Anomalous ecosystem dynamics following the apparent collapse of a keystone forage species

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Supplement

Additional capelin surveys in the NL region

In addition to the long-term Div. 3L surveys, several other capelin surveys were run for a limited time in the NL region (Figure S1). These include Div. 2J3K Canadian and Russian fall surveys, and a 3LNO Russian spring survey (Tretyakov 2013). These surveys generally began in the early 1980s and stopped about 1994. Their biomass estimates are in agreement with the long-term spring Div. 3L survey, showing increased biomass estimates in the mid- to late 1980s and falling to low values in 1991. Based on the linear correlations, the Canadian Div. 3L and Russian Div. 3LNO surveys were most strongly related (r = 0.81).
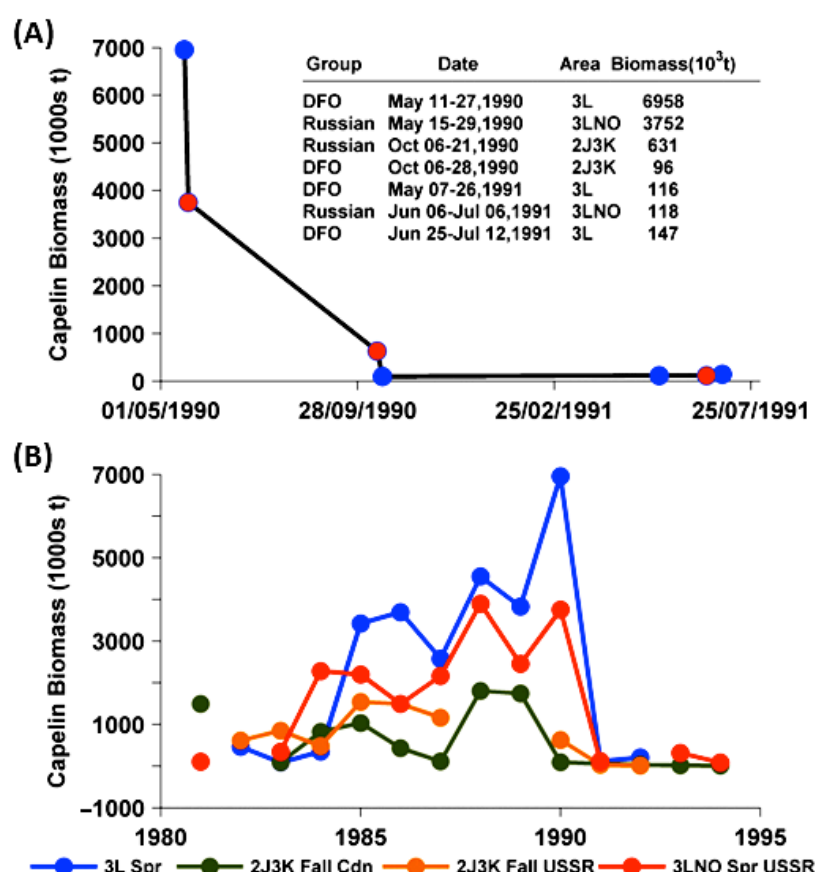
Figure S1 (A). Offshore acoustic survey biomass estimates pinpointing the timing of the apparent capelin collapse from 1990-1991 in the NL region based on DFO (blue) and Russian (red) acoustic surveys. **(B).** Biomass estimates from capelin surveys in the NL region compared to the ongoing Div. 3L survey up to 1994. The strongest correlation coefficient, r = 0.81 was between the two spring surveys, other values ranged from r = 0.23 to 0.50.

Ecosystem overview through Principal Component Analysis (PCA)

Table S1. Time series used as input to PCA, 1982-2012. Data series which are complete from 1982-2008 are indicated with an asterisk.

Variable Name	Source	Comment
Capelin biomass (CplnMss)	Mowbray (2012)	Estimate from May acoustic survey Div. 3L
Capelin average age trapped fish* (Age3KL)	DFO (2013)	
Capelin female body length* (CplnLgth)	DFO (2013)	Female-Male correlation = 0.98
Capelin timing of inshore spawning* (SpawnDay)	DFO (2013)	
Capelin inshore school area index	DFO (1999)	
Capelin CPUE inshore fishery (CplnTrap)	DFO (2001)	Div. 3KL trap fishery
Capelin component of harp seal diet* (CplnHarp)	Stenson (2012)	Model estimate using time varying diet assessment
Cod 2J3KL biomass (CodMss)	Shelton et al. (2006)	Spawning stock biomass
Cod liver condition index 1* (CodLiver1) See Figure S5	Brattey et al. (2010)	
Cod liver condition index 2* (CodLiver2) See Figure S5	Brattey et al. (2010)	
Cod weight at age 1* (CodWgt1) See Figure S3	Brattey et al. (2010)	
Cod weight at age 2* (CodWgt2) See Figure S3	Brattey et al. (2010)	
Arctic cod component of harp seal diet* (ACodHarp)	Stenson (2012)	Model estimate using time varying diet assessment
Snow crab CPUE 2HJ3KLNO* (Snow Crab)	DFO (2014)	CPUEs from 2HJ, 3K, 3LNO combined based on landings
Shrimp CPUE SFA6 (Shrimp)	Orr and Sullivan (2013)	Shrimp fishing area 6 includes S Labrador shelf (Hamilton Bank) and Div. 3K
Combined physical variables*	Colbourne et al. (2014)	PC1 of physical variables; see *Ocean Climate Variability*, Supplement

Centre of concentration of capelin from the annual fall groundfish surveys

To assess and correct for possible changes in the capture efficiency of capelin resulting from the change of gear and sampling intensity, we undertook a simulation analysis. For each gear type used (n=2), we randomly sampled the Newfoundland fall survey database using sample sizes (hauls) ranging from 2 to 100 with 1000 replicates each. We then estimated the probability of detecting capelin as a function of sample size using a binomial model (appropriate for presence/absence measurements). These analyses indicate that the probability of capelin capture by the Campelen trawl was significantly greater than that for the Engels trawl, and that the probability of detection by both gear types was an asymptotic function of sample size with sample sizes of eight (Engels Trawl) and three (Campelen trawl) yielding a common 95% probability of capelin detection. Based on these findings, we standardized for the influence of gear efficiency and sample effort by dividing the survey area into a 0.5 by 0.5 degree grid and excluding all cells containing less than 8 trawls during the 1971-1994 period when the Engels trawl was employed, and all cells that containing less than 3 trawls during the 1995-2013 interval when Campelen trawls were used. Having thus standardized the data, we evaluated whether changes in capelin distribution have occurred in response to their reported collapse. To do so, we divided the data into four time periods *a) 1971 to 1984); b) 1985 to 1994; c)* 1995 to 2004; and *d)* 2005 to 2013 (Figure 4).

We estimated spatial and temporal changes in the capelin center of biomass concentration using Generalized Additive Models (GAMs; Wood, 2006). GAMs are a flexible class of statistical models which are useful in estimating the response as a non-monotonic (*i.e.* multi-modal) function of one or several predictors. Using DFO fall groundfish survey data, we estimated capelin abundance as:

$$\mu_i = \beta_0 + \beta_1 Time_i + f_1(Longitude_i, Latitude_i, Time_i) + f_2(Day_i) + \varepsilon_i$$

where μ_i is the $\log_{10} + 1$ capelin abundance, β_0 is the model intercept, β_i and f_i are parametric and functional effects estimated from the data, and ε_i is an error term. The $f_1(Longitude_i, Latitude_i, Time_i)$ term allows the estimation of the spatial variability in capelin distribution at each discrete level of time ($Time_i$). The $f_2(Day_i)$ term accounts for the average intra-annual variability in capelin abundance. We fitted the above equation to the data using both 5 and 1 year time increments. Since the response was $\log_{10} + 1$ transformed, we used a Gaussian distributed error structure and identity link. We also explored other distributions such as the Gamma, negative binomial, and Tweedie, but the results were similar and there was no significant change in overall model fit (Nakagawa & Schielzeth 2013).

The above equation was used to predict the average capelin abundance across the entire spatial domain of the capelin within each year. Center of mass predictions were made on the same day of the year (331), which corresponds to the day when most measurements were available.
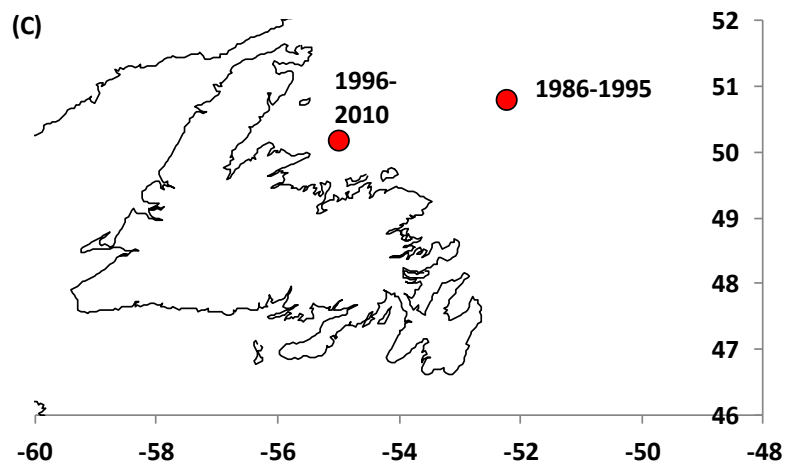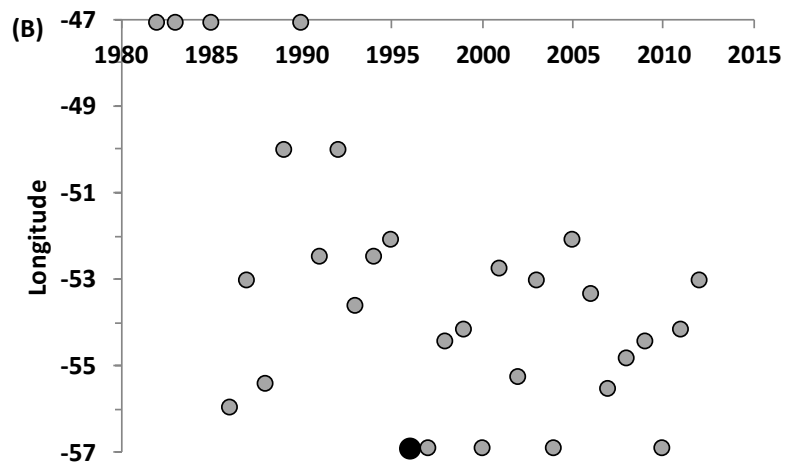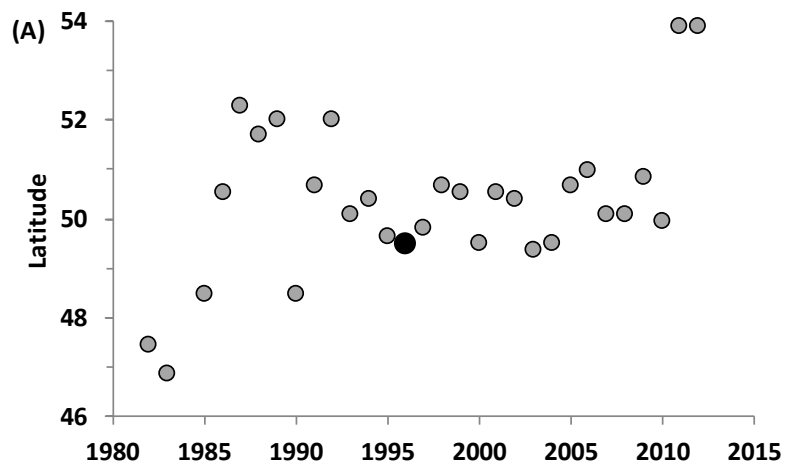
(D)
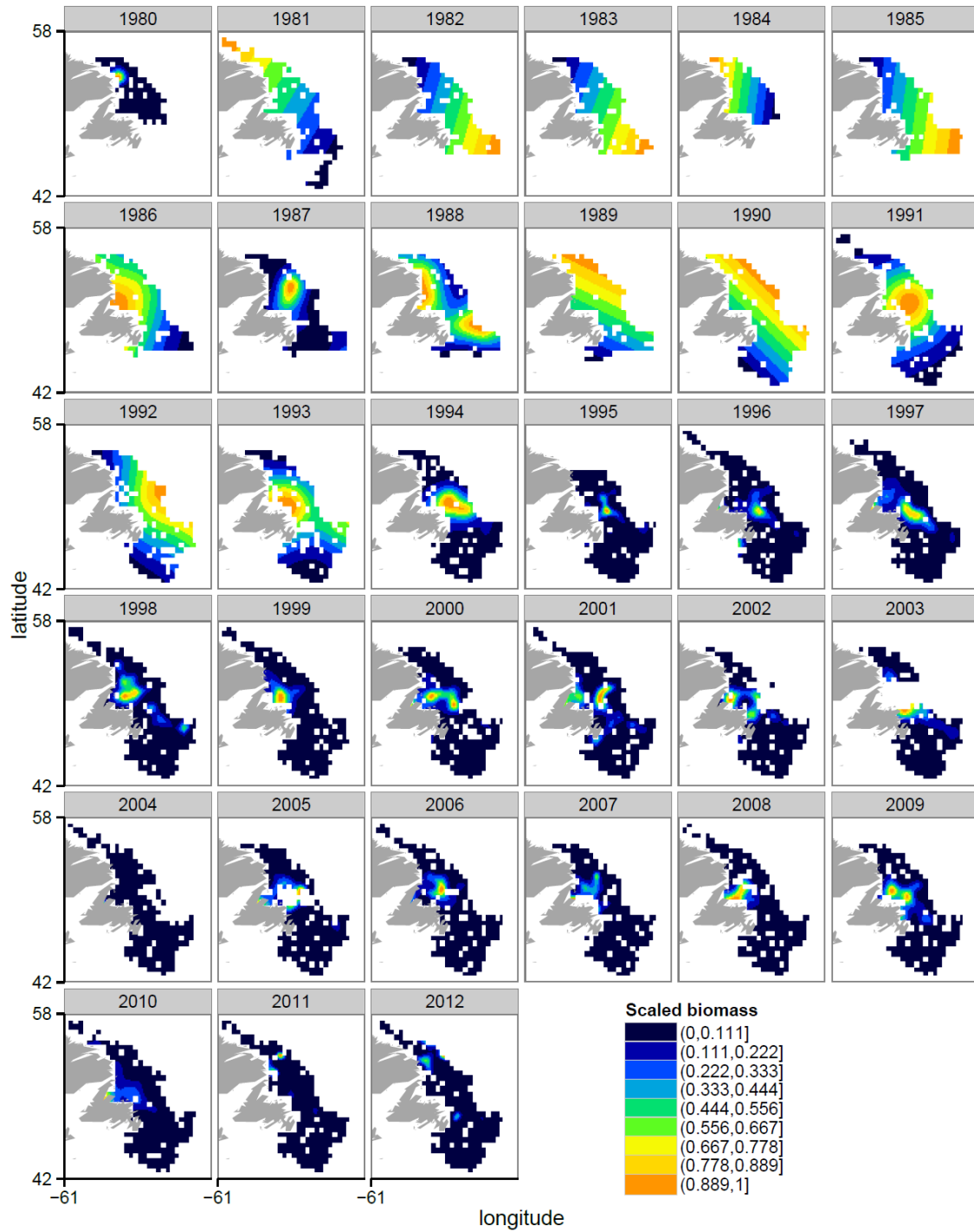
Figure S2. Time series of centres of concentration of capelin from the annual fall groundfish survey by (A) latitude and (B) longitude. The year 1996 is marked by a large black point. (C) The average centres of concentration for the periods 1986-1995 and 1996-2010. (D) Spatial representation of capelin biomass concentration from each annual survey from 1980 to 2012.
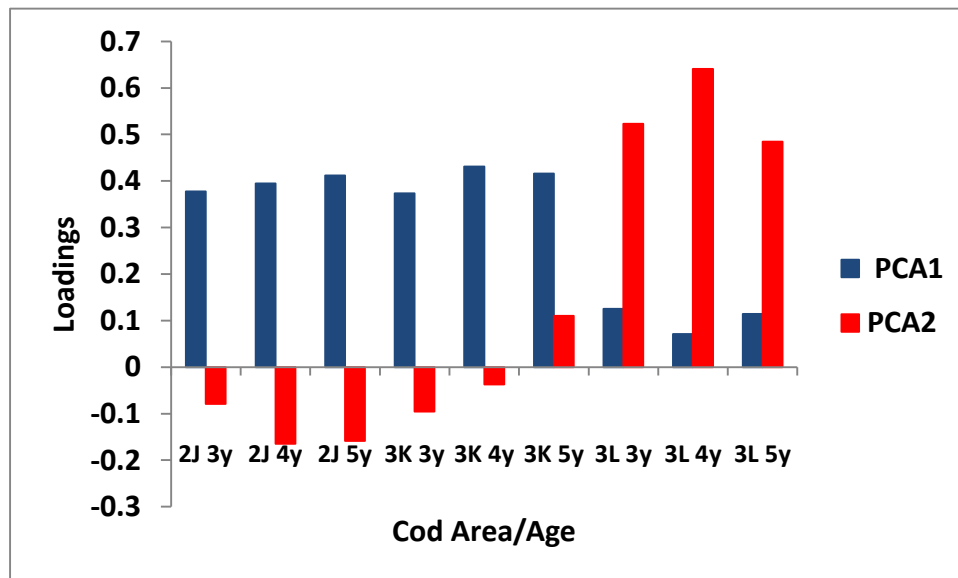
Cod weight at age

A principal component analysis (PCA) was performed on the weight at age time series (Figure 9) to determine whether the variability was coherent among series and therefore whether data could be compactly summarized by the leading PCA modes. Two year old cod showed weak temporal variability and were excluded from the analysis. A correlation matrix was constructed from the 9 remaining time series and subjected to a PCA analysis. Much of the variability can be summarized by the two leading modes.

The loadings for mode 1 indicate that the variability for areas 2J and 3K is very similar, capturing 46% of the overall variance (Figure S3). Mode 1 reaches a minimum in 1992 from whence it begins a long-term trend of increasing weight at age (Figure S4). Area 3L differs somewhat, featuring maximum loadings in mode 2 and capturing 22% of the overall variance. Its time series does not show a distinct separation associated with 1991 rather, it exhibits an overall increasing trend over the entire period. The 2 time series mirror what is seen in Figure 9. Comparison of the average weights for the pre- and post-1991 periods is shown in Table S2.

Table S2. Comparison of average weights at age for the pre- and post-1991 periods.

Weights (kg)	2J 2y	2J 3y	2J 4y	2J 5y	3K 2y	3K 3y	3K 4y	3K 5y	3L 2y	3L 3y	3L 4y	3L 5y
Pre-1991	0.212	0.480	0.867	1.338	0.199	0.505	0.949	1.410	0.190	0.438	0.779	1.328
Post-1991	0.209	0.442	0.770	1.127	0.199	0.459	0.832	1.308	0.226	0.520	0.909	1.386
Gain (kg)	-0.003	-0.038	-0.097	-0.212	0.000	-0.046	-0.117	-0.102	0.036	0.082	0.130	0.058
% Gain	-1.5	-8.0	-11.2	-15.8	0.1	-9.1	-12.3	-7.2	18.9	18.8	16.7	4.4
p	0.870	0.264	0.077	0.016	0.985	0.141	0.035	0.199	0.002	0.002	0.017	0.419

Figure S3. Loadings for PC1 and 2 based on the correlation matrix derived from 3-5 year old cod weight at age for NAFO Div. 2J, 3K and 3L.
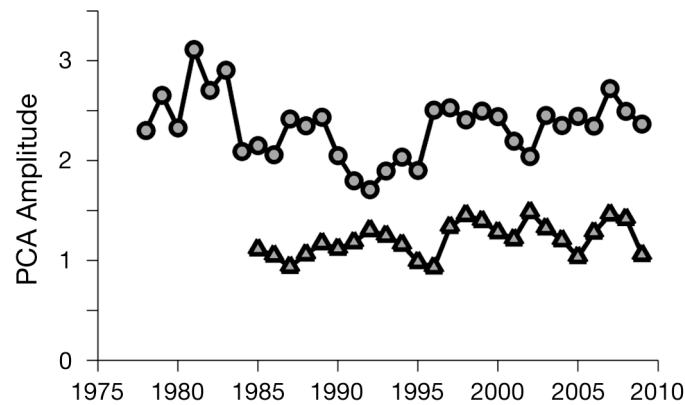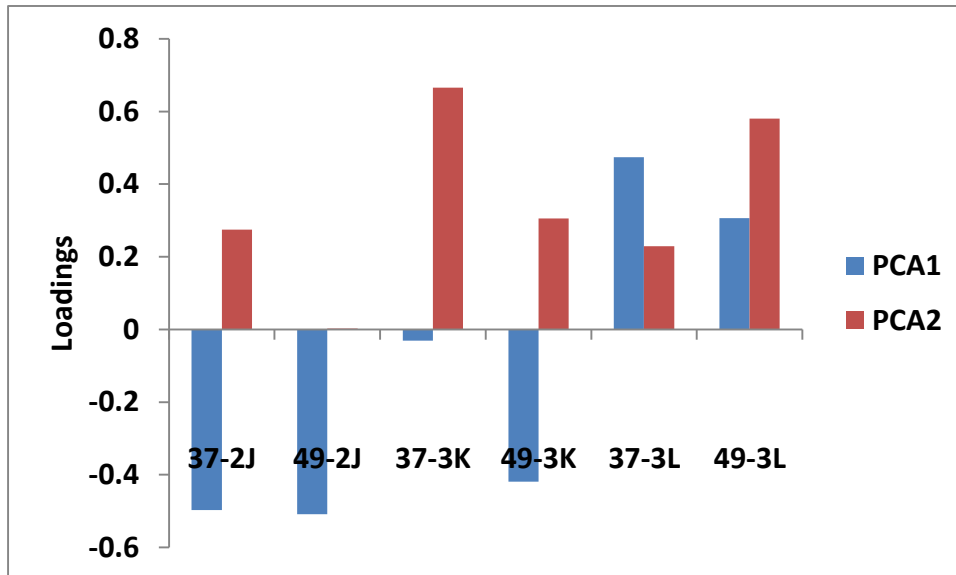
Figure S4. Time series of PC1 and 2 based on the correlation matrix derived from 3-5 year old cod weight at age for NAFO Div. 2J, 3K and 3L.

Cod liver condition index

In a similar fashion, the time series of cod liver condition (Figure 10) were subjected to a PCA. The results indicate that PC1, with 49% of the variance, has strong in phase loadings for 2J and the 49 cm component of 3K; there is also an out of phase (opposing) component in 3L for both lengths (Figure S5). This captures a result similar to that revealed by the analysis of cod weight at age (Figure S3), namely, 2J and 3K acting alike, 3L acting separately. PC2 captures 27% of the variance and features in phase contributions from all but the 2J 49 cm cod. The time series of PC1 coupled with the loadings indicates that for both lengths in 2J and the 49 cm length in 3K the liver index decreased from above average to below average 1990 to 1991 and remained below average thereafter (Figure S6, Table S3). This favours the interpretation that a collapse occurred. On the other hand, both components in 3L, the site of the capelin survey, varied in the opposite manner supporting the conclusion that the capelin population did not collapse. The 37 cm 3K component varied little, as PC2 indicates that from about 1983 onwards, condition oscillated around 0.

Table S3. Comparison of cod liver condition for the pre- and post-1991 periods.

	Liver Index	Div. 2J		Div. 3K		Div. 3L	
Period		37 cm	49 cm	37 cm	49 cm	37 cm	49 cm
Pre-1991	Average	0.67	1.01	-0.54	0.25	-1.00	-1.35
	SD	1.15	0.63	1.18	1.35	0.63	1.47
	Npts	12	12	13	13	9	9
Post-1991	Average	-0.45	-0.61	0.36	-0.19	0.41	0.37
	SD	0.61	0.56	0.68	0.68	0.73	0.87
	Npts	18	18	18	18	18	18
	P	0.0016	<0.0001	0.0273	0.2429	<0.0001	0.0008

Figure S5. Loadings for PC1 and 2 based on the correlation matrix derived from 37 and 49 cm cod liver index for NAFO Div. 2J, 3K and 3L.
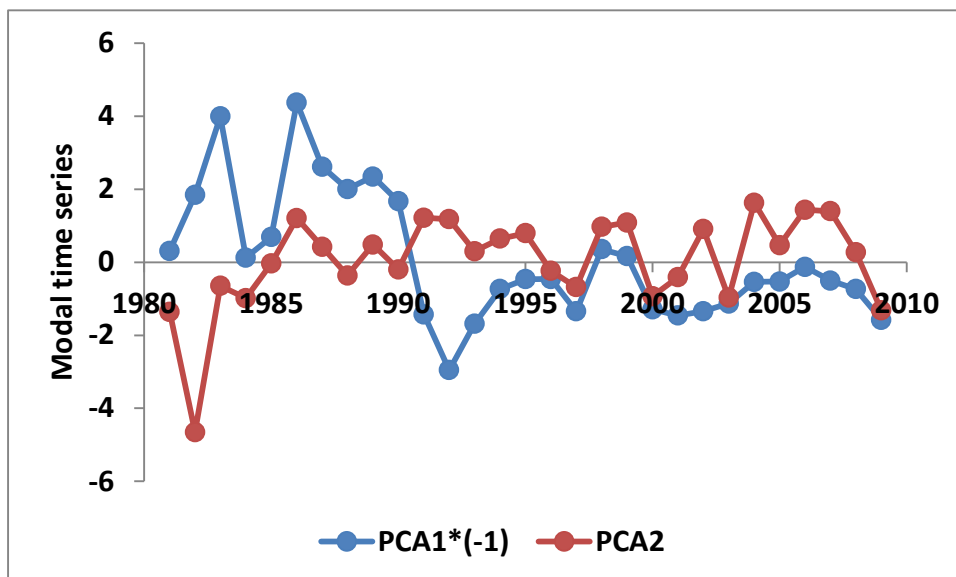

Figure S6. Time series of PC1 and 2 based on the correlation matrix derived from 37 and 49 cm cod liver index for NAFO Div. 2J, 3K and 3L.

Ocean climate variability

The input variables for a PCA are shown in (Figure S7) and include ice cover, measures of the quantity of sub-zero temperature water, temporally and vertically integrated ocean temperatures, and proxies representing ocean currents. The leading mode, which accounts 56% of the variance, suggests that 1991 was the coldest year on record (Figure S7). If the years are ranked from coldest to warmest based on the 7 thermally-related variables of Figure 12, 1991 also emerges as the coldest year with an average ranking of 3.3; then next coldest year (1993) has a ranking of 5.9.
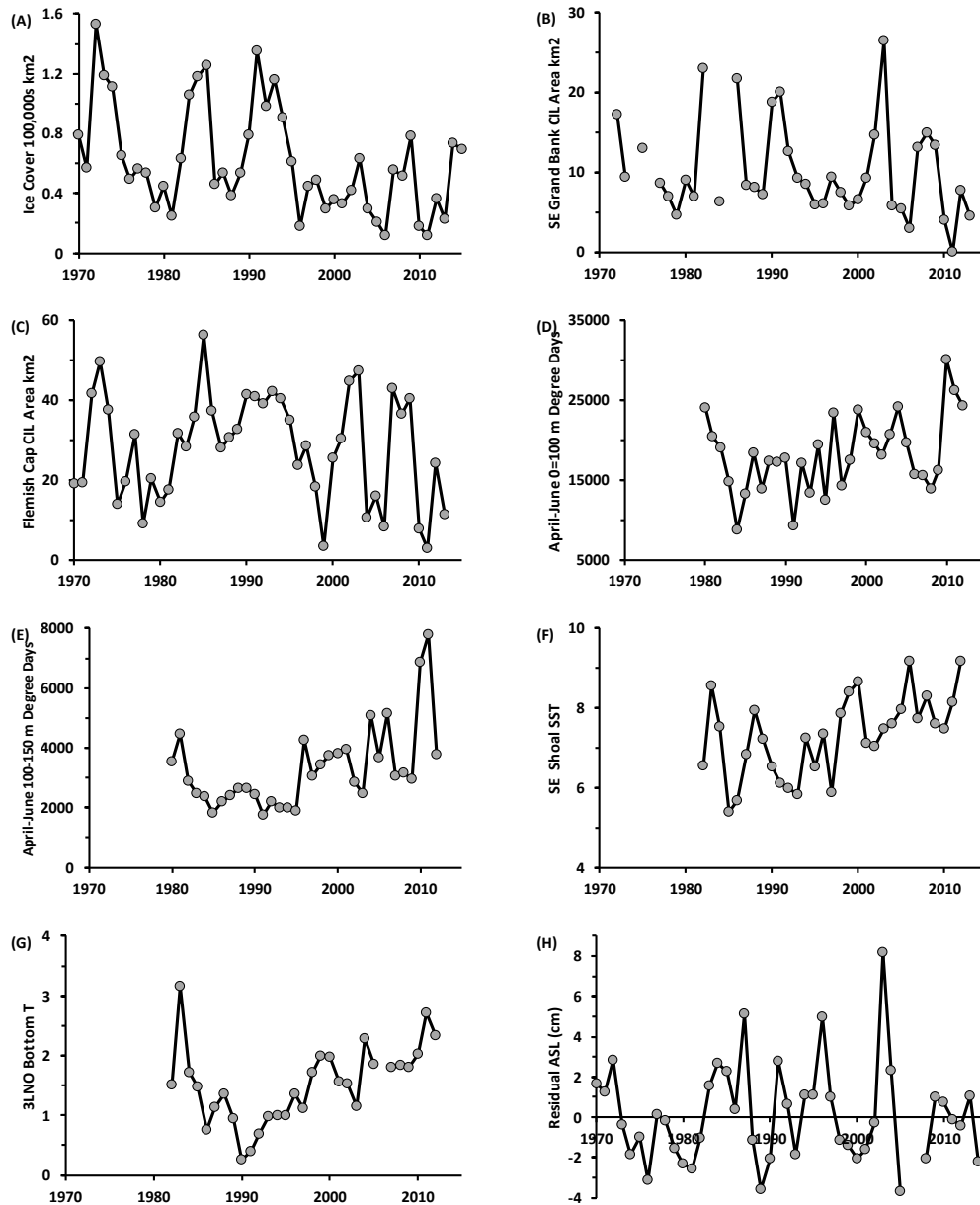
Figure S7. Time series of ocean climate variables include (A) the April-June ice cover south of 55°N; the area of the Cold Intermediate Layer (CIL) during spring for the (B) SE Grand Bank and (C) Flemish Cap (47°N) hydrographic sections; (D) the April-June 0-100 m and (E) 100-150 m integrated temperatures from Station 27 located 7 km offshore of St. John's (A-E, Colbourne et al. 2014); (F) annual average sea surface temperature from SE Shoal (Petrie et al. 2008); (G) Div. 3LNO annual bottom temperature (Colbourne et al. 2014); and, (H) annual residual adjusted sea level (ASL) at St. John's (http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html).

Acoustic survey grids

Two grids were generally used for the Div. 3L acoustic surveys (Figure S8). Based on the surveys from 1985-1990 (7 surveys, 2 in 1985, Figure S8B) the percentage distributions of capelin biomass were derived for each survey and A*tanh[(y-y0)/L)], where A is the asymptotic amplitude, y the latitude, y0 the reference latitude and L the decay scale, fitted to the observations. The best fit was for A=30.1, y0 = 46.1 and L=1.2 with R^2=0.32. The centre of mass of the capelin concentration is at 47.83 °N. In contrast, the available observations from 1991ff (1991, 1992 and 1996 surveys with the data readily available in six subareas of the latitudinal grid) show no latitudinal dependence (R^2=0).

If the shift to later spawning times (Figure 8) represented a shift in the movement of capelin through 3L, what does that mean to a fixed survey? If we further assume that the variability in the spawning time (SD, 11.9 d) represents the variability in the timing of the peak concentration through 3L, then we can estimate (Gaussian distribution) the likelihood of a peak concentration in 3L on May

31 or earlier. Using the statistics of the observed peak beach spawning time (average spawning occurred on day 197.4, SD = 11.9 d) for 1991 and thereafter, and that the average observed maximum capelin concentrations occurred 28 d prior to peak spawning, we ran 10,000 simulations of the occurrence of maximum concentrations in Div. 3L.

Under these assumptions, the probability that the peak concentration occurs before June 1 is about 6% (Figure S8C). For a single survey in Div. 3L, it is likely that the peak capelin concentration would not be observed. However, we need to determine the probability of 25 successive years (1991-2015) when the peak occurrence was later than May 31 in all years. This turns out to be about 22%; so it is unlikely that we should not see sustained low values over the 25 year period if the statistics for beach spawning reflect the time of occurrence of peak concentrations in 3L and the only factor operating was a change in the timing of the capelin migration.
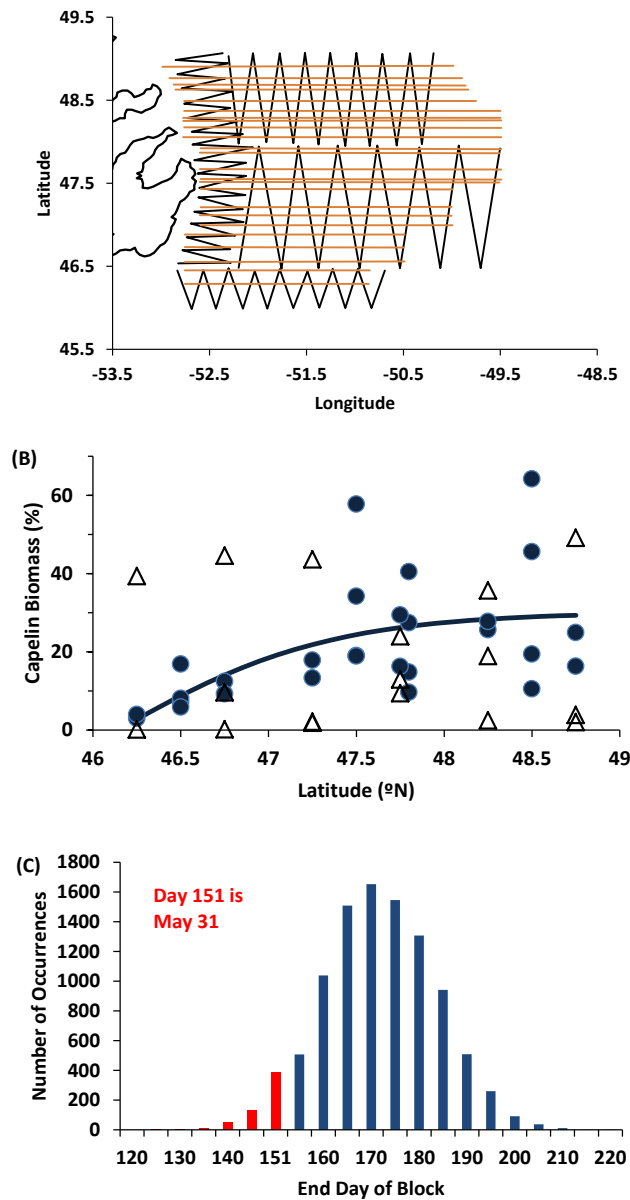
Figure S8. (A) Ship's tracks for the saw-tooth (pre-1989, black) and latitudinal (1989 and thereafter, red) acoustic survey grids. The earlier grid was composed of 4 subareas or strata, A at the coast, and B-D, the successive sawtooth patterns from north to south. The latitudinal grid was subdivided into 6 zones from A in the north to F in the south (Miller 1991). (B) Distribution of biomass with latitude from DFO surveys 1985-1990 (circles) and 1991, 1992 and 1996 (triangles). The curve is the fit of A*tanh[(y-y0)/L)] where A is the asymptotic amplitude, x the latitude, x0 the reference latitude and L the decay scale. The best fit was for A=30.1, y0 = 46.1 and L=1.2 with R^2=0.32. (C) Probability distribution of the time of occurrence of maximum capelin concentration in Div. 3L.

*Comparsion of average body lengths between offshore and inshore capelin*

On average, twenty-nine (±8, SD) mid-water trawl sets were made during the Div. 3L acoustic surveys to serve as ground truth data. From these, the distribution of capelin ages was determined and can be related to the average age of the fish caught during the inshore fishery (Figure 7; Mowbray 2014). In Figure S9, we compare the average age based on the distribution of the ≥2 year old capelin from the spring survey with the average age of the inshore catch for the pre-1991 and the 1991-2012 periods. The results suggest a greater connection between the inshore-offshore populations pre-1991 ($R^2 = 0.37$) than for the period 1991 and thereafter ($R^2 = 0.0006$).
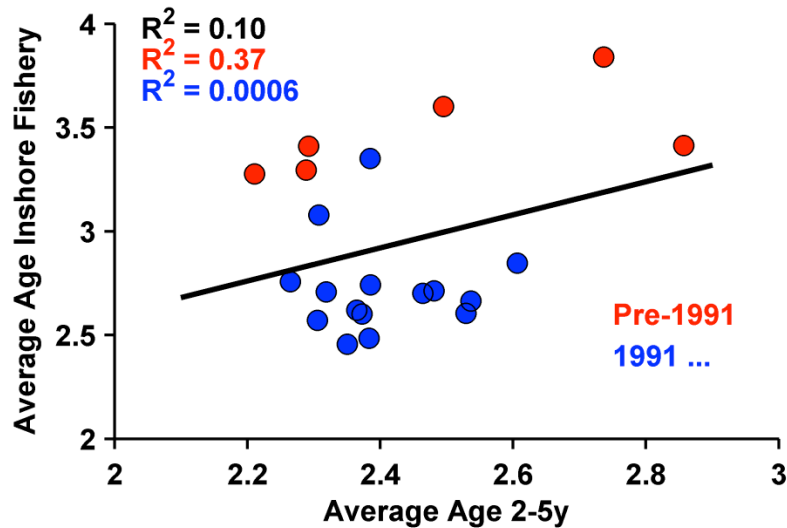
Figure S9. Relationship between the average ages of the 2-5 year old capelin from mid-water trawl sets taken during the Div. 3L acoustic survey and the average ages of fish captured by the inshore fishery. The black line is a linear fit to all of the observations.

Changes of size at age for offshore capelin

Observations of length at age were collected for offshore capelin from mid-water trawl sets during the spring acoustic survey (1985-1992, 1996-2012 omitting 1997, 1998 and 2006, Mowbray 2014). The 1985-1992 period features significantly smaller capelin for the 2 and 3 year old fish, whereas the 4 and 5 year olds were significantly larger than those during the 1996-2012 period (Figure S10).
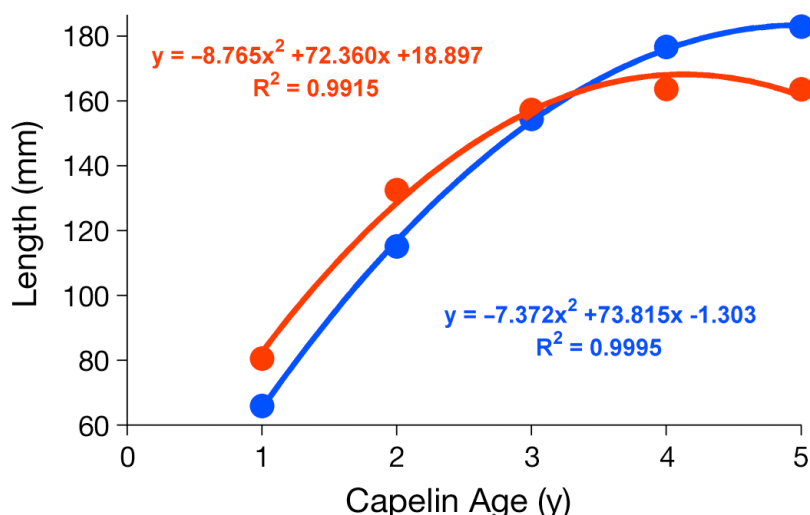
Figure S10. Capelin length at age from mid-water trawl sets collected during the offshore spring survey for 1985-1992 (blue) and 1996-2012 (red). A second degree polynomial fit is shown for illustration. Statistics and p values for data displayed in Figure S10 are as follows:

		Averages		SE		
Age		1985-92	1996-12	1985-92	1996-12	P
	1	65.9	80.5	1.2	3.9	0.0120
	2	115.2	132.5	2.2	1.4	0.0001
	3	154.5	157.3	2.5	1.5	0.3200
	4	176.8	163.8	2.9	1.3	0.0001
	5	183.0	163.7	1.9	4.8	0.0037

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