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

Kenneth T. Frank[1,2,*], Brian Petrie[1], Daniel Boyce[2], William C. Leggett[2]

[1]Fisheries and Oceans Canada, Bedford Institute of Oceanography, Ocean Sciences Division, Dartmouth, Nova Scotia B2Y 4A2, Canada
[2]Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT: Major groundfish populations in the western Atlantic north of Georges Bank/Western Scotian Shelf experienced near-total population collapses beginning in the late 1980s–early 1990s. Explosive increases in the abundance of their pelagic fish and invertebrate prey (notably capelin, sand lance, herring, shrimp and snow crab) generally followed. However, several investigators have concluded, based on the results of annual acoustic surveys, that the lightly exploited capelin stock in the Newfoundland/Labrador (NL) region experienced a sudden 6.8 Mt (98%) decline in biomass from 1990 to 1991 coincident with the groundfish collapse. Given the enormity, duration and unexpected nature of this decline, it was characterized as a collapse. The contrasting response of this capelin stock to the groundfish collapse relative to other North Atlantic (NA) ecosystems prompted us to undertake systematic analyses of the NL ecosystem. The reported capelin collapse in NL should have induced significant responses of trophically linked species, as have been reported in other NA ecosystems. We found little evidence of changes in the population abundance, diet and condition of marine mammals, cod, seabirds and zooplankton, in indexes of the areal occupancy and spawning biomass of capelin, or of environmental effects. These results strongly support the hypothesis that the reported collapse did not occur. Profound seasonal distribution changes, a fixed in time and space acoustic survey in a restricted portion of the distributional range of capelin, and the possibility that NL capelin stock has become less migratory provide a more robust and consistent explanation of the observations.

KEY WORDS: Forage fish · Stock collapse · Ecosystem response · North Atlantic · Acoustic surveys · Migration

INTRODUCTION

Beginning in the mid-1980s, the abundance of several groundfish species, including Atlantic cod *Gadus morhua*, experienced rapid, near-synchronous declines across the western North Atlantic Ocean from Labrador to the eastern Scotian Shelf off Nova Scotia (Fig. 1). In this region, cod biomass declined by 85% from 1.47 Mt in 1985 to 0.22 Mt in 1993. This downturn occurred in 7, which account for 98% of the total biomass, of the 8 regional cod stocks in the NW Atlantic. This decline, largely a conse-quence of overfishing (Petrie et al. 2009), precipitated a chain of trophically connected events that fundamentally changed the structure of these ecosystems (Frank et al. 2005, 2006). One response, common to all of the affected ecosystems, was an irruptive increase in the biomass of their macro-invertebrate prey (shrimp *Pandalus borealis* and snow crab *Chionoecetes opilio*; Worm & Myers 2003, Frank et al. 2005, Boudreau & Worm 2012). In addition, the biomass of forage fish species exhibited rapid, order of magnitude increases in response to the groundfish collapse (Frank et al. 2006, 2013).
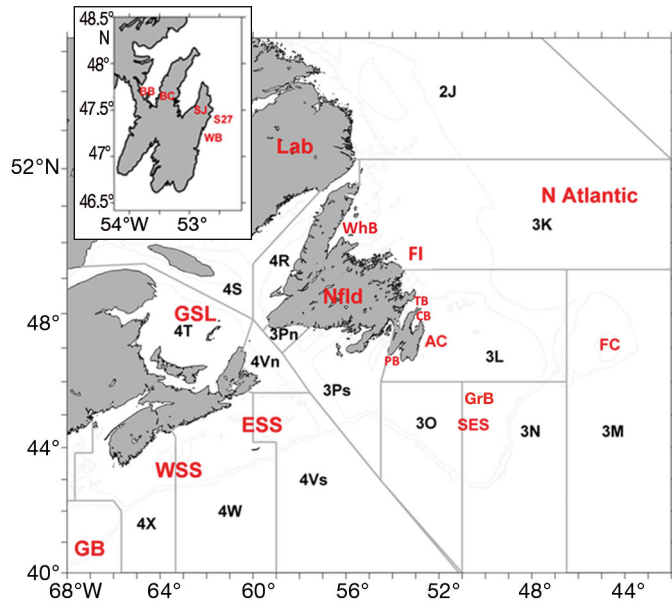
Fig. 1. Study area, including Labrador (Lab), White Bay (WhB), Fogo Island (FI), Trinity Bay (TB), Conception Bay (CB), Avalon Channel (AC), Flemish Cap (FC), Grand Bank (GrB), Southeast Shoal (SES), Placentia Bay (PB), Newfoundland (Nfld), Gulf of St. Lawrence (GSL), Eastern Scotian Shelf (ESS), Western Scotian Shelf (WSS) and Georges Bank (GB). Inset shows Avalon Peninsula, including Bellevue Beach (BB), Bryant's Cove (BC), St. John's (SJ), Stn 27 (S27) and Witless Bay (WB). NAFO Divisions (2J, 3K, etc.) are displayed in black characters

With the decline of cod from 1970 (1.6 Mt) to 1977 (0.2 Mt) due to overfishing by foreign fleets in the Newfoundland/Labrador (NL) ecosystem, defined as the combination of Northwest Atlantic Fisheries Organization (NAFO) Divisions (Div.) 2J, 3K and 3L, capelin *Mallotus villosus*, the dominant forage fish species, exhibited a rapid increase from 2.4 Mt in 1972 to 4.2 Mt in 1976, then to 2.9 Mt in 1977 (Fig. 2A). In stark contrast, the cod collapse of ~1 Mt (a 95% decline) from 1985 to 1992 was accompanied by a 6.8 Mt (98%) decline of capelin in Div. 3L (Fig. 2A). Additional surveys covering all or part of the NL region confirm the decline seen in the spring Div. 3L survey (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m553p185_supp.pdf).

From the late 1980s to early 1990s, a similar response was witnessed in an adjacent area (Div. 3NO), where capelin biomass declined from ~0.4 to ~0.03 Mt (Miller 1993). For other NW Atlantic (with the exception of Iceland) and the Barents Sea fisheries, cod declines were accompanied by increases in capelin stocks (Fig. 2B).

Capelin is a short-lived, migratory, planktivorous, schooling species. Historically, the centre of abundance and distribution in the NW Atlantic has been

in Div. 2J3KL (Fig. 1). Capelin appear to spend most of their lives offshore, with the exception of summer, when the mature stock, composed mainly of age 3 and 4 yr olds, spawns on beaches along eastern/northeastern Newfoundland during June and early July. Juvenile capelin are generally widely distributed, occurring in major coastal bays and in offshore areas, but the northern Grand Bank is considered the main nursery and overwintering area for the stock (Carscadden et al. 2013). Capelin occupy a central position in the food chain serving as a conduit for energy transfer from lower to higher trophic level predators, which include several groundfish species, marine mammals and a variety of seabird species.

Spring offshore acoustic surveys of capelin in NL by the Canadian Department of Fisheries and Oceans (DFO), intended to quantitatively assess the biomass of the capelin stock prior to its onshore
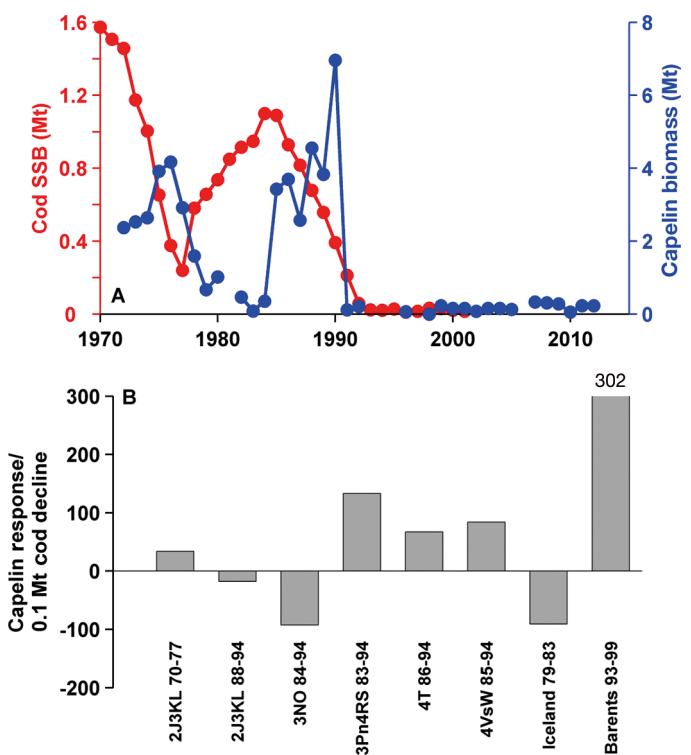

Fig. 2. (A) Spawning stock biomass (SSB) estimates of cod *Gadus morhua* (ages 3+; red) and capelin *Mallotus villosus* (blue) from NAFO management area Division 2J3KL from 1970 to present. Capelin biomass estimates were obtained from 2 sources: from 1972 to 1980 using a sequential capelin abundance model (Carscadden & Miller 1981, Carscadden et al. 1981) and an offshore acoustic survey thereafter (Mowbray 2012). (B) Capelin response in numbers per tow for Divisions 2J3KL to 4VsW and 1000s t per 100 000 t decrease of cod for Iceland and the Barents Sea. *x*-axis labels correspond to the cod management unit area and years of the cod decline

spawning migration, began in 1982 and have been conducted annually since 1999, with the exception of 2006. On the basis of these surveys, several authors have concluded (Table 1) that, following an initial positive response (1987 to 1990) when biomass increased from 2 to 7 Mt, the capelin stock experienced a precipitous, single-year decline of 6.8 Mt in 1991 from which it has yet to recover (Fig. 2). This decline has occurred irrespective of the fact that capelin have been exploited at levels of 10% or less in this ecosystem (Shelton et al. 1992).

The ecosystem and species-level impacts of biomass declines of capelin in other North Atlantic regions (Iceland and Barents Sea) provide insight into what might have been expected in the NL marine environment. In the Iceland ecosystem, overfishing led to a dramatic decline of capelin biomass from 2 Mt in 1978 to 0.3 Mt (85% decrease) in 1982 and, in response, the weight at age of Icelandic cod (ages 5–8 yr) declined by 25–30% (Vilhjálmsson 2002). Similar responses were observed in the Barents Sea, where overfishing of capelin during the 1980s resulted in a sudden 6 Mt collapse (Gjøsæter et al. 2009). This was followed by a 1–2 kg reduction in the average weight at age of 4–6 yr old cod (Mehl & Sunnanå 1991). In addition, the population of harp seals *Pagophilus groenlandicus*, a principal capelin predator, which had previously been increasing at a rate of 5% per year, exhibited a pronounced levelling off of population growth during the period of the capelin collapse (Gjøsæter et al. 2009). A massive influx of starving harp seals into the near-shore zone followed the collapse, resulting in an unprecedented bycatch of 57 000 and 21 000 seals in the 1987 and 1988 coastal fisheries (Haug et al. 1991). Coincident with the capelin collapse, the population of common murres *Uria aalge* at 2 breeding colonies (Hornoya and Bear Island) experienced precipitous 85–90% declines from a peak of 245 000 breeding pairs (Erikstad et al. 2013). Finally, the area occupied by the collapsed Barents Sea capelin stock shrank by 50–60% (Michalsen et al. 2013), and the abundance of their principal zooplankton prey increased (Gjøsæter et al. 2002).

The abundance and behaviour of capelin in the NL region during their annual migration cycle has been

Table 1. Publications commenting on the status of the Newfoundland–Labrador capelin (*Mallotus villosus*) stock and the dynamics of this ecosystem after 1991

Reference	Comment
Rose (2003, p. 3)	'The best known example of decline is the northern Atlantic cod, but this is only one of many species that is likely at all time historic low levels of abundance, including … pelagic fishes, especially capelin'
Rose (2007, p. 505)	'The capelin stock collapsed over most of its former range in Newfoundland and Labrador just before the final collapse of the cod stocks'
DFO (2010, p. 28)	'A dramatic increase in the biomass of invertebrates (e.g. crab and shrimp) occurred coupled with the loss and lack of recovery of capelin, a key forage species'
Dwyer et al. (2010, p. 442)	'Today there is consensus that since the 1990s capelin biomass in the study area has been significantly lower than it was in the mid to late 1980s'
Dawe et al. (2012, p. 246)	'…, it is clear (especially for Newfoundland) that depletion of predators did not result in increased abundance of the primary forage species, but rather that capelin declined as part of a collapse of the entire finfish community'
Lilly et al. (2013, p. 110)	'Reasons for the collapse and non-recovery of capelin are not well understood'
Buren et al. (2014a, p. 1)	'Capelin stock suffered a major biomass decline in 1991, from which it has not yet recovered'
Buren et al. (2014b, p. 278)	'The changes in capelin biology and ecology that took place during the1990s, and most importantly its severe abundance decline, must have represented a serious burden'
Mullowney & Rose (2014, p. 785)	'An often overlooked part of the many descriptions of the collapse of Northern cod is that its chief food source, capelin, collapsed at about the same time'
Obradovich et al. (2014, p. 775)	'Capelin stocks collapsed in the early 1990s, concurrent with declines in Northern cod. Neither has yet fully recovered'
DFO (2014, p. 2)	'The Newfoundland marine ecosystem underwent a regime shift in the early to mid-1990s and included the collapse of historically dominating groundfishes, and key forage species like capelin. Shellfish became the dominant functional group in the ecosystem'
Mullowney et al. (2016, p. 144)	'The capelin stock off the northeast coast of Newfoundland and southern Labrador collapsed in the early 1990s along with most of the finfish community. We postulated that the later spawning of northern capelin over the past 2 decades has led to poorer recruitment and created a 'mismatch pit' in which stock productivity has been held at a low level'

monitored and quantitatively assessed in several ways from the late 1970s to present. In Div. 3L, these include (1) offshore acoustic surveys of about 2 wk duration, generally taking place during May, targeting maturing capelin, (2) inshore aerial photographic surveys about 1 mo later (generally during June) of pre-spawning capelin schools, (3) determination of commercial catch rates of pre-spawning capelin for the inshore fishery, (4) annual recording of the timing of peak spawning on beaches and estimation of larval production following a 2–4 wk egg incubation period (DFO 2013), and (5) in Div. 2J3KL, estimates of post-spawning adult and maturing capelin abundance in annual DFO offshore bottom-trawl research surveys during November and December.

Given the ecosystem responses that followed the collapse of Icelandic and Barents Sea capelin, we expected to find evidence of similar impacts in NL. We therefore examined population growth rates, condition factors and diet composition of major fish, mammal and avian predators, the geographic range and behaviour of capelin, and zooplankton abundance, as well as variability in the physical environment. We begin with an integrated overview of the NL ecosystem. We next investigate the nature of these inter-connections in greater detail with particular emphasis on whether the evidence does or does not support the reported collapse of capelin. Finally, we explore 2 hypotheses that could account for the interpretation that the capelin stock has collapsed: changing migratory patterns against the background of a temporally and spatially fixed capelin survey; and the possibility that the capelin stock has become less migratory since the early 1990s.

INTEGRATED OVERVIEW OF NL ECOSYSTEM

Interconnections and coherence among a suite of biotic and abiotic variables were examined using principal component analysis (PCA). We assembled 11 complete time series (1982–2008; Table S1 in the Supplement) that reflected the biological variability associated with capelin (4 series), their predators (4 series associated with cod), species occupying the same trophic level as capelin (2 series), and the physical environment (8 series). Note that 3 variables — cod liver condition, cod weight at age and the physical environment — consisting of 6, 9 and 8 series respectively, were well represented by 2 (variables associated with cod) or 1 (physical environment) series derived from separate PCAs of these variables (Figs. S3 to S7 in the Supplement). The

leading PCA mode (PC1) based on the correlation matrix of these 11 series accounts for 51% of the variance, has moderate to strong loadings for 10 of the 11 variables (Fig. 3A), and features a clear transition from positive to negative values during the period 1987–1993, with the greatest change centred on 1991, the year of the reported capelin collapse (Fig. 3C). The time series of PC1 is positively related to the biomass estimates of capelin ($R^2 = 0.39$; Fig. 3D), and more strongly of cod ($R^2 = 0.91$; Fig. 3E). The strong relationship of cod to PC1 arises from the dominance of low-frequency variability in both series: initially both series have high values, followed by a 6–7 yr transition period, then to sustained low magnitudes. It also suggests a more dominant role for cod as an ecosystem driver than for capelin.

Restricting the PCA to complete series directly excludes several important variables, including capelin biomass from the acoustic surveys, cod biomass, capelin inshore school area, capelin catch per unit effort (CPUE) from the inshore trap fishery, and shrimp CPUE. However, by including these series with the original 11 and extending the analysis period from 1982 to 2012 (84% data coverage to estimate the correlation matrix), a set of loadings with strong contributions from the added variables was found (Fig. 3B). Moreover, the loadings of the 11 variables common to both analyses are highly coherent ($R^2 = 0.995$). Cod biomass remained the leading component emerging from this analysis.

The general overview derived from the PCA indicates strong connections among capelin, species occupying an equivalent trophic level and capelin predators, and a moderate coupling with environmental variability (3rd or 4th weakest loading; Fig. 3A,B). It is also clear that 1991 was a pivotal year, not just for the estimate of capelin biomass but for many of the NL ecosystem variables included in the analyses. Though it was one of the weaker components of the PCA, we note that the physical series indicates that 1991 was the coldest year in the period 1982–2012 based on the analysis of 7 variables reflecting the thermal state of the environment (Fig. S7 in the Supplement).

CAPELIN

Offshore capelin distribution: acoustic surveys

Following a spring migration from offshore banks to inshore spawning grounds, post-spawning and maturing capelin normally undertake a fall migration
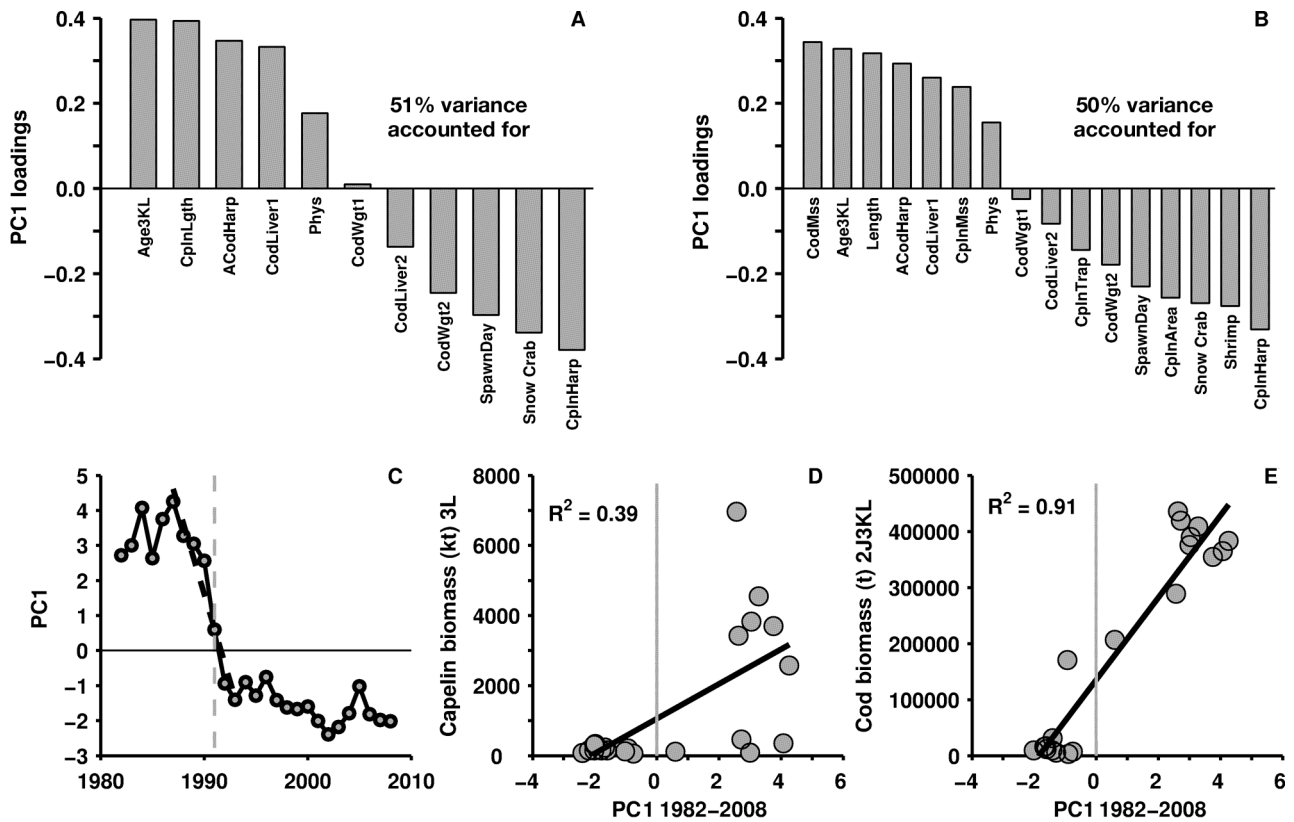
Fig. 3. (A) Principal component 1 (PC1) loadings based on 11 complete series (Table S1 in the Supplement) for 1982–2008. (B) PC1 loadings based on 16 series (Table S1) for 1982–2012. Overall data coverage for these series was 84%. (C) Time series of PC1 based on loadings shown in (A). Vertical broken line marks 1991. (D) Comparison of PC1 time series with capelin (*Mallotus villosus*) biomass estimates derived from acoustic surveys. (E) Comparison of PC1 time series with cod (*Gadus morhua*) biomass estimates derived from annual groundfish surveys

to areas off the coast of Labrador and northern New-foundland in Div. 2J3K (Carscadden et al. 2013). These offshore concentrations of capelin once supported a short-lived, intensive commercial fishery during the 1970s prosecuted mainly by Russian (former USSR) mid-water trawlers (Carscadden & Nakashima 1997). DFO and Russian fall acoustic surveys (1981–1994) both showed a shift in the location of the highest capelin densities from Div. 2J during the 1980s to the southern half of Div. 3K in the early 1990s, albeit at very low densities (Carscadden & Nakashima 1997). The fall survey biomasses were unexpectedly low in 1990, given the large spring values of 7 Mt (DFO, Div. 3L) and 3.8 Mt (Russian, Div. 3LNO) recorded that same year (Fig. S1A in the Supplement). Extremely low biomass estimates were found in the post-1990 fall surveys in Div. 2J3K (Fig. S1B in the Supplement). These observations suggest the possibility that capelin did not migrate offshore, particularly in the fall of 1990, at least not into Div. 2J3K.

Carscadden et al. (2013) reported that maturing capelin occur in deep water of the inshore bays along eastern Newfoundland but could not establish whether these aggregations represented separate, resident stocks or were part of a continuous distribution of one stock that occurred both in the bays and offshore. The only inshore, year-round study of capelin, in Trinity Bay during 1967–1968, revealed the presence of large inactive concentrations over-wintering at depths of 140–200 m; the concentrations were not quantified but were deemed large enough to support a commercial mid-water trawl fishery (Winters 1970).

Offshore capelin distribution: annual bottom-trawl surveys

It has been widely observed that the area occupied by marine fishes varies directly with their abundance (reviewed in Fisher & Frank 2004). This response has

been documented for Barents Sea capelin (Michalsen et al. 2013). We therefore analysed pre- and post-1991 capelin distributions in NL with the expectation that the post-collapse area inhabited would be considerably smaller. In this analysis, we used the 1971–2013 capelin observations from the DFO autumn bottom-trawl surveys conducted in Div. 2J3KL. The survey gear type changed from an Engels trawl (1971–1994) to a Campelen trawl (1995–present). Trawl tow time also decreased from 30 to 15 min coincident with this gear change, requir-

ing the development of corrections to inter-compare the data series (Section 'Centre of concentration of capelin from the annual fall groundfish survey' in the Supplement).

Following the standardization, we calculated the proportion of capelin occupancy for each time period and cell. This analysis was performed using numbers of capelin per tow. Linear and binomial models fitted to the data indicate that there have been no significant changes in the geographic area occupied (p = 0.47) by capelin prior to or after 1991, the year of the reported capelin collapse (Fig. 4). There was, however, evidence of a systematic onshore displacement of the centre of capelin biomass concentration (Fig. S2 in the Supplement). From 1986 to 1995, the average centre of concentration was located at 50.8° N (SD: ±1.2), 52.2° W (SD: ±2.6); for the period 1996–2010, it was found at 50.2° N (SD: ±0.5), 55° W (SD: ±1.7), 195 km onshore of the earlier position (p = 0.025). Our result for the post-1996 period is consistent with the catch-weighted centre of mass analysis using the Campelen trawl survey data alone (DFO 2015b). The timing of this geographic displacement corresponded to a general increase of ocean temperatures in the Div. 2J3KL region (Colbourne et al. 2014).

Changes in the distribution of capelin have been observed in other regions of the western North Atlantic. Frank et al. (1994, 1996) reported a progressive increase in capelin bycatch (from one to several hundred per standard tow) in the 1988–1993 spring and summer groundfish surveys on the eastern Scotian Shelf. The largest increase, from 1991 to 1992, was coincident with the transition identified by the PCA for the NL region (Fig. 3C). Frank et al. (1996) hypothesized that the most likely source of these capelin was the Gulf of St. Lawrence, but could not rule out the possibility of immigration from NL. Kenchington et al. (2015), who applied genetic methodologies on samples of Scotian Shelf capelin collected from 2002 to 2008, con-
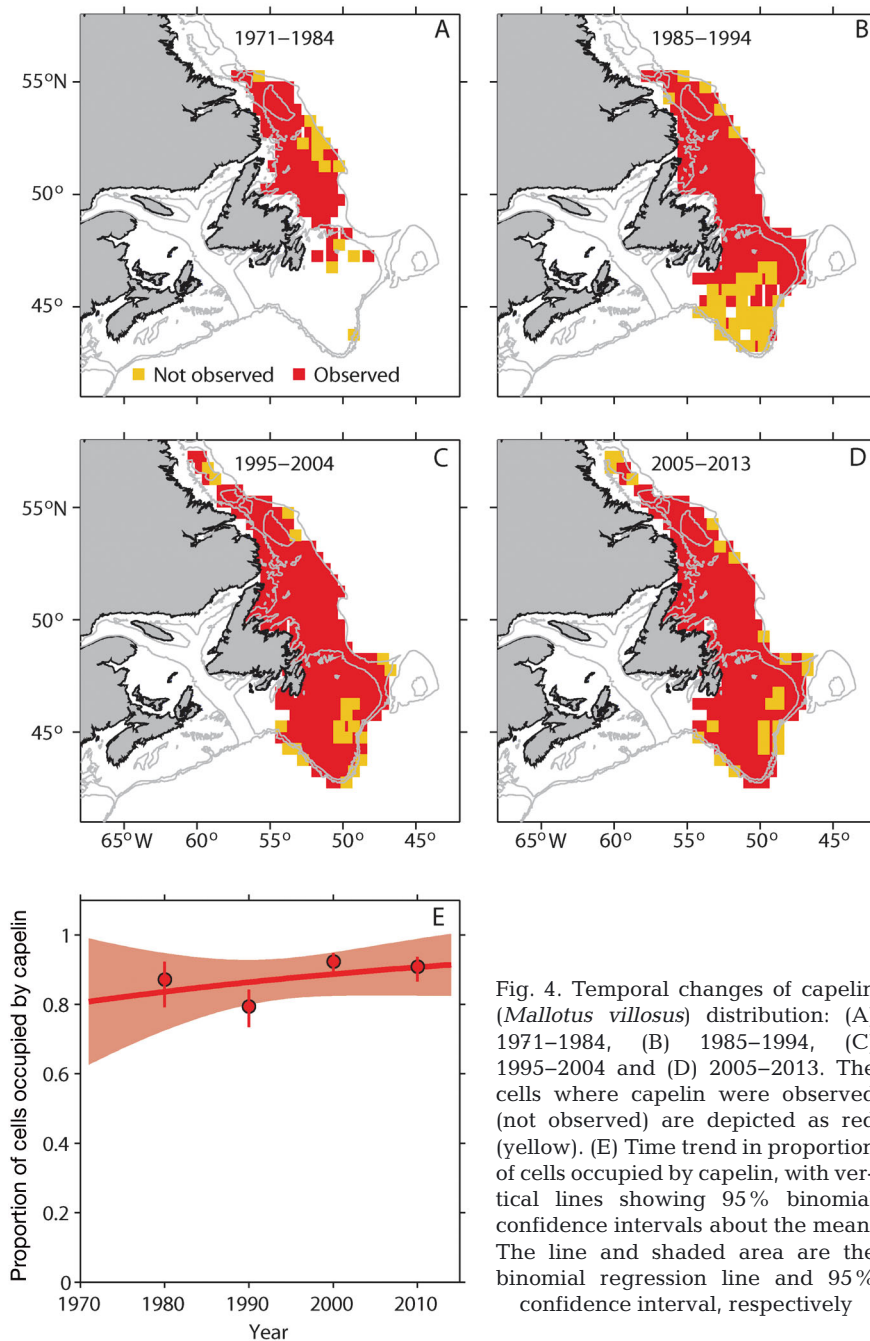

Fig. 4. Temporal changes of capelin (*Mallotus villosus*) distribution: (A) 1971–1984, (B) 1985–1994, (C) 1995–2004 and (D) 2005–2013. The cells where capelin were observed (not observed) are depicted as red (yellow). (E) Time trend in proportion of cells occupied by capelin, with vertical lines showing 95% binomial confidence intervals about the mean. The line and shaded area are the binomial regression line and 95% confidence interval, respectively

cluded that the offshore demersal spawners on the eastern Scotian Shelf were related to the inshore demersal spawners from eastern Newfoundland and southern Labrador, and to beach spawners from the Gulf of St. Lawrence. Concurrent increases of capelin were evident as bycatch in the shrimp fishery on Flemish Cap (Div. 3M), where, in 1993, capelin were present in 72% of the sets. In the case of Flemish Cap, below-normal ocean temperatures were believed to be the primary cause of migration into this area (Frank et al. 1996).

Capelin depth distributions during offshore acoustic surveys in Div. 3L

Prior to 1991, capelin undertook extensive diel vertical migrations throughout the survey area (DFO 2013). Beginning in 1991, capelin altered this behaviour and remained at much greater depths throughout the day, a pattern which persisted until 2011. For the 3 yr (1988−1990) before the reported collapse, capelin were found at an average depth of 79 m, 87 m above the mean bottom depth. From 1991 to 2012, eleven NL acoustic surveys reported capelin at an average depth of 201 m, 25 m above the mean bottom depth. During 1991, capelin were on average 4 m off the bottom, the closest to the bottom in the 14 yr record (DFO 2013).

Residence time of capelin concentrations during offshore acoustic surveys in Div. 3L

When assessing the abundance of a species during the migratory phase of its life cycle, it is vital that the survey design fully encompasses the residence time of the species in the surveyed area. This will provide reliable assessments of population biomass. As designed and implemented, Div. 3L acoustic surveys for capelin were typically centred on 24 May (SD: 15.8 d) and lasted 2 wk. There are no estimates of the residence time of capelin in this region, so there is a possibility that the survey duration is inadequate. Assuming that the results of each year's survey prior to 1991 represent a stage in the build-up or decline of capelin concentrations in Div. 3L, and that capelin migration occurs with the same timing each year, it is possible to estimate residence time of capelin in the survey area by combining all data from 1984 to 1991. This provides an approximation of how a synoptic, continuous survey within a single year might appear. We fitted the survey results with symmetric exponen-
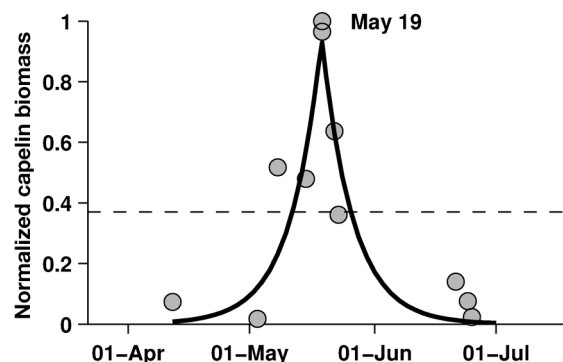

Fig. 5. Normalized capelin (*Mallotus villosus*) biomass estimates from 1984 to 1991 acoustic surveys of Div. 3L (circles) centred on mid-survey date and fit of $A \cdot \exp(-|t-t_0|/\tau)$, where A is amplitude, t is survey time, t_0 is time of peak concentration, and τ is temporal decay scale. Horizontal dashed line represents the e-folding amplitude (= 0.37)

tials of the form $A \cdot e^{(-|t-t_0|/\tau)}$, where A is the amplitude, t is the survey time, t_0 is the time of peak concentration, and τ is the temporal decay scale. The value $2 \cdot \tau$, the e-folding time, is the duration of concentrations greater than $A \cdot e^{-1}$ (=$0.37 \cdot A$). For the fit, concentrations were normalized by dividing by the highest value. The results indicate that the time scale for concentrations greater than e^{-1} is about 20.8 d, with a peak concentration around 19 May ($R^2 = 0.80$; Fig. 5). This time scale is comparable to the duration of the Div. 3L acoustic survey and should produce a reliable estimate of capelin biomass, provided that the timing of capelin migration to inshore spawning areas does not vary.

Independent indexes of inshore capelin abundance

Two independent indexes of mature capelin abundance spanning the period of the reported collapse have been developed for the inshore region of Div. 3L. The number and size of capelin spawning schools adjacent to the major spawning beaches of eastern Newfoundland have been monitored since the mid-1980s using aerial photographic techniques (Evans & Nakashima 2002). The index of capelin abundance derived from these surveys increased progressively from the mid-1980s to the mid-1990s (Fig. 6). These observations are not consistent with the reported 1991 collapse of capelin based on the acoustic surveys. Commercial catch rates from the inshore trap fishery for capelin (DFO 2001) also indicate an increase in capelin abundance from the early to mid-1980s through 1996−1997 (Fig. 6). These catch rates
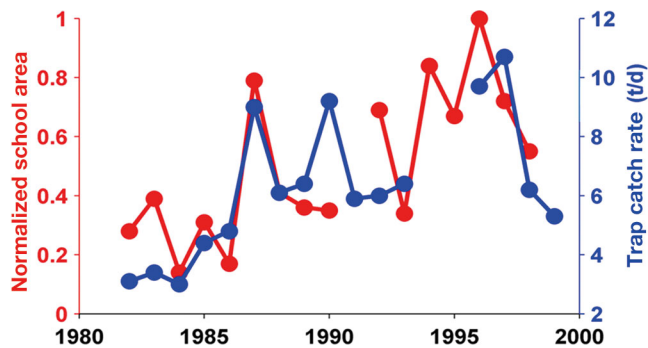
Fig. 6. Time series of 2 indexes of capelin (*Mallotus villosus*) stock size from inshore areas off eastern Newfoundland: area of aggregations of adult capelin in Conception and Trinity Bays near spawning beaches based on aerial surveys from fixed-wing aircraft (red) and catch rates of capelin from capelin traps in Div. 3KL (blue)

are strongly correlated (r = 0.73) with the abundance index derived from the aerial surveys. The inconsistency between the trend of increasing capelin abundance reflected in these inshore indexes and the reported 1991 collapse and subsequent lack of recovery indicated by the offshore acoustic data was raised by Carscadden & Nakashima (1997). The authors questioned the wisdom of the continuing use of the acoustic survey data in the capelin stock assessments. The capelin stock status report (DFO 2000, p. 5) notes, 'There is still an unreconciled difference between the low acoustic estimates during the early 1990's and in 1999, and inshore indices.' However, to date, the acoustic surveys remain one of the fundamental inputs for these assessments and for the conclusion that a major capelin collapse occurred in 1991 (Table 1).

Demographic change of harvested inshore capelin

The average age and length of male and female adult capelin harvested in Div. 3KL show clear transitions from higher to lower values centred on 1991 (Fig. 7). The pre-1991 average age (±SD) of harvested fish was 3.4 ± 0.2 yr, while the post-1991 average age was significantly (p = 0.001) lower at 2.7 ± 0.2 yr. Similarly, adult body lengths (±SD) were significantly (p < 0.001) longer (male, 186 ± 3 mm; female, 165 ± 3 mm) pre- compared to post-1991 (male, 166 ± 4 mm; female, 148 ± 4 mm). These 3 series (male and female body length, harvested fish age) are strongly correlated (range of r: 0.9–0.98). The temporal coincidence, magnitude and persist-

ence of these demographic parameters imply that significant changes occurred in 1991.

Timing of inshore capelin beach spawning

The peak spawning time of beach-spawning capelin in NL exhibited a pronounced shift at the time of the reported capelin collapse (Fig. 8A,B). Prior to 1991, peak spawning occurred on average on 21 June, 28 d after the mid-point (24 May) of the offshore acoustic surveys. Beginning in 1991 and thereafter, average peak spawning shifted to 16 July, 53 d after the acoustic survey midpoint. If this 25 d delay in the average timing of capelin spawning activity on the beaches is representative of a similar 25 d delay in the timing of the arrival of high concentrations in the offshore acoustic survey area, it is possible that the post-1990 acoustic surveys, which remained largely unchanged in time and duration, were conducted too early to accurately assess the annual biomass of capelin in Div. 3L. Temporal shifts in migration timing of as much as 45 or more days have been observed for the Icelandic capelin stock (Vilhjálmsson 1994). The shifts relative to the timing of acoustic surveys could have dramatically reduced capelin detection frequencies in this region unless other adaptive measures were taken (Vilhjálmsson & Carscadden 2002).

In 1991, two acoustic surveys in Div. 3L were conducted; the first from 7 to 26 May gave a biomass estimate of 0.12 Mt, and the second from 25 June to 12 July gave an estimate of 0.15 Mt (Miller & Carscadden 1991; see also our Fig. S1A in the Supplement). Peak beach spawning occurred on 21 July 1991. If the peak offshore concentration of capelin
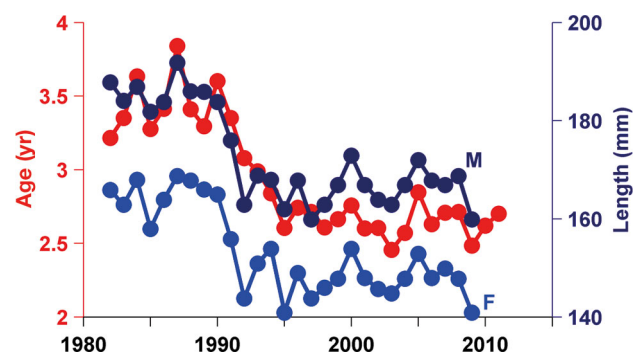

Fig. 7. Time series of age of harvested inshore capelin *Mallotus villosus* (red), and adult body length of male (M, dark blue) and female (F, light blue) capelin in Div. 3KL (DFO 2013). Note that F and M capelin body lengths are highly correlated (R² = 0.96)
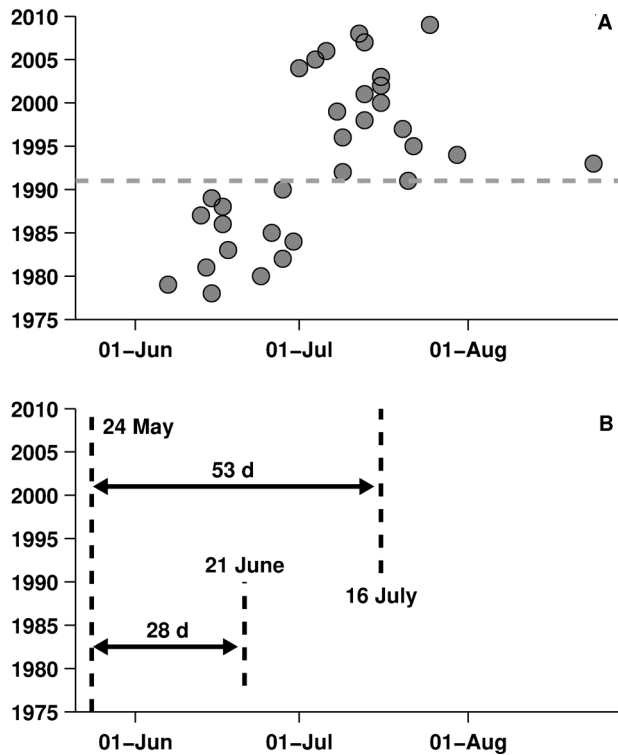
Fig. 8. (A) Timing of peak beach spawning of capelin (*Mallotus villosus*), illustrating later spawning times after 1990. Data from Bryant's Cove and Bellevue Beach (DFO 2013). (B) Average date (24 May) of the offshore acoustic survey in relation to the average of the peak spawning times prior to 1991 (21 June) and 1991 and later (16 July). Time intervals separating peak spawning dates and the offshore acoustic survey are shown

occurred roughly 28 d prior to peak inshore spawning, then in 1991 it should have taken place about 23 June, just before the start of the acoustic survey (see Fig. 8B). However, given our estimate of the temporal decay scale (i.e. residence time in the offshore; Fig. 5), the survey would likely have been positioned to detect high concentrations of capelin if they were present. Russia also conducted an acoustic survey from 6 June to 6 July in 1991 in Div. 3LNO, which yielded a biomass estimate of 0.12 Mt. Russian surveys in Div. 3LNO were also conducted in 1993 (8–25 June) and 1994 (14–24 June), yielding biomass estimates of 0.32 and 0.08 Mt, respectively (Fig. S1B in the Supplement).

Inshore recruitment index

Nakashima & Mowbray (2013) reported 5 indexes of capelin recruitment for Div. 3KL. Only the time series for the August larval capelin production index for Trinity Bay (Div. 3L) has sufficient data with

which to compare pre- and post-1991 recruitment levels. The average larval capelin concentration during the pre-1991 years (48 m^{-2}, SD: 15, surveys from 5 yr) did not differ significantly from the post-1991 average (39 m^{-2}, SD: 27, surveys from 5 yr). This finding is inconsistent with a sustained ~6 Mt reduction in capelin biomass in the NL ecosystem beginning in 1991.

ECOSYSTEM RESPONSE

Temporal dynamics of cod weight at age and condition

Capelin are a major component of the diet of cod in NL, and the growth and condition of cod have been shown to be sensitive to variation in the abundance of capelin in the ecosystem (Rose & O'Driscoll 2002). Cod weights at age have been assessed annually in Div. 2J3KL from fall research bottom-trawl surveys beginning in 1978 (Fig. 9). We evaluated the coherence of the temporal variation in the 3–5 yr old cod weight at age time series through a PCA. The first 2 PCA modes effectively separated Div. 2J and 3K from 3L, captured 46 and 22% of the overall variance, respectively, and featured comparable loadings for all 6 series for Div. 2J and 3K (leading mode) and for all 3 series from Div. 3L (second mode; Figs. S3 & S4 in the Supplement). Weight at age of 3–5 yr old cod in Div. 2J and 3K declined to minimum values in the early 1990s, about the time of the reported capelin collapse in Div. 3L. Of the 12 time series of weight at age, 5 showed significant (p < 0.05) differences between the pre- and post-1991 periods: the weight at age of Div. 2J 5 yr and Div. 3K 4 yr old cod declined, whereas the weights of Div. 3L 3–4 yr old cod increased (Fig. 9; Table S2 in the Supplement). The increase of weight at age in Div. 3L is inconsistent with the reported capelin collapse. Krumsick & Rose (2012) determined the diets of cod collected between March and September in 1997–2003, 2008 and 2011 from Div. 2J, 3K, 3L and 3Ps. Over the entire region, capelin was the leading prey item at 31.6% by weight. On average, capelin constituted <7.4% of the cod diet from Div. 2J, but made a progressively larger contribution in Div. 3K (13.5%) and Div. 3L (61.3%). In Div. 3Ps, capelin contributed 33.5% to the total diet. However, we note that cod biomass had reached low values in the early 1990s, which were sustained, and therefore it is possible that capelin availability had not declined relative to the diminished cod biomass.

Rose & O'Driscoll (2002) reported a strong positive relationship ($R^2 = 0.73$) between the ratio of liver to gutted body weight of 30–65 cm cod and a measure of the local (within a 40 km radius) availability of capelin, as assessed by acoustic surveys conducted during 1996–2001, independent of those run by DFO. We therefore examined temporal trends in the pre- and post-1991 liver condition index for 37 cm (immature) and 49 cm (mature) cod sampled in annual DFO research surveys (Taggart et al. 1994). Annual standardized anomalies of the index for 37 and 49 cm cod in Div. 2J and 49 cm cod in Div. 3K varied coherently,

Fig. 10. Normalized ((Observation − Average)/SD) annual liver index for 37 (open circles) and 49 (filled circles) cm cod *Gadus morhua* in Div. (A) 2J, (B) 3K and (C) 3L based on the DFO fall research vessel surveys (Brattey et al. 2011). Dashed vertical line denotes 1991

with peak values in 1986, decreasing to sustained low values in 1991, the time of the reported capelin collapse (Fig. 10; see also Figs. S5 & S6 in the Supplement). In Div. 3K (37 cm) and 3L, the opposite occurred. The differences of the pre- and post-1991 liver indexes were significant for all but the Div. 3K 49 cm cod (Table S3 in the Supplement). The index decreased for both size classes in Div. 2J and increased for both in Div. 3L as well as for Div. 3K 37 cm cod. The increased condition index in Div. 3L is inconsistent with the reported capelin collapse there.

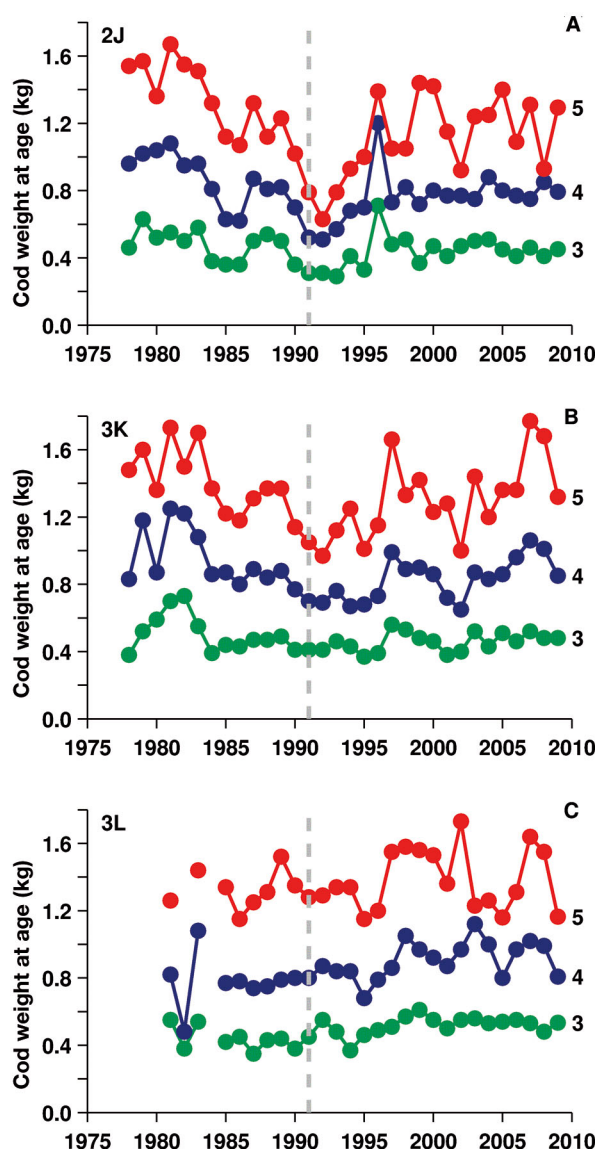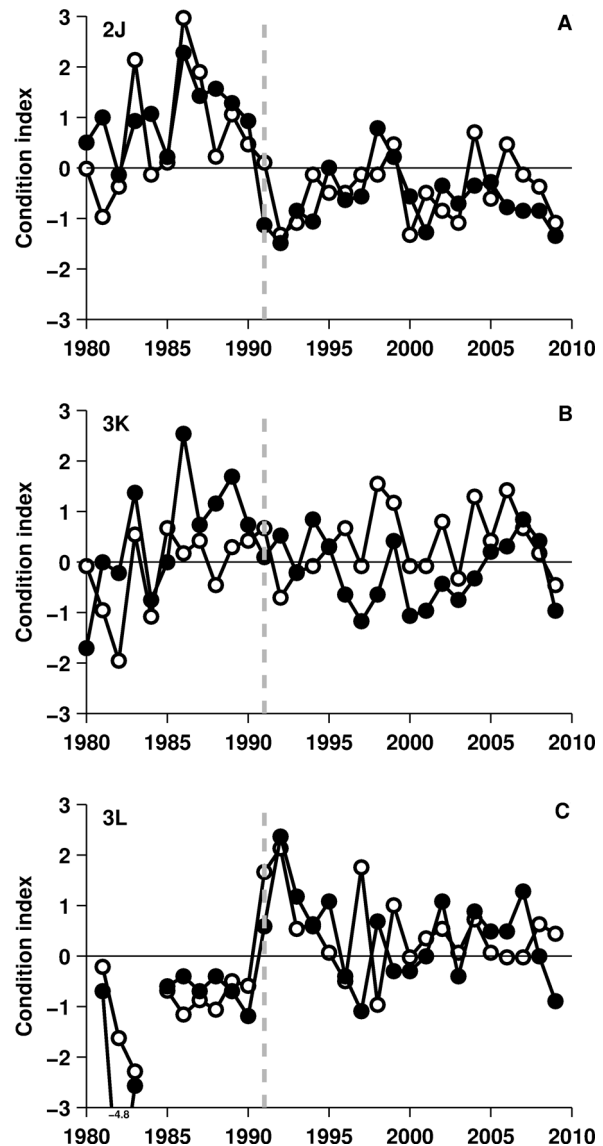In summary, both the analysis of cod weight at age

Fig. 9. Annual weight at ages 3 yr (green), 4 yr (blue) and 5 yr (red) for cod *Gadus morhua* in Div. (A) 2J, (B) 3K and (C) 3L from fall research vessel surveys conducted by DFO (Brattey et al. 2010). Dashed vertical line denotes 1991

and liver condition indicate that changes occurred in the cod-capelin trophic dynamics in the early 1990s, particularly in Div. 2J, that were roughly coherent with the dramatic decline in biomass estimates from the Div. 3L capelin acoustic surveys. However, this was not the case in the southern part of the region (Div. 3L), and mixed results were obtained in Div. 3K.

Harp seal population trends and diet

The NL harp seal population, a major predator of capelin, experienced a sustained increase from a low of ~1.7 million in 1977 to ~7 million animals in the mid- to late 2000s (Fig. 11A). Contrary to expectation based on observations in the Barents Sea, there was no evidence of a slowing of seal population growth following the reported 1991 collapse of capelin. Indeed, the rate of population increase continued undiminished until the mid-1990s. The slowing in the rate of population increase that occurred post-1998 has been attributed to increased rates of exploitation (Templeman 2010). Moreover, while large numbers of weakened or starving harp seals were observed following the collapse of capelin in the Barents Sea, there have been no reports of such occurrences in NL prior to or after 1991. In fact, Stenson (2012) estimated that the annual consumption of capelin by harp seals increased from ~0.5 Mt in 1991 to ~1.4 Mt in 2008. Notably, Stenson's estimate of capelin consumption by seals in 2008 alone (1.4 Mt) exceeded, by 8-fold, the post-1991 average biomass of NL capelin as assessed by the acoustic survey (Fig. 2). When the seal consumption estimates of capelin calculated by Stenson (2012) are combined with estimates of capelin consumption by fish (includes cod, turbot, American plaice, redfish and yellowtail flounder) and whales (species unspecified), it ranged from 2.8 to 3.4 Mt (DFO 2015a).

Seabird population trends

The Funk Island (Div. 3L) colony of common murres off eastern Newfoundland has been monitored continuously since the mid-1980s. Capelin is a primary food of this species (Davoren & Montevecchi 2003). Contrary to expectation and co-incident with the reported collapse of capelin, the number of breeding adults with chicks increased from 10 000 to 100 000 and has remained near 100 000 individuals (Davoren & Montevecchi 2003; our Fig. 11B). During the same time period, the contribution of capelin

dominated the diet of murre chicks ranging from 74 to 99% (Davoren & Montevecchi 2003).

The diets of northern gannets *Sula bassana* during the month of August at the Funk Island colony have been examined annually from 1977 to 2004 (Montevecchi & Myers 1997, Montevecchi 2007; our Fig. 11C). From 1977 to 1989, capelin constituted <12% of their diet. However, from 1990 to 2004, during the period of the reported collapse, capelin was the most common item of the northern gannets' diet
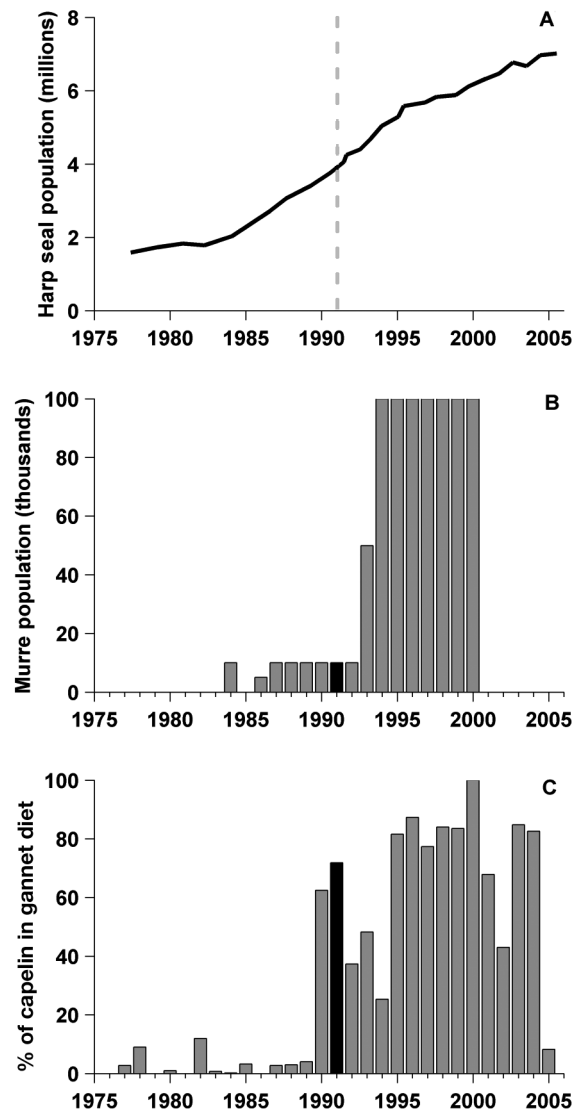

Fig. 11. Temporal changes in population sizes of (A) harp seals *Pagophilus groenlandicus* in the Newfoundland–Labrador region, (B) common murres *Uria aalge* (order of magnitude estimates) at the Funk Island colony and (C) percentage contribution of capelin *Mallotus villosus* in the diets of northern gannets *Sula bassana* at the Funk Island colony. Dashed vertical line in (A) and blackened bar in (B,C) marks the 1991 timing of the reported capelin collapse

(26–100%). Montevecchi & Myers (1997) hypothe-sized that the increased prevalence of capelin in the gannets' diets in August was linked to the delayed inshore spawning of capelin in the 1990s, leading to greater local availability of capelin within the forag-ing range of gannets from the Funk Island colony.

The breeding colonies of Atlantic puffin *Fratercula arctica*, a major predator of capelin, at Great and Gull Islands in Witless Bay (Div. 3L) have been monitored continuously since 1979 (Robertson et al. 2004). At the Great Island site, puffin populations increased by 3.5% yr^{-1} from 1984 to 1994 and at Gull Island by 8.3% yr^{-1} from 1984 to 2003. Neither the Great Island nor Gull Island puffin colonies showed any evidence of a negative population response to the reported capelin collapse. In a review of the status of these and other seabird species colonies along the coastal areas of NL, Carscadden et al. (2002) concluded that their population sizes remained stable or increased throughout the 1990s — a time of changing capelin behaviour and ecology.

Zooplankton response: *Calanus finmarchicus* abundance

The copepod *Calanus finmarchicus* dominates the diet of both juvenile and adult capelin in the NL re-gion, comprising over half or more of their stomach content (O'Driscoll et al. 2001, Dalpadado & Mowbray 2013). In the Barents Sea, a strong inverse relation-ship between zooplankton abundance and capelin biomass has been observed, indicating that grazing by capelin has a negative effect on zooplankton abundance (Dalpadado et al. 2001, Gjøsæter et al. 2002). Given the magnitude of the reported collapse of capelin in 1991, a significant increase in the abun-dance of *C. finmarchicus* might have been expected.

The Sir Alister Hardy Foundation for Ocean Sci-ence (SAHFOS 2015) provides an index of *C. fin-marchicus* abundance for standard areas of the North Atlantic Ocean. We evaluated the pre- and post-1991 annual integrated *Calanus* abundance for SAHFOS region E9, which overlaps the area of the Div. 3L acoustic survey. We included all years for which com-plete (12) monthly averages, or for which 11 of 12 monthly values were available. In the latter instance, we substituted the relevant annual monthly mean for the pre-1991 or 1991–2007 periods as appropriate. Contrary to expectation, based on the assumption of a sustained ~6 Mt collapse of capelin beginning in 1991, there was no significant difference between the pre- and post-1991 annual integrated *Calanus*

abundance (±SE) (pre-1991: 229 ± 20 individuals; post-1991: 236 ± 36 individuals). On the other hand, if our estimate of ~21 d residence time for migrating capelin in Div. 3L is correct, the impact of capelin grazing pressure on the *Calanus* population would be small. Combined with the fact that during spring, ~60% of capelin sampled for diet determination in the offshore (southern Labrador and Northeast Grand Banks) had empty stomachs (O'Driscoll et al. 2001), this makes it highly unlikely that changes in copepod abundance in this region from one time to another could be attributed to biomass variability of capelin.

Physical variability

Ocean climate, and in particular temperature, is an important driver of coherent, broad-scale ecosystem variability (e.g. Drinkwater et al. 2010) which could have contributed to the reported collapse of capelin in NL. Nakashima (1992) hypothesized that pre-spawning capelin may follow migration patterns guided by a detectable current, such as the inshore branch of the Labrador Current. Consequently, we investigated 7 time series that represented the tem-perature field and the nearshore current of the New-foundland ecosystem (Fig. S7 in the Supplement). The variables considered included (from Colbourne et al. 2014) (1) April–June ice cover south of 55° N, (2) area of the cold intermediate layer (CIL) for both the SE Grand Bank and (3) Flemish Cap (47° N) hydrographic sections, (4) April–June 0–100 m and 100–150 m integrated temperatures from Stn 27 located 7 km offshore of St. John's, (5) bottom tem-peratures from NAFO Div. 3LNO, (6) sea surface temperature for the SE Shoal (Petrie et al. 2008), and (7) calculated residual adjusted sea level (ASL) at St. John's (www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html). The ASL is re-lated to the current, v, through geostrophy, where $v = -(g/f)(\Delta\zeta/L)$, g is the gravitational acceleration, f is the Coriolis parameter, $\Delta\zeta$ is the residual adjusted sea level and L is the width of the Avalon Channel, taken as 80 km. Comparison of the calculated ASL values with a limited number of current meter observations made in the Avalon Channel for 10 months in 1980–1981 and for 8 months in 1994–1995 indicated that ASL was only weakly correlated ($R^2 = 0.007$) with the observed Avalon Channel flows. However, given that the ASL was the only multi-decadal series available that could be used as a proxy for ocean current, it was included in the PCA.

The first mode of the PCA accounted for 56% of the variance, the second 13%. Consequently, only PC1 results are presented (Fig. 12). As anticipated, the weakest loading was for the ASL component. The remaining loadings, which are related to heat content, were uniform in amplitude (SD ~10% of the average value; Fig. 12A), indicating that the variability in these measures was broadly coherent. Positive mode 1 loadings corresponded to years characterized by greater ice cover, more extensive CIL areas and colder water temperatures. Negative mode 1 values, in contrast, were associated with the inverse, i.e. reduced ice cover, less extensive CIL areas and warmer water temperatures. Notably, the PC1 time series was distinguished by a transition from colder to warmer conditions in the mid-1990s, well after the reported 1991 capelin collapse. Several authors (Frank et al. 1996, Carscadden & Nakashima 1997) have shown that changes in ocean climate can influence the distribution and abundance of capelin and could have contributed to the apparent collapse reported in 1991. However, the change in ocean climate as identified in our analysis occurred ~5 yr after the reported collapse.

Over the length of the record and particularly between 1985 and 2005, the ASL was highly variable (Fig. S7H in the Supplement). This indicates that the coastal current is not likely a consistent mechanism to guide the capelin migration as hypothesized by Nakashima (1992). The evidence is weak, therefore, that changes in the physical environment were responsible for the reported 1991 collapse of capelin.

REVISITING THE DIV. 3L OFFSHORE ACOUSTIC SURVEY

The inconsistencies between expectation and observation in the responses of the NL ecosystem to the reported capelin collapse, and between the near-shore and offshore indexes of capelin abundance, prompted us to review some elements of the design and results of the Div. 3L acoustic survey. The review consisted of (1) an inter-comparison with capelin acoustic surveys conducted in other regions, (2) the influence of a grid design change that occurred near the time of the reported collapse, (3) characterization of the pattern of capelin distribution within the acoustic survey domain prior to and after the reported collapse and (4) determination of the probabilities of acoustic detection of peak capelin concentrations after the reported capelin collapse.

Iceland and Norway, both with major capelin fisheries yielding ~1 Mt annually, carry out extensive annual offshore acoustic surveys critical to the development of reliable biomass estimates upon which the fisheries are managed. The surveys employ multiple dedicated ships, flexibility in survey timing and spatial coverage to accommodate interannual changes in capelin distribution and migratory behaviour, and cooperative interactions with the commercial fleets (Gjøsæter et al. 1998, Vilhjálmsson & Carscadden 2002, Gjøsæter 2011). In the Barents Sea, multiple ships have surveyed the resident capelin stock synoptically each September since 1972. The autumn survey is considered an ideal time period because the stock is well dispersed off bottom and actively feeding during the non-migratory phase of its life cycle. In Icelandic waters, acoustic surveys are frequently repeated when initial surveys yield questionable biomass estimates. There, in 7 of the 15 years between 1987 and 2001, 2 surveys were required to achieve reliable estimates, and in 3 years, 5 surveys were conducted. A single survey was judged satisfactory in only 2 of 15 years (Vilhjálmsson & Carscadden 2002).
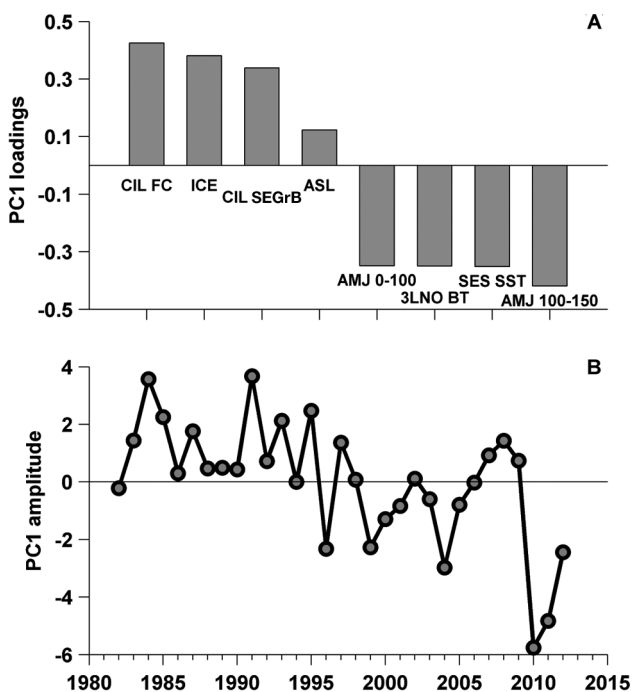

Fig. 12. (A) Loadings for principal component 1 (PC1) of physical variables accounting for 56% of the overall variance. CIL: cold intermediate layer, for Flemish Cap (FC) and SE Grand Bank (SEGrB); ICE: Apr–Jun ice cover south of 55° N; ASL: annual residual adjusted sea level at St. John's; AMJ: Apr–Jun 0–100 m and 100–150 m integrated temperatures from Stn 27; 3LNO BT: Div. 3LNO annual bottom temperature; and SES SST: annual average sea surface temperature from SE Shoal. (B) Time series of PC1

In the 13 years in which >1 survey was required, an upward biomass revision of 250 000 to 900 000 t resulted. Clearly, the intensity of these surveys reflects the economic importance of their respective fisheries. In Canada, where the capelin fishery is of modest economic importance, the survey design for NL capelin differs markedly from those of Iceland and Norway. The timing of the NL survey is chosen to correspond with the seasonal distribution patterns of the different stocks. For Div. 3L, the choice is May to correspond to the pre-spawning concentrations congregating there. It is a single, fixed in time and space survey employing a single vessel. There were some years when multiple surveys were conducted, but these were discontinued after 1994. This 2 wk survey, centred on 24 May, was initiated in 1982 and has been conducted in 25 of the years from 1982 to 2012. Midwater trawl fishing sets are conducted throughout the survey. The survey is restricted to Div. 3L, one-third of the capelin management area (Div. 2J3KL).

Two grid designs have been used to survey capelin in Div. 3L: the pre-1989 grid consisted of a series of 4 saw-tooth transects, 1 in a north–south orientation along the coast, and the other 3 oriented in an east–west direction over the shelf (Fig. S8A in the Supplement at www.int-res.com/articles/suppl/m553 p185_supp.pdf). Subsequently, a latitudinal grid was employed where the initial positions of the lines were randomly determined but remained fixed thereafter. We mapped the observations from the 1990 latitudinal survey, a year featuring high capelin biomass, onto the saw-tooth grid. The total biomass and variance estimates differed, one from the other, by <1%. We also overlaid the longitudinal grid on the 1986 saw-tooth survey, which featured a high biomass; the longitudinal grid captured all of the features of the 1986 survey. We conclude that the change in survey design implemented in 1989 is unlikely to have significantly affected the efficacy of the survey.

It is also important to examine the pattern of capelin distribution within the acoustic survey domain to determine whether or not capelin tended to reside within a particular area and how well the survey resolved the major concentrations of capelin biomass. Capelin biomasses for the pre-1989 surveys were compiled for 4 subareas or strata, whereas for 1989 and subsequent surveys, biomasses were compiled for 6 subareas for a limited number of years (Miller 1991; see also our Fig. S8A in the Supplement). If capelin were strongly confined to a limited area, the relevant duration of the survey required to capture most of the biomass would be less than the typical 2 wk; in that case, it would be more likely that the survey could miss peak capelin concentrations. Based on the 1985–1990 pre-collapse surveys, the latitudinal centre of capelin biomass was located at 47.83° N, i.e. 50% of the biomass was contained in the northern 40% of the survey range, indicative of a northern bias in the distribution (Fig. S8B in the Supplement). This weak latitudinal dependence indicates that 2 wk should be sufficiently long to assess the biomass of capelin in the survey area. However, the analysis shows little decrease of biomass at the northern limit of the survey, implying only partial resolution of the capelin stock. In addition, limited biomass observations by subarea from the post-collapse era show a nearly uniform distribution, unlike what was seen earlier and implying a change in the capelin distribution during the May survey period.

If the shift in the peak capelin spawning times inshore beginning in 1991 represents the same shift in the maximum concentrations in Div. 3L prior to migration, then we estimate the probability that the maximum concentration occurs before 1 June is about 6% and likely missed by the typical May acoustic survey (Figs. 5 & 8; Fig. S8C in the Supplement). However, the observed low biomasses from 1991–2015 necessitate 25 successive years that the survey would have to miss the peak concentration; we estimate the probability that this occurred as ~22%. It is unlikely under these assumptions that the survey would observe a sustained low capelin biomass in Div. 3L if the only change were caused by a delay, i.e. a temporal change, in migration. It does not rule out the possibility of a change in the spatial pattern of the onshore migration.

DISCUSSION

The annual capelin acoustic survey conducted in Div. 3L of the NL ecosystem was the basis for concluding that a sustained ~6 Mt decrease in the biomass of Div. 2J3KL capelin stock occurred beginning in 1991. Concurrent with this and subsequent surveys, several of the inshore indexes, the population growth and dietary requirements of predatory species, and the growth of species occupying an equivalent trophic level indicate a resilient capelin population. Despite these factors and warnings by Carscadden et al. (2013) concerning over-reliance on this survey for the assessment of the NL capelin stock, the results of the spring Div. 3L acoustic survey have generally been taken at face value as an indicator of stock status. From our analyses of the NL ecosystem prior to, during and after the reported

decline, and our inter-comparison with Barents Sea and Icelandic ecosystems, where dramatic ecosystem level impacts of capelin failures were observed, we conclude that no such collapse occurred.

We advance 2 hypotheses which may explain the inability of the offshore acoustic surveys to adequately detect significant quantities of capelin: (1) changes in the timing of life cycle events in capelin; and/or (2) shifts in the behaviour of capelin from a highly migratory stock to one that has become predominantly non-migratory.

Beginning in 1991 and continuing thereafter, the average timing of shoreward migration and peak spawning of capelin on the beaches of Newfoundland experienced an abrupt 25 d average delay. If this delay reflected a similar shift of the timing of the appearance of high concentrations of shoreward migrating capelin in the offshore acoustic survey area, and our estimate of ~21 d residence time on the shelf were true (i.e. comparable to the length of the survey), then biomass estimates could be grossly underestimated. As noted earlier, the low estimated capelin biomasses during subsequent DFO and Russian surveys in June–July 1991 argue against this conclusion, as does the sustained low stock biomasses. However, variability in the delay between peak offshore concentrations and peak onshore spawning, uncertainty in the residence time on the shelf and a changed migration path allow for the possibility that the reported collapse of capelin in 1991, and its virtual absence thereafter, could have resulted from a sustained spatiotemporal disconnect between the timing of the acoustic survey in Div. 3L and the arrival of onshore migrating capelin schools in the survey region. Additional evidence suggests a decoupling of the offshore and inshore capelin populations beginning in 1991. A comparison of the average age based on the distribution of the ≥2 yr old capelin from the spring acoustic survey with the average age of the inshore catch for the pre-1991 and the 1991–2012 periods shows 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; Fig. S9 in the Supplement).

An alternative interpretation involves a modification of the historical view of the annual migration pattern of capelin characterized by over-wintering offshore and a return to nearshore spawning locations each summer. Evidence points to the possibility that ~7 Mt capelin stock seen in the spring 1990 Div. 3L survey did not migrate offshore en masse during the fall when multiple acoustic surveys detected only 0.1–0.6 Mt of capelin in Div. 2J3K, and moreover, that this absence of a fall migration offshore continued (Fig. 2; Figs. S1 & S2 in the Supplement).

Fish migration normally serves to maximize access to productive habitats, and consequently, migrant populations may be quite large due to utilization of resources of vast geographic areas (Gross 1987). Compared to residents, migrants tend to delay maturation, thus attaining larger adult body sizes and higher condition (Jonsson & Jonsson 1993, Gillanders et al. 2015). On this basis, we would expect that if a large fraction of the post-1990 capelin population became coastal residents of the major embayments of eastern NL (i.e. from White Bay in the north to Placentia Bay in the south), noticeable reductions in condition, growth, maturation timing and eventually population size would be expected. There is support for most of these expectations. Annual condition factors (Fulton's K) derived for both male and female capelin from inshore areas in Div. 3KL from 1982 to 1999 switched from mainly positive to negative anomalies in 1991 and persisted in that state (Carscadden & Frank 2002, DFO 2015b). The timing of these changes coincides closely with the hypothesized change in migration behaviour. Observations of capelin length at age (Mowbray 2014) revealed the existence of significantly smaller 2 and 3 yr old capelin during 1985–1992, whereas 4 and 5 yr olds were significantly larger than those during 1996–2012, which suggests that the growth potential of the population has shifted toward smaller adult sizes (Fig. S10 in the Supplement). Further, the proportion of capelin maturing at younger ages has increased dramatically since the early 1990s (Mowbray 2014). Collectively, these shifts in the demographic characteristics of capelin are consistent with the notion of a capelin population dominated by non-migratory individuals.

While it may be biologically challenging for the NL capelin population to remain inshore through the winter and nearshore on nearly a year-round basis, such a distributional shift would clearly increase the availability of capelin to the benefit of the suite of predators that normally inhabit the coastal zone (e.g. Fig. 11B,C). This trophic amplification effect may be responsible for the recent documented recovery of Div. 2J3KL cod, first reported to occur in the nearshore in Trinity Bay and subsequently spreading to offshore areas (Rose et al. 2011, Rose & Rowe 2015). NL cod is considered a stock complex, and it has been argued that the Smith Sound (Trinity Bay) aggregation of cod, the largest inshore concentration ever reported in the region, arose through immigra-

tion occurring in 1995 (Rose et al. 2011). Smith Sound cod experienced relatively low mortality rates, and in 7 yr, doubled in biomass, contrasting dramatically with offshore stock components of cod, most of which exhibited zero or negative growth (Lilly et al. 2006). Since 2007, the biomass of cod located immediately offshore in proximity to Trinity Bay, a region known as the Bonavista Corridor, has increased from a few thousand to >200 000 t. Rose & Rowe (2015) argued that this dramatic recovery in the offshore was supported by a cross-shelf migration of Smith Sound cod. We further hypothesize that the directed immigration of cod from the offshore in 1995 and its subsequent growth and development inshore were supported by the resident capelin population in that region.

CONCLUSION

Our interpretation of the available observational data leads us to conclude that the reported capelin collapse in NL was not the result of food chain dynamics driven by bottom-up processes as has been previously suggested (Table 1). There are, however, clear indications that 1991 was a pivotal year in the NL ecosystem, highlighted by the onset of declines in the average age and adult body length of capelin captured by the inshore fishery, delays in the timing of peak inshore spawning, increases in the depth distribution of capelin during the May acoustic surveys, limited fall migration of juvenile and post-spawning capelin into Div. 2J3K in the fall of 1990 and beyond, changes in cod weight at age in Div. 2J and 3K, and in the cod liver index in Div. 2J3KL (Figs. 3 & 7–11). We argue that these changes were not indicative of a collapsed capelin stock, but rather one experiencing profound phenological/migratory alterations shaped by the dynamics of a complex ecosystem that we do not understand fully. In fact, the sustained feeding and breeding success of coastal seabirds, the continued upward trajectory of the seal population in the Newfoundland area, the positive trajectory of the inshore aerial capelin survey and inshore capelin catch data post-1991, and the estimated consumptive demand by capelin predators of ~3 Mt, are all consistent with an increase in capelin biomass. Capelin biomass may have peaked at 7 Mt in 1990 and remained near that level during and subsequent to the late 1980s/early 1990s collapse of their major groundfish predators. Such an increase in capelin biomass, when coupled with the reported increases in the biomass of shrimp and snow crab in this ecosystem following the NW Atlantic groundfish

collapse, would be fully consistent with the well-documented response of other NA ecosystems to the groundfish collapse (Petrie et al. 2009).

Given these findings, the several hypotheses relating to the post-1991 species interactions and ecosystem function in NL, advanced on the assumption of a 1991 capelin collapse (Table 1), would appear to warrant reconsideration.

LITERATURE CITED

Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. Mar Ecol Prog Ser 469:195–213

Brattey J, Cadigan NG, Dwyer K, Healey BP and others (2010) Assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J+3KL in 2010. DFO Can Sci Advis Sec Res Doc 2010/103

Buren AD, Koen-Alonso M, Pepin P, Mowbray F and others (2014a) Bottom-up regulation of capelin, a keystone forage species. PLoS ONE 9:e87589

Buren AD, Koen-Alonso M, Stenson GB (2014b) The role of harp seals, fisheries and food availability in driving the dynamics of northern cod. Mar Ecol Prog Ser 511: 265–284

Carscadden JE, Frank KT (2002) Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. ICES J Mar Sci 59: 950–958

Carscadden J, Miller DS (1981) Analytical assessment of the capelin stock in Subarea 2+ Div. 3K using SCAM. NAFO SCR Doc 81/II/4, Ser No. N268

Carscadden JE, Nakashima BS (1997) Abundance and changes in distribution, biology, and behavior of capelin in response to cooler waters of the 1990s. Proc Symp Forage Fish Mar Ecosyst AK-SG-97-01, p 457–468

Carscadden J, Winters GH, Miller DS (1981) Analytical assessment of the capelin stock in Subarea 2+ Div. 3L using SCAM. NAFO SCR Doc 81/II/3, Ser No. N267

Carscadden JE, Montevecchi WA, Davoren GK, Nakashima BS (2002) Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES J Mar Sci 59:1027–1033

Carscadden JE, Gjösaeter H, Viljálmsson H (2013) A comparison of recent changes in distribution of capelin (*Mallotus villosus*) in the Barents Sea, around Iceland and in the Northwest Atlantic. Prog Oceanogr 114:64–83

Colbourne E, Holden J, Craig J, Senciall D, Bailey W, Stead P, Fitzpatrick C (2014) Physical oceanographic conditions on the Newfoundland and Labrador Shelf during 2013. DFO Can Sci Advis Sec Res Doc 2014/094

Dalpadado P, Mowbray F (2013) Comparative analysis of feeding ecology of capelin from two shelf ecosystems, off

Newfoundland and in the Barents Sea. Prog Oceanogr 114:97–105

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58: 876–895

Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. Mar Ecol Prog Ser 258:253–261

Dawe EG, Koen-Alonso M, Chabot D, Stansbury D, Mullowney D (2012) Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change. Mar Ecol Prog Ser 469:233–248

DFO (2000) Capelin in SA 2 + Div. 3KL. DFO Sci Stock Status Rep B2-02

DFO (2001) Capelin in SA 2 + Div. 3KL during 1999. DFO Res Doc 2001/161

DFO (2010) Canadian marine ecosystem status and trends report. DFO Can Sci Advis Sec Sci Advis Rep 2010/030 (revised)

DFO (2013) Assessment of capelin in SA2 + Div. 3KL in 2013. DFO Can Sci Advis Sec Sci Advis Rep 2013/011

DFO (2014) Short-term stock prospects for cod, crab and shrimp in the Newfoundland and Labrador region (Divisions 2J3KL). DFO Can Sci Advis Sec Sci Resp 2014/049

DFO (2015a) Proceedings of the regional peer review meeting of the framework for Atlantic herring (*Clupea harengus*) and reference points for Capelin (*Mallotus villosus*) in the Newfoundland and Labrador Region; November 19-21, 2013. DFO Can Sci Advis Sec Proc Ser 2014/049

DFO (2015b) Assessment of capelin in Subarea 2 and Divisions 3KL in 2015. DFO Can Sci Advis Sec Sci Advis Rep 2015/036

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S and others (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388

Dwyer KS, Buren A, Koen-Alonso M (2010) Greenland halibut diet in the Northwest Atlantic from 1978 to 2003 as an indicator of ecosystem change. J Sea Res 64: 436–445

Erikstad KE, Reiertsen TK, Barrett RT, Vikebø F, Sandvik H (2013) Seabird–fish interactions: the fall and rise of a common guillemot *Uria aalge* population. Mar Ecol Prog Ser 475:267–276

Evans GT, Nakashima BS (2002) A weighted multiplicative analysis to estimate trends in year-class size of capelin. ICES J Mar Sci 59:1116–1119

Fisher JAD, Frank KT (2004) Abundance-distribution relationships and conservation of exploited marine fishes. Mar Ecol Prog Ser 279:201–213

Frank KT, Simon J, Carscadden JE (1994) Recent excursions of Capelin (*Mallotus villosus*) to Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. NAFO SCR Doc 94/68

Frank KT, Carscadden JE, Simon J (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can J Fish Aquat Sci 53:1473–1486

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623

Frank KT, Petrie B, Shackell NL, Choi JS (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecol Lett 9:1096–1105

Frank KT, Fisher JAD, Petrie B, Leggett WC, Shackell NL, Taggart CT (2013) Irruptive prey dynamics following the groundfish collapse in the Northwest Atlantic: an illusion? ICES J Mar Sci 70:1299–1307

Gillanders BM, Izzo C, Doubleday ZA, Ye Q (2015) Partial migration: growth varies between resident and migratory fish. Biol Lett 11:20140850

Gjøsæter H (2011) The Barents Sea capelin autumn investigations 1972-2011 – a 40 years anniversary. Institute of Marine Research, Bergen

Gjøsæter H, Dommasnes A, Rottingen B (1998) The Barents sea capelin stock 1972–1997. A synthesis of results from acoustic surveys. Sarsia 83:497–510

Gjøsæter H, Dalpadado P, Hassel A (2002) Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. ICES J Mar Sci 59:959–967

Gjøsæter H, Bogstad B, Tjelmeland S (2009) Ecosystem effects of the three capelin stock collapses in the Barents Sea. Mar Biol Res 5:40–53

Gross MT (1987) Evolution of diadromy in fishes. Am Fish Soc Symp 1:14–25

Haug T, Krøyer AB, Nilssen KT, Ugland KI, Aspholm PE (1991) Harp seal (*Phoca groenlandica*) invasion in Norwegian coastal waters: age composition and feeding habits. ICES J Mar Sci 48:363–371

Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes. Rev Fish Biol Fish 3: 348–365

Kenchington EL, Nakashima BS, Taggart CT, Hamilton LC (2015) Genetic structure of capelin (*Mallotus villosus*) in the Northwest Atlantic Ocean. PLoS ONE 10:e0122315

Krumsick KJ, Rose GA (2012) Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador. ICES J Mar Sci 69:1701–1709

Lilly GR, Murphy EF, Healey BP, Brattey J (2006) An assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2K3KL in April 2006. Can Sci Adv Sec Res Doc 2006/043

Lilly GR, Nakken O, Brattey J (2013) A review of the contributions of fisheries and climate variability to contrasting dynamics in two Arcto-boreal Atlantic cod (*Gadus morhua*) stocks: persistent high productivity in the Barents Sea and collapse on the Newfoundland and Labrador Shelf. Prog Oceanogr 114:106–125

Mehl S, Sunnanå K (1991) Changes in growth of Northeast Arctic cod in relation to food consumption in 1984-1988. ICES Mar Sci Symp 193:109–112

Michalsen K, Dalpadado P, Eriksen E, Gjøsæter H and others (2013) Marine living resources of the Barents Sea — ecosystem understanding and monitoring in a climate change perspective. Mar Biol Res 9:932–947

Miller DS (1991) Estimates of biomass from an acoustic survey for capelin (*Mallotus villosus*) in Division 3L, May 1991. NAFO SCR Doc 91/37

Miller DS (1993) Results from an acoustic survey for capelin in Divisions 3NO in 1992. NAFO SCR Doc 93/21

Miller DS, Carscadden JE (1991) Results of two acoustic surveys for capelin (*Mallotus villosus*) in Divisions 3L in 1991. NAFO SCR Doc 91/123

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Mar Ecol Prog Ser 352: 213–220

Montevecchi WA, Myers RA (1997) Centurial and decadal

oceanographic influences on changes in Northern Gannet populations and diets in the Northwest Atlantic: implications for climate change. ICES J Mar Sci 54: 608–614

Mowbray FK (2012) Some results from spring acoustic surveys for capelin (*Mallotus villosus*) in NAFO Division 3L between 1982 and 2010. Can Sci Adv Sec Res Doc 2012/143

Mowbray FK (2014) Recent spring offshore acoustic survey results for capelin, *Mallotus villosus*, in NAFO Division 3L. DFO Can Sci Advis Sec Res Doc 2013/040

► Mullowney DRJ, Rose GA (2014) Is recovery of northern cod limited by poor feeding? The capelin hypothesis revisited. ICES J Mar Sci 71:784–793

► Mullowney DRJ, Maillet G, Dawe E, Rose G, Rowe S (2016) Spawning delays of northern capelin (*Mallotus villosus*) and recovery dynamics: a mismatch with ice-mediated spring bloom? Prog Oceanogr 141:144–152

► Nakashima BS (1992) Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*). Can J Fish Aquat Sci 49:2423–2429

Nakashima B, Mowbray F (2013) Capelin (*Mallotus villosus*) recruitment indices in NAFO Division 3KL. DFO Can Sci Advis Sec Res Doc 2013/091

► Obradovich SG, Carruthers EH, Rose GA (2014) Bottom-up limits to Newfoundland capelin (*Mallotus villosus*) rebuilding: the euphausiid hypothesis. ICES J Mar Sci 71:775–783

► O'Driscoll RL, Parsons MJD, Rose GA (2001) Feeding of capelin (*Mallotus villosus*) in Newfoundland waters. Sarsia 86:165–176

Petrie B, Pettipas R, Petrie W (2008) An overview of meteorological, sea ice and sea surface temperature conditions off eastern Canada during 2007. DFO Can Sci Advis Sec Res Doc 2008/016

► Petrie B, Frank KT, Shackell NL, Leggett WC (2009) Structure and stability in exploited marine ecosystems: quantifying critical transitions. Fish Oceanogr 18: 83–101

Robertson GJ, Wilhelm SI, Taylor PA (2004) Population size and trends of seabirds breeding on Gull and Great islands, Witless Bay Islands Ecological Reserve, Newfoundland up to 2003. Tech Rep Ser No. 418. Canadian Wildlife Service, Dartmouth, NS

Rose GA (2003) Fisheries resources and science in New-foundland and Labrador: an independent assessment. Royal Commission on renewing and strengthening our place in Canada, St. John's, NL

Rose GA (2007) Cod: the ecological history of the North Atlantic fishery. Breakwater Books, St. John's, NL

► Rose GA, O'Driscoll RL (2002) Capelin are good for cod: can the northern stock rebuild without them? ICES J Mar Sci 59:1018–1026

► Rose GA, Rowe S (2015) Northern cod comeback. Can J Fish Aquat Sci 72:1789–1798

► Rose GA, Nelson RJ, Mello LGS (2011) Isolation or meta-population: whence and whither the Smith Sound cod? Can J Fish Aquat Sci 68:152–169

SAHFOS (Sir Alister Hardy Foundation for Ocean Science) (2015) www.sahfos.ac.uk

Shelton PA, Carscadden J, Hoenig JM (1992) Risk evaluation of the 10% harvest rate procedure for capelin in NAFO Division 3L. Publ Spec Can Sci Halieut Aquat 120: 193–201

Stenson GB (2012) Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL. DFO Can Sci Advis Sec Res Doc 2012/156

Taggart CT, Anderson J, Bishop C, Colbourne E and others (1994) Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar Sci Symp 198: 140–157

Templeman ND (2010) Ecosystem status and trends report for the Newfoundland and Labrador shelf. DFO Can Sci Advis Sec Res Doc 2010/026

Vilhjálmsson H (1994) The Icelandic capelin stock. Capelin (*Mallotus villosus* Muller) in the Iceland–Greenland–Jan Mayen area. Rit Fiskideildar 13:1–281

► Vilhjálmsson H (2002) Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. ICES J Mar Sci 59:870–883

► Vilhjálmsson H, Carscadden JE (2002) Assessment surveys for capelin in the Iceland-East Greenland-Jan Mayen area, 1978-2001. ICES J Mar Sci 59:1096–1104

► Winters GH (1970) Biological changes in coastal capelin from the over-wintering to the spawning condition. J Fish Res Board Can 27:2215–2224

► Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162–173