



Re-visiting the drivers of capelin recruitment in Newfoundland since 1991

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ABSTRACT

Capelin is a small forage fish that plays a key role in the transfer of energy from secondary producers to vertebrate predators in Arcto-boreal food webs. Profound changes in abundance and distribution of capelin occurred in 1991 in Newfoundland, which corresponded with the collapse of the groundfish stocks. There has been minimal recovery of capelin biomass since 1991. We re-assessed the relationships between larval survival, recruitment, and onshore winds post-1991. We also investigated the link between larval capelin vital rates (growth) and recruitment for three current years of data: 2002, a collapsed population state; 2006, a transitioning state; and 2013, a recovering state. Like research pre-1991, we found a positive relationship between the age-2 recruitment index and larval abundance of the same cohort. However, the relationship between onshore winds and recruitment failed post-1991. Capelin are spawning persistently later since 1991 when there are fewer onshore wind events, which is likely a factor hindering the recovery of the capelin stock. Instead, the age-2 recruitment index was related to *Pseudocalanus* spp. density during the larval stage. Increased availability of preferred prey in autumn, due to a shift in zooplankton phenology seen around 2006, may have improved larval survival in recent years. We found faster growth in the recovering population state (2013) which suggests better larval growth conditions in recent years. Low larval survival from beach spawning may be inhibiting the recovery of the capelin stock, but enhanced productivity of small copepods in autumn can potentially compensate for the negative effect of later spawning.

1. Introduction

Identifying the drivers of recruitment variability and changes in productivity of marine fish is a fundamental aim of fisheries science. Marine fishes are characterized by high fecundity and high mortality rates in the pelagic larval stage, and even small changes in growth and mortality rates in the first weeks of life can result in orders of magnitude differences in adult abundance (Houde 2008). Larval fish are vulnerable to both starvation and predation. The “growth-mortality hypothesis” (Anderson 1988) predicts that survival rate is positively related to growth rate during the larval stage and is based on three complementary mechanisms: “bigger is better”, where larger-at-age individuals are less vulnerable to predation (e.g. Litvak and Leggett 1992; Leggett and DeBlois 1994); “stage duration”, where faster-growing larvae metamorphose into juveniles earlier, reducing cumulative mortality risk (Chambers and Leggett 1987); and “growth-selective predation”, where variability in individual growth rate may influence probability of capture by a predator, independent of size (Takasuka et al., 2003, 2007). The growth-mortality hypothesis is a

broadly accepted paradigm, with recruitment often positively linked to larval growth (Robert et al., 2007; Murphy et al., 2013; Kamimura et al., 2015).

Even though prey availability and predation are fundamental components of the growth-mortality hypothesis, the physical environment also plays an important role in setting the fate of fish larvae. In particular, the levels of windstress, upwelling, and microturbulence modulate growth and survival rates by generating variability in the encounter rates between larvae and their prey (Lasker, 1978, 1981; Roy et al., 1992; Dower et al., 1997). Temperature regulates both growth and developmental rate of fishes (Houde 1989). However, correlative studies between temperature and recruitment often break down (reviewed in Myers 1998), as the same climatic variable influencing temperature may also be affecting other drivers of larval survival such as prey availability.

Capelin (*Mallotus villosus*) is a small forage fish that plays a key role in the transfer of energy from secondary producers to vertebrate predators in the pelagic food webs of the subarctic Atlantic oceans (Vesin et al., 1981; Vilhjalmsen 1994; Carscadden et al., 2001). There are

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three main capelin populations in the North Atlantic: Barents Sea, Iceland, and Newfoundland and Labrador (NL). These three capelin populations have all undergone periods of boom and bust; however, while all three populations collapsed around the same time in the early 1990s during a cold period in the North Atlantic, the Barents Sea and Iceland populations subsequently recovered and continued with their boom-bust cycles (reviewed in Carscadden et al., 2013), while the NL population has remained at low levels of abundance for more than two decades until recently (DFO, 2015). These three capelin fisheries are managed using the precautionary approach; however, the Iceland and Barents Sea capelin fisheries have each set a B_{lim} , which is the minimum spawning stock biomass required to achieve average recruitment, and use assessment models. The capelin fishery in these two regions is closed if the spawning stock biomass is below the B_{lim} , which occurred during the early 1990s and more recently (Gjosæter et al., 2015; ICES, 2016). In NL, where the capelin fishery is considered to be lightly exploited (Carscadden et al., 2001) with no stock-recruitment relationship (Carscadden et al., 2000), the total allowable catch is adjusted based on the bi-annual stock assessment with no closures of the fishery to date (DFO, 2015).

In NL, recruitment is set early during the larval stage (Frank and Leggett, 1981a; Leggett et al., 1984; Dalley et al., 2002). Larval survival in the first two weeks, as the larvae emerge from the sediments at beach sites, was previously related to both temperature and the occurrence of onshore winds for the years 1966–1978 (Leggett et al., 1984). However, when a longer time series was considered (1974–1994), temperature dropped out and onshore winds explained 25% of recruitment variability for the years 1974–1990, after exclusion of the 1991–1994 year classes from the analysis given the strong impact on recruitment from the capelin stock collapse (Carscadden et al., 2000). Onshore winds were identified as important for larval survival as they provide a mechanism for larval emergence from the sediments, and larval condition and survival is a negative function of residency time in the sediments (Frank and Leggett 1981b, 1982; Leggett et al., 1984). Furthermore, onshore wind events allow for a rapid coastal water mass replacement where cold, high-salinity waters were replaced with warmer, less-saline waters (Frank and Leggett 1982). This water mass replacement was positively related to increased availability of small zooplankton prey ($< 250 \mu\text{m}$) and a decrease in abundance of invertebrate predators (Frank and Leggett 1982).

Profound changes in NL capelin spawning biomass distribution and abundance were first observed in 1991, which corresponded with other major changes in the ecosystem, namely the collapse of the groundfish stocks and a shift to cold oceanographic conditions (Carscadden et al., 2001; Carscadden et al., 2013). Fundamental changes in capelin biology occurred at the same time, including maturation shifting from ages 3–4 to age 2, and delayed spawning by up to four weeks (Nakashima and Mowbray, 2014). Anomalous meteorological and

oceanographic conditions were hypothesized to have driven this collapse in capelin biomass with colder temperatures associated with extensive changes in distribution of capelin (Frank et al., 1996); decreased or changed prey availability (Carscadden et al., 2001); and delayed spawning times and smaller size-at-age (Carscadden et al., 1997). While there has been a general warming in oceanographic conditions from 1995 to 2010 (Colbourne et al., 2016), capelin biomass has not yet recovered to pre-1991 levels. Recent acoustic surveys indicate that capelin in NL waters are currently experiencing an increase in biomass (2011–2015) with capelin distribution suggestive of that seen in the 1980s (Mowbray, 2014; DFO, 2015).

The aim of our study was to identify potential mechanisms underlying the lack of recovery of capelin post-1991. We re-tested the relationships between capelin larval survival, the age-2 recruitment index, and onshore wind events for the years 1991–2013. We predicted that the age-2 recruitment index is still related to larval abundance, but that the drivers of recruitment variability have changed due to persistently later spawning in capelin since 1991, which has resulted in a mismatch between capelin peak spawning and onshore wind events. Pre-1991, capelin spawned in June when north-easterly onshore winds dominate; post-1991, capelin spawn in July and August when south-westerly winds dominate. In addition to onshore wind events, we tested potential effects of prey availability and temperature on age-2 recruitment. To gain further insight into the relationship between capelin larval vital rates and recruitment variability, we collected larval growth data using three contrasting years: 2002, a year of collapsed population state; 2006, during a transitioning state with increasing temperature and changing zooplankton phenology; and 2013, during a recovering state. We predicted that larval growth varied among years, with faster growth and higher recruitment in the recovering state compared to the collapsed and transitioning states.

2. Material and methods

2.1. Recruitment indices

We used the absolute biomass estimate of age-2 capelin obtained from the spring (May) acoustic survey conducted by Fisheries and Oceans Canada (DFO) in NAFO Division 3L (1991–1992, 1996, 1999–2005, 2007–2015) as our recruitment index (DFO, 2015). The recruitment index was lagged by 2 years in order to compare survival in the same cohort. Details of the acoustic survey methods are given in Mowbray (2014).

To test if there was still a relationship between the age-2 recruitment index and larval abundance post-1991, we used two larval indices collected by DFO. As capelin larvae emerge into the nearshore area from one large and four small spawning beaches and two demersal sites ($< 20 \text{ m}$ water depth), they were sampled by boat off Bellevue beach,

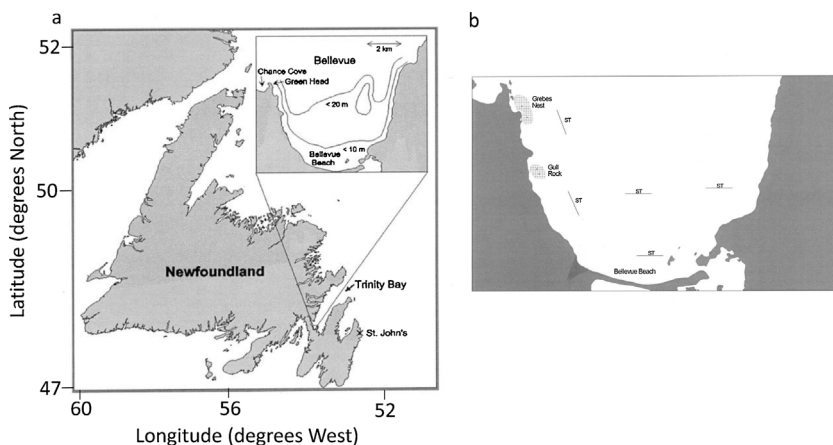


Fig. 1. (a) Map of the Bellevue Beach nearshore area, Trinity Bay, Newfoundland, Canada; (b) map of surface tow sampling stations (ST) in the Bellevue beach nearshore area and the two demersal spawning beds (Grebes Nest and Gull Rock).

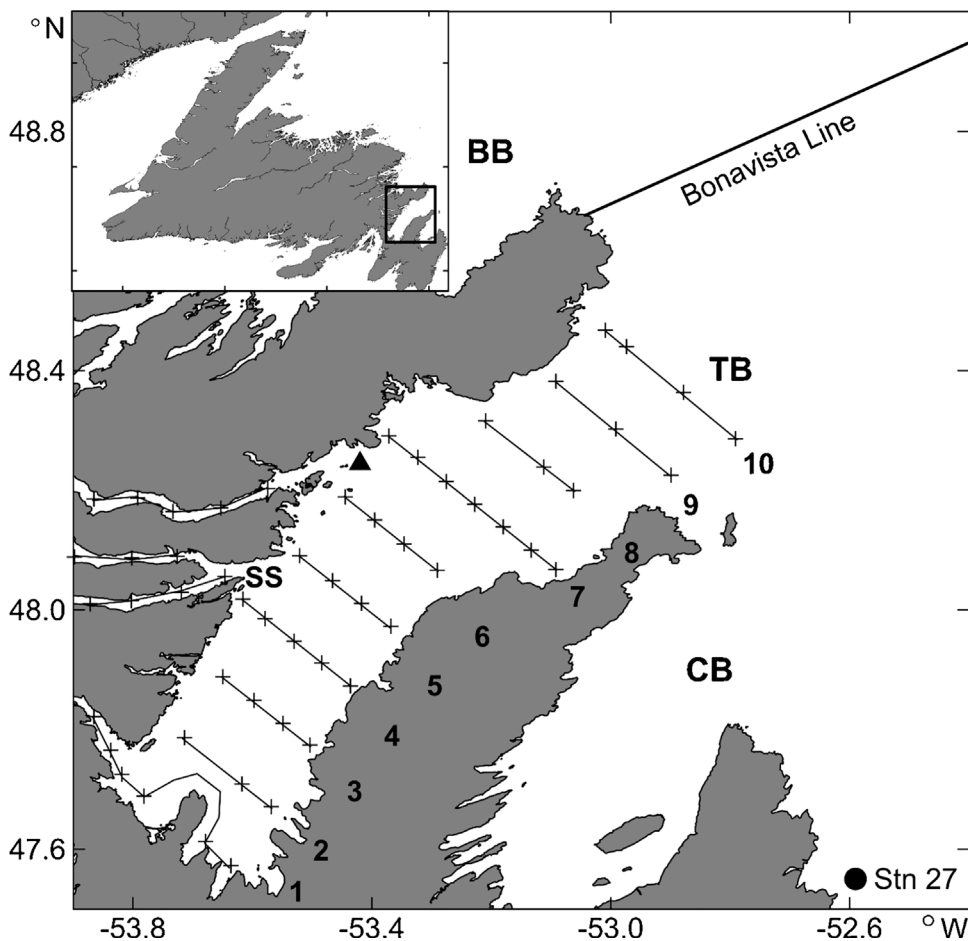


Fig. 2. Map of sampling stations for late-larval capelin in Trinity Bay (TB), Newfoundland, Canada. In 2002, all 52 sites were sampled; from 2003 to 2013, 19 sites were sampled in the centre of the bay (transects 4–7). Zooplankton and temperature data were collected at station 27 and Bonavista Line as part of the Atlantic Zone Monitoring Program (AZMP), Fisheries and Oceans Canada. BB (Bonavista Bay), CB (Conception Bay).

Trinity Bay, NL (48°N, 53.5°W) (2001–2015; DFO, 2015; Fig. 1). Briefly, emergent larval densities were sampled at 5 stations in the nearshore area from the onset to the end of emergence (sampling typically lasts 4–6 weeks in July and August) using a 270 µm mesh size net on a 0.75 m diameter ring. Larvae were collected every 24–48 h during daylight hours in surface tows of 10 min duration at 2.1 knots (Nakashima and Mowbray, 2014; Fig. 1). Material from the cod-end was filtered through a 270 µm mesh sieve and immediately preserved in 5% formalin and seawater. A General Oceanic® flowmeter was attached to the mouth of the ring net to measure water volume sampled at each station. Annual production of larvae per m³ was calculated using the trapezoidal integration method (Nakashima and Mowbray, 2014):

$$N = \sum (t_n - t_{n-1})^{1/2} [X(t_n) + X(t_{n-1})] \quad (1)$$

where t is the day of the year, n is the number of sampling days, and $X(t)$ is the number of larvae per m³ on day t . If a sample was missed for 2 or more days then the missing values were set to 0.

Late-larval densities were collected annually (2002–2015) in Trinity Bay, NL (Fig. 2). Methods have previously been described in Dalley et al. (2002). Briefly, bongo nets measuring 61 cm in diameter with 333 µm mesh nets were towed in a double oblique pattern to a maximum depth of 200 m at a winch speed of 20 m min⁻¹ for descent and 10 m min⁻¹ for ascent, and a vessel speed of 2–2.5 kt. In 2002, 56 stations were sampled, while 19 stations were sampled in the middle of the bay (transects 4–7) from 2003 to 2015 in August, September and/or October (Fig. 2). Material from the cod-end was filtered through a 333 µm mesh sieve and immediately preserved in 5% formalin and seawater. General Oceanic® flowmeters were attached to the mouth of the bongo nets to measure water volume sampled at each station. Annual larval densities per m² were calculated as a mean of all sampling

stations.

For three years only (2002, 2006, and 2013), one of the two bongo net samples was preserved in 95% ethanol. The capelin larval otoliths from these three years were used to investigate the link between larval vital rates and capelin recruitment. In 2002, sampling was conducted across the whole bay at 56 stations in September and October, and five larvae from 20 randomly chosen stations were analyzed from each month ($n = 200$). In September 2006, capelin larvae were captured at only 10 of the 19 stations in the centre of the bay, and ten larvae from each station were analyzed ($n = 100$). In 2013, capelin larvae were captured at 18 of the 19 stations in the centre of the bay in both August and September, and five larvae were analyzed from each station and month ($n = 180$).

2.2. Environmental drivers of recruitment variability

We considered interannual variability in the abundance of *Pseudocalanus* spp., which was identified as the main zooplankton prey species contributing to the diet of larval capelin in Trinity Bay (D. Kamada, Memorial University of Newfoundland, pers. comm.). *Pseudocalanus* spp. abundance data were obtained from DFO's Atlantic Zone Monitoring Program (AZMP) and used as an alternative index since the 333 µm mesh nets used for sampling fish larvae do not allow us to sample the appropriate size range of zooplankton comprising the diet of fish larvae. We used 1 June–1 October *Pseudocalanus* spp. densities sampled at the high frequency sampling site, station 27 (47.55°N, 52.59°W, 165 m depth), located south of Trinity Bay along the east coast of NL (Fig. 2). We used station 27 for the larval capelin prey abundance index, rather than the less frequently sampled Bonavista Line, as station 27 is sampled approximately bi-weekly to monthly

throughout the year and is considered representative of the zooplankton population in our study area (Wilson et al. in review; Fig. 2). Zooplankton samples were collected using a dual 0.75 m diameter ring net with 202 μm mesh towed vertically with a retrieving speed of 1 m s^{-1} . Samples were preserved in 2% formalin for later taxonomic identification and enumeration. A minimum of 200 organisms per sample were counted and identified to the lowest taxonomical level possible, and additional aliquots were taken until approximately 75–100 *Calanus* spp. were identified and staged (Mitchell et al., 2002). Given that the 202 μm mesh of the AZMP sampling gear cannot provide quantitative estimates of copepod nauplius stages, which are commonly ingested by first-feeding larvae, abundance of the adult copepod stage (C6) was used as a proxy for nauplii and early copepodite production in the system (Ringuette et al., 2002).

Sea temperature at a depth of 20 m was provided by the high frequency fixed sampling station 27 located outside St. John's harbour. We were interested in measuring interannual variability in mean temperatures from 1 June to 1 October, which corresponded with capelin spawning and larval occurrence in Trinity Bay. Temperature measured at station 27 was representative of seasonal and interannual variations in regional ocean temperature (Ouellet et al., 2003).

Daily wind data from the monthly wind summaries from the St. John's meteorological site were used to determine the number of days between onshore wind events within a 10-day period following the first day of hatch (Leggett et al., 1984). Longer intervals between onshore wind events were related to lower condition in emergent capelin larvae (Frank and Leggett 1981a).

2.3. Laboratory analyses

Capelin larvae were identified based on the descriptions in Fahay (2007). The standard length (tip of snout to tip of notochord) of 5–10 randomly chosen capelin larvae from each station was measured to the nearest 0.1 mm under a dissecting microscope (Olympus SZX16) linked to an image analysis system. A larva was placed in a drop of water on a glass slide and the otoliths were illuminated with cross-polarizing filters under a dissecting microscope (60 \times) (Olympus SZX16). The otoliths were removed from the head of the larva using insect pins, cleared of any adhering tissue, and left to air dry on a glass slide. A drop of Krazy Glue™ was added once the otoliths were dry.

Otolith radii and increment width were measured along the rostral axis under oil immersion at 1000 \times magnification using a compound microscope (Zeiss AX10) coupled to an image-analysis system (ImagePro Plus 6.3) with a video camera. The otoliths were all read twice. If the percentage of standard deviation around the mean increment width from the two otolith measurements was greater than 10% and/or the increment counts were not the same, the otolith was analyzed a third time (Murphy et al., 2013). This third reading was related to the first reading only. Using these criteria, 31 otoliths (6%) were rejected after a third reading.

2.4. Data analyses

Using methods outlined in Leggett et al. (1984), annual incubation temperatures of the eggs spawned at one beach site (Bellevue Beach) in Trinity Bay were calculated using peak spawning time collected by DFO since 1991 using Formula (2) (Frank and Leggett 1981b).

$$Y = 0.607 \times x_1 + 0.348 \times x_2 + 0.392 \times x_3 + 0.142 \times x_4 - 0.297 \quad (2)$$

where Y = incubation temperature (degrees Celcius), x_1 = water temperature (degrees Celcius), x_2 = h of bright sunlight per day, x_3 = minimum daily air temperature (degrees Celcius), and x_4 = maximum daily air temperature (degrees Celcius).

Mean monthly water temperature was calculated from the surface measurement (0–20 m) at station 27, daily minimum and maximum air

temperatures were provided by the St. John's meteorological site, and hours of sunlight was provided by National Research Council Canada (<http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html>).

Peak spawning time was used as the starting point for the calculation and the average incubation temperature was the mean of estimated daily temperatures over the following 14 days. Using the mean incubation temperatures from Formula (2), we calculated the number of days until hatch using Formula (3) from Frank and Leggett (1981b). A recent study has confirmed that the relationship between temperature and days to hatch for capelin eggs is still valid post-1991 (Purchase 2017).

$$\text{Days to hatch} = e^{(4.27 - 0.63 \cdot (\ln(Y + 1)))} \quad (3)$$

In a robust multiple regression model ('lmer' function in R package 'robustbase') (Maechler et al., 2017), the relationship between the age-2 recruitment index and the three environmental variables (wind, temperature and *Pseudocalanus* spp. densities) was tested. A robust multiple regression model was used because *Pseudocalanus* spp. densities in 2012 was three times as high as the next highest year. Best model selection was based on adjusted R^2 values as this model function does not provide AIC values.

Capelin larvae have previously been found to initiate otolith increment formation approximately 12 days post hatch (Ivarjord et al., 2008). For this reason, we used the absolute increment counts as a proxy for age with no correction for delayed increment formation and we assumed the delay in increment formation would be the same among years. Daily increment formation was found for capelin larvae reared in large basins (Gjosæter and Monstad, 1985), although another study found daily otolith increment deposition occurred in only fast-growing ($> 0.30 \text{ mm day}^{-1}$) capelin larvae (Ivarjord et al., 2008). Due to this uncertainty, we did not back-calculate length-at-age (Campana 1996).

In all three years, one of the surveys was conducted in mid-September, so we compared mean otolith increment widths (MIW) in larvae captured in September among years using a one factor (year) repeated-measures analysis of variance (ANOVA). We did not include sampling site as a factor as the majority of larvae in all three years were sampled in the middle of the bay (transects 4–7; Fig. 2). We binned the increment widths into groups of five increments over the first 20 increments. Comparisons of MIW amongst years were performed using *post-hoc* Tukey tests.

We used non-parametric local density estimators (Dower et al., 2009; Robert et al., 2014) to describe the change in variability of larval growth with age. This approach has the advantage of avoiding potential biases from traditional linear models where there may be individual age-dependent departures from the overall response. Further details of age-dependent serial autocorrelations can be found in Pepin et al. (1999). Briefly, this method produces a locally weighted estimate of the cumulative distribution function (CDF) of observations, using kernel smoothing, as a function of age as a covariate. The weighting function was

$$w(d) = e^{-d} \quad (4)$$

where $d = |x_i - x|/b$, and b is a bandwidth parameter. The bandwidth parameter describes how far 'local' extends and it is calculated by cross validation. Our bandwidth was 2.75 days, which is due to widely spaced observations, which was also encountered by Dower et al. (2009). Periods characterized by rapid increases in otolith growth autocorrelation are potential survival bottlenecks where high growth-selective mortality may operate (Pepin et al., 2015).

Assumptions of ANOVA were examined using box and normal probability plots, and MIW, temperature, prey densities, larval densities and recruitment were $\log(x + 1)$ transformed to satisfy the assumptions of homogeneity of variances. C + + was used for the CDF analysis and R v. 3.3.2 (R Core Team 2016) was used for all other statistical analyses.

Table 1

The age-2 recruitment index (lagged by 2 years) of capelin in Newfoundland (NL), Canada obtained from the spring acoustic survey in NAFO Division 3L since 1991; the peak spawning day at Bellevue Beach, Trinity Bay collected by Fisheries and Oceans Canada; incubation temperature in the beach sediments based on Formula (2) from Leggett et al. (1984); the number of days for eggs to hatch based on Formula (3) from Leggett et al. (1984); peak hatch date of eggs; the number of days between onshore wind events for the first 10 days post-hatch where > 10 indicates that there were no onshore wind events in the first 10 days post hatch; emergent capelin larval densities sampled from the nearshore in Trinity Bay, NL; capelin late-larval densities sampled in Trinity Bay, NL; *Pseudocalanus* spp. adult copepod stage (C6) densities sampled from 1 June to 1 October; and mean temperature at 20 m at Station 27 from 1 June to 1 October.

Year	age-2 recruitment (billions)	Peak spawning (Julian Day)	Incubation temperature (Y) (°C)	Days to hatch	Peak hatch date (Julian Day)	Days between onshore wind events	Emergent larval densities (m ⁻³)	Late-larval densities (m ⁻²)	<i>Pseudocalanus</i> spp. C6 densities (m ⁻²)	Mean temp. at 20 m (°C)
1991		203	12.0	14	217	> 10				3.4
1992		191	14.4	13	204	> 10				7.7
1993		237	13.4	13	250	> 10				6.7
1994	2.96	214	18.3	11	225	> 10				8.7
1995		204	15.8	13	217	> 10				7.9
1996		193	15.9	12	205	> 10				8.7
1997	8.21	202	14.4	13	215	> 10				7.6
1998	8.46	204	16.7	12	216	> 10				6.0
1999	6.71	191	17.3	12	203	6			5882	7.8
2000	3.28	200	14.2	13	213	9			8150	6.9
2001	3.99	198	16.8	12	210	> 10	753		6754	8.6
2002	8.59	201	14.4	13	214	> 10	1031	23	6049	7.3
2003	2.91	198	19.5	11	209	> 10	578	48	5603	8.3
2004		183	14.4	13	196	> 10	606	15	5828	6.9
2005	15.62	190	17.6	11	201	> 10	2736	10	4154	7.3
2006	9.98	189	17.2	12	201	> 10	2245	18	8710	8.8
2007	18.55	199	17.3	12	211	> 10	3700	75	6491	5.2
2008	1.19	197	17.0	12	209	5	1899	26	4148	7.5
2009	10.60	217	16.3	12	229	9	1881	22	9418	7.0
2010	18.40	191	18.9	11	202	7	1276	45	8114	7.8
2011	26.03	186	17.1	12	198	> 10	2620	83	8839	8.3
2012	91.16	195	16.8	12	207	> 10	2867	10	27659	6.7
2013	35.05	184	16.5	12	196	8	3770	14	7065	9.5

3. Results

3.1. Recruitment indices and drivers of recruitment variability

The densities of emergent capelin larvae varied among years, ranging from a low of 578 m⁻³ in 2003 to a high of 3770 m⁻³ in 2013 (Table 1). Emergent larvae entered the nearshore area in pulses lasting for 1–5 days (Nakashima and Mowbray, 2014). The sampling stations closer to the beach had higher densities of larvae compared to the sampling stations further from the beach. The densities of late-stage capelin larvae ranged from a low of 10 m⁻² in 2005 and 2010 to a high of 83 m⁻² in 2011 (Table 1). The distribution of late-stage larvae in Trinity Bay did not show any patterns among months or years (Nakashima and Mowbray, 2014).

The age-2 recruitment index was related to emergent larval abundances at Bellevue beach (2001–2013) ($y = 0.40x + 2.80$; $p = 0.017$; $R^2 = 0.42$) but not to late-larval abundances in Trinity Bay (2002–2013) ($y = -0.16x + 1.61$; $p > 0.05$; $R^2 = 0.05$) (Fig. 3).

Since 1991, the timing of annual peak spawning has varied over a period of nearly two months, from 2 July in 2004–25 August in 1993 (Table 1). Egg incubation times ranged from 11 to 14 days over the 23 years (Table 1). The best model selection, based on adjusted R^2 values, included only *Pseudocalanus* spp. densities from 1 June to 1 October (Table 2; Fig. 4). There was an increasing trend in *Pseudocalanus* spp. densities from 2006, with the highest density of *Pseudocalanus* spp. in 2012, which was also the highest recruitment year in the time series (Fig. 4).

3.2. Interannual variability in environmental variables

Mean temperature at 20 m at station 27 from 1 June to 1 October varied from 3.4 °C (1991) to 9.5 °C (2013) (Table 1). Incubation temperatures on the beach ranged from 12.0 °C in 1991–19.5 °C in 2003 (Table 1). There were no daily onshore wind events in the 10-day period immediately following peak hatch day in 74% (17 out of 23) of

the years since 1991 (Table 1).

3.3. Interannual variability in larval growth

Of the 480 otoliths available for larval growth analysis, age and growth measurements from 449 otoliths were used in this study. The length frequency distributions of larvae sampled from all three years were similar with the majority of larvae sampled in each year ranging from 10–22 mm SL (Fig. 5).

Mean increment widths (groups 1–5, 6–10, 11–15, 16–20) of larvae captured in September varied among years (repeated measures ANOVA: $F_{6,255} = 2.490$, $p = 0.023$, G.G. statistic = 0.034) (Fig. 6), with highest MIW in 2013 for all increment groups except for MIW 6–10 where growth was higher in 2006 (post hoc Tukey's test: $p < 0.001$) (Fig. 6). Furthermore, when MIW in August 2013 and October 2002 are compared to the September values, August 2013 has highest MIW compared to other sampling times while MIW was similar between September and October 2002 (Fig. 6). With only three years of data, it is not possible to assess quantitatively the relationship between growth and the age-2 recruitment index; however, the year with the fastest growth recorded (2013) corresponded with one of the strongest years in the age-2 recruitment index.

There was a consistent trend in age-dependent serial autocorrelations in capelin larval growth until increment 17 (potentially 12–28 days post hatch) (Fig. 7), and then an increase in serial autocorrelations from increments 17–21 (potentially 29–33 days post hatch) (Fig. 7).

4. Discussion

The strong relationship between the age-2 recruitment index from the acoustic survey in NAFO Div. 3L and emergent larval densities from the Bellevue beach nearshore area supports previous research on the synchronicity of capelin larval emergence in NL. Onshore wind events are now rare when capelin larvae are emerging from beach sites, but

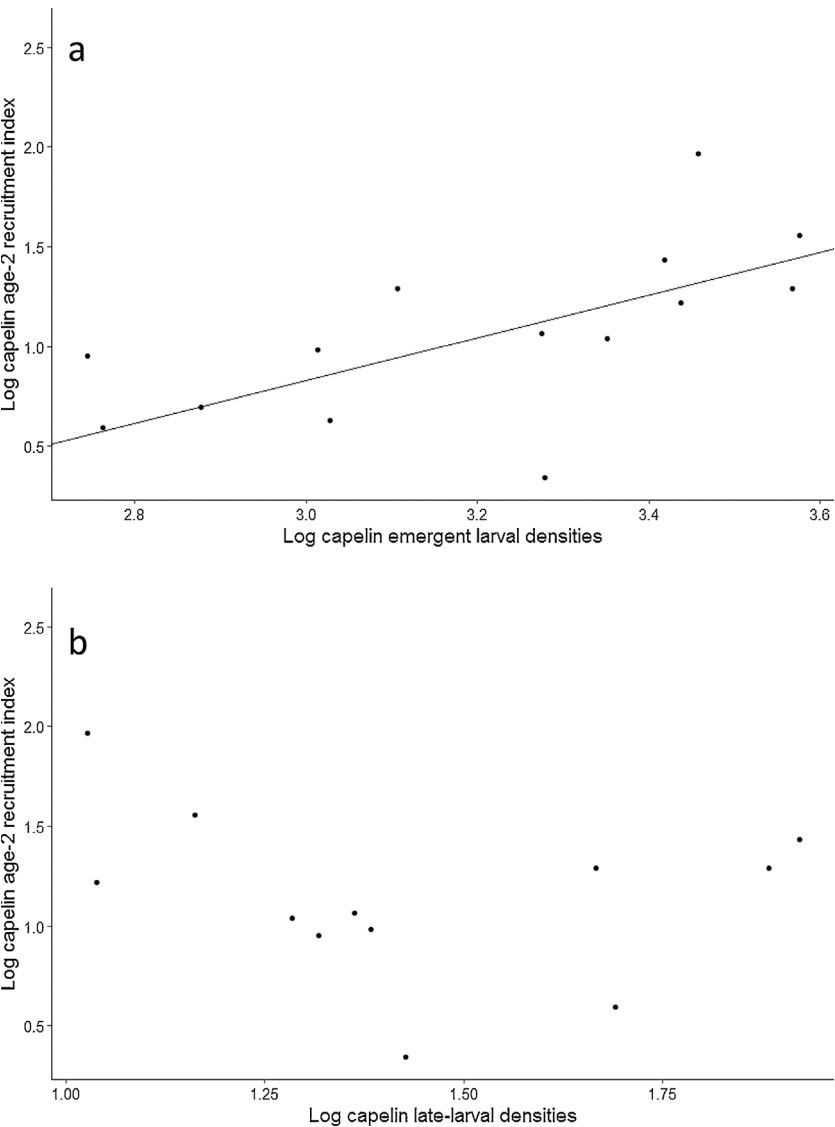


Fig. 3. Linear regressions of the age-2 recruitment index and (a) emergent capelin larval densities from surface boat tows (2000–2015), and (b) late-larval capelin larval densities from Trinity Bay (2002–2015).

Table 2
Robust multiple linear regression of the age-2 recruitment index and *Pseudocalanus* spp. densities from 1 June to 1 October, the number of days between onshore wind events 10 days post-hatch (WIND), and mean temperature at 20 m from 1 June to 1 October at station 27 (Temperature).

Model	Adjusted R ²	P value
<i>Pseudocalanus</i> spp.	0.33	0.005
<i>Pseudocalanus</i> spp., WIND	0.31	
<i>Pseudocalanus</i> spp., WIND, Temperature	0.27	

when they do occur, our results support the hypothesis that there is still a synchronous release of emergent larvae post-1991. While our study is restricted spatially to one main spawning beach on the east coast of NL, previous research has found synchronous release of emergent larvae at various sites across the east coast of NL due to widespread hydrology and meteorological forcing (Frank and Leggett 1981a). In the 1990s, Bellevue beach was found to be representative of larval emergence at other south-eastern beach sites (NAFO Div. 3L), and larval emergence was approximately one week later at sites further north (NAFO Div. 3K) (Nakashima 1996). Expanding surveys of spawning and larval emergence timing at suitable capelin spawning beaches [eastward facing to ocean with median grain size of 2.4–11.4 mm (Nakashima and Taggart 2002)] would provide a valuable update on the synchrony of

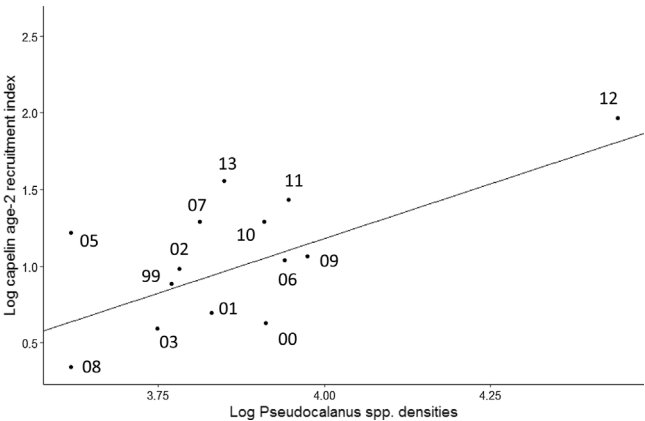


Fig. 4. The best fit model of a multiple linear regression between the age-2 recruitment index and days between onshore wind events 10 days post hatch, mean temperature at 20 m, and *Pseudocalanus* spp. includes only variable, which is the densities of *Pseudocalanus* spp. from 1 June to 1 October. Each point is labelled with the year (last two digits).

capelin larval emergence in NL, allowing us to further examine the potential factors influencing the release of emerging larvae from beach sediments.

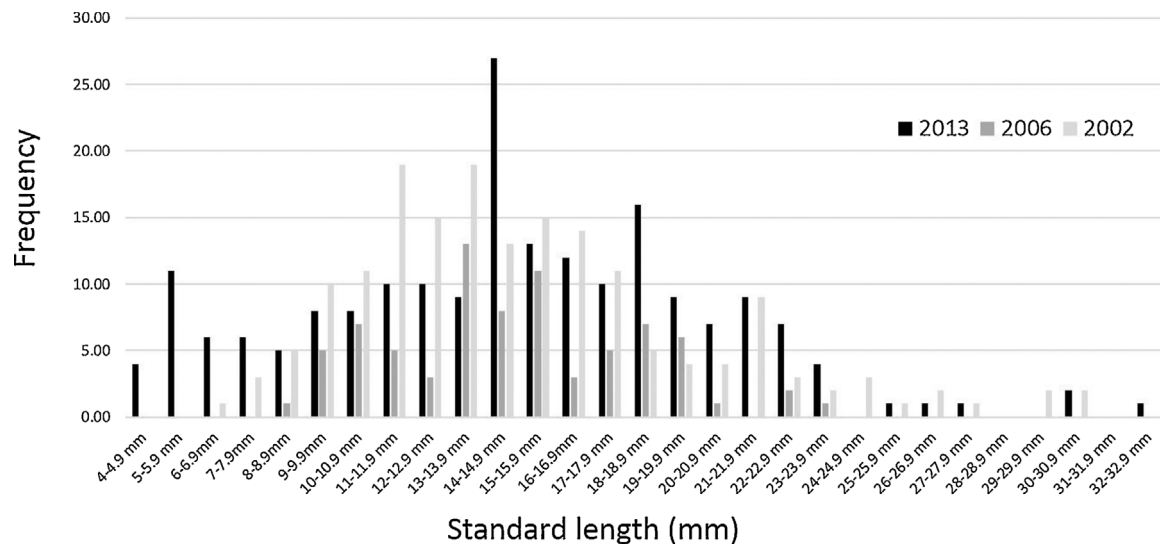


Fig. 5. Length frequency distributions of capelin larvae sampled in Trinity Bay, Newfoundland in the years 2002, 2006, 2013.

Since the population crash of 1991 and subsequent non-recovery of capelin biomass over the past two decades to pre-1991 levels, a re-assessment of the drivers of recruitment variability of capelin is vital to understanding why there has been minimal recovery of capelin. For capelin in NL, larval survival and year-class strength were related to meteorological and hydrological factors from 1966 to 1990 (Frank and Leggett, 1981a; Leggett et al., 1984; Carscadden et al., 2000; Dalley et al., 2002). Post-1991, capelin survival was still set in the first two weeks post-hatch, with the age-2 recruitment index related to the emergent larval densities; however, the age-2 recruitment index was no longer related to onshore wind events. The lack of relationship between the age-2 recruitment index and onshore wind events post-1991 may be due to a delay in spawning that has persisted since 1991. With predominately south-westerly wind events later in the summer, the number of onshore wind events has decreased during the capelin spawning period, going from a mean of 1.78 (range 0–7) onshore wind events in June to a mean of 0.73 (range 0–4) onshore wind events in July. Onshore wind events are still required to release emergent larvae from the beach sediments, but infrequent onshore wind events later in

the summer likely results in high interannual variability in release success of larvae emerging from the sediments in good condition (Frank and Leggett 1981a, 1982). While our larval index also includes demersal sources of larvae, demersal habitat is thought to contribute little to recruitment in Newfoundland (Nakashima and Wheeler 2002), due to longer incubation times in cooler water (Penton et al., 2012) resulting in extended exposure to egg predators and less time for larvae to grow prior to winter. Furthermore, fewer onshore wind events are also likely having a negative impact on survival of demersal sources of larvae as a mismatch with rapid coastal water mass replacements would decrease the availability of small prey and increase overlap with invertebrate predators (Frank and Carscadden 1989). High mortality in the larval stages is likely one of the main factors inhibiting the recovery of capelin in NL.

There was a positive relationship between the age-2 recruitment index and *Pseudocalanus* spp. abundance. This suggests that once the larvae are released from the sediments, the availability of this specific prey type is an important driver of recruitment variability. The importance of prey availability to capelin larval survival has previously

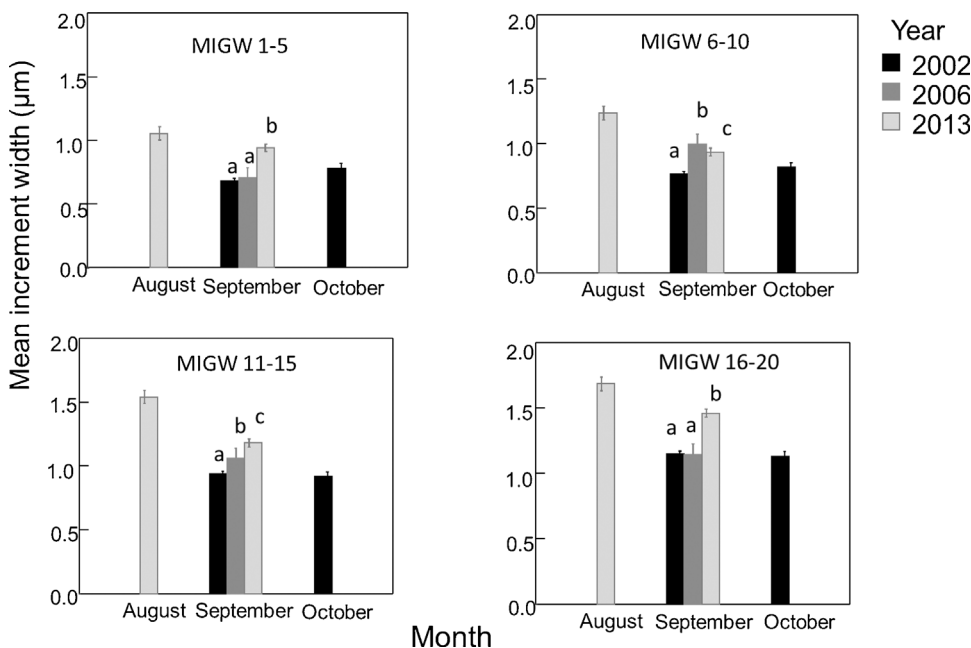


Fig. 6. Mean otolith increment widths (MIW) (increments 1–5, 6–10, 11–15, 16–20) of capelin larvae varied among three years (2002, 2006, 2013) in September (repeated measures ANOVA: $F_{6,255} = 2.490$, $p = 0.023$, G.G. statistic = 0.034). MIW was higher in 2013 for all increment groups except MIGW 6–10 where growth was higher in 2006 (Post hoc Tukey's test: $p < 0.001$).

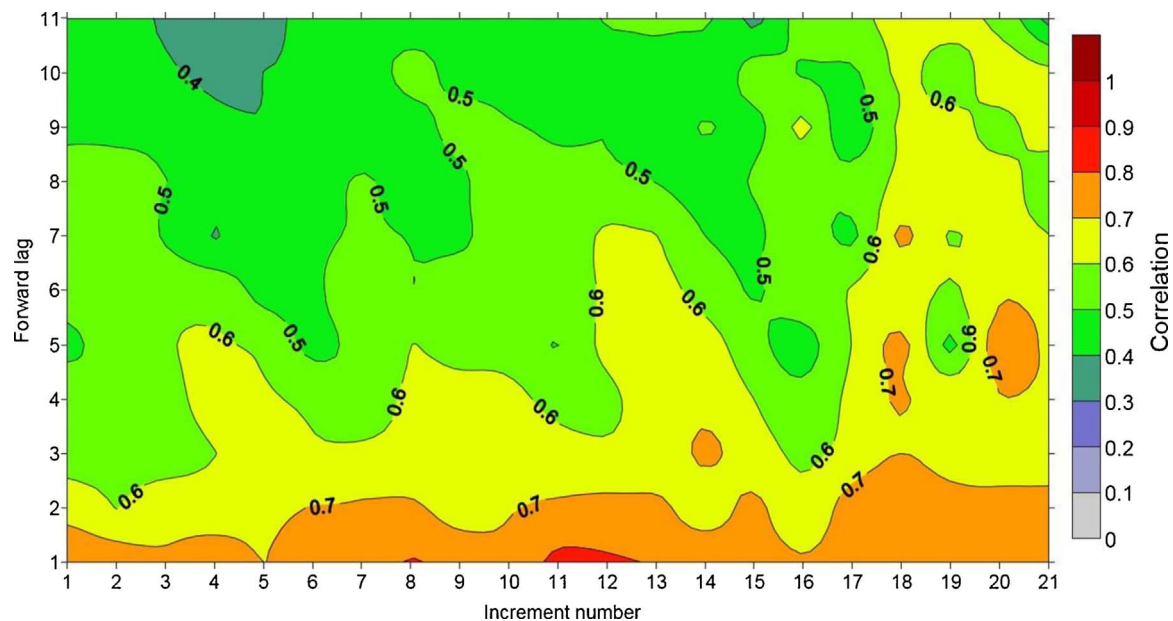


Fig. 7. Age-dependent serial autocorrelations (r value represented by colour of scale) of otolith increment widths of capelin larvae. Forward lag is the number of daily increments after a given increment number.

been identified in NL (Frank and Leggett, 1982, 1986). Larval capelin (5–30 mm SL) feed on small prey, such as nauplii and copepodite stages of small copepods, and *Pseudocalanus* spp. was found to dominate the diet of capelin larvae in Trinity Bay, NL for the years 2002, 2006, and 2014 (D. Kamada, Memorial University of Newfoundland, pers. comm.). In the NL ecosystem, there has been a shift in zooplankton phenology from a spring to an autumn bloom, which occurred around 2006 (Pepin et al., 2013). This change in phenology was particularly evident for *Pseudocalanus* spp., with peak adult abundance shifting from April–May prior to 2005 to August–September after that period. Furthermore, the abundance of *Pseudocalanus* spp. was at or above normal across the Newfoundland Shelf from 2009 to 2015 (DFO, 2016). Such drastic changes in the phenology and dynamics of this preferred prey species may have resulted in increased foraging opportunities for larval capelin. Since capelin larvae feed on both naupliar and copepodite stages of *Pseudocalanus* spp., the importance of a prey match-mismatch may extend from the first-feeding stage, as emergent larvae leave nearshore areas, to the late-larval stage.

Parallel to an increase in *Pseudocalanus* spp. prey abundance, we observed higher daily larval growth during the recovering population state (2013) compared to the collapsed (2002) and transitioning (2006) states suggesting better larval growth conditions for capelin in recent years. Faster-growing individuals are predicted to experience relatively high survival rates due to increased resilience to starvation and increased ability to avoid predation (e.g. “growth-mortality hypothesis” Anderson 1988). Temperature (Houde 1987) and prey availability (Cushing 1972, 1990) have been identified as two of the most important drivers of larval growth and survival. Post-1991, we did not find a relationship between the age-2 recruitment index and temperature or the onshore wind regime previously described by Leggett et al. (1984). The “breaking” of environmental-recruitment relationships when being re-tested with new data is well documented (Myers 1998; Lindegren and Checkley, 2012; Hare et al., 2015). However, the abrupt change in the ecosystem structure of NL in 1991, which resulted in a decline in finfish predators, an increase in seals and macro-invertebrates, and changes in zooplankton phenology, could have masked the environment-recruitment link (Keyl and Wolff 2008). We recognize that the potential drivers of recruitment variability can be tightly coupled and there is a possibility that temperature still has an important – but indirect – effect on recruitment by triggering the observed change

in phenology of the main prey *Pseudocalanus* spp.

Increment widths of an individual larva are not independent from each other, and an individual's growth rate at an earlier age is likely indicative of future growth (Pepin et al., 2015). In fast-growing species like scrombrids, serial correlation is high from the early larval stage, suggesting that first-feeding success is an important predictor of future growth and survival (Robert et al., 2014; Pepin et al., 2015). Moreover, periods characterized by rapid increases in otolith growth autocorrelation are potential survival bottlenecks where high growth-selective mortality may operate (Pepin et al., 2015). In capelin, because the first increment is deposited approximately 12 days post hatch (Ivarjord et al., 2008), it is not possible to back-calculate growth performance during the critical first-feeding stage. Otolith growth autocorrelation for increments 1–16 (~12–28 days post hatch) was stable at a relatively strong level, which suggests we missed the increase in autocorrelation typically observed during first-feeding in multiple species (Pepin et al., 2015). We observed an additional increase in serial correlation from increment 17 (~29 days post hatch). Even though we did not detect a relationship between the age-2 recruitment index and late-larval abundance, this change in serial correlation indicates the potential for a significant increase in selective mortality at approximately 4 weeks post-hatch. This supports the existence of a secondary survival bottleneck beyond larval emergence from beach sediments, and suggests that late-larval dynamics could play a role in fine-tuning recruitment strength (e.g., Köster et al., 2003; Zhang et al., 2016; Takahashi et al., 2016), possibly through availability of the main prey.

Larval survival is a key component of recruitment success in capelin. However, later spawning is having a profound effect on larval survival in NL. Post-1991, capelin are smaller, mature earlier, and spawn later, which may be driven by low productivity of larger copepods in the NL ecosystem having a negative effect on capelin adult growth and condition (Dalpadado and Mowbray 2013; DFO, 2016). Later spawning results in a mismatch between peak larval emergence and onshore wind events, and, consequently, capelin larvae are trapped on beaches for longer in late summer and have less time to grow before their first winter. Low larval survival from beach spawning may be inhibiting the recovery of the NL capelin stock. However, enhanced food productivity of small copepods in autumn has generated a positive effect on larval survival that can potentially compensate for the negative effect of later spawning.

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