



Original Article

Identifying possible drivers of the abrupt and persistent delay in capelin spawning timing following the 1991 stock collapse in Newfoundland, Canada

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Spawning timing in fish is generally cyclical in temperate regions in order to increase the probability of matching larval occurrence with ideal environmental conditions. The capelin stock in Northwest Atlantic Fisheries Organization Divisions 2J3KL collapsed in 1990–1991 and has not recovered. This collapse was concomitant with collapses in groundfish stocks and cold oceanographic conditions. Using citizen science data, newspaper archives, grey and primary literature, and monitoring data, a century of capelin beach spawning times were compiled. Capelin beach spawning has been persistently 3 weeks later since the stock collapse. To identify potential predictors of capelin spawning timing, an exploratory analysis was conducted using environmental and biological variables and a period factor that categorized a year as either pre-collapse (1990 and earlier) or post-collapse (post-1990) in a step-wise multiple regression model. Spawning timing was predicted to be delayed in the post-collapse period when there were negative anomalies in the Newfoundland and Labrador Climate Index and summer (June–August) North Atlantic Oscillation, and when there was a decrease in mean length of the spawning population. The production of weak year-classes is predicted when spawning is delayed, suggesting that late spawning is severely inhibiting the recovery of the stock.

Keywords: Bottom-up processes, *Mallotus villosus*, Northwest Atlantic climate, recruitment, regime shift

Introduction

Fish spawning timing in temperate regions is often cyclical to allow for the synchronous occurrence of early life stages and environmental conditions conducive to their growth (i.e. temporal overlap with seasonal zooplankton blooms) in order to improve the probability of offspring survival (Cushing, 1975, 1990; Kristiansen *et al.*, 2011). Since recruitment variability is the outcome of multiple complex trophodynamic and physical processes that act on the early life stages of fishes (Houde, 2008), a match between fish spawning and zooplankton blooms does not guarantee high recruitment. However, a mismatch between these two factors will likely produce a poor recruiting year (Leggett and Deblois, 1994; Durant *et al.*, 2007; Régnier *et al.*, 2019) due to high levels of larval starvation and/or increased predation on slow-growing larvae (Hjort, 1914; Anderson, 1988; Cushing, 1990). The timing of fish spawning can be influenced by both environmental factors and phenotypic char-

acteristics of spawners, such as age and size (Wright and Trippel, 2009). The impact of inter-annual variability in spawning timing on recruitment and productivity of fish populations is of vital interest to fisheries science.

Capelin (*Mallotus villosus*) is a forage fish that plays a key role in the transfer of energy from secondary producers to vertebrate predators of the North-East Pacific, Arctic, and subarctic Atlantic oceans (Vesin *et al.*, 1981; Anderson and Piatt, 1999; Carscadden *et al.*, 2001; Vilhjálmsson, 2002). A collapse of the capelin stock in Newfoundland and Labrador (NL) in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL (hereafter, NL capelin stock) occurred in 1990–1991 with no recovery over the subsequent three decades (reviewed in Buren *et al.* 2019). While “boom-bust” population dynamics are typical of short-lived forage species (Schwartzlose *et al.*, 1999; Chavez *et al.*, 2003), the NL capelin stock has been in a “bust” phase for a prolonged period of time (~ 30 years) compared to other known capelin stock collapses in the Bar-

ents Sea (Gjøsæter *et al.*, 2009; Hjermann *et al.*, 2010) and around Iceland (Pálsson *et al.*, 2012; Carscadden *et al.*, 2013). This collapse of the NL capelin stock was concomitant with other major changes in the ecosystem, namely the collapse of commercial and non-commercial groundfish stocks (Rice, 2002; Lilly, 2008; Pedersen *et al.*, 2017), a shift to an invertebrate-dominated ecosystem (Lilly *et al.*, 2000; Dawe *et al.*, 2012), and cold oceanographic conditions (Drinkwater, 1996). These pervasive ecosystem changes in the early 1990's are suggestive of a regime shift (Buren *et al.*, 2014; Pedersen *et al.*, 2017, 2020), but see also deYoung *et al.* (2004).

Cold temperatures were hypothesized to be a major driver of the observed changes in capelin biology in the early 1990's including persistently delayed beach spawning times (Carscadden and Nakashima, 1997). Since NL capelin year-class strength is set early during the larval stage (Frank and Leggett, 1981a; Leggett *et al.*, 1984; Dalley *et al.*, 2002; Murphy *et al.*, 2018), a change in the timing of spawning may be leading to a mismatch in environmental conditions (i.e. onshore wind events, zooplankton prey availability) and larval emergence (Murphy *et al.*, 2018). Carscadden *et al.* (1997), using a dataset from 1978–1994, found negative relationships between spawning timing, summed sea surface temperature from February to June, and fish lengths. However, these findings were driven by three years of data that were collected following the collapse of capelin in 1990–91, but prior to the collapse of the capelin stock being recognized (Frank *et al.*, 1996, 2016; DFO, 1998; Buren *et al.*, 2019). Furthermore, there has been a general warming in oceanographic conditions from 1995–2011 (Cyr *et al.*, 2021), and capelin spawning times are still delayed. Buren *et al.* (2014) re-tested the relationships described in Carscadden *et al.* (1997) using data from 1978–2010 and included two new variables: a period term [pre-collapse (1990 and earlier) and post-collapse (post-1990)] and the maximum area of sea ice south of 55°N. They found that spawning timing was related to both the period term and the maximum value of sea ice area, and, although the mechanisms that regulate capelin spawning are unknown, the impact of changing sea ice conditions on prey availability and subsequent capelin condition may be driving later spawning (Buren *et al.*, 2014).

Capelin is an iconic species in Newfoundland and Labrador. Due to its annual beach spawning events, the public has witnessed first-hand the change in timing of capelin beach spawning since the 1990's. Capelin are subject to a personal-use fishery for food, bait, and fertilizer during their annual beach spawning events, and a commercial roe fishery with a full utilization requirement since 2006 (i.e. both females and males are retained; DFO, 2019). The inshore commercial fishery closely tracks the spawning migrations of capelin in order to target the spawning females. The total allowable catch for the commercial fishery is small (on average 25000 metric tonnes annually since 1991) compared to other capelin fisheries (ICES, 2020; Marine and Freshwater Research Institute, 2021). Capelin fisheries around Iceland and in the Barents Sea are managed using a harvest control rule (i.e. escapement strategy) (Gjøsæter *et al.*, 2015; Marine and Freshwater Research Institute, 2021), while the NL capelin stock is assessed using trends from two main survey indices (spring hydroacoustic and summer larval), a capelin forecast model, and trends in other biological and ecological data series (DFO, 2019; Lewis *et al.*, 2019).

The first objective of this study was to compile a century of capelin beach spawning data to determine if the abrupt and persistent shift in capelin spawning timing since 1991 was seen during other cold periods in the past century. The second objective was

to explore the relationships between spawning timing and environmental and biological variables in NAFO Divs. 3KL (Buren *et al.*, 2014; Figure 1a). The third objective was to explore if the change in timing of capelin spawning and/or the environment since the population collapse has had an impact on recruitment (year-class strength).

Materials and methods

Capelin beach spawning timing

Newspaper archives (1919–1963; 1991–2019)

The online digital newspaper archive at Memorial University of Newfoundland http://collections.mun.ca/cdm/landingpage/collect/cns_news was searched by the authors; and hard copies of newspaper clippings and online news articles were searched by a librarian. Only newspaper editions from June, July and August were considered in the search, and the search terms “caplin” and “capelin” were used. While peak beach spawning day was not necessarily reported, capelin rolling on a beach and/or the start of the inshore fishery was often reported. We used reporting of these events as a proxy for peak spawning day. When a newspaper did not provide the date when capelin arrived in a specific area, the authors used the date of publication of the newspaper as the date of arrival in the area. An absence of reporting on capelin spawning in a given year was not treated as an absence of spawning *per se* but rather that the capelin “roll” did not make the news. Four digitally archived newspapers provided capelin spawning times in NAFO Divs. 2J3KL for five decades (1919–1963): Evening Telegram (St. John's); Twillingate Sun; Newfoundland Weekly (Boston); and Daily News (St. John's) (Supplementary Table S1). A variety of newspaper and online news articles provided beach spawning times in NAFO Divs. 2J3KL for 1991–2019: The Telegram (St. John's); The Evening Telegram (St. John's); Northern Pen (St. Anthony); and CBC-NL (online news) (Supplementary Table S1).

Scientific literature (1940–1990)

Primary and grey literature sources were searched for data on capelin beach spawning times. We were primarily interested in the time period 1960–1980 due to the lack of spawning data for these two decades from other data sources (i.e. newspaper archives, monitoring beaches). Examples of the types of spawning data reported in the literature were observations of beach rolling and sampling of spawning capelin (Atkinson, 1977; Misra and Carscadden, 1984; Theriault *et al.*, 1996); hydroacoustic surveys of inshore capelin schools (Whitehead *et al.*, 1980); and aerial surveys of inshore spawning aggregations (Nakashima, 1995) (Supplementary Table S1).

Capelin spawning diaries (1991–2019)

Fisheries and Oceans Canada (DFO) developed a network of paid citizen scientists, on average 18 per year ($n = 0–27$) located on the southern and northeastern coasts of the island of Newfoundland (Figure 1b), to monitor their local beaches every 1–2 d in the summer (between June and August from 1991–2019). Citizen scientists looked for evidence of capelin spawning and categorized what they observed: beach spawning (light, medium, or intense); evidence of recent spawning based on dead capelin on beach (few, medium amount, or heavy concentrations); and capelin schools close to a beach that may result in spawning soon (few fish present, small

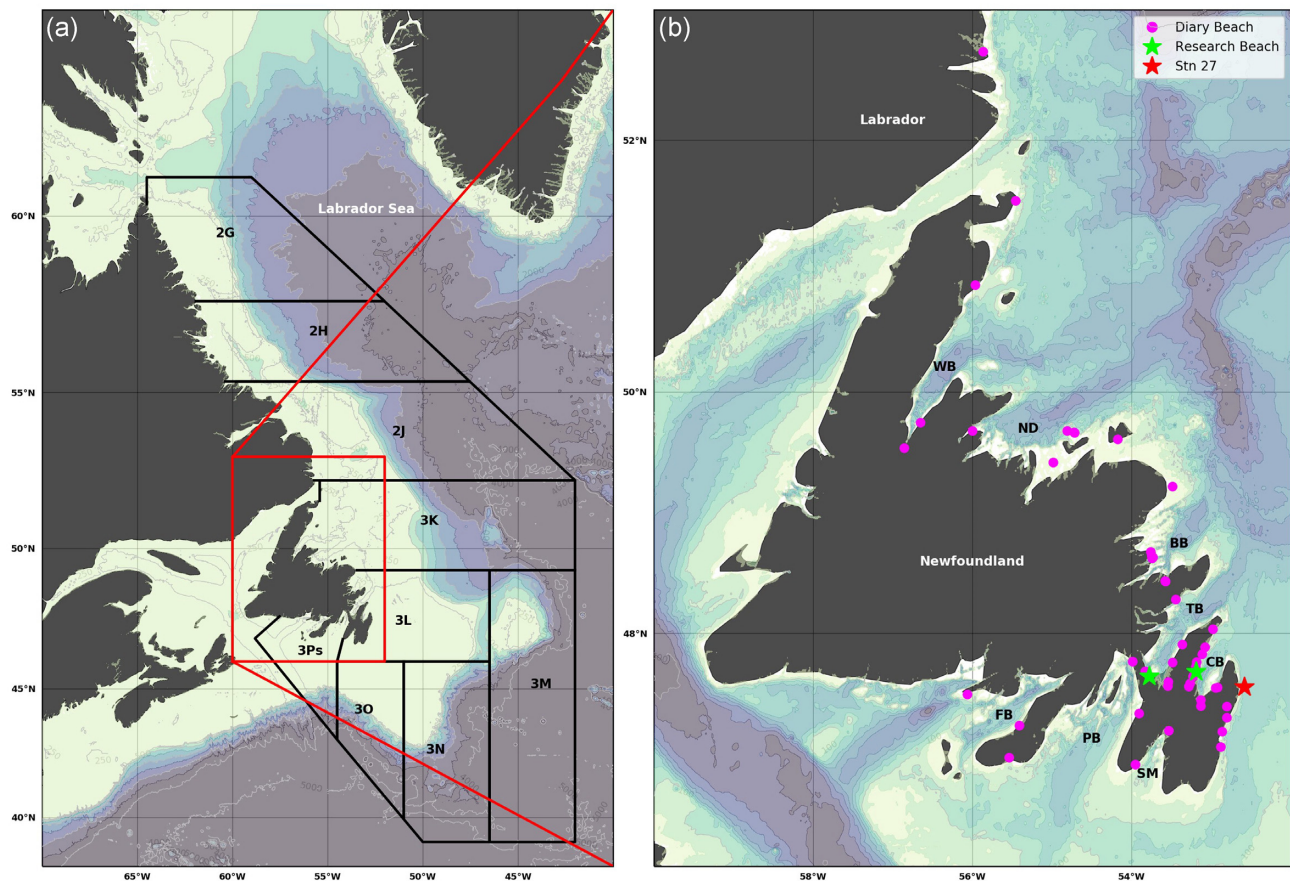


Figure 1. Panel (a) The island of Newfoundland and southern Labrador, Canada (in red box). Capelin stock area in NAFO Divisions 2J3KL + 3Ps. Panel (b) Embayments of Newfoundland (FB: Fortune Bay; PB: Placentia Bay; SM: St. Mary's Bay; CB: Conception Bay; TB: Trinity Bay; BB: Bonavista Bay; ND: Notre Dame Bay; WB: White Bay), with beaches monitored by the Fisheries and Oceans Canada's capelin spawning diary network (pink dots). Two research beaches (Bryant's Cove in CB and Bellevue Beach in TB; green stars), and Station 27 (Stn 27) off St. John's (red star).

schools, or many/dense schools) (Supplementary Table S2). The spawning diaries were returned to DFO each autumn. The diaries provided information on peak spawning day, which was either the first entry of intense, heavy spawning or, if no heavy spawning was seen that summer, then first day of medium spawning.

Scientific research beaches (1978–2016)

There were two long-running monitoring projects at capelin spawning beaches in Div. 3L. At Bryant's Cove, Conception Bay, capelin spawning timing was monitored from 1978–1990 and this beach was subsequently included in the spawning diary program in 1992 (Figure 1b). At Bellevue Beach, Trinity Bay, capelin spawning timing was monitored from 1990–2016, and from 2017, this beach was included in the spawning diary program (Figure 1b). These two research beaches used egg density measurements from sediment cores and detailed monitoring of the beaches to determine peak spawning day (Frank and Leggett, 1981b; Nakashima and Taggart, 2002; DFO, 2019).

Capelin population demographics

Commercial fishery (1978–2019)

To obtain population demographic data of spawning capelin (i.e. size-at-age and age at maturation), commercial samples were ob-

tained from fish processing plants by DFO. A maximum of ten samples of 200 frozen fish were collected from each of five bays in NAFO Divs. 3KL (Conception, Trinity, Bonavista, Notre Dame, White; see Figure 1b). Of these 50 collected samples, 20 were processed each year depending on gear type (fixed: cast nets, beach seines, capelin traps, dip nets, and tuck seines; mobile: purse seines and ring nets), bay, and week of fishery as a function of the total annual fishery landings. Length, weight, sex, and maturity were determined for all fish in the sample, and age (using otoliths) was determined for two fish per sex, per 5 mm length class in each sample. There were some exceptions to the methods described above. In 1978, 1979, 1984, and 1991, all fish in 1–15% of processed commercial samples underwent detailed sampling, including ageing. In 1999, approximately 8% of the commercial samples were processed for length, sex, and maturity only (no ageing), and in 1995, there was no commercial fishery.

Two biological variables were used as predictor variables in the models: mean length of fish (\bar{L}) from the commercial catch, and proportion of age-2 female fish in the female portion of the commercial catch (Mat_2). For \bar{L} , data were pooled for sex, gear, and NAFO division in order to mitigate the effects of highly variable sex ratios in the first 5 years of sampling (1978–1982) before the commencement of the roe fishery. Mean lengths were calculated for each year by NAFO division, gear type, and sex, and then averaged across sex for each combination of NAFO division and gear

types, assuming an equal sex ratio. The resulting mean lengths were then averaged across gear types (e.g. purse seine, traps, tuck seines) within sectors (fixed or mobile) by NAFO division. Finally, \bar{L} was estimated by averaging the mean lengths by gear sector and NAFO division by the proportion of the commercial catch that was taken annually in each NAFO division and gear sector.

For Mat_2 , an age-length key was developed for the female capelin in each year and NAFO division using fish whose lengths were measured and their otoliths aged. Ages were generated for fish that only had length measurements using the `alkIndivAge` function in the FSA package in R (Ogle *et al.*, 2021). All female fish were provided an age, except for fish that were smaller than the smallest aged fish in a particular year and NAFO division, and fish that were not sexed. Fish that were larger than the largest aged fish were categorized in the oldest age class.

Mat_2 and \bar{L} were both standardized. Standardizing the data by dividing the difference between an observation (X_i) and the mean observation value over a defined period (\bar{X}_{period}) by the standard deviation over the same reference period ($s(X)_{\text{period}}$) was conducted using Equation (1):

$$\bar{X} = \frac{X_i - \bar{X}_{\text{period}}}{s(X)_{\text{period}}}. \quad (1)$$

We used the years 1981–2010 as the reference period, which corresponds with the climatological period (World Meteorological Organization, 2017). Environmental variables described in the Environmental Predictors section were also standardized using Equation (1).

Year-class index

Capelin have been subject to an annual DFO spring (May) acoustic survey in NAFO Divs. 3KL since the 1980's (1985–1992, 1996, 1999–2005, 2007–2015, 2017–2019) (DFO, 2019). The spring acoustic survey primarily targets the juvenile portion of the stock (i.e. age-2 fish). The age-2 recruitment index from the acoustic survey was lagged by 2 years in order to evaluate year-class strength. Details of the spring acoustic survey methods are in Mowbray (2014).

Environmental predictors of capelin spawning

As this was an exploratory analysis of the predictors of capelin spawning timing, we considered a large number of environmental variables plus a climate index which is composed of ten environmental sub-indices (details below). Generally, there was no duplication between the individual environmental variables and the ten environmental sub-indices of the climate index (with two exceptions: salinity and temperature). Variable selection is discussed in more detail in the Data Analyses section.

Newfoundland and Labrador (NL) climate index

The NL climate index (*NLCI*) is the mean of the standardized anomalies of ten environmental time series derived annually by DFO (Cyr and Galbraith, 2021). It represents the large-scale climate conditions and state of the physical environment over the NL shelf and the Northwest Atlantic in general. The *NLCI* and its sub-indices are available at <https://doi.org/10.20383/101.0301> (Cyr and Galbraith, 2020).

The ten environmental time series used in the *NLCI*, which all commence in 1951 unless specified, are the following: winter (December–March) North Atlantic Oscillation (NAO) index; air temperature at 5 sites around the northwest Atlantic (Nuuk, Greenland; and Iqaluit, Cartwright, Bonavista, and St. John's, Canada); sea ice season severity (starts in 1969); the number of icebergs crossing 48°N; SSTs in NAFO Divs. 2GHJ3KLNOP (starts in 1982); vertically averaged temperature and salinity at Station 27 (47° 32.8' N, 52° 35.2' W) located in the Avalon channel just outside St. John's harbor in NAFO Div. 3L (see Figure 1b); Cold Intermediate Layer (CIL) core temperatures at Station 27; the summer CIL area at Seal Island, Bonavista, and Flemish Cap hydrographic sections; and the spring and fall bottom temperatures in NAFO Divs. 3LNOPs and 2HJ3KLNO, respectively (both start in 1980). Five of these sub-indices (winter NAO, sea ice severity, icebergs, salinity, and CIL area) had their anomaly signs reversed, since positive anomalies for these time series indicate cold conditions. We included the *NLCI* as well as its 10 sub-indices in the exploratory models.

Summer North Atlantic Oscillation (1951–2019)

The NAO index refers to the anomaly in the sea-level pressure difference over the North Atlantic between a sub-tropical high near the Azores, and a sub-polar low near Iceland. This index is usually a good indicator of the general air circulation above the North Atlantic (e.g. strength of the westerly winds), with consequences for the regional climate (e.g. air temperature, precipitation, etc.) (Hurrell, 1995). The winter NAO, which is the average of the NAO index over the winter months (December–March), was linked to fisheries productivity in the North Atlantic (Parsons and Lear, 2001; Brander and Mohn, 2004; Buch *et al.*, 2004) and is included in the *NLCI*. The summer (June–August) NAO (NAO_s) is considered a proxy for the strength of the westerly winds and may impact the timing of the annual capelin summer spawning migration into the bays of Newfoundland. The NAO is based on empirical orthogonal functions for which monthly values are accessible via the National Oceanic and Atmospheric Administration (NOAA) website (<https://www.ncdc.noaa.gov/teleconnections/nao/>).

Sea surface temperature (1982–2019)

Temperature can act as a cue for spawning migrations and the onset of spawning (e.g. Ware and Tanasichuk, 1989) as well as exert overall control on metabolic rates for many species (O'Connor *et al.*, 2007). We used NOAA's 1/4° Optimum Interpolation Sea Surface Temperature (OISST v2.0) data product (Banzon *et al.*, 2016), which is accessible online at <https://www.ncdc.noaa.gov/oisst/optimum-interpolation-sea-surface-temperature-oisst-v20>. The daily SST maps for the months of February to June were converted into a daily SST time series by averaging all pixels inside the shelf area (< 1000 m) of NAFO Div. 3L (Figure 1a) and converted into a standardized SST time series. SST was calculated using the climatological period 1982–2010 since 1982 was the first complete year of this dataset.

Station 27 temperature, salinity, and stratification (1951–2019)

Salinity is associated with water column stratification and timing of the spring bloom (Greenan *et al.*, 2019) as well as vertical structuring of the water column which may alter the degree of spatial overlap between capelin and their prey and predators (e.g.

Neuenfeldt and Beyer, 2003; Kempf *et al.*, 2013). Multiple temperature and salinity profiles obtained from Station 27 were averaged into monthly means before being vertically averaged into three different depth ranges (0–20 m for surface, 150–176 m for bottom, and 0–176 m for the entire water column). Vertically averaged salinity and temperature variables for the entire water column (0–176 m) were included in the *NLCI*. We were interested in including a range of depths for these variables as potential predictors of spawning timing. The standardized anomalies (\tilde{T}_{0-20m} , $\tilde{T}_{150-176m}$, \tilde{T}_{0-176m} , \tilde{Sal}_{0-20m} , $\tilde{Sal}_{150-176m}$ and \tilde{Sal}_{0-176m}) were calculated using the 1981–2010 climatological period.

Water column stratification is known to impact the plankton bloom by controlling both nutrient uptake in the surface layers and the retention of the plankton cells in the photic zone (e.g. Behrenfeld *et al.*, 2006). Timing of the spring bloom may impact capelin spring condition and timing of spawning migrations (Buren *et al.*, 2014). For profiles where both temperature and salinity were available from Station 27, the density (ρ) of the water was derived using the TEOS-10 toolbox (McDougall and Barker, 2011). These profiles were used to produce monthly means, from which April and July stratification were approximated by the density difference between 5 and 50 m divided by the depth range (i.e. $\Delta\rho/\Delta z$). These two months represented spring and summer stratification. The standardized anomalies (\tilde{S}_{April} and \tilde{S}_{July}) were calculated using the 1981–2010 climatological period. Positive anomalies indicated stronger stratification, while negative anomalies indicated a more mixed water column.

Seasonal sea ice (1969–2019)

Prior work by Wu *et al.* (2007) found that sea ice affects the timing of the spring plankton bloom in the NL region. Three seasonal sea ice variables were considered for use in our model: maximum area of sea ice south of 55°N, minimum latitude of sea ice extent, and timing of the sea ice retreat (t_{ice}) (Buren *et al.*, 2014; Lewis *et al.*, 2019). Maximum area and minimum latitude of sea ice were negatively correlated ($r = -0.79$) because more southerly extents (latitude is closer to 0°N) is associated with a large area of sea ice while a more northerly extent (latitude is closer to 90°N) is associated with a small area of sea ice, and t_{ice} was not correlated with either variable ($r < 0.2$). Further, both maximum area and minimum latitude of sea ice were strongly correlated (positively or negatively) with several of the other environmental time series being considered while t_{ice} was only weakly correlated with these time series. Consequently, t_{ice} was chosen as the seasonal sea ice variable. To determine t_{ice} , digital versions of weekly regional ice charts for the NL region were obtained from the Canadian Ice Service (<http://iceweb1.cis.ec.gc.ca/Archive/page1.xhtml>) (see Buren *et al.*, 2014; Lewis *et al.*, 2019 for more details). Briefly, t_{ice} was determined as day-of-the-year corresponding to the week for which the southernmost extent of the NL shelf sea ice sheet (between 55°N and 43°N) was observed. Our analysis included sea ice concentrations as low as 1/10–3/10 according to the World Meteorological Organization's Colour codes (<https://www.canada.ca/en/environment-climate-change/services/ice-forecasts-observations/publications/interpreting-charts/chapter-2.html#concentration-sea>). Ice that was not part of the main ice pack, such as ice trapped in bays around the island of Newfoundland or in Lake Melville in Labrador and isolated patches of sea ice in open waters, was not considered

when determining the value of t_{ice} . The standardized anomalies (\tilde{t}_{ice}) were calculated using the 1981–2010 climatological period.

Data analyses

A century of capelin beach spawning data (1919–2019)

To construct a seven-decade timeline of capelin beach spawning times before the stock collapse (1919–1990) in NAFO Divs. 2J3KL, we used newspaper archives, primary and grey literature, and a research beach (Bryant's Cove, Conception Bay). To construct a three-decade timeline of capelin spawning during the post-collapse period (1991–2019) in NAFO Divs. 2J3KL, we used capelin spawning diaries, newspaper archives, and a research beach (Bellevue Beach, Trinity Bay). We used all data sources to calculate annual median peak spawning day.

Environmental and biological predictors of capelin spawning timing (1978–2019)

To predict peak spawning day, we performed step-wise multiple regressions with forward and backward Akaike information criterion (AIC) selection. Biological and environmental data used in the model were primarily from NAFO Divs. 3KL with the exception being some of the sub-indices included in the *NLCI* (see above). Annual median peak spawning day was calculated from the spawning diaries in NAFO Divs. 3KL and from research beaches in NAFO Div. 3L. Environmental data were examined and anomalous data were removed or retained after inspection following Zuur *et al.* (2010). Due to the sheer number of environmental data time series available for this analysis, some decisions were made prior to the regression analysis to create a hierarchy of preferences for which variables would be retained when pairs of variables had high collinearity ($r > 0.5$). For time series that covered multiple depth intervals and demonstrated collinearity, we selected the time series that covered a broader depth range. When a time series for a single variable was collinear with the *NLCI*, then the *NLCI* was chosen to provide a holistic impression of conditions in the system. In all remaining cases, we dropped the variable that resulted in the least number of variables being dropped in the analysis. This process resulted in the following variables being retained for the step-wise multiple regression analysis: \tilde{t}_{ice} , NAO_s , *NLCI*, \tilde{Sal}_{0-176m} , \tilde{S}_{April} and \tilde{S}_{July} . These environmental variables were then combined with the standardized anomalies of the biological variables (\tilde{L} and \tilde{Mat}_2). Since temporal dependency was detected in the residuals of preliminary fitted models, we included a period factor that categorized the data source as either 1990 and earlier (pre-collapse) or post-1990 (post-collapse) to attempt to address temporal dependency similar to Buren *et al.* (2014). Prior to beginning the step-wise regression, we omitted any year for which one of the input variables was missing. After running the step-wise regression, we would repeat the data omission step, this time only omitting years that were missing data for variables that were included in the fitted model, and would then repeat the step-wise regression. This process was repeated until no further changes occurred in the model or the data included. Following the step-wise multiple regression, model residuals were examined for temporal dependency by plotting residuals vs. year and were further examined for additional departures from model assumptions by plotting residuals vs. variables that were included or dropped from the final model. After determining the best-fitting model based on

AIC, we simplified the model by removing any variables with parameters that were not significantly different from zero.

Predictors of year-class strength (1985–2019)

To predict year-class strength (age-2 recruitment, lagged by two years), a step-wise multiple regression model with forward and backward AIC selection was used. Environmental variables included in the model were \tilde{t}_{ice} , NAO_s , $NLCI$, \tilde{Sal}_{0-176m} , \tilde{S}_{April} and \tilde{S}_{July} , and biological variables included in the model were the standardized anomalies of annual median peak spawning day in NAFO Divs. 3KL ($\tilde{Peak_day}$; standardized using Equation 1), \tilde{L} , and \tilde{Mat}_2 . Due to the shorter data series and increased number of predictor variables in the year-class model, we had to use a two-stage analytical approach as there was an insufficient number of observations in the data set to handle the number of terms in the full model. The first step of the two-stage approach reduced the number of environmental variables considered in the model. Prior to beginning the step-wise regression, we omitted any year for which one of the input variables was missing. Once an initial model was fit, we repeated the data omission step with only the input variables that were included in the model and refit the model. This process was repeated until there were no further changes in the model or the data included in the fitting of the model. Once this first stage was completed, model residuals were examined for temporal dependency by plotting residuals vs. year and were further examined for additional departures from model assumptions by plotting residuals vs. variables that were included or dropped from the final model. If temporal dependency was detected in the residuals of the fitted model, we refit the model with the addition of the period term (pre-collapse and post-collapse) that included first-order interactions with the terms in the initial fitted model. Prior to refitting the model, we re-did the data omission step, this time only omitting years for which any of the remaining variables were missing. We then repeated the model validation process with the residuals of the refitted model. After determining the best-fitting model based on AIC, we simplified the model by removing any variables with parameters that were not significantly different from zero.

Coefficient of partial determination

In order to rank the importance of each of the predictors in the step-wise multiple regression models, we determined the coefficients of partial determination (PD_i) for each of the predictors. The PD_i is the proportion of the variance that a reduced model (i.e. one without a given predictor) cannot explain. The higher the PD_i , the more important the excluded predictor. The PD_i of the reduced models were calculated using Equation (2):

$$PD_i = \frac{R^2_{full} - R^2_i}{1 - R^2_i}, \quad (2)$$

where i indicates the reduced model.

To show the effect of different predictor variables on the dependent variable (either spawning timing or year-class strength), we held all the predictors to their average value with the exception of the predictor of interest. We then created figures to show the trends in the responses of the dependent variables to changes in significant predictor variables across the complete range of values for that predictor.

All statistical analyses were done in R (v. 3.6.2/3) using base R (R Core Team, 2019), the MASS package (Venables and Ripley, 2002)

for the step-wise multiple regressions, and FSA package (Ogle et al., 2021) for the age-length key.

Results

Capelin beach spawning timing

From 1919–1990, pooling all data sources, median peak spawning day was 25 June [day-of-year (DOY): 176; Figure 2]. By decade, there was a consistency in median peak spawning timing [18–29 June (DOY: 169–180); Figure 2]. We also evaluated spawning timing during known warming and cooling periods in the past century (Drinkwater, 2006; Cyr et al., 2021). Peak spawning day was later (4 July; DOY: 185) in the cooling period of 1925–1929 compared to the subsequent warming period from 1930–69 (22 June; DOY: 173); however, the two subsequent cooling periods in the mid-1970's and mid-1980's were not associated with delayed spawning [16 June (DOY: 167, based on limited spawning data from 1976–1979) and 19 June (DOY: 170), respectively; Figure 2, Supplementary Table S1].

From 1991–2019, pooling all data sources, median peak spawning day was 13 July (DOY: 194), which is 18 days later than median peak spawning day in the pre-collapse period (Figure 2). Median peak spawning days were fairly consistent among the decades even though there was a warming period from 1995–2011 (Cyr et al., 2021): 15 July (DOY: 196) in both the 1990's and 2000's, and 11 July (DOY: 192) in the 2010's (Figure 2). Only one data point was available for Labrador (NAFO Div. 2J) in the post-collapse period (Supplementary Table S1), and there has been either an absence of or minimal capelin beach spawning reported in Labrador since 1991 (DFO, 2019).

Capelin population demographics

Capelin caught in the commercial fishery experienced a near step-like decline in \tilde{L} between 1990 and 1991 and have remained at relatively short lengths for the past three decades (Figure 3a), primarily due to the increased proportion of mature age-2 capelin and the decline of older and larger ages 4, 5, and 6 fish in the commercial catch (DFO, 2019). Capelin experienced a brief resurgence in \tilde{L} between 2012 and 2014 when there was a partial recovery in stock size (DFO, 2019; Figure 3a).

Prior to the collapse of capelin in 1990–91, \tilde{Mat}_2 only occasionally exceeded 10% of the female portion of the catch (Figure 3b). Following their collapse, \tilde{Mat}_2 was consistently greater than 10% of the catch and often exceeded 50% (Figure 3b).

Estimates of age-2 recruit abundance from the spring acoustic survey decreased by an order of magnitude in 1990–1991 and have remained at low levels for the subsequent three decades with a moderate increase in 2013–2016 (DFO, 2019; Figure 3c).

Environment

Both NAO_s and \tilde{Sal}_{0-176m} had mainly positive anomalies in the pre-collapse period and predominately negative anomalies in the post-collapse period (Figure 4a, b). There was a negative anomaly in $NLCI$ from the mid-1980's to mid-1990's and there was a generally positive trend in $NLCI$ from 1996–2013 (Figure 4c). \tilde{t}_{ice} had a positive anomaly (late retreat of sea ice) in the late 1980's and early 1990's, with no real trend from the late 1990's onwards (Supplementary Figure S1a). There was no clear trend in the anomaly

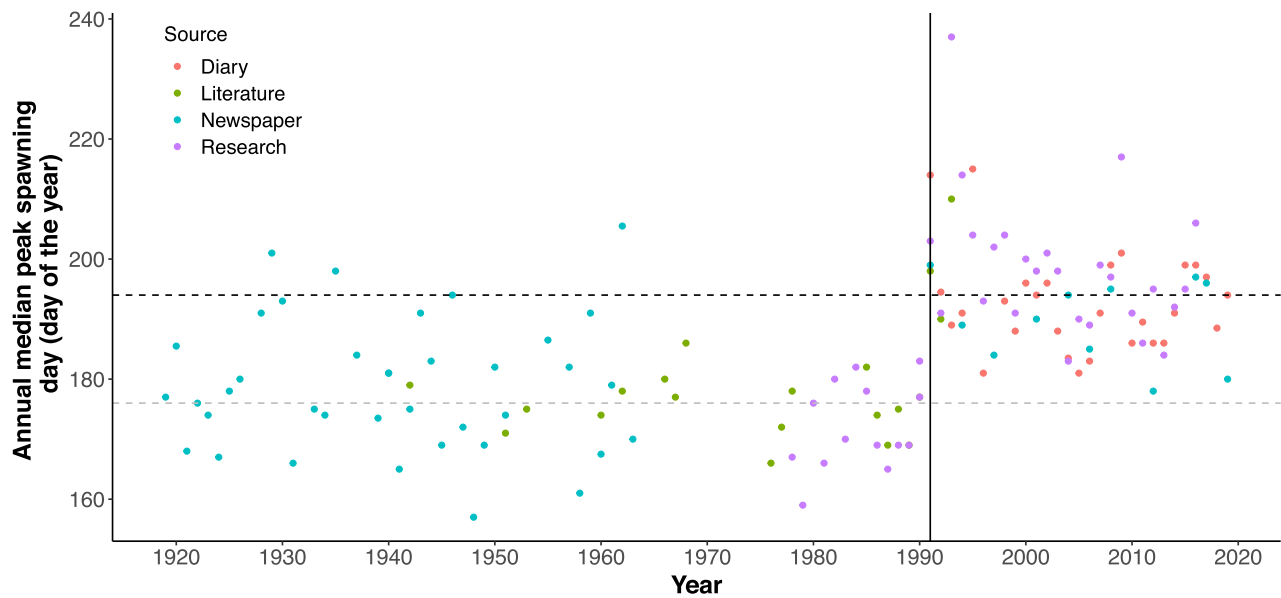


Figure 2. Annual median peak capelin spawning day using all data sources [i.e. newspaper archives, research beaches (Bryant's Cove and Bellevue Beach), primary and grey literature, and capelin spawning diaries] from NAFO Divs. 2J3KL. Solid vertical line is 1991 (timing of collapse; Buren *et al.*, 2019). Horizontal lines are mean peak spawning times pre-1991 [25 June; day-of-year (DOY): 176; grey dashed line] and post-1991 (13 July; DOY: 194; black dashed line).

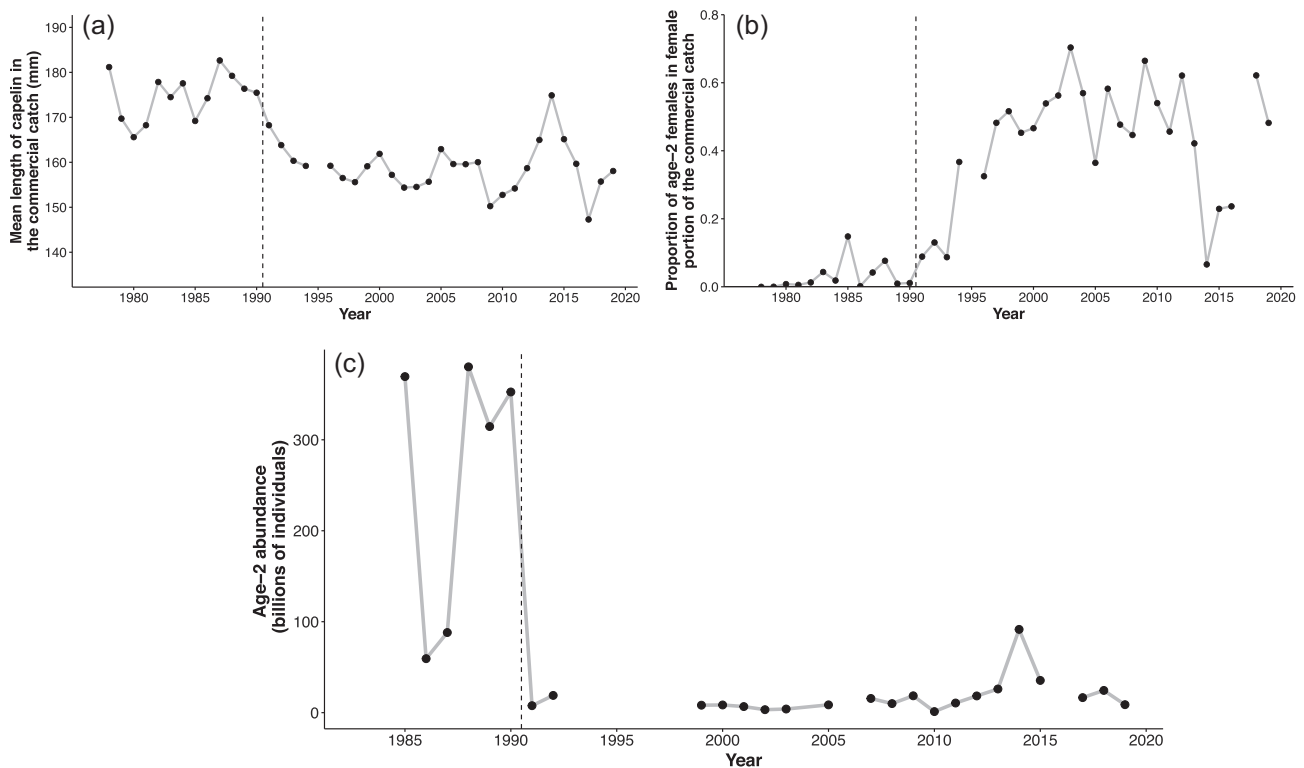


Figure 3. Panel (a): mean length of capelin in the commercial catch from 1978–2019. Panel (b): the proportion of mature age-2 female capelin in the female portion of the commercial catch from 1978–2019. Panel (c): the abundance of age-2 capelin surveyed in the annual spring (May) offshore acoustic survey by Fisheries and Oceans Canada (1985–2019). The vertical dashed line indicates the approximate timing of the collapse of the capelin stock in NAFO Divs. 3KL (Buren *et al.*, 2019).

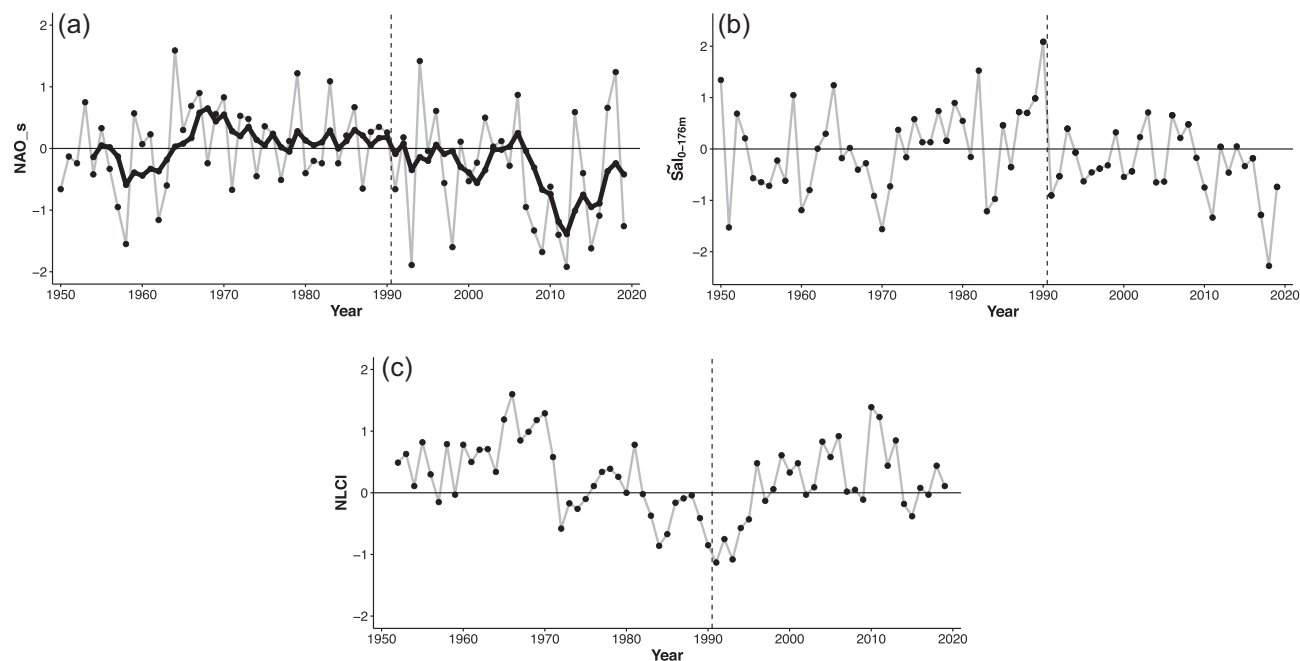


Figure 4. Three environmental variables used in the spawning timing and year-class models: Panel (a) summer (June–August) North Atlantic Oscillation average (NAO_s) that includes annual data (thin grey line) and five-year moving average (thick grey line) Panel (b) Vertically averaged salinity Sal_{0-176m} from Station 27, and Panel (c) Newfoundland and Labrador climate index (NLCI) which is composed of 10 sub-indices (Cyr and Galbraith, 2020).

Table 1. Best model fit for the spawning timing step-wise multiple regression model with only the significant predictors included. The significant predictors were ranked using their coefficients of partial determination (PD_i). The PD_i is the proportion of the variance that a reduced model (i.e. one without a given predictor) cannot explain. The higher the PD_i , the more important the excluded predictor. With the exception of the full model, the R^2 , adjusted R^2 and PD_i values correspond to models performed with one of the four predictors of interest removed.

Model version	Estimate	Std. Error	t-value	F-statistic	p-value	R^2	Adjusted R^2	PD_i
Full model				69.3	$<2.2e^{-16}$	0.93	0.92	
Intercept	192.73	1.02	189.18		$<2.0e^{-16}$			
period	−20.02	2.67	−7.50		$1.56e^{-8}$	0.75	0.70	0.72
NLCI	−9.70	1.06	−9.12		$2.07e^{-10}$	0.74	0.70	0.72
NAO_s	−2.01	0.72	−2.77		0.009	0.88	0.86	0.42
\bar{L}	−4.35	1.21	−3.58		0.001	0.90	0.89	0.29
Period* \bar{L}	4.71	2.40	1.97		0.058			
Period* NAO_s	−6.34	2.22	−2.85		0.008			

NLCI (Newfoundland and Labrador climate index), NAO_s [summer (June–August) North Atlantic Oscillation], \bar{L} (mean fish length). Period term categorizes the data as either pre-collapse or post-collapse.

lies of \tilde{S}_{April} and \tilde{S}_{July} , although there does appear to be an increase in positive anomalies of \tilde{S}_{April} in the post-collapse period compared to the pre-collapse period (Supplementary Figure S1b and c).

Environmental and biological predictors of spawning timing (1978–2019)

The best model for predicting spawning timing is shown in Table 1 (Figure 5a). The coefficient on the period term, which applies to the pre-collapse period, indicates that spawning was ~ 20 days earlier prior to the collapse in the capelin population. Further, spawning timing is predicted to be delayed by decreases in \bar{L} , NAO_s , and NLCI. The interaction term between period and NAO_s indicates

that NAO_s had more of an effect on predicted spawning timing in the pre-collapse period, while the interaction term between period and \bar{L} indicates that the change in \bar{L} had more of an effect on predicted spawning timing in the post-collapse period. The best model based on AIC included insignificant predictors (\tilde{f}_{ice} and \tilde{S}_{July} and the interaction between the period term and \tilde{S}_{July}) (Supplementary Tables S3 and S4, Figure S2). An analysis of variance (ANOVA) found no significant difference in AICs between the best model based on AIC and the final model that only included significant predictors ($F_{29,32} = 1.57$, $p = 0.22$; Supplementary Table S5).

As the NLCI is composed of ten sub-indices (Cyr and Galbraith, 2021), we wanted to identify which of the ten environmental variables were important for predicting peak spawning day, so we re-ran the step-wise multiple regression model re-

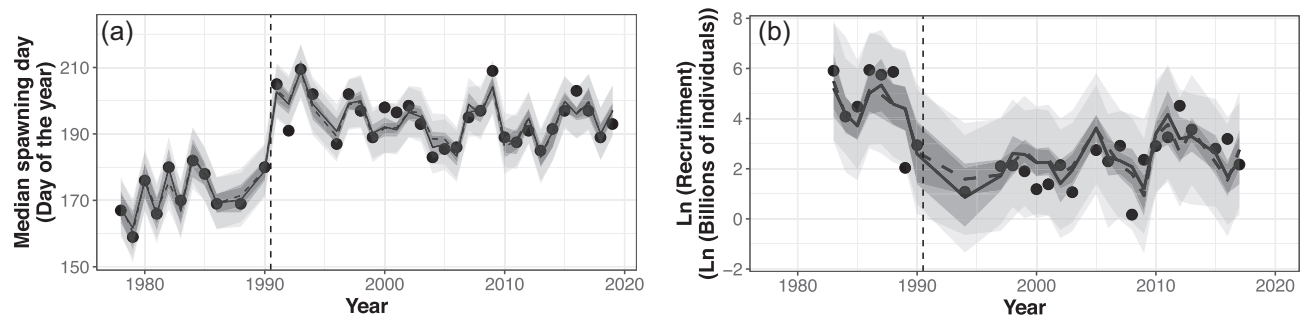


Figure 5. Panel (a) The best model to predict annual median peak spawning day in northeastern Newfoundland (NAFO Divs. 3KL) included the period term, mean length of the commercial catch (\bar{L}), summer (June–August) North Atlantic Oscillation average (NAO_s), and Newfoundland and Labrador climate index ($NLCI$), and interactions between the period term and NAO_s and between the period term and \bar{L} . Panel (b) Capelin year-class strength was predicted by annual peak spawning timing ($Peak_day$) and salinity (Sal_{0-176m}). Solid line is the best-fitting model and the dashed line is the reduced model with only significant variables included. Light grey is the 95% prediction interval, dark grey is the 95% confidence interval. Shading is the same for both ribbons with small differences in shading indicating where the intervals diverge between model versions. Solid black symbols are the observed values. Dashed vertical line corresponds with the collapse of the capelin stock in Div. 2J3KL (Buren *et al.*, 2019). Note the log scale of capelin year-class strength (time-lagged by two years).

Table 2. Best model fit for the year-class step-wise multiple regression model with only significant predictors included. The significant predictors were ranked using their coefficients of partial determination (PD_i). The PD_i is the proportion of the variance that a reduced model (i.e. one without a given predictor) cannot explain. The higher the PD_i , the more important the excluded predictor. With the exception of the full model, the R^2 , adjusted R^2 and PD_i values correspond to models performed with one of the two predictors of interest removed.

Model version	Estimate	Std. error	t-value	F-statistic	P-value	R^2	Adjusted R^2	PD_i
Full model				18.02	$1.43e^{-5}$	0.59	0.56	
Intercept	2.95	0.20	14.92		$5.92e^{-14}$			
\widetilde{Sal}_{0-176m}	−0.55	0.27	−2.03		0.053	0.52	0.50	0.14
$Peak_day$	−1.39	0.23	−5.97		$3.10e^{-6}$	0.006	−0.03	0.59

\widetilde{Sal}_{0-176m} (vertically averaged salinity at Station 27), $Peak_day$ (median peak spawning day).

placing the $NLCI$ with its ten sub-indices. One variable was retained from the $NLCI$: sea ice season severity (sea ice) (Supplementary Tables S6 and S7, Figures S3 and S4). The coefficient on the period term, which applies to the pre-collapse period, indicates that spawning was ~ 17 days earlier prior to the collapse in the capelin population. Further, spawning timing is predicted to be delayed by negative anomalies in \bar{L} , NAO_s , and sea ice season severity. The interaction term between period and NAO_s indicates that the change in NAO_s had more of an effect on predicted spawning timing in the pre-collapse period. The best model based on AIC included an insignificant predictor (\hat{S}_{July} and the interaction between period and \hat{S}_{July}). Replacing the $NLCI$ with its component parts did not improve the model fit based on the R^2 values of the two regression models (Supplementary Table S8).

Environmental and biological predictors of year-class strength (1985–2019)

The best model for predicting year-class strength is shown in Table 2 (Figure 5b). The year-class model required the addition of the period term due to temporal dependency in its residuals (Supplementary Tables S9 and S10, Figures S5 and S6). This simple model, with a moderate R^2 , predicted that strong year-classes would occur when spawning is earlier (negative anomaly in $Peak_day$) and there is a negative anomaly in \widetilde{Sal}_{0-176m} . The best model based on AIC included insignificant predictors (period term and NAO_s) (Supplementary Table S11). An ANOVA

found no significant difference in AICs between the best model based on AIC and the final model that only included significant predictors ($F_{23,25} = 2.51$, $p = 0.10$; Supplementary Table S12).

Coefficient of partial determination (PD_i)

For the spawning timing model, the two most important predictors were the period term and $NLCI$ (Table 1). NAO_s and \bar{L} were the next most important predictors. Examining the sensitivity of spawning timing to each of the three significant predictor variables ($NLCI$, NAO_s , and \bar{L}) by period [pre- and post-collapse; Figure 6(a)–(c)] showed that median spawning day was predicted to be later in the post-collapse period for all values of NAO_s and \bar{L} . However, extremely negative values for the $NLCI$ could result in predicted spawning time during the pre-collapse period to occur at the same time as or a few days later than years with some of the most positive values of the $NLCI$ in the post-collapse period. Comparing across predictors and periods, the $NLCI$ in both the pre- and post-collapse periods and \bar{L} during the post-collapse period had the greatest effect on spawning timing and resulted in similar amounts of change in predicted spawning timing across their ranges.

For the year-class model, $Peak_day$ had a much larger PD_i than \widetilde{Sal}_{0-176m} (Table 2). Year-class strength is predicted to weaken with later dates for $Peak_day$ and more positive values of \widetilde{Sal}_{0-176m} , although $Peak_day$ had a much larger effect on year-class strength over its range of values compared with \widetilde{Sal}_{0-176m} (Figure 7a and b).

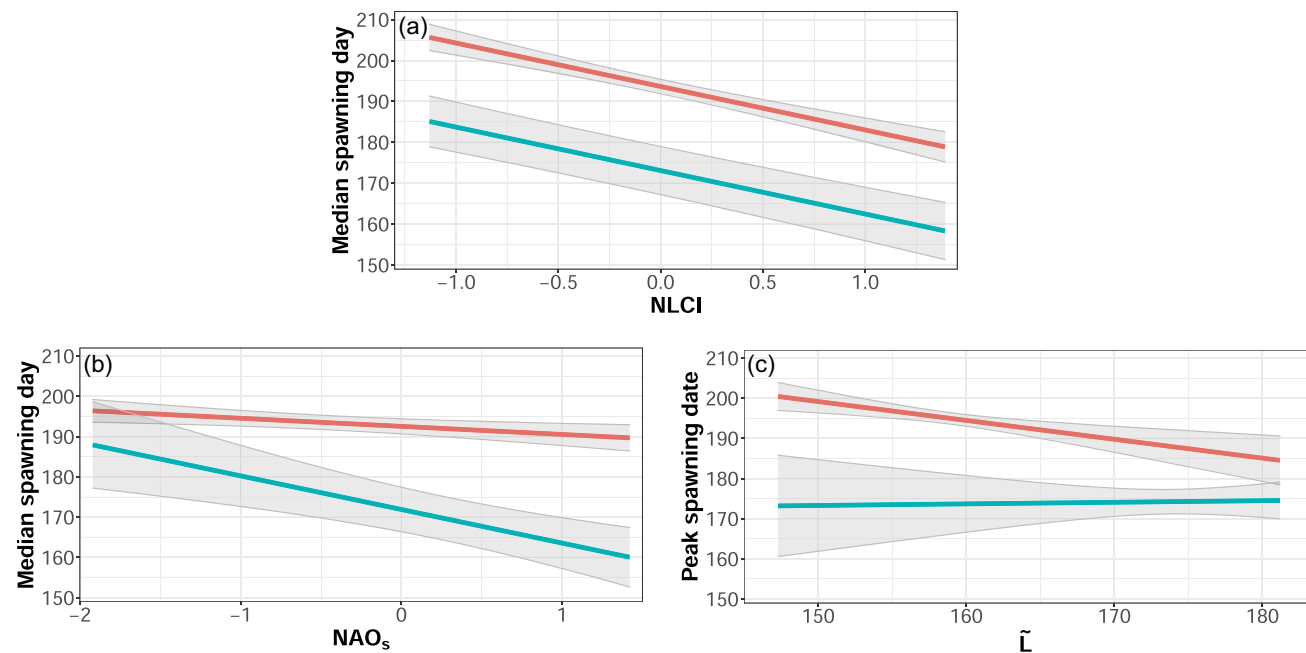


Figure 6. Spawning timing was most sensitive to the period term, which is seen in all panels, followed by changes in Panel (a). Newfoundland and Labrador climate index *NLCI*, Panel (b) summer (June–August) North Atlantic Oscillation average *NAO_s*, and Panel (c). mean length of the commercial catch \bar{L} . The pre-collapse period is the teal line and the post-collapse period is the red line. The light shaded grey area are 95% confidence intervals.

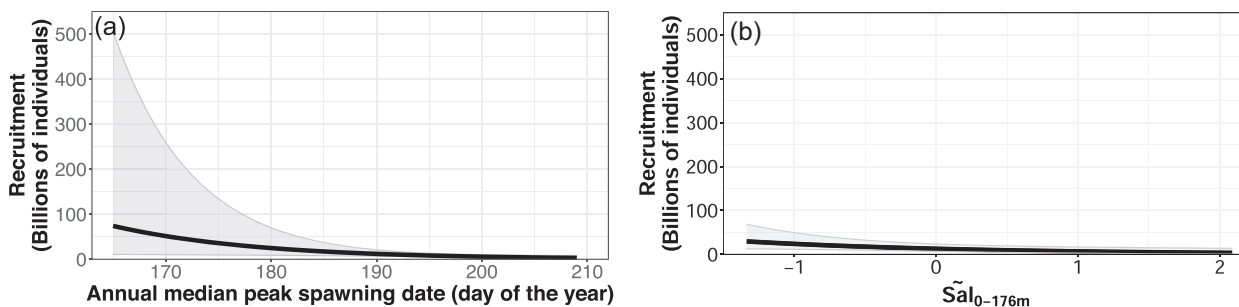


Figure 7. Year-class strength was sensitive to changes in Panel (a) annual median peak spawning date (day of year; *Peak_day*) and Panel (b) salinity (\tilde{Sal}_{0-176m}). The light shaded grey area are 95% confidence intervals.

Discussion

Predictors of spawning timing and year-class strength

In 1991, capelin abruptly shifted the timing of their spawning, with beach spawning beginning approximately three weeks later than it had during the prior 71 years (from at least 1919). This shift to later spawning has persisted for the subsequent three decades (1991–2019). Weaker year-classes are predicted to be produced when spawning time is delayed. There are multiple potential mechanisms to support this finding. Delayed spawning is likely promoting a mismatch between larval occurrence and ideal environmental conditions for larval growth and survival (Frank and Leggett, 1982a; Leggett *et al.*, 1984; Murphy *et al.*, 2018) and may also be reducing overwinter survival because 0-group larvae have less time to grow and forage before their first winter (Gudmundsdottir and Vilhjálmsson, 2002; Vilhjálmsson, 2002). Furthermore, the NL capelin stock are facultative spawners that move between beaches and off-beach sites, with the proportion of capelin spawning at off-beach sites increasing when beaches become too warm ($> 12^{\circ}\text{C}$)

for spawning later in the summer (Templeman, 1948; Dodson *et al.*, 1991; Nakashima and Wheeler, 2002; Crook *et al.*, 2017). An increase in off-beach spawning has been observed since the collapse in the capelin stock (Nakashima and Clark, 1999). However, productivity from these off-beach sites may be low as eggs spawned at these sites have slower development rates (Penton *et al.*, 2012) and can have lower hatching success (Nakashima and Wheeler, 2002).

Spawning phenology has been shown to be influenced by temperature in many fish species with temperature acting as a cue for spawning migrations and onset of spawning (Ware and Tanasichuk, 1989; Sims *et al.*, 2004; Taylor, 2008; Fincham *et al.*, 2013) as well as directly affecting the rate of oocyte growth and development (Kjesbu *et al.*, 2010). Typically, warmer temperatures increase the speed of ovarian development (Kjesbu *et al.*, 2010), although warmer than optimal temperatures have been associated with delayed spawning (Tveiten and Johnsen, 1999; Wright *et al.*, 2017) and other studies have found no effect of temperature on spawning timing (Morgan *et al.*, 2013). We found that negative anomaly

lies in NAO_s and $NLCI$ (specifically severe sea ice seasons) predicted delayed spawning. A positive NAO_s is generally indicative of a strengthening of the westerly winds over the Northwest Atlantic. The NAO_s was predominantly positive between 1965 and 1990, while being predominantly negative afterward. While the causal relationship between spawning timing and NAO_s is not clear, increased westerly winds may have impacted the subpolar gyre and thus the strength and pathways of the Labrador current system (Holliday *et al.*, 2020). This, in turn, may have promoted earlier spawning migrations via faster transit times into the bays of NL in the pre-collapse period while decreased westerly winds in the post-collapse period may have promoted slower transit times and delayed spawning migrations. Furthermore, the predicted impact of NAO_s on spawning timing decreased in the post-collapse period. Delayed spawning migrations are also predicted when there are colder ocean conditions, which has ramifications for timing of stratification and spring bloom, and may also impact gonad development. A negative anomaly in the $NLCI$ occurred from the mid-1980's to mid-1990's; however, the observed delay in spawning timing has persisted, including some of the latest peak spawning dates recorded, even though there has been a positive anomaly in the $NLCI$ from 1996–2013, suggesting that the delay in spawning is not solely due to a phenotypic response to a cooling climate.

Demographic structure of a fish population impacts life-cycle events like spawning timing, with age-related differences in spawning timing and duration. Larger and older fish may spawn earlier (Lambert, 1987; Ware and Tanasichuk, 1989) or later (Hutchings and Myers, 1993; Morgan *et al.*, 2013) and for a longer duration (Hutchings and Myers, 1993) compared to smaller and younger fish. For NL capelin, larger fish arrived first to spawn at beaches in the pre-collapse period (Vandeperre and Methven, 2007). Mean length (\bar{L}) of the capelin spawning population predicted spawning timing, with delayed spawning predicted when there was a decrease in \bar{L} in the post-collapse period. When the capelin stock collapsed, growth rates of immature fish increased (DFO, 2019), likely a compensatory response due to less competition for food rather than an evolutionary response due to selective effects of fishing (Law, 2000). Evolutionary responses to fishing has been seen in fisheries where both immature and mature large fish are targeted (e.g. Atlantic cod *Gadus morhua*: Olsen *et al.*, 2004; Swain *et al.*, 2007), although a recent study on heavily exploited Atlantic cod stocks found that while there have been phenotypic changes in these stocks, there has been no substantial loss of genetic diversity (Pinsky *et al.*, 2021). The collapse of the NL capelin stock appears to have been environmentally driven with an order of magnitude decline occurring between May and November 1990 (e.g. Bakanev and Zubov, 1991) with no apparent selection on the basis of spawning timing. During periods where immature fish have high growth rates, year-classes will mature and spawn at a younger age (Ricker, 1981; Olsen *et al.*, 2004; De Roos *et al.*, 2006); and since the majority of NL capelin are semelparous (Shackell *et al.*, 1994), increased immature growth rates and earlier maturation results in a spawning population that is both younger and smaller in length compared to fish maturing and spawning at older ages. This change in demography of the capelin stock may be affecting timing of reproduction at the population level.

In summary, these exploratory analyses have provided a foundation for further hypothesis testing of the potential drivers of capelin spawning timing. The period term is the most important predictor of spawning timing for the NL capelin stock which suggests that either we have not identified all of the relevant environmental and biological variables that can be used to predict the dramatic change

in spawning timing in 1991 (Buren *et al.*, 2014); or the rapid cooling in the early 1990's caused a non-linear perturbation of the stock and a positive anomaly in $NLCI$ from 1996–2013 was not sufficient for a return to the previous equilibrium in spawning timing (Scheffer and Carpenter, 2003; Robertson *et al.*, 2021). Instead, it appears that two less important, but significant, variables (i.e. a demographic change to smaller mature fish and a negative anomaly in NAO_s) have created unfavourable conditions for earlier spawning despite warming conditions in the ecosystem. In turn, delayed spawning migrations are predicted to negatively impact year-class strength perhaps due to match-mismatch dynamics and overwinter survival of 0-group larvae.

Long-term implications

As a consequence of anthropogenic climate change, there is an ongoing increase in the surface (0–200 m) density stratification of the world's ocean (Bindoff *et al.*, 2019), including in the Northwest Atlantic, due to increased freshwater input and near surface temperature increases (Greenan *et al.*, 2019). In NL, climate projections forecast an increase in SST of 0.4°–2.2°C in 50 years (Han *et al.*, 2015). Increased stratification was found to have negative consequences for fisheries productivity as projected increases in ocean stratification was related to a mismatch between fish spawning timing and phytoplankton blooms (Asch *et al.*, 2019). Persistently delayed capelin spawning timing could result in an even greater mismatch between spawning timing and primary productivity if the spring bloom occurs progressively earlier due to increased stratification. These changes in the physical environment may also impact zooplankton community structure and, consequently, the prey available for larval capelin. Since 1999, small-bodied copepods like *Pseudocalanus* spp., which are a preferred prey of larval fish (Möller *et al.*, 2004; Heath and Lough, 2007; Wilson *et al.*, 2018), have increased in abundance in the Northwest Atlantic (Bélanger *et al.*, 2020). This suggests that current and forecasted oceanographic conditions may be supportive of increased survival rates of the early life history stages due to improvements in the larval prey field. However, with capelin spawning timing persistently delayed, capelin larvae are emerging later in the summer which has resulted in a mismatch between larval emergence and infrequent onshore wind events that predominately occur earlier in the summer (Murphy *et al.*, 2018). These onshore wind events have previously been identified as important for NL capelin larval survival as the release of emergent larval pulses from beach sediments were triggered by onshore wind events with higher larval mortality occurring when the interval between onshore wind events increased (Frank and Leggett, 1981a); and onshore wind events were associated with increased larval prey availability and decreased occurrence of invertebrate predators in nearshore waters due to coastal water mass replacement (Frank and Leggett, 1982b). So even with an increase in the abundance of preferred larval prey in the post-collapse period, emergent larvae may not be able to capitalize on this resource due to delayed spawning timing.

Limitations of study

There is a relative lack of mechanistic explanations for how the different environmental predictors may be affecting spawning timing and year-class strength. Capelin spawning timing was predicted by large-scale and regional climate indices (NAO_s and the $NLCI$). While the causal relationship between these climate signals and

spawning timing has not been clearly established, we have hypothesized the mechanisms by which NAO_s predicts spawning timing (i.e. changes in winds and the Labrador Current system transport), but more direct hypothesis testing is required to link large-scale atmospheric forcing and ocean circulation changes in the Northwest Atlantic to the smaller-scale NL ecosystem level changes (e.g. sea ice, freshwater input, timing of the bloom, plankton assemblage, etc.).

Conclusions

By building on previous research by Carscadden *et al.* (1997) and Buren *et al.* (2014), a model was developed to predict the timing of capelin spawning using biological and environmental variables. We found that post-1990, delayed spawning migrations are predicted when there is a decrease in mean length in the spawning stock. This shift to earlier maturation and smaller mean lengths occurred when the stock collapsed in 1991 and was concomitant with a change in the ecosystem (i.e. decrease in summer NAO and a cold anomaly in the early 1990's). The persistent change in capelin maturation timing since the early 1990's appears to be a compensatory response as a shift to later maturation at age-3 occurred when the stock size increased in the early 2010's although there wasn't a strong shift to earlier spawning timing during those years with spawning on average only four days earlier in the early 2010's compared to the post-collapse median. There was still a negative anomaly in the NAO_s during the 2010's. This suggests that a shift back to beach spawning in June is possible, but requires changes to both capelin population demographics and broad-scale and regional climate indices. The persistent delay in beach spawning is predicted to have negative ramifications for the recovery potential of the NL capelin stock.

Supplementary Data

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

Data availability statement

The time series of beach spawning data is available in the online supplementary material while all other data are available on request.

Acknowledgements

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