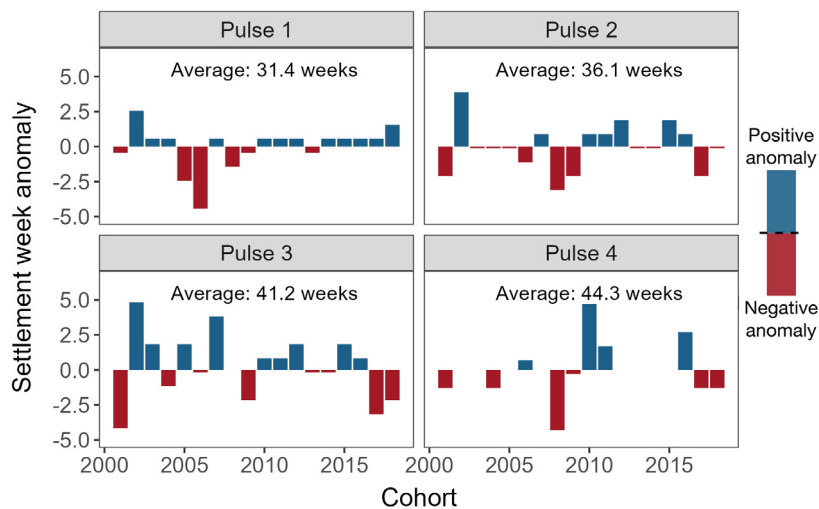


Fig. 2. Settlement week anomalies for age-0 *Gadus morhua* in Newman Sound, Newfoundland. Anomalies were calculated as differences from average. Positive and negative anomalies denote later and earlier than average settlement times, respectively

During winters with 98 d or less below 1°C, our model predicted high survival probability in Pulse 1 juveniles with low pre-winter Fulton's *K*, in contrast

to high survival probability in Pulse 3 juveniles with high pre-winter *K*. During winters with 130 d or more below 1°C, Pulse 1 juveniles showed the same trend as Pulse 2 and Pulse 3 juveniles, with high survival probability associated with high pre-winter Fulton's *K*. Pulse 1 juveniles did best with high condition during longer winters, followed by Pulse 2, whereas Pulse 3 had the lowest relative survival probability (Fig. 5a).

Settlement week anomaly was significantly associated with survival probability; survival odds decreased by 48 % (OR = 0.52:1) for every week settled later than average. Survival probability estimate was 0.49 (95 % CI: 0.25–0.73) when pulses settled 5 wk earlier than the average settlement time. The survival probability estimate was 0.022 (95 % CI: 0.0078–0.061) when pulses settled 4 wk later than the average settlement time (Fig. 5b).

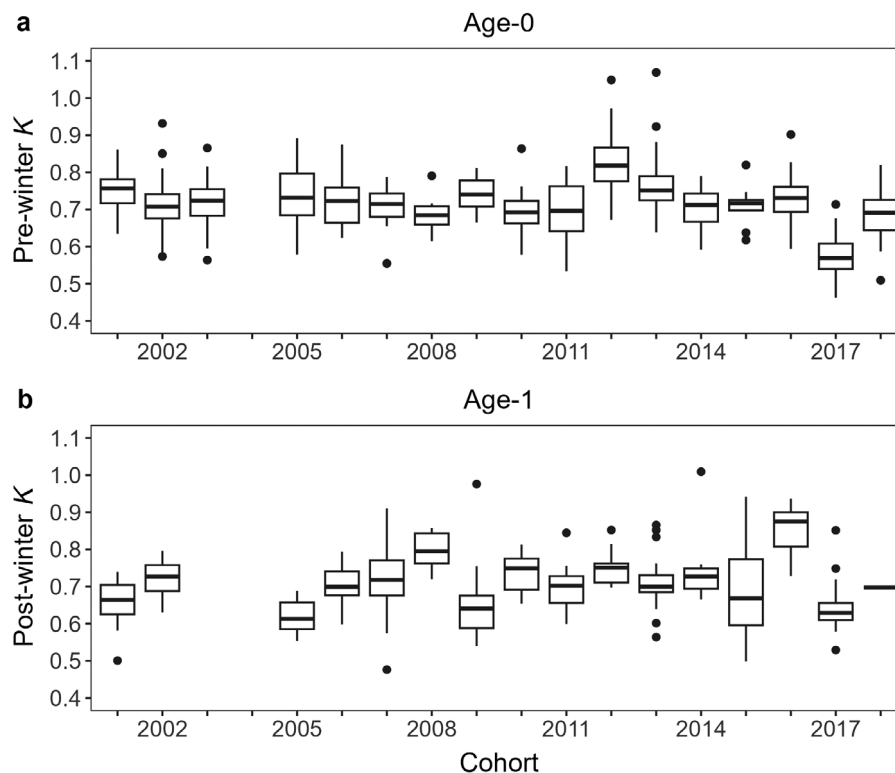


Fig. 3. Fulton's *K* condition factor of age-0 *Gadus morhua* for (a) October (pre-winter) and (b) May (post-winter) for each annual cohort from 2001 to 2018. The horizontal bold line represents the median of all sampled juveniles for each cohort, the lower and upper hinges correspond to the first and 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 outliers

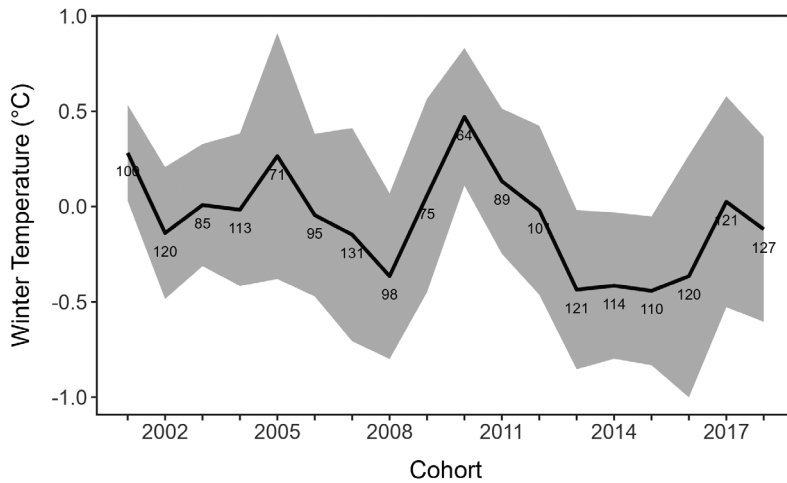


Fig. 4. Mean winter temperature in Newman Sound, Newfoundland, for each *Gadus morhua* cohort (2001–2018). Grey shading represents  $\pm$  SD. Numbers represent days below 1°C each winter

### 3.3. Winter duration

To understand the interactive effect between pulse, condition, and winter duration, we divided the dataset into 2 categories: (1) short winter ( $\leq 90$  d below 1°C), and (2) long winter ( $\geq 120$  d below 1°C). We only used long and short winters to clarify interactive effects; the remaining 8 winters were excluded because these winters were between the criteria of 'short' and 'long' and limited our ability to understand the interactive effect between pulse, condition, and winter duration. Short winters ( $n = 5$ ) had an average winter temperature of  $0.19 \pm 0.19^\circ\text{C}$ , and long winters ( $n = 6$ ) had an average winter temperature of  $-0.20 \pm 0.17^\circ\text{C}$ . Pulse, condition, and settlement anomaly had no effect on survival probability during short winters (GLM:  $\chi^2 = 7.8$ ,  $df = 4$ ,  $p = 0.10$ ; Fig. 6). Pulse also had no effect during long winters; however, condition and settlement anomaly significantly affected survival probability (GLM:  $\chi^2 = 21.98$ ,  $df = 4$ ,  $p = 0.0002$ ; Fig. 6). Early settlement and high Fulton's  $K$  were associated with higher survival probability during longer winters. There was high uncertainty in survival probability estimates for short winters relative to long winters (Fig. 6).

### 3.4. Settlement timing

Early settlement (negative anomaly) was associated with increased length

(SL, mm) within each pulse relative to late settlement (positive anomaly;  $\chi^2 = 40.11$ ,  $df = 1$ ,  $p < 0.001$ ). Warmer autumn temperatures were associated with negative settlement anomalies ( $\chi^2 = 43.04$ ;  $df = 1, 52$ ;  $p = 0.0006$ ). Our model predicted settlement 1 wk earlier for every 1.1°C increase in temperature in the autumn (Fig. 7). The largest anomaly in settlement timing occurred in 2008 ( $12.4 \pm 2.2^\circ\text{C}$ ), with Pulse 2 settling 3.1 wk earlier than average, and Pulse 3 settling 5.2 wk earlier. The Pulse 1 anomaly in 2008 was not as large as the later pulses, but was nonetheless negative, at 1.4 wk earlier than average.

### 3.5. Condition

Pulse, mean length, settlement anomaly, and autumn temperature did not affect pre-winter condition (Fulton's  $K$ ;  $p > 0.05$ ). Additionally, we found no significant relationship between pre-winter and post-winter condition ( $\chi^2 = 3.21$ ,  $df = 1$ ,  $p = 0.07$ ).

Settlement anomalies significantly affected post-winter condition (Fulton's  $K$ ) for Pulse 2 and Pulse 3 juveniles ( $\chi^2 = 4.60$ ;  $df = 1$ ,  $p = 0.032$ ), with no effects from winter duration or pulse ( $p > 0.5$ ). Our model predicted post-winter condition of 0.64 (95% CI: 0.59–0.71) with a  $-4.0$  wk anomaly and 0.77 (95% CI: 0.70–0.84) with a  $+4.0$  wk anomaly (Fig. 8).

Table 3. Type-III analysis of deviance of the effect of pulse, settlement anomaly (weeks), pre-winter condition (Fulton's  $K$ ), and days below 1°C on survival probability of age-0 *Gadus morhua* from the 2001–2018 cohorts from Newman Sound, Newfoundland. Data modeled with a generalized linear model, using a binomial error distribution and logit link. Degrees of freedom (df), likelihood ratio chi-square test statistic (LR chi-square) and p-value (p) are reported for each source variable. Residual deviance was 27.6 on 14 degrees of freedom

Source	df	LR chi-square	p
Pulse	2	10.1	0.0065
Settlement anomaly	1	18.2	<0.001
Pre-winter $K$	1	22.3	<0.001
Days below 1°C	1	23.3	<0.001
Pulse $\times$ Pre-winter $K$	2	8.93	0.012
Pulse $\times$ Days below 1°C	2	8.7	0.013
Pre-winter $K \times$ Days below 1°C	1	21.9	<0.001
Pulse $\times$ Pre-winter $K \times$ Days below 1°C	2	7.73	0.021

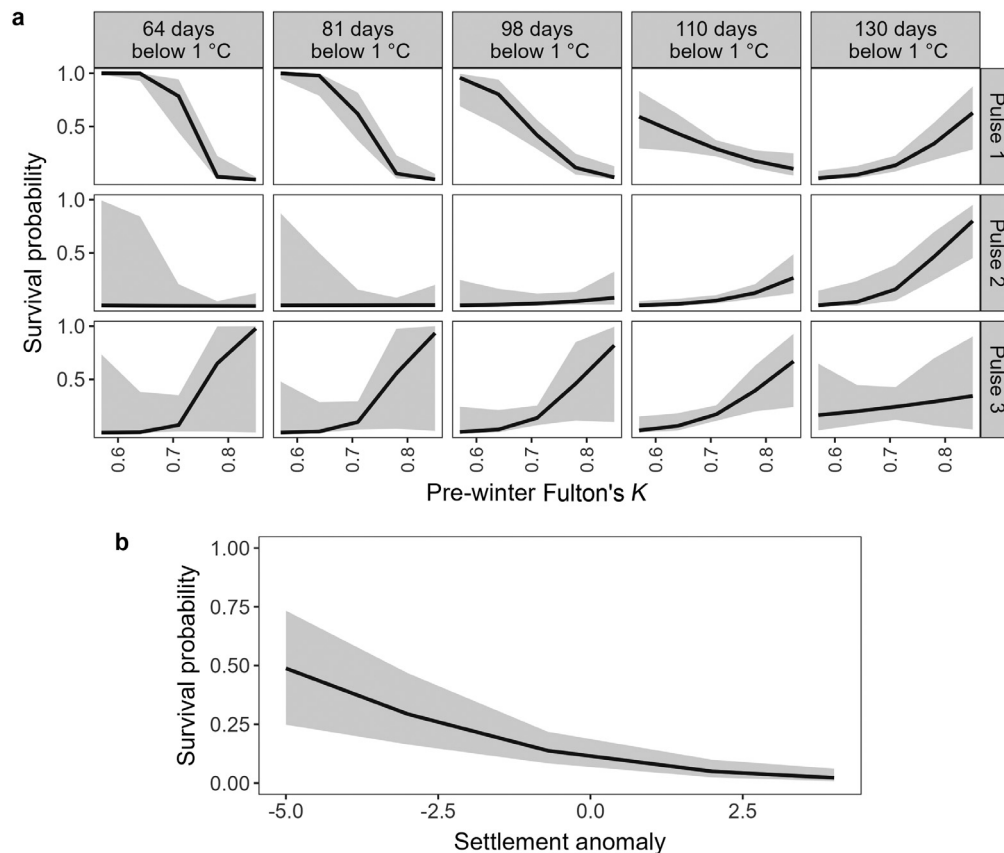


Fig. 5. Predictor effects for survival probability of age-0 *Gadus morhua* for Pulse 1, Pulse 2, and Pulse 3 from 2001 to 2018. Generalized linear model (binomial error distribution and logit link) results show (a) the interactive effect of pulse, winter duration, and pre-winter condition on survival probability, and (b) the effect of settlement anomaly on survival probability of age-0 *G. morhua*. Settlement anomaly is represented by weeks, with negative values representing earlier than average settlement, and positive values representing later than average settlement. Gray shading represents 95% confidence intervals

#### 4. DISCUSSION

The challenges of winter sampling have limited the characterization of overwintering survival in marine systems (Hurst 2007), but our long-term field dataset indicates that multiple factors influence survival probability of juvenile Atlantic cod in their first winter. *A priori*, we expected higher age-1 survivorship among age-0 cod entering winter in high body condition and at a larger size (resulting from early pre-winter settlement) compared to juveniles in low condition and at a smaller size (resulting from later pre-winter settlement). Similarly, we expected higher survival in cohorts experiencing mild annual winter conditions than those experiencing harsher winters (longer, colder). Our results show that: (1) early settlement, regardless of settlement pulse, promotes higher winter survival (support for  $H_1$ ); (2) winter duration had an interactive effect between settlement pulse (body size) and condition on survival, with high survival for

smaller individuals (late pulses) with high pre-winter condition during shorter winters; in contrast, larger individuals (early pulses) with high pre-winter condition had high survival only during the longest winters (130 d below 1°C; partial support of  $H_2$ ); and (3) high pre-winter body condition increased survival probability, but only for the smallest individuals or during the longest winters (partial support for  $H_3$ ). These results challenge several assumptions of overwintering ecology (e.g. 'bigger is better', low temperature stress) but emphasize the importance of settlement timing, winter duration, and fish condition on future survival. We discuss these results below in the context of current and future climate scenarios.

##### 4.1. Settlement timing

Settlement timing of pulses significantly influenced their survival probability, with a survival ad-



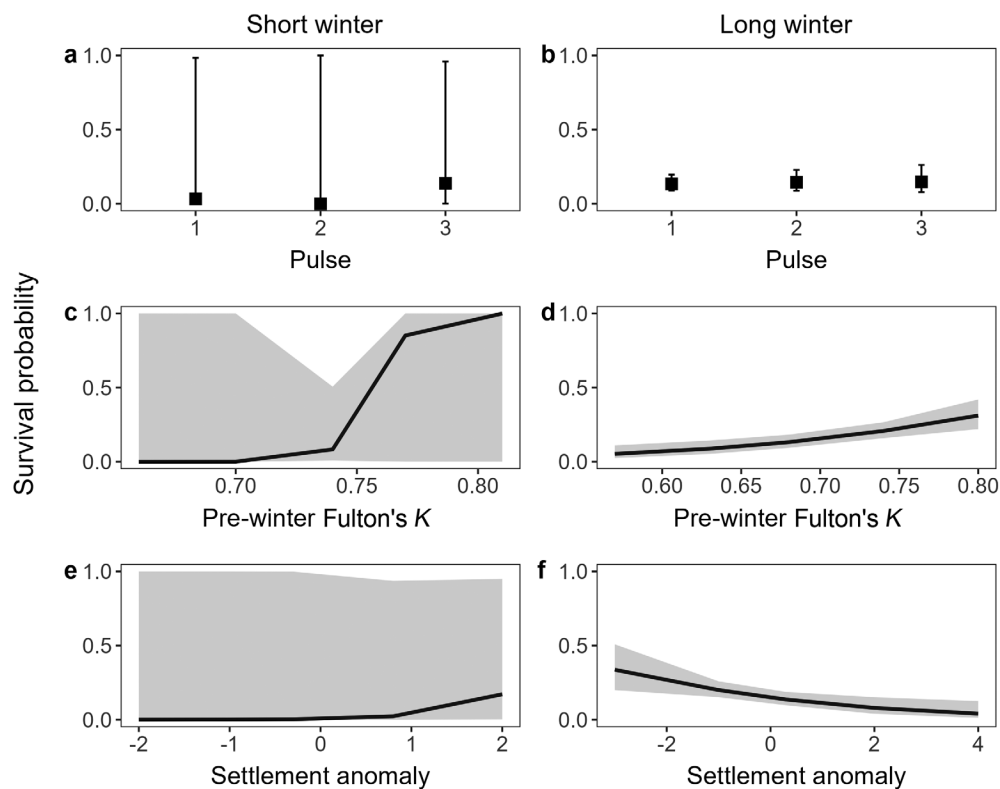


Fig. 6. Predictor effects for survival probability of age-0 *Gadus morhua* separated by winter duration. Binomial logistic regression models were split into short winters ( $\leq 90$  d below  $1^{\circ}\text{C}$ ) and long winters ( $\geq 120$  d below  $1^{\circ}\text{C}$ ). Data include Pulse 1, Pulse 2, and Pulse 3 from 2001 to 2018. Binomial logistic regression results show the effect of (a,b) pulse, (c,d) pre-winter Fulton's  $K$  and (e,f) settlement anomaly on survival probability during (a,c,e) short winters and (b,d,f) long winters. Error bars (a,b) and gray shading (c,d,e,f) represent 95% confidence intervals

vantage for early settlement in a given year. Settlement timing for all pulses shifted earlier under warmer autumn conditions, which may simply represent faster pre-settlement growth and earlier settlement competency (Dolan et al. 2021). However, waves dominate circulation within Newfoundland inlets (Syvitski et al. 1987), and timing of settlement for age-0 cod and nearshore temperature are both linked to coastal winds and resultant upwelling events (Ings et al. 2008). The physical oceanography of the coastal system in the late summer–early autumn period (temperature, upwelling/downwelling events) may therefore structure biological processes for juvenile cod both immediately (settlement timing and condition) and into the following year (overwintering success).

Despite clear evidence that higher survivorship occurs in large juveniles of most fishes (Werner & Gilliam 1984, Moss et al. 2005, Hurst 2007), we observed high survival probability in our smallest (Pulse 3) groups of juveniles with short winter duration when body condition entering winter was high. In contrast, large juveniles (Pulse 1) had low survival during shorter winters with high body

condition entering winter, and high survival with low body condition. Larger juveniles have an increased ability to survive low-food scenarios during winter (Geissinger et al. 2021) and may focus on increasing length rather than increasing energy stores. The intermediate size class (Pulse 2) had low survival regardless of body condition except in long winters. The difference in survival between the second and third pulses indicates a survival advantage for small juveniles over intermediate juveniles (Pulse 3 vs. Pulse 2) during shorter, mild winters, a surprising result given the general ability of larger fish to evade predators (Van der Veer et al. 1997, Lundvall et al. 1999, Cowan et al. 1996).

Predation likely contributes to the size-structured survival we observed. A time- or size-dependent predator window may explain the high survival probability of large-sized, early-pulse juveniles and smaller-sized, late-pulse juveniles. Early pulses settle early in the season and have greater length relative to later settlement pulses (Grant & Brown 1998, Geissinger et al. 2022). Smaller-sized, late-pulse juveniles may experience a predator window by way

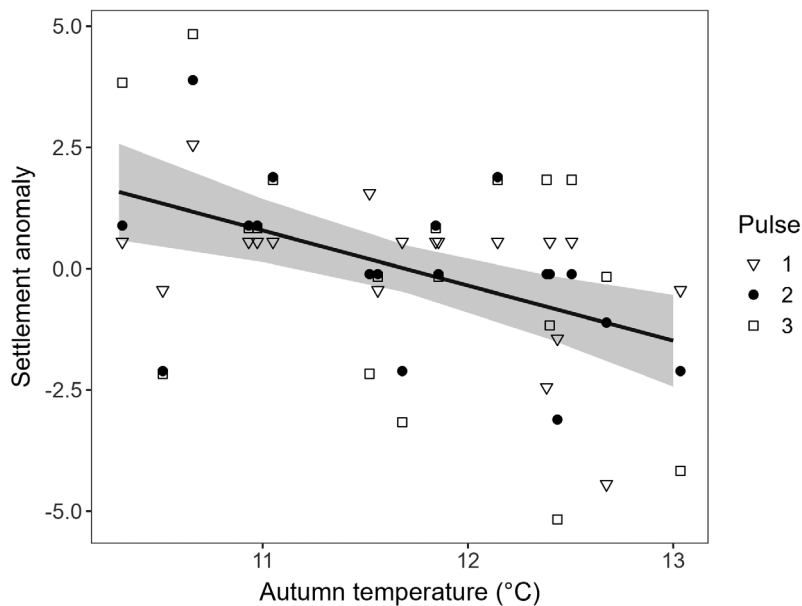


Fig. 7. Settlement week anomalies for age-0 *Gadus morhua* in the 2001–2018 cohorts from Newman Sound, Newfoundland, across mean autumn temperatures. Estimates are produced from a general linear model with autumn temperature as an explanatory variable. Settlement time anomalies were associated with autumn temperature. Regression lines estimated from a Gaussian distribution. Gray shading represents 95 % confidence intervals and individual points represent settlement anomalies for Pulse 1, Pulse 2, and Pulse 3

of several potential mechanisms. For example, late-pulse fish settle into nearshore structured habitats (e.g. eelgrass, kelp) after predators move into deeper water in the autumn, thereby significantly reducing predation rates (Linehan et al. 2001, MacRobert 2020). Alternatively, energy reserves could differ in later pulses that retain reserves from their pelagic phase, which help them survive winter (sensu Copeman et al. 2008).

Pulse assignments add some uncertainty, with special consideration given to individuals on the upper and lower bounds of their respective pulses. Assessing pulse structure in isolation (e.g. 1 sampling trip per season) would increase uncertainty in pulse assignments. However, our protocol of sampling every 2 wk minimizes potential error in pulse assignment and settlement time estimates because we measured and released juveniles back into their habitats, providing the opportunity to re-measure and track cohorts over short time intervals (~14 d). This sampling protocol provides an opportunity to assess growth trajectories throughout the course of seasons (Gregory et al. 2019). Settlement pulses result in multiple size classes throughout autumn and into winter (Grant & Brown 1998, Dolan et al. 2021), and size differences can lead to differential survival within annual cohorts (Geffen et al. 2011, Geissinger

et al. 2022). Understanding settlement pulses in relation to winter survival provides a more holistic understanding of juvenile population dynamics in coastal nurseries.

Delineating the contrasting advantages between early versus late settlement pulses will require further research. Otolith studies that further characterize settlement pulses and confirm settlement times would support better understanding of the complex size structure in fishes with multiple pulses (Geffen et al. 2011, Dolan et al. 2021). Studies on settlement time at a coarser scale can help determine if either settlement time or size entering winter drive winter survival. Additionally, a better assessment of energetic benefits for early vs. late settlement and predator windows will enhance understanding of this complex and counter-intuitive result.

#### 4.2. Condition

Favorable pre-winter condition resulted in high overwintering survival, with the exception of Pulse 1 during short winters. High survival with high condition aligns with other studies on high-latitude fish species (Heintz et al. 2013, Sewall et al. 2019). In our study, condition did not vary among pulses within cohorts, indicating similar rates of increase in *W/L* ratios annually among settlement pulses. Potentially, once cod settle (regardless of pulse), they switch to a growth allocation strategy leading to increased length, presumably to avoid predation (Post & Parkinson 2001, Copeman et al. 2008, Siddon et al. 2013). Juvenile fish often favor one of 2 alternative strategies: (1) maximize somatic growth or (2) maximize lipid storage (Post & Parkinson 2001). Energy allocation strategies in Arctic gadid species (e.g. polar cod *Boreogadus saida* and saffron cod *Eleginus gracilis*) under laboratory conditions appear to favor energy storage over growth as temperatures decline in autumn (Copeman et al. 2016), and presumably individual Atlantic cod can allocate more energy to fat as metabolic demands decrease with temperature (Jobling 1995). Despite this allocation, increased condition may be associated with higher temperatures in coastal nurseries (e.g. Pacific cod *Gadus macro-*

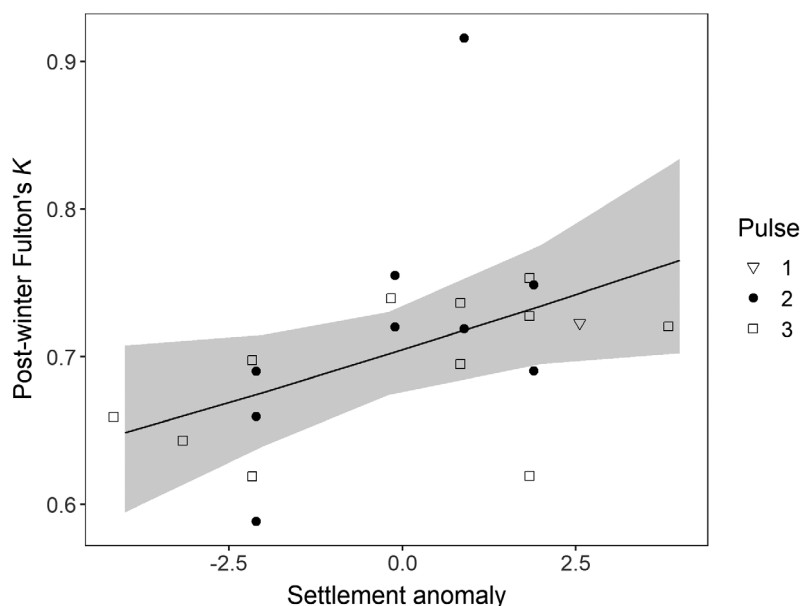


Fig. 8. Post-winter Fulton's  $K$  for age-0 *Gadus morhua* in the 2001–2018 cohorts from Newman Sound, Newfoundland, based on settlement anomalies (weeks). Estimates are produced from a general linear model with settlement anomaly as an explanatory variable. Regression lines estimated from a Gaussian distribution. Individual points represent post-winter Fulton's  $K$  for Pulse 1, Pulse 2, and Pulse 3

*cephalus*; Abookire et al. 2022). In our study, pre-winter condition was relatively consistent across pulses and thermal conditions within a given year, although we acknowledge that wet Fulton's  $K$  may be too coarse of a condition metric to detect modest differences in annual autumn temperature.

Condition post-winter can indicate whether fish needed to use their energy stores (low food) or were able to maintain or improve their energy reserves (high food). We were only able to measure post-winter condition in fish that survived winter, which limits our ability to draw inferences on the relationship between post-winter condition and survival. Regardless, post-winter condition of the survivors still provides useful insight. Condition loss throughout winter typically results from low food availability, in worst years leading to death (Geissinger et al. 2021). In the absence of food, condition of juvenile roach *Rutilus rutilus* decreases at a faster rate during warm winters than cold winters (Brodersen et al. 2011). In contrast, juvenile Atlantic cod can increase their body condition at temperatures ranging from  $-0.7$  to  $2.5^{\circ}\text{C}$  when food is available even in small quantities (Geissinger et al. 2021). Across most years, poorer condition of juvenile cod after winter suggests limited winter foraging opportunities in coastal Newfoundland. Low food availability, competition for available resources, or predation risk (including can-

nibalism within the cohort) could all limit foraging opportunities. Surprisingly, winter duration had no effect on post-winter condition. These results highlight the fact that juvenile cod are well suited to cold temperatures, despite susceptibility to metabolic (energy storage) and behavioral (foraging) stressors in winter environments.

We showed that settlement time explained variance in post-winter condition, highlighting the complexity of a multi-pulsed population. Later settlement was associated with higher post-winter condition. We interpret our findings as evidence of a trade-off to settling later in the season. Food quality and availability may differ throughout the autumn season and could explain observed differences in post-winter condition based on settlement time. Although Fulton's  $K$  can reflect total available energy reserves in cod (Lambert & Dutil

1997), it offers limited information on types of energy reserves available. Fulton's  $K$  provides no direct information on food quality or the total available energy between pulses or settlement times. However, lipid class and fatty acid composition changes when juvenile cod transition from pelagic to demersal prey types following settlement (Copeman et al. 2008). Although beyond the scope of our study, evaluating multi-pulse diet and energetics within coastal Newfoundland Atlantic cod would provide further insight but would require finer temporal measurement of autumn growth and energy allocation.

#### 4.3. Winter duration

The difference in effects of explanatory variables on survival between short ( $\leq 90$  d below  $1^{\circ}\text{C}$ ) and long ( $\geq 120$  d below  $1^{\circ}\text{C}$ ) winters was unexpected. The high uncertainty around survival probability estimates during short winters indicates that unmeasured variables contribute to survival during short winters (e.g. food resources, predation). Our study could not evaluate predation (including cannibalism), acknowledging its likely contribution to winter survival. Short winters are warmer and can increase metabolic demand in fishes (Soofiani & Hawkins 1982, Chipps et al. 2000). In contrast to short winters,

pre-winter condition and settlement time explained survival probability during long winters with higher confidence.

During long winters only, favorable condition and early settlement increased survival, and settlement pulse did not contribute to change in survival. In laboratory settings, wild-caught juvenile cod maintain growth in low food environments with cold conditions ( $<1^{\circ}\text{C}$ ) for months at a time (Brown et al. 1989, Geissinger et al. 2021). Winter thermal refuges may also exclude predators in nearshore ecosystems (Kristiansen et al. 2001). For example, tagging studies indicate that age-2 Greenland cod *G. macrocephalus ogac*, a known predator on age-0 cod, move away from nearshore habitats in winter (Shapiera et al. 2014), but predation through cohort cannibalism may possibly occur throughout winter. Noting the primary importance of high pre-winter condition for survival, juveniles likely depend on their winter fat reserves until spring, although favorable post-winter condition in some years suggests periodic winter foraging (Geissinger et al. 2022, this study). Therefore, coastal cod in Newfoundland may require sufficiently long winters to reduce metabolic demand and predation risk during periods of low productivity.

## 5. CONCLUSIONS

We showed that large body size does not always favor overwintering survival in juvenile Atlantic cod, and a potentially high survival probability may characterize smaller individuals (i.e. later settlement pulses). Smaller fish experiencing high survival contradicts most assumptions based on size. Smaller size entering winter may represent a trade-off with settlement time (including variation among and within pulses) and indicates a bet-hedging strategy for Atlantic cod in Newfoundland coastal waters, increasing the probability of survival for at least one settlement pulse in a year of typical annual environmental variability in the Atlantic subarctic.

Autumn temperatures may play an important role in survival trade-offs because: (1) survival probability decreased when settlement pulses arrived later in the season, and (2) warmer autumns were associated with earlier settlement across all settlement pulses. Therefore, warm autumns may promote high winter survival for all pulses settling earlier in the season, with an increased advantage for late pulses. However, warmer temperatures can also result in shorter, warmer winters, thereby decreasing survivorship in larger, early-settling juveniles.

Our study emphasizes the importance of characterizing age-0 Atlantic cod cohort demographics (size, condition) to assess survival in juvenile fish populations and highlights the importance of seasonal sampling to assess multiple settlement pulses. Simple metrics, such as Fulton's condition factor  $K$ , can complement size and abundance measures from surveys, and could potentially be further enhanced through energetic measures to improve predictions of survival probability to age-1. The dynamic pulse structure of coastal cod populations in Newfoundland is complex, and such variability in settlement time and pre-winter size may be an important component of historical and future climate resiliency in this population.

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