

High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in subarctic coastal habitat during their first winter

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In subarctic Newfoundland, age-0 juvenile Atlantic cod (*Gadus morhua*) settle into coastal habitats in several summer and fall pulses, yielding a broad length-frequency distribution prior to their first winter. The first winter is often associated with physiological and metabolic stress and has been considered a critical survival period determining cohort strength. We evaluated size-structured overwinter mortality and movement using mark-recapture and condition metrics by marking 226 cod in two batches one week apart, in October 2016. We estimated fall and overwinter mortality, and documented movement of fish recaptured in May 2017 using Cormack–Jolly–Seber models. We recaptured 30 marked juveniles. High fall mortality characterized late settling cohorts relative to earlier settling cohorts (16.6% d⁻¹ vs. 4.5–7.7% d⁻¹). Overwinter mortality was unexpectedly low (0.0052 and 0.0022% d⁻¹). Individual condition (Fulton's K) of juvenile cod remained high throughout winter across all size groups. We expected higher mortality of juvenile cod and broad dispersal of juveniles over winter (32 weeks). In contrast, our results indicated low mortality and high site-fidelity in their first winter. This study indicates the period leading up to winter is important for survival, suggesting winter is not a survival bottleneck and may even provide a refuge compared to the rest of the year.

Keywords: coastal nursery, Cormack–Jolly–Seber, juvenile fish, marine, natural mortality, site-fidelity.

Introduction

Natural mortality at early life stages strongly influences recruitment potential. Natural mortality represents a critical defining variable in fish ecology and population dynamics, yet quantifying mortality is challenging in open, marine systems. Despite many gaps in current understanding of natural mortality, published evidence suggests that three main factors affect fish survival: size, growth rate, and ambient temperature (Pauly, 1980; Sewall *et al.*, 2019). Numerous studies have examined mortality rates for many species, from larval to adult stages (Peterson and Wroblewski, 1984; Gulland, 1987). Extensive research has considered natural mortality of north-east Arctic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*), providing an important baseline for juvenile population dynamics (Nash and Geffen, 2012; Ottersen *et al.*, 2014; Bogstad *et al.*, 2016). However, limited data availability on natural mortality rates in young-of-the-year juveniles across regions and species continues to constrain our understanding of the relationship between early juvenile abundance and recruitment to fisheries.

Size-structured mortality dominates early life stages, particularly in juvenile fish in their first year of life (Sogard, 1997; Sewall *et al.*, 2019). The complex factors that influence size-structured mortality in young-of-the-year juveniles involve the interplay of physiology and bottom-up processes (e.g. size-dependent energetics; Sogard and Olla, 2000) combined with behaviour and top-down processes (e.g. size-dependent movement and predation risk; Akimova *et al.*, 2019; MacRobert,

2020). Broadly speaking, large juvenile fish should have a survival advantage compared to small conspecifics because larger fish have more energy stores to endure periods of low productivity, reduced exposure to gape-limited predators (“predator window”; Cowan *et al.*, 1996; Beamish and Mahnken, 2001), improved swim-performance, and reduced need to forage in risky habitats (Heintz and Vollenweider, 2010; Sewall *et al.*, 2019). Numerous studies document size-dependent mortality across a wide range of fish species, recognizing that mortality may involve one or more of these processes (Sogard, 1997; Schindler, 2011).

Size-structured mortality may be especially important during winter. Research on Atlantic cod from the Barents Sea and haddock (*Melanogrammus aeglefinus*) from the Barents Sea, the southern Scotian Shelf, and the Bay of Fundy shows a strong positive relationship between body size (length) at age-0 and abundance at age-1 (Stige *et al.*, 2019). In seasonal environments, highest rates of size-dependent mortality may occur in juveniles entering their first winter. Early spawning in sand smelt (*Atherina boyeri*) confers a survival advantage from their increased size at onset of winter, compared to later spawning individuals (Henderson *et al.*, 1988). Similarly, in bluefish (*Pomatomus saltatrix*), spring-spawned juveniles had higher survival than summer-spawned juveniles, although some of the latter group may also survive (Morley *et al.*, 2013). Juvenile rainbow trout (*Oncorhynchus mykiss*) rarely survive their first winter unless they achieve a critical size and energy threshold (Mogensen and Post, 2012). Similarly,

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young-of-the-year walleye pollock (*Gadus chalcogrammus*) rarely survive their first winter following poor fall growth conditions (Heintz and Vollenweider, 2010). Yet, overwinter mortality and ecosystem dynamics during winter are poorly characterized for most species, especially in marine systems (Beamish and Mahnken, 2001; Hurst, 2007). Even in freshwater systems, where juvenile overwinter mortality has well-established links to year-class strength and poleward range (Post and Evans, 1989; Morley *et al.*, 2013), juvenile fish may actually experience lower mortality throughout winter compared to other times of the year. For example, Atlantic salmon (*Salmo salar*) parr experience higher initial mortality leading into winter compared to mid-winter when ice covers streams (Linnansaari and Cunjak, 2010). Additionally, size-dependent mortality during winter may not be evident when there is sufficient productivity (Geissinger *et al.*, 2021a). Therefore, overwintering mortality and size-dependent processes likely vary by species, region, and ecosystem.

Natural mortality rates in early life stages of cod have been difficult to characterize. Alteration in relative abundance of a cohort occurs sometime between egg production and the onset of their first winter (Campana, 1996; Bogstad *et al.*, 2016; Lunzmann-Cooke *et al.*, 2021). However, mortality rates for juveniles remain poorly studied due to size limitations for tagging and high mortality rates, necessitating the need to tag large numbers of individuals (Seber, 1982). Additionally, juvenile distributions are coarsely linked to dynamic seasonal and annual environmental conditions (Laurel *et al.*, 2017). Estimates of instantaneous mortality rates of Atlantic cod from Newfoundland range between 5.4 and 4.4% $\cdot y^{-1}$ from age-1 to age-3 (Anderson and Gregory, 2000), with reported daily instantaneous mortality rates of age-0 cod in northeast Arctic cod (*G. morhua*) ranging from 0.005 to 0.021% d^{-1} (Bogstad *et al.*, 2016). These estimates provide a starting point to understanding natural mortality in young-of-the-year fish. However, poor understanding on the mechanisms and seasonal regulation of young-of-the-year natural mortality for most marine fish species persist (i.e. size, energetics, predation, environment).

Reliable estimation of natural mortality requires understanding movement. One difficulty in estimating natural mortality is disentangling movement from mortality in fish populations (Pine *et al.*, 2003). We also know little on winter movement in young-of-the-year marine fish. Few studies have characterized the distances travelled away from coastal habitats and movement patterns during winter (although see Shapeira *et al.*, 2014). In the Barents Sea, juvenile cod are relatively stationary until age-3 (Ottersen *et al.*, 1998). In the North Sea, pelagic juvenile cod (age 0–2) move inshore to shallow coastal nurseries during winter (Riley and Parnell, 1984). In contrast, juvenile cod (age 1–2) in the Gulf of St. Lawrence move out of shallow coastal nurseries during winter to depths ranging between 100 and 200 m with the younger, smaller cod not migrating as far as the older juveniles (Hanson, 1996). These regional differences highlight the importance of understanding movement when estimating natural mortality.

In this study, we use capture–mark–recapture techniques and demographic information on cohorts (size, condition) to quantify overwintering mortality in age-0 Atlantic cod in coastal Newfoundland. Complementary otolith microchemistry analysis (trace elements) looked for evidence of changing habitat use over time. Trace elements, such as Mg, Ba, and Sr, capture temperature and salinity changes in marine fish (Els-

don and Gillanders, 2002) indicative of habitat and movement (Miller, 2011; Stanley *et al.*, 2016). Following settlement, age-0 cod in Newfoundland spend the summer and fall in or near eelgrass habitats (Gotceitas *et al.*, 1997; Grant and Brown, 1998; Laurel *et al.*, 2004), which provide cover from predators (Linehan *et al.*, 2001). Evidence suggests that juvenile cod do not move more than a few kilometers within a single season (Grant and Brown, 1998), but nonetheless mix and move at scales of ~ 100 m (Laurel *et al.*, 2004) in contiguous eelgrass meadows. Winter studies suggest juvenile cod likely use deeper water to avoid freezing (Methven and Bajdik, 1994; Grant and Brown, 1998), but their movement and mortality have not been quantified. Atlantic cod in Newfoundland are an excellent model species to test hypotheses of overwinter survival given their broad size distributions in the fall (Methven and Bajdik, 1994; Ings *et al.*, 2008). We hypothesize that (1) large individuals are more likely to survive their first winter compared to smaller individuals, and (2) juvenile cod randomly disperse among suitable habitats during their first winter after leaving coastal eelgrass habitats.

Methods

Study sites and fish sampling

Eelgrass habitat dominates the shoreline of Newman Sound, a fjord in Bonavista Bay, Newfoundland Canada, where we conducted our field work. We selected three sites within Newman Sound for this study: Newbridge Cove, Canning's Cove, and Mistaken Cove. In Newbridge Cove, a somewhat isolated, protected cove, eelgrass beds extend out to ~ 7 m depth. Canning's Cove is ~ 1.67 km across the sound from Newbridge Cove, and Mistaken Cove is located ~ 750 m east along the north coast of the sound (Figure 1). We collected fish using a demersal seine net 25 m long and 2 m high, consisting of 19-mm stretched mesh. The beach seine can quantitatively sample juvenile cod as small as 30 mm standard length. We excluded fish smaller than 30 mm from our study because they are not considered fully settled. The net was deployed 55 m from the shore using a small open boat and retrieved by two individuals standing 16 m apart along the shore. The seine samples ~ 880 m² of habitat from the bottom substrate to 2 m into the water column with a capture efficiency of $\sim 95\%$ (Gotceitas *et al.*, 1997).

We assigned sampled fish into recruitment pulses (see Ings *et al.*, 2008) using size–frequency distributions and finite mixture distribution models (Macdonald and Du, 2018) in the R programming language (R Core Team, 2021). Pulse assignments were derived from the Newman Sound long-term monitoring program from Fisheries and Oceans Canada. A biweekly sampling program enables detection of new pulses by tracking the growth of each pulse over time and thus detection of new pulses in the population (Methven and Bajdik, 1994; Ings *et al.*, 2008). We use finite mixture distribution models to determine the size-class distributions for each sampling trip, and then assign the pulses based on growth trajectories over the course of the season (Gregory *et al.*, 2019).

Marking technique

We applied fluorochrome markers—calcein (Sigma-Aldrich: C0875-25G) or alizarin red S (Sigma-Aldrich: A5533-25G)—to batch mark otoliths (Lü *et al.*, 2020). Fluorochrome dyes bind with calcium in the otolith and, while exposed to the dye,

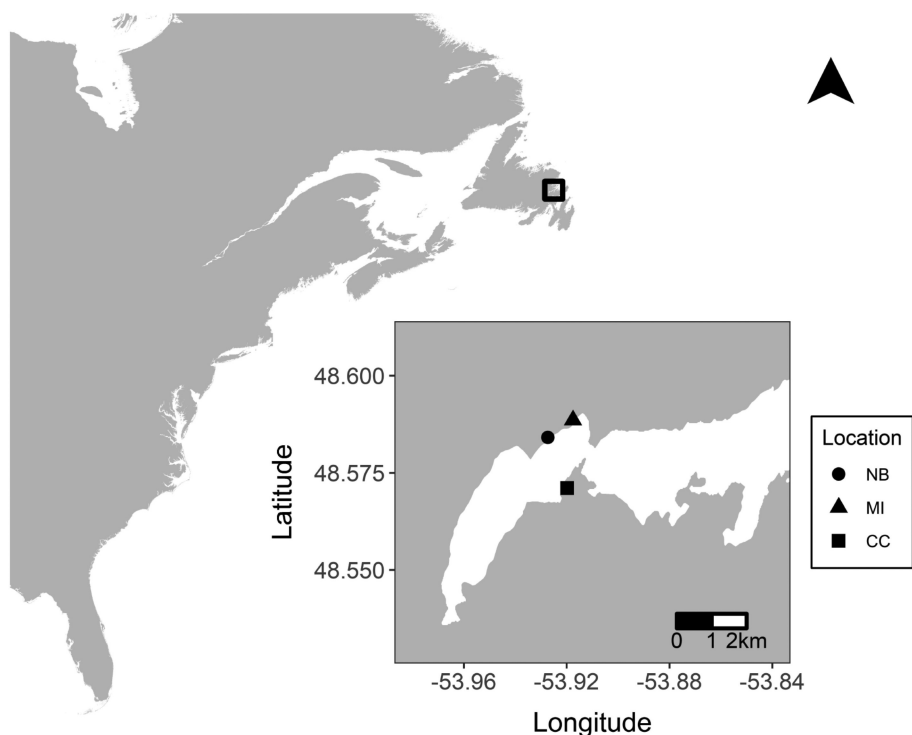


Figure 1. Newman Sound, Newfoundland in the context of eastern North America, showing fish sampling locations in October 2016 and May 2017 (circle, Newbridge Cove (NB); triangle, Mistaken Cove (MI); square, Canning's Cove (CC)).

fish lay down a distinct mark in the daily growth rings that can be read with confidence after recapture (Schmitt, 1982; Campana and Neilson, 1985). We marked age-0 juvenile cod in our study by immersing them for 24 h (Schmitt, 1982). Calcein fluoresces yellow and alizarin red S fluoresces red. This method produces a persistent mark that minimizes detrimental tagging effects induced by other common external tagging methods—e.g. fin clipping or externally visible markings (e.g. tattoos, brands, or various manufactured tags). We conducted validation trials to establish tag retention at effective and non-toxic concentrations. Validation trials focused predominantly on juvenile Greenland cod (*Gadus macrocephalus ogac*) because of availability of fish at an appropriate size at sampling. We further validated marks on Atlantic cod throughout the marking period by confirming application of marks on the subsampled fish (see supplementary material). Although we confirmed 100% tag retention, observer effort nonetheless added a risk of tag-loss. To minimize tag-loss from observation, we analysed both sagittal otoliths from each sampled fish.

Mark-recapture

We set up tanks at Salton's Marine Interpretation Centre in Terra Nova National Park, near our capture-release site to mark fish for our mark-recapture experiment. We placed two 80-L treatment aquaria inside 120-L plastic water baths with a flow-through water source to maintain ambient temperature (10.4–11.4°C). Temperature, dissolved oxygen, and pH were monitored regularly throughout the 24-h marking period. Fluorochrome can decrease pH levels; therefore, we maintained a consistent pH level using Na_2CO_3 . Fluorochrome solutions were prepared as a stock solution, which we slowly added into the tanks.

We collected age-0 Atlantic cod from Newbridge Cove (Figure 1) in five to six beach seine hauls on each of 13, 14, and 18 October in 2016. We measured a random subsample ($n = 51$ on 13 October; $n = 30$ on 18 October) of cod to the nearest mm Standard Length (mm SL; snout to the caudal peduncle) from each date to determine size distribution of individuals captured. We captured 184 age-0 juvenile cod in seine hauls on 13 and 14 October and held them in calcein (50 mgL^{-1}) treatment aquaria. A total of six juvenile cod mortalities occurred during the marking period, which we attributed to handling stress prior to the treatment. Mortalities were sampled to validate mark retention. On 15 October, we released 178 of these marked fish at the capture-release site. We observed no evidence of mark-induced mortality among 30 marked individuals we held in a submerged 40-L cage at our study site for 1 h prior to release.

We captured another 149 juvenile cod on 18 October and held them in alizarin red S baths (250 mgL^{-1}) for 24 h, prior to releasing a total of 129 fish into Newbridge Cove on 19 October. Twenty fish did not survive the overnight marking treatment; however, again, we observed no additional mark-induced mortality among 30 individuals we held at our study site for 1 h prior to release; in our experience, most mortalities occur relatively quickly after marking and prolonged holding times beyond 1 h can add additional handling stress.

We captured marked and unmarked age-1 Atlantic cod on 24 and 25 May 2017 using the same seining technique, at the release cove and at two nearby coves—289 cod at Newbridge Cove (capture-release-recapture), 50 cod at Canning's Cove (recapture), and 62 cod at Mistaken Cove (recapture). We conducted two seine hauls at Newbridge Cove, three at Canning's Cove, and one at Mistaken Cove. These fish were frozen at -10°C on site, then transported to the laboratory and stored

frozen until we could examine their otoliths for marks. We calculated catch per haul across Newman Sound for the first marking period (14 October 2016) and recapture period (25 May 2017).

The juvenile cod sampled in May then formed the basis for our capture–mark–recapture analysis (see details below). Recapture rates could not be calculated from the October marking periods, since the fluorescent marks were internal. Therefore, the fall recapture rate is dependent on marked fish surviving winter. Research was conducted under Memorial University of Newfoundland and Labrador Animal Care protocol #16–02-RG.

Otolith analysis

For all fish captured in May 2017, we measured standard length and extracted sagittal and lapillus otoliths. Sagitta were mounted, sulcus facing upwards, on slides using Crystal Bond™. Sagittal otoliths were ground on the longitudinal plane using a 15- μm finishing film and polished with a 3- μm lapping film. We then viewed the otoliths for potential marks using a Zeiss Axio Imager A1™, 10x/23 eye and 10x/0.3 objective lenses. The microscope was fitted with an AmScope Microscope Digital Camera™ (MU1203-FL). We examined otoliths for calcein marks using a filter that excites at 450–490 nm wavelengths, allows emission at 515 nm, and has a beam splitter at 510 nm. Alizarin red S was viewed using an alizarin red S filter set (Chroma Technology™) that excites at 510–560 nm with a 590 nm barrier filter.

Sample preparation for trace elements

To provide inference on environmental histories in recaptured juvenile cod, we selected a subsample of 60 otoliths from our May 2017 recaptures for trace element analysis using secondary ion mass spectrometry (SIMS). Through this analysis, we aimed to determine whether juvenile cod move to deep, isothermal water. Cod that move to deep water, would show minimal trace element variation among fish, and Mg levels would decrease from the fall band to the winter band (Stanley *et al.*, 2015). A Cameca IMS 4f Secondary Mass Spectrometer was used to perform spot analysis of Na/Ca, Mg/Ca, Sr/Ca, and Ba/Ca in the fall and winter growth bands of otoliths. The fall and winter bands were traced based on visual assessment. We selected marked and unmarked individuals from two size groups—large (99–132 mm SL; Pulse 1) and small (71–96 mm SL; Pulse 2) individuals. The large size group contained 4 marked and 15 unmarked individuals, whereas the small-size group included 14 marked and 27 unmarked individuals. Given the limited information on trace element levels in relation to temperature in juvenile cod, we sampled cross-sections, from the edge of the otolith to the core, of an additional four otoliths from a previous experimental study (Geissinger *et al.*, 2021a) to provide a limited comparison between field caught juveniles, and those with a known winter temperature profile (see supplementary material). We sectioned sagittal otoliths with a thin kerf Beuhler Isomet™ low-speed saw and hand polished them to the core before mounting otolith sections into a SIMS sample ring (aluminium ring with 25.4 mm outside diameter) and embedding them in the ring using epoxy resin. Polishing the casts and SIMS analyses followed the methods of Aranha *et al.* (2014). Otolith elemental compositions were converted into molar values and standardized to calcium concentrations (Me:Ca). Trace element

analysis for this study has unknown predictive power given it is used in a small-scale winter marine coastal environment (Stanley *et al.*, 2016).

Statistical analysis

We ran capture–mark–recapture models with Cormack–Jolly–Seber formulation using the programs MARK (version 9.0) and RMark (Laake, 2013). These models allowed us to calculate period-specific apparent survival rates. Survival rates, ϕ_i , denote the probability of survival from release occasion i to release occasion $i + 1$. Recapture probability, p_i , describes the probability of capture or recapture on occasion i . We ran eight models with ϕ and p under different constraints: constant (ϕ , p), varying with time (ϕ , p), and varying with size (ϕ), and chose the top model, using Akaike information criteria (AIC). We calculated the overdispersion parameter, \hat{c} , by dividing the observed, \hat{c} from the model by the mean, \hat{c} from simulations; we considered a \hat{c} value greater than 1 meant overdispersed.

Daily natural mortality (M) is reported as % per day using the formula

$$M = ((1 - \phi) \cdot d^{-1}) \cdot 100. \quad (1)$$

The marking period (d) for the fall sample was 6 d (13–19 October 2016), and the marking period for the overwinter period was 223 d (19 October 2016–24 May 2017). We calculated condition of captured fish in May (marked and unmarked) using Fulton's K condition factor (Fulton, 1904; Grant and Brown, 1999), with dry weight as

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

with W_{DRY} as the dry eviscerated weight (g) and L as the standard length (cm). We calculated Hepatosomatic Index (HSI , Lambert and Dutil, 1997) as

$$HSI_{\text{DRY}} = 1000 \cdot (L W_{\text{DRY}} \cdot W_{\text{DRY}}^{-1}), \quad (3)$$

with $L W_{\text{DRY}}$ as the dry liver weight (g). We analysed the condition and HSI using a generalized linear model, with a Gamma distribution to determine whether condition changed between size class (pulse) or sampling location post-winter. The models used Fulton's K and HSI as response variables, respectively, with pulse and location (Newbridge, Canning's, or Mistaken) as fixed explanatory variables (categorical). The models included an interactive effect between pulse and location, but the interactive effect was removed when $p \geq 0.05$.

Trace element (Mg, Ba, Sr) analysis used a generalized linear mixed effect model with a Gamma distribution and log link. Pulse, season, and location were fixed explanatory variables, and otolith ID was a random effect. All statistical analyses were conducted using the R statistical programming language (R Core Team, 2021). Associated data are available on Scholars Portal Dataverse (Geissinger *et al.*, 2021b).

Results

Initial size distribution

Size distribution from the subsample ($n = 51$) ranged from 41 to 84 mm SL during our first marking period on 14 October 2016. The marked population contained three settlement pulses—Pulse 1 ($n = 39$) ranged from 66 to 84 mm SL (76.0 ± 5.9 , mean \pm SD), Pulse 2 ($n = 46$) ranged from 46 to 65 mm SL (58.3 ± 5.5), and Pulse 3 ($n = 3$) contained one size at 41 mm SL (Figure 2a). On 19 October, subsampled ($n = 30$)

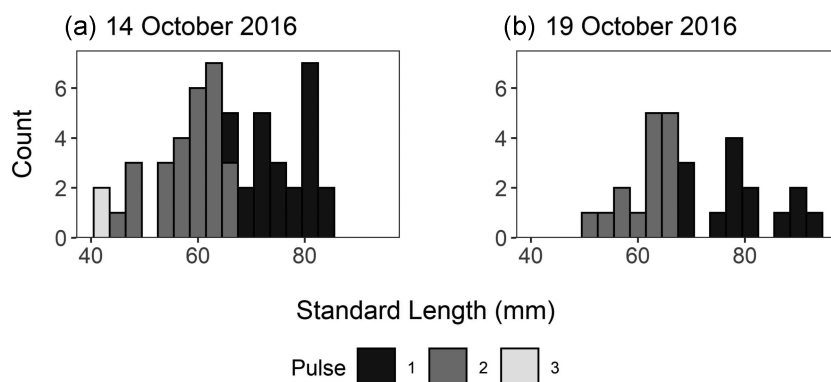


Figure 2. Size distribution of subsampled age-0 Atlantic cod caught on (a) 14 October 2016 ($n = 51$) and (b) 19 October 2016 ($n = 39$). Shading represents pulse assignment for each size-class.

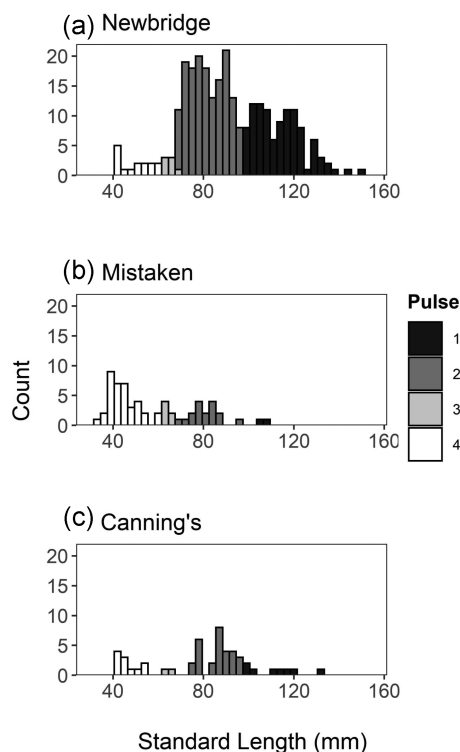


Figure 3. Size distribution of age-1 Atlantic cod caught on 24 May 2017, from (a) Newbridge Cove, (b) Mistaken Cove, and (c) Canning's Cove. Shading represents pulse assignment for each size class.

size distribution ranged from 52 to 93 mm SL: Pulse 1 ($n = 24$) ranged from 68 to 93 mm SL (79.4 ± 8.0) and Pulse 2 ($n = 52$) ranged from 52 to 67 mm SL (61.7 ± 4.4).

Recaptures

We captured a total of 281 cod on 24 May 2017, at our Newbridge Cove release site and the two nearby sites (Figure 1). We captured 103 Pulse 1 fish ranging from 98 to 151 mm SL (114.0 ± 11.0) and 156 Pulse 2 fish ranging from 69 to 97 mm SL (81.2 ± 8.5). There were seven Pulse 3 ranging from 62 to 68 mm SL (64.9 ± 2.3). Additionally, we captured 15 individuals from Pulse 4, which ranged from 41 to 60 mm SL (49.7 ± 7.0 ; Figure 3a); we captured no Pulse 4 individuals in Newbridge Cove in October 2016 because these fish had yet to settle into our study site when we began our marking experi-

ment. Therefore, we excluded all Pulse 4 fish captured in May from CMR analysis. The size distribution at Mistaken Cove ranged from 32 to 109 mm SL, including elements of Pulse 1 (106–109 mm SL; $n = 2$), Pulse 2 (69–96 mm SL; $n = 17$), Pulse 3 (62–67 mm SL; $n = 6$), and Pulse 4 (32–61 mm SL; $n = 37$; Figure 3b). At Canning's Cove, Pulse 1 ranged from 99 to 132 mm SL ($n = 8$), Pulse 2 ranged from 75 to 97 mm SL ($n = 29$), Pulse 3 ranged from 63 to 66 ($n = 2$), and Pulse 4 ranged from 41 to 55 mm SL ($n = 11$; Figure 3c).

We recaptured a total of 33 marked juvenile cod in May 2017, 32 weeks after initial marking the previous fall. The majority of marked juvenile cod we recaptured (30 individuals) were taken at our Newbridge Cove marking site, including five cod from the first marking period (14 October), 24 cod from the second marking period (19 October), and one double-marked individual (exhibiting both a calcein and an alizarin red S mark; Figure 4). At this site, three recaptures were from Pulse 1, with the remainder (27) from Pulse 2. The three recaptures at Mistaken Cove (a recapture site only) all came from the 14 October marking period and they were from Pulse 2; we observed no individuals from the 19 October marking at this site. There were no recaptures from Canning's Cove (a recapture site only).

Condition

A generalized linear model showed that the interaction between pulse and site significantly influenced Fulton's K condition factor, K_{DRY} (ANODEV; $\chi^2 = 25.71$; $df = 6$ 381; $p < 0.001$). Pulse 1 fish at Mistaken Cove, which had an average $K = 2.13 \pm 0.41$, likely drove the interaction between site and pulse. Mean values of all other pulses and sites ranged from 1.57 to 1.86 (Figure 5a).

HSI varied with pulse (ANODEV; $\chi^2 = 57.28$; $df = 3$ 372; $p < 0.001$), but not site (ANODEV; $\chi^2 = 0.38$; $df = 2$ 372; $p = 0.83$). Pulse 1 HSI averaged 1.46 ± 0.40 compared to 1.43 ± 0.41 for Pulse 2. Pulse 3 HSI (1.19 ± 0.46) and Pulse 4 HSI (0.94 ± 0.41) were significantly lower than Pulse 1 and Pulse 2 (Figure 5b).

Capture-mark-recapture models

Given the low recapture rates at neighbouring sites, we only modeled marked and recaptured cod at Newbridge Cove, acknowledging the limitations associated with evidence of post-winter migration of marked fish after 32 weeks at large. The best-fit model was φ (time \times pulse) and p (time) with

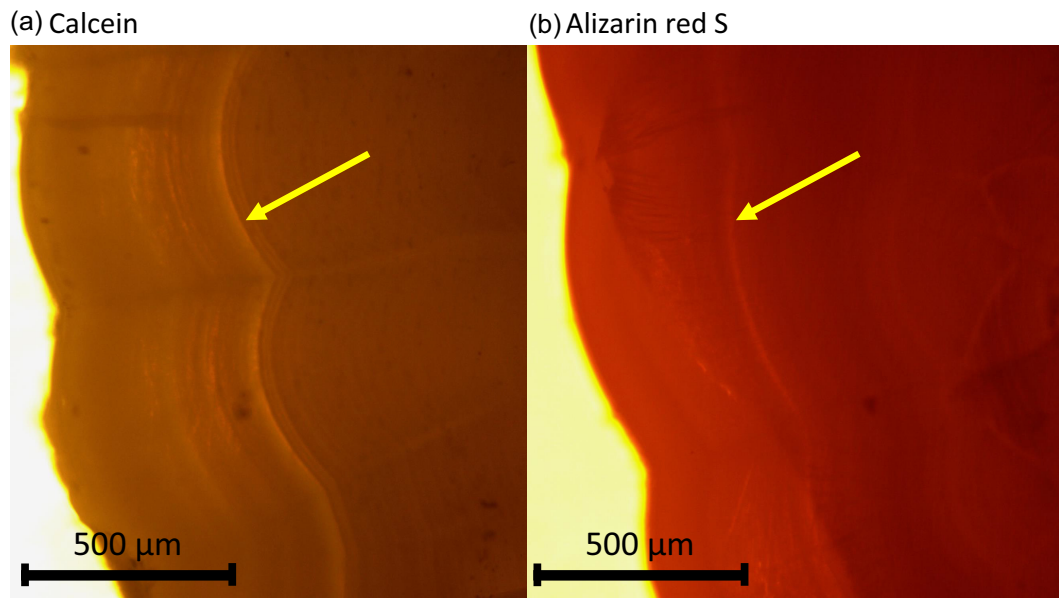


Figure 4. Sagittal otoliths from two mark–recaptured juvenile Atlantic cod (*Gadus morhua*) (May 2017), initially marked and released with (a) calcein (14–15 October 2016) and (b) alizarin red S (19 October 2016).

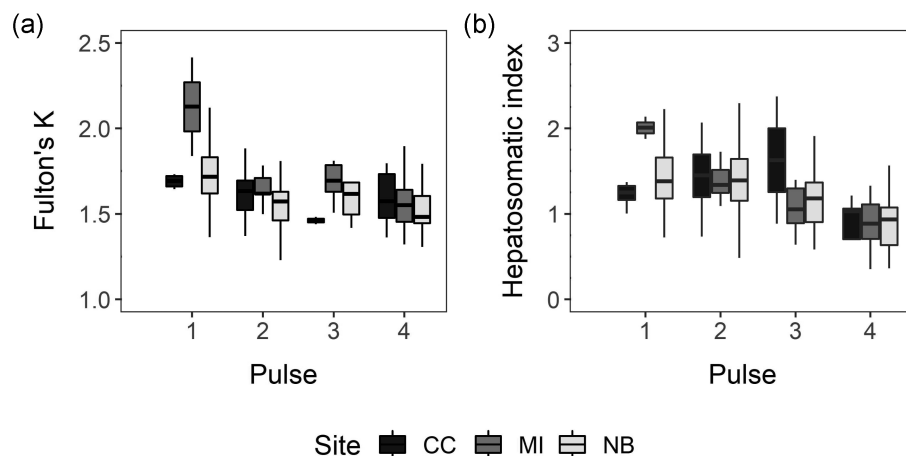


Figure 5. Fulton's condition factor, K_{DRY} (a) and hepatosomatic index (HSI) for age-1 Atlantic cod collected in Newman Sound on 24 May 2017. Fulton's K had a significant interaction between site (CC: Canning's Cove; MI: Mistaken Cove; NB: Newbridge Cove) and pulse (ANODEV; $\chi^2 = 22.76$; $df = 4$ 377; $p < 0.001$). HSI differed significantly between pulses (ANODEV; $\chi^2 = 56.44$; $df = 2$ 366; $p < 0.0001$). 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.

$AIC = 166.26$. A bootstrap goodness-of-fit with 1000 simulations showed reasonable likelihood of the observed model deviance of 4.96, with 124 of the simulated values exceeding the observed value ($p = 0.123$). The model $\hat{c} = 4.96$ indicates slight overdispersion.

Mortality rate varied by pulse and time, and recapture probability varied with time (Table 1). Pulse 1 mortality $M = 7.71\% \text{ d}^{-1}$ ($\pm 1.6\% \text{ d}^{-1}$ SE) in the October 2016 sampling strongly contrasted $M = 0.00515\% \text{ d}^{-1}$ (± 0.001) over the 32-week period at-large (over winter). Pulse 2 mortality $M = 4.52\% \text{ d}^{-1}$ (± 0.99) in the October sampling period greatly exceeded $M = 0.0022\% \text{ d}^{-1}$ (± 0.0003) over winter. In contrast, we observed higher Pulse 3 mortality in October of $M = 16.63\% \text{ d}^{-1}$ relative to the other pulses, but overwinter mortality consistent with the first two pulses with $M = 0.39\% \text{ d}^{-1}$. However, small sample size resulted in low

precision and high error for Pulse 3 estimates during both time periods (Table 1). Lower sample size in the initial marking period characterized juvenile cod from Pulse 3 along with low abundance during our sampling in May 2017. Catch per haul for Pulse 1 in Newman Sound of 31.9 cod haul⁻¹ on 14 October 2016 contrasted 7.3 cod haul⁻¹ on 24 May 2017. We collected 11.6 cod haul⁻¹ in October 2016 and 16.9 cod haul⁻¹ in May 2017 from Pulse 2. Lastly, there were 0.4 cod haul⁻¹ in Pulse 3 in October 2016 and 0.0 cod haul⁻¹ in May 2017.

Trace elements

Trace elements (Mg, Ba, Sr) did not vary significantly by pulse or site (see supplementary material; $p > 0.05$). Mg and Ba values both differed significantly among field fish between fall and winter (Mg: ANODEV, $\chi^2 = 35.28$; $df = 1$ 124, $p < 0.01$; Figure 6), with an increase in mean Mg from

Table 1. Cormack–Jolly–Seber (CJS) model output for Newbridge Cove ($N = 249$), specified as φ (\sim time + pulse), p (\sim time), with the marking–recapture period, estimated as the apparent survival probability (φ) and apparent capture probability (p), standard error (SE), 95% lower confidence limits (lcl), and 95% upper confidence limits (ucl).

Parameter	Pulse	Marking/recapture period	Estimate (survival period ⁻¹)	SE	lcl	ucl
φ	1	Fall (1 week)	0.54	0.094	0.36	0.71
φ	1	Winter (32 weeks)	0.99	0.0022	0.98	0.99
φ	2	Fall (1 week)	0.73	0.060	0.60	0.83
φ	2	Winter (32 weeks)	0.99	0.76×10^{-3}	0.993	0.996
φ	3	Fall (1 week)	0.0022	40.23	0.00	1.00
φ	3	Winter (32 weeks)	0.14	2210.12	0.00	1.00
p	1; 2; 3	Fall (1 week)	0.054	0.057	0.0063	0.34
p	1; 2; 3	Winter (32 weeks)	1.00	1.64×10^4	0.00	1.00

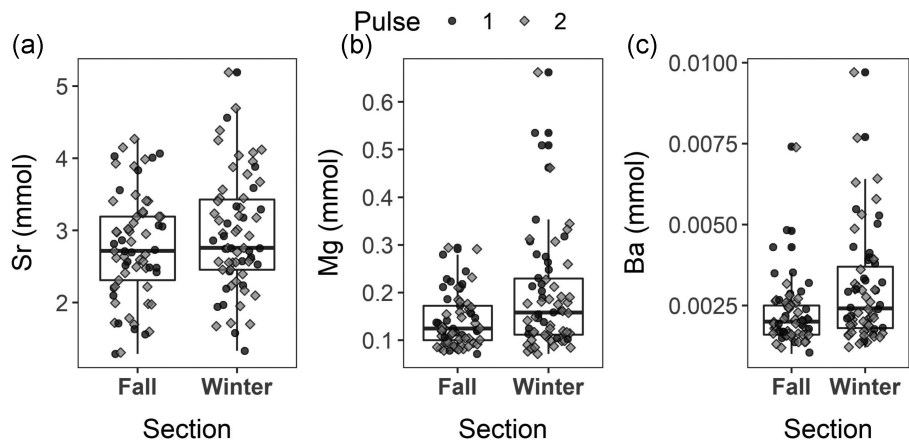


Figure 6. Trace element (a) Sr, (b) Mg, and (c) Ba of age-1 juvenile Atlantic cod sagittal otoliths on the fall and winter bands ($n = 60$). No differences were detected between pulses. The bold line represents the median, the lower and upper hinges correspond to the first and third quartiles, and the upper and lower whiskers extend to the largest and smallest value within 1.5 times the interquartile range. Points represent individual measurements for each fish.

0.131 ± 0.009 mmol (mean ± SE) in the fall to 0.166 ± 0.011 mmol in the winter. Standard deviation of Mg in the winter (0.071–0.662 mmol) was twice that in fall (0.071–0.294 mmol, Table 2). Ba differed significantly between fall and winter (ANODEV, $\chi^2 = 24.549$; $df = 1$ 124, $p < 0.01$), with a mean increase from 0.0021 ± 0.00 013 mmol in the fall to 0.0026 ± 0.00 016 mmol in the winter. Sr values did not differ significantly among field fish between fall and winter (ANODEV, $\chi^2 = 3.21$; $df = 1$ 124, $p = 0.07$). Ba, Sr, and Mg cross-sections from four individual cod from a controlled lab experiment did not vary substantially (Supplementary Figure S1). The winter temperatures at our sites in 2016–2017 ranged from −1.3 to 5.3°C overwinter (1 December 2016–24 May 2017), whereas the temperature experienced by the control fish ranged from −0.7 to 3.1°C.

Discussion

Past studies point to the overwinter period as a significant survival bottleneck for both freshwater and marine species (Henderson *et al.*, 1988; Garvey *et al.*, 1998; Ellis *et al.*, 2017). Despite strong evidence for this bottleneck, the factors driving winter survival remain inconclusive. Some studies support energetic-based mortality (Norcross *et al.*, 2001) whereas others support predation-based mortality (Cowan *et al.*, 1996). The observed low mortality—0.005% d⁻¹ or less for the largest juveniles in their first winter indicates that winter does

not cause a significant survival bottleneck for young-of-the-year cod in Newfoundland.

This overwinter mark–recapture study provides the first information on juvenile overwinter mortality and habitat use for cod *in situ*. Our results do not support our first hypothesis that the size of juvenile fish entering winter is an important component of overwinter mortality. We observed lower mortality in the first two settlement pulses (i.e. largest individuals) compared to the smaller third pulse fish, which arrived in our coastal site in mid-October. However, winter mortality was also low for the third pulse (0.39% d⁻¹), but our limited sample size for Pulse 3 cod limits our confidence in the Pulse 3 mortality estimate. Our results indicate that 60+ mm cod in the fall have a distinct survival advantage over the 50–58 mm cod arriving later in the fall. The third settlement pulse had high mortality in the fall, with few Pulse 3 fish detected in Newman Sound in the spring or summer. Additionally, a fourth pulse (~30–60 mm in the spring) appeared in our nearshore sites after November 2016 and maintained unexpectedly high abundances through May 2017 (Gregory *et al.*, 2019). The high representation of a fourth settlement pulse further supports our assertion that small size does not limit overwinter survival in our study area. However, we do not know the initial abundance of Pulse 4, which limits our full understanding of their survival.

Energetics impacts overwinter mortality in many freshwater and marine juvenile fishes (Sogard and Olla, 2000; Heintz

Table 2. Trace elements for age-0 Atlantic cod sagittal otoliths ($N = 60$), including fall and winter measurements with means, standard deviations (SD), and ranges (min–max).

	Section	Mean (mmol)	SD (mmol)	Range (mmol)
Sr	Fall	2.77	0.741	1.29–4.27
	Winter	2.97	0.790	1.33–5.19
Ba	Fall	2.21×10^{-03}	9.62×10^{-04}	1.00×10^{-03} – 7.40×10^{-03}
	Winter	2.88×10^{-03}	1.44×10^{-03}	1.20×10^{-03} – 7.70×10^{-03}
Mg	Fall	0.14	0.0559	0.071–0.290
	Winter	0.19	0.1180	0.071–0.660

and Vollenweider, 2010; Mogensen and Post, 2012). Harsh winter conditions can often intensify size-structured mortality in fishes due to cold temperatures and food limitation (Fullerton *et al.*, 2000; Huss *et al.*, 2008). Freshwater studies show substantial starvation mortality during winter (e.g. Post and Evans, 1989), where mortality regulators include size, food availability (Garvey *et al.*, 1998), and winter severity—i.e. duration, photoperiod, and temperature (Fullerton *et al.*, 2000). Winter mortality rates as low as 0% characterize warm, high-resource freshwater environments, in contrast to 18% in warm winters with low resource abundance (Mogensen and Post, 2012). However, in cold lakes, when size and lipid availability in fish fall below threshold levels, mortality levels increase to 94% (Mogensen and Post, 2012). Studies of marine systems yield similar results. For example, sand smelt (*Atherina boyeri*) showed almost 50% mortality in two consecutive winters (Henderson *et al.*, 1988). Additionally, low winter temperatures impact temperate systems in the most severe winters, where marine fish (*Micropogonias undulatus*; *Cynoscion nebulosus*) cannot tolerate low temperatures (Lankford and Targett, 2001; Ellis *et al.*, 2017). However, low temperatures do not always have a negative effect. Increased condition and growth can occur in northern latitude species, such as Pacific herring (*Clupea pallasii*) during cold years (Sewall *et al.*, 2019). In contrast to Atlantic cod and herring, extreme winter temperatures in temperate regions lead to “winterkills”, which expose fish to lethal thermal conditions (Ellis *et al.*, 2017), sometimes caused by osmoregulatory failures (Johnson and Evans, 1996). Thus, our finding of low mortality in juvenile cod contrast our initial expectations as well as some published findings for freshwater and temperate marine species.

Based on experimental studies of Fulton’s K condition, juvenile Atlantic cod remained in relatively high condition post-winter in our study, averaging 1.5 or greater for all pulses and locations. Fulton’s K (DRY) condition factor can vary from ~1.0 for juvenile cod under starvation conditions, to ~1.5 when food exceeds 5% body weight per day (Geissinger *et al.*, 2021a). Therefore, the Fulton’s K data suggest age-0 cod were likely not energy limited during winter. However, the HSI condition metric varied with size of fish, with Pulse 1 and 2 values of ~1.4, and Pulse 4 values less than 1.0. This distinct change in HSI between size groups indicates either (1) larger juveniles accumulate more relative liver energy pre-winter (either through foraging opportunity or size-dependent energy allocation) or (2) smaller juveniles consume more energy stores in the liver during winter. Testing these hypotheses will require further studies, although our data suggest winter survival was neither size-dependent nor overly impacted by energy limitation in the winter of 2016–2017.

Atlantic cod possess physiological adaptations to minimize the impact of low winter temperatures. Increased concentrations of antifreeze glycoproteins in juvenile Atlantic cod entering the winter period allow them to endure sub-zero temperatures (Fletcher *et al.*, 1987). Nevertheless, we had expected high mortality overwinter in young-of-the-year cod, given our *a priori* perception of limited resources and low mean temperatures during this period. We had anticipated that low productivity in the coastal zone during the winter period (Foy and Paul, 2004) would have led to depleted energy stores in juveniles, increasing metabolic stress and increasing mortality over winter. Geissinger *et al.* (2021a) showed that young-of-the-year Atlantic cod can survive and grow in low temperatures (−0.8 to 2.7°C) assuming availability of at least some food. Low mortality rate and high condition indices of overwintering juvenile cod suggest that the juveniles in our study may have had sufficient access to food throughout the winter (Geissinger *et al.*, 2021a), although we did not expect this outcome given published accounts of winter zooplankton availability in Newfoundland (Wilson *et al.*, 2018).

A critical size threshold can be challenging to measure during overwinter periods (Beamish and Mahnken, 2001). Winter mortality rates alone do not demonstrate size-structured predation *per se*. However, using our fall capture–mark–recapture period, we infer the unexpected presence of a “predator window” prior to winter. Pulse 3 fish were estimated to experience high mortality in the late fall (16.63% d^{−1}), which suggests that Pulse 3 cod did not likely survive to the start of winter. Pulse 3 mortality rates require cautious interpretation given the small sample size. We attribute this high fall mortality to predation based on two lines of evidence. First, emigration is unlikely a factor based on a concurrent study in the system that showed juvenile cod limit movement to similar habitats (MacRobert, 2020). Second, we predict that predators likely consumed the Pulse 3 fish prior to winter while ambient conditions remained comparatively warm and metabolic demands and foraging activity were presumably higher. Pulse 1 and Pulse 2 fish survived to the start of winter, possibly due to their ability to evade predators or outgrow the size that predators can capture them (Schmitt and Holbrook, 1984; Persson *et al.*, 1996). Examples of predators in this system are cunner (*Tautoglabrus adspersus*) sculpin (*Myoxocephalus scorpius*), age 1–2 cod (*G. morhua*; *G. ogac*) and white hake (*Urophycis tenuis*; Linehan *et al.*, 2001). High abundances of age-1 cod (2015 cohort) at our study site persisted throughout the fall in 2016, only relocating away from shore into winter habitat in late November in 2016 (Gregory *et al.*, 2019), after we had deployed our marks.

We offer two complementary hypotheses to explain why mortality was lower than expected in age-0 cod facing their

first winter in coastal Newfoundland. First, predators in the area likely overwinter in deeper, warmer habitats to reduce the risk of freezing, whereas age-0 juveniles produce sufficient antifreeze glycoprotein to remain in the nearshore and survive sub-zero temperatures (Fletcher *et al.*, 1987). Second, juvenile cod may also reduce their encounter rates with predators by restricting movement and occupying structured “refuge” habitats typically found in the nearshore e.g. kelp, eelgrass (e.g. Gregory and Anderson, 1997). This age-0 overwintering strategy would also explain the high site-fidelity in the nearshore observed in our study. Laurel *et al.* (2004) and Ryan *et al.* (2012) indicate that juvenile cod indeed move among neighboring eelgrass patches within a limited area. Our evidence supports overall high site-fidelity overwinter. Had juvenile cod exhibited random dispersal behaviour, marked fish would have dispersed broadly to numerous locations along the shore of the sound. In such a scenario, recapture of any juveniles in the post-winter period (May) at our mark-release site would have been unlikely given the availability of suitable habitat in the immediate study area. In contrast, the large number of recaptures (~15%) strongly suggests that juvenile cod remain close to their pre-winter habitat overwinter, possibly due to reduced swimming activity related to cold temperatures (Laurel *et al.*, 2016). Alternatively, juvenile cod could be active during the winter period, similar to age-1 Greenland cod who have a larger home range in the winter relative to other seasons (Shapiera *et al.*, 2014). In this scenario, juvenile Atlantic cod would actively return to their settlement sites, further supporting strong site-fidelity.

The trace element analysis of otoliths did not provide conclusive insight into the environmental histories of mark-recaptured juvenile cod. Although non-significant discrimination among samples analysed by trace elements is inconclusive, we report results as they will be valuable for future studies using these tools at different scales, seasons and ontogenetic stages. The high variation in Mg levels in the winter section of otoliths, along with overlap in Mg values in the fall sections, defied our expectations. Based on an experimental study on the impacts of temperature and salinity on trace elements in juvenile Atlantic cod, Stanley *et al.* (2015) showed decreased Mg:Ca ratios in otoliths with decreased temperature. Instead of an overall decrease in Mg levels in the winter compared to the fall, we observed high variation and strong overlap between the two time periods. If we assume a clear trace element signal, then this observation suggests two potential scenarios. Juveniles either (1) do not overwinter in the same location or (2) remain close to shore, in shallow water with greater thermal variation relative to deep water. However, we cannot draw firm conclusions from these data because trace element incorporation in otoliths has not been verified in field studies for Atlantic cod, and temperature and salinity both impact incorporation rates (Miller, 2011). Juvenile cod presumably remain close to their settlement sites, and do not move to deep water for thermal refuge. Instead, they remain close to the coast where they experience large temperature changes associated with oceanographic processes. Few published studies address juvenile overwinter movements in marine ecosystems (however, see Hanson, 1996; Gregory and Anderson, 1997; Shapiera *et al.*, 2014). Although we do not know how far they move, our collective data indicate that age-0 cod make microhabitat shifts pre-winter (i.e. depart eelgrass beds) but likely exhibit little movement during winter.

Conclusions

Young-of-the-year fish in sub-arctic marine ecosystems experience unique physical and physiological challenges compared to those in temperate waters. Length and severity of winter certainly contribute to these challenges. The northern population of Atlantic cod in Canada has not recovered since the fisheries moratorium was first declared three decades ago through to the time when we conducted this study (DFO, 2019). The transition from age-0 to age-1 has remained poorly understood in the context of population assessment (e.g. Boudreau *et al.*, 2017; Rose and Walters, 2019), with little specific focus on the overwinter period. In contrast to previous studies, especially in freshwater ecosystems, the winter period does not appear to be a major source of additional mortality following settlement in the first year of life. This study provides important insight into overwinter dynamics seldom investigated in marine environments. Determining whether these seasonal conditions broadly represent a longer time series will require further studies.

Critical periods can provide information on recruitment patterns and vulnerable phases of early-life histories of juvenile fishes. Age-0 cod are important in determining juvenile cod year class strength, especially for weak year classes (Lunzmann-Cooke *et al.*, 2021). Therefore, understanding mortality from age-0 to age-1 can clarify the relationship between pre-recruits and adult populations. Our study indicates late fall may be a critical period which needs to be considered in recruitment processes for cod, and that winter mortality may be significantly lower than other times of the year.

Supplementary material

Supplementary material is available at the ICESJMS online version of the manuscript.

Author Contributions

EAG, RSG, and PVRS conceptualized research questions. EAG, RSG, PVRS, and BJL developed experimental design. EAG and RSG conducted field work. EAG completed otolith analysis, condition measurements, and statistical analyses. EAG wrote the paper, with comments and revisions by RSG, PVRS, and BJL.

Data Availability Statement

The data underlying this article are available in Scholars Portal Dataverse at <https://doi.org/10.5683/SP3/NPQSLV>.

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