## Title:

Rebuttal to Frank et al 2016

## Authors:

NAFC1Montevecchi WA2  
Robert D3  
Davoren GK4  
Rose G5?

## Affiliations:

1. Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, NL, Canada
2. Cognitive and Behavioural Ecology Programme, Departments of Biology and Psychology, Memorial University of Newfoundland, St. John’s, NL, Canada
3. Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada
4. Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada
5. CFER/ UBC ?

## Abstract

## Introduction

Forage fish play a crucial role in many ecosystems, acting as a conduit of energy between lower trophic levels and large vertebrate predators. Forage fish are small shoaling species that characteristically have rapid growth, short life expectancies, and population responses tightly linked to environmental control. These characteristics lead this group of species to exhibit boom and bust dynamics, i.e. their abundances change rapidly and substantially and undergo phases of extremely high and extremely low abundances (Soutar & Issacs 1969, Schwartzlose et al. 1999, Chavez et al. 2003, Alheit et al. 2009, Pikitch et al. 2012). Forage fish species can experience prolonged periods of ‘bust’ dynamics. For example, Norwegian spring-spawning herring stock collapsed in the late 1960s and remained at very low levels until the late 1980s (Toresen & Østvedt 2000, Skagseth et al. 2015); and sardine and anchovy have decade-scale regimes of high and low abundances where populations thrived for 20 to 30 years and then disappeared for similar periods (Schwartzlose et al. 1999, Chavez et al. 2003). Capelin is the focal forage species in ecosystems of the northern Atlantic Ocean (Templeman 1948, Jangaard 1974, Vilhjálmsson 1994, Carscadden et al. 2001). The three most important capelin populations in the North Atlantic are in the Barents Sea, off Iceland, and off Newfoundland and Labrador (Canada). The Barents Sea capelin stock underwent three collapses during the last 4 decades, during the mid- to late 1980s, mid-1990s, and mid-2000s. The size of the stock fluctuated between 3 - 7 million tonnes during the boom and around 200 thousand tonnes during the bust phases. There is general agreement that ecosystem changes were the driving forces behind these dynamics (Gjøsæter et al. 2009). The Icelandic capelin stock underwent similar dynamics, with three bust phases in the last 4 decades, in the early 1980s, in the early 1990s, and during most of the 2000s. The size of the stock was around 1.5 - 2 million tonnes during the boom and between 100 and 500 thousand tonnes during the bust phases (ICES 2017).The first two cases were due to a combination of poor recruitment and the stock being easily available to the fishing fleet, while the last case was likely associated to a climate-related shift in distribution (Pálsson et al. 2012, Carscadden et al. 2013).

Fisheries and Oceans Canada is responsible for the assessment of the Newfoundland and Labrador capelin stock; it has concluded that there was an order of magnitude decline in the stock in the early 1990s, and that capelin abundance declined to less than 1% of historic levels in 2010 (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015). The size of the stock fluctuated between 2 - 6 million tonnes prior to 1991, and between 25 and 900 thousand tonnes during the ensuing period (DFO 2015).This decline was concomitant with drastic changes in the ecosystem during the late 1980s and early 1990s (Hutchings & Myers 1994, Gomes et al. 1995, Lilly et al. 2000, Rice 2002, Koen-Alonso et al. 2010, Hammill et al. 2011, Pedersen et al. 2017), including major changes in the biology and ecology of capelin (Carscadden & Nakashima 1997, Carscadden et al. 2001, Nakashima & Wheeler 2002, DFO 2010). The collapse was identified as an important signal contributing to a regime shift that occurred in the early 1990s (Buren et al. 2014a, Pedersen et al. 2017). Several aspects of the stock’s dynamics, such as recruitment, growth, and mortality of pre-spawners, have been linked to bottom-up processes (Frank & Leggett 1981, Leggett et al. 1984, Dalley et al. 2002, Buren et al. 2014a, Obradovich et al. 2014, Murphy et al. 2018) with little empirical evidence of top-down processes (Carscadden et al. 2001) driving capelin population dynamics in Newfoundland.

Frank et al. (2016) concluded that the capelin stock off Newfoundland and Labrador did not collapse. The debate over the collapse or non-collapse of capelin in the NL region is not new, and it stems from the unexplained discordance between the inshore and offshore indices in the 1990s, where inshore indices suggested little change in capelin biomass since the 1980s while the offshore acoustic survey found a dramatic decrease in capelin biomass (Nakashima 1996, Carscadden & Nakashima 1997, Carscadden et al. 2001, DFO 2001b). And while this discordance resulted in the exclusion of the offshore acoustic survey as an input into the capelin multiplicative year-class model, this model still had large statistical uncertainties ((Evans & Nakashima 2002), suggesting that the inshore indices alone did not explain capelin year class variability. This model is no longer in use as the number of inshore indices collected has been reduced over time (DFO 2000). Since 1999, the offshore acoustic survey is considered the best method to obtain an index of the immature capelin biomass in NL (O'Driscoll et al. 2002, Mowbray 2014), which is in accordance with Iceland and the Barents Sea (e.g. Gjøsæter et al. 2009, ICES 2017). In Frank et al. (2016), support for the non-collapse of capelin was based on changes in biology of capelin post-1991 (i.e. distribution and demography), re-analysis of the offshore research surveys (multi-species bottom trawl and acoustic), and the response of various components of the ecosystem (e.g., zooplankton, northern cod, birds, seals) to the large scale changes that occurred during the early 1990s. These authors postulated that the reported collapse was not real and proposed two hypotheses to interpret why the offshore spring acoustic surveys have failed to detect large capelin aggregations since 1991: 1) capelin changed its migratory patterns while the timing of the acoustic survey has remained constant leading to a spatio-temporal mismatch between the survey and the stock, and 2) the capelin stock has become less migratory and are remaining in inshore waters, and therefore undetected by the offshore surveys. The objective of this paper is to assess the empirical support for the hypotheses of stock collapse (DFO 2015) vs non-collapse (Frank et al. 2016) using all available data.

## Integrated overview of NL ecosystem

## Capelin

### Offshore capelin distribution: acoustic surveys

In the NL region, the capelin stock has been surveyed using acoustic methods since the 1980s (see Mowbray 2014 for more details). From 1982 to 1993 there were two acoustic surveys annually that initially targeted what was thought to be two separate stocks (Div. 2J3K and Div. 3L) (Campbell & Winters 1973); however, meristic (Misra & Carscadden 1984) and tagging studies (Nakashima 1992) supported one single stock unit in NAFO Div. 2J3KL in 1992. Following the change in stock definition, the two acoustic surveys targeted different life stages of the stock. Spring acoustic surveys in May targeted the immature portion of the stock in NAFO Div. 3L. This survey provided an abundance estimate of immature capelin that will be recruiting into the fishery the following year. The second acoustic survey was conducted in October in NAFO Div. 2J3K that targeted the maturing portion of the stock to provide a revised estimate of the size and number of maturing fish recruiting to the fishery the following year. The dramatic decline in the spring acoustic estimate in 1991, which was not reflected in the inshore indices (Carscadden & Nakashima 1997), instigated dropping the spring survey in favour of an expanded fall survey (NAFO Div. 2J3KL) in 1993-1994. However, this expanded fall acoustic survey did not find the ‘missing’ capelin biomass and reconcile the inshore and offshore indices. The fall survey was subsequently cancelled and the spring acoustic survey in NAFO Div. 3L has been conducted annually since 1996 (except in 1997, 1998, 2006 and 2016).

The acoustic survey design and implementation has changed significantly over time and a more detailed description of the acoustic survey program is provided in Mowbray (2014). The current spring acoustic survey consists of a series of equidistant parallel transect lines every 15 to 30 nautical miles with survey effort being partitioned amongst a number of strata that were classed as core (e.g., highest priority) or non-core (e.g., lowest priority). The position of the initial transect line is randomly determined while the positions of subsequent lines are dependent on the position of the initial line. Targeted fishing sets were conducted to determine the species composition of the acoustic backscatter. Additional fishing sets were conducted periodically to confirm the absence of fish signal with at least one fishing set conducted every 12 hour period during all surveys. Prior to 1996, a large mid-water trawl (Diamond IX) was used to collect biological samples. Since 1996, both mid-water (IYGPT) and bottom trawls (Campelen 1800) have been used to collect samples. Set duration ranged from 15 to 120 minutes depending on mode of deployment and the intensity of the backscatter to be verified. Detailed sex-length stratified biological sampling of capelin, including age, length, weight, maturity, diet, is conducted annually.

*Spatio-temporal mismatch post-1991*

Frank et al. (2016) hypothesized that delays in the timing of capelin spawning post-1991 may have led to a mismatch in capelin availability to the acoustic survey. However, due to the age-dependent distribution of capelin with older capelin in the north (Div. 2J3K) and immature capelin in the south (Div. 3L), the spring acoustic survey in NAFO Div. 3L was only ever designed to survey the immature portion of the stock rather than the spawning migration. Specifically, the spring acoustic survey provides an index of abundance of the immature age-2 portion of the stock, as age-1 capelin have a weak acoustic signal and are only detected when they are present in large numbers at high densities. Age-1 capelin are also poorly recruited to the sampling gears, resulting in an underestimation of their overall contribution to the acoustic signal. The proportion of maturing age-2 capelin has increased post-1991 (varies annually between 37-79% compared to 4% pre-1991) (Mowbray 2014), and this change in biology may have introduced a bias in the acoustic survey post-1991 by artificially depressing the immature capelin acoustic estimate, which relies solely on age-2 fish. However, the acoustic survey has had high internal consistency, with the abundance of the age-3 cohort highly correlated with the abundance of the age-2 cohort of the previous year (reference to res doc). Cohort tracking in the acoustic survey failed in only two years (1990 and 2010), which affected all ages rather than just the age-2 and age-3 cohorts(Mowbray 2014).

For spawning capelin, there is a spatio-temporal mismatch between spawning migrations and the spring acoustic survey due to persistently later spawning post-1991. Moreover, if mature capelin are present in the area, they are unlikely to be detected due to highly aggregated shoals relative to the survey effort. Capelin surveys in other countries are timed to avoid spawning migrations (Gjøsæter 1998). An exception is Iceland, where if capelin are not detected in surveys during the fall feeding period due to shifting stock distribution, follow-up surveys are conducted during spawning migrations (reviewed in Carscadden et al. 2013). In recognition of the difficulty involved in locating highly aggregated spawning shoals within a large expanse of water, Iceland increases their survey efforts for spring spawning migrations and utilizes commercial fleet information to exclude survey areas with no capelin, allowing the survey vessels to conduct a more concentrated survey for highly aggregated shoals of migrating capelin. This level of survey effort is not possible during the spring survey in the NL region resulting in these migratory spawners rarely being intercepted (Figure FM-3). However, when concerns were raised that the spring acoustic survey may be missing capelin due to a change in spawning timing, repeat acoustic surveys in June of 1991 and 2003 were conducted(Mowbray 2014). These repeat surveys failed to detect a marked change in capelin biomass between survey months (Mowbray 2014). A delay in migration timing also does not explain the coincidental sudden decline of capelin in the fall acoustic surveys starting in 1990, a year when spawning timing was similar to that observed prior to 1991 (Figure FM-4). Consequently, we find no evidence that the persistent delay in the spawning migration of capelin post-1991 is responsible for creating an illusion of a sudden and sustained loss of capelin in the spring acoustic surveys conducted by Canada and the USSR. The offshore spring and fall acoustic surveys support the hypothesis of a capelin collapse.

*Capelin stock is non-migratory and inshore post-1991*

Frank et al. (2016) suggested that an alternate explanation to the apparent offshore acoustic survey collapse was an abrupt change in capelin migration patterns post-1991, with capelin now remaining inshore year round. The migration hypothesis postulates that a non-migratory capelin stock post-1991 will mature at an earlier age (Frank et al. 2016). To test this hypothesis, we examined trends in capelin maturity from 1982-2015 using data from the spring acoustic survey with capelin partitioned into spatial strata based on both depth and latitude. Annually, the fraction of capelin in each age-class and strata that were classed as mature were divided by the total number of capelin from that age-class. There were a number of changes in capelin maturation trends from 1982-2015. Prior to 1991, ~7% of age-2 and ~58% of age-3 capelin were classed as mature and there was substantial variability in the fraction of individuals within an age-class that were mature in a particular year. At age-4, nearly all capelin were classed as mature on a consistent basis. Between 1991 and 1999, data on capelin maturity was sparse, but from the limited data that were available, it appears that there was a general increase in the percentages of ages-2 and 3 that were mature. From 2000-2010, 57% age-2 and 99% age-3 were mature, which was a significant increase from 1982-1990. Since 2010, the proportion of mature age-2’s declined substantially to 40% and the proportion of mature age-3’s experienced a smaller decline to 93%.

While our analysis on maturity pre- and post-1991 is consistent with Frank et al. (2016)’s hypothesis that a capelin population that is no longer migrating will have a younger age at maturity, our results are also consistent with the hypothesis that age at maturity will decline in fish populations that are stressed (Trippel 1995), with a stressed population being defined by Shuter (1990) as “one that has undergone a substantial decline in size”. Furthermore, it is possible to see rapid changes in age at maturity in response to shifts in stock size (Trippel 1995); for example, as Atlantic herring stocks increased in the mid-1980s in Georges Bank, there was a 50% decrease in the percentage of mature age-3 fish(Melvin et al. 1995). There has been a similar response recently in NAFO Div. 2J3KL with a recent decline in the fraction of mature ages-2 and -3 capelin since 2010, which corresponded with a recent increase in capelin biomass.

Younger ages at maturity have a number of potentially negative implications for capelin biomass that challenge Frank et al. (2016)’s migration hypothesis. Male capelin are essentially semelparous, with typically one reproductive period before dying, while females are iteroparous, reproducing in multiple years (Huse 1998). A shift towards earlier maturation post-1991, with most capelin being mature by age-3, has resulted in a substantial reduction in the number of age-4 male capelin. The reduction in the number of age-4 males impacts age-4 females because, if all other factors remain equal, age-4 females will experience a greater share of predation pressure due to there being fewer age-4 males available to absorb predation. Maturing at a younger age requires capelin to divert energy away from somatic growth towards developing gonads. This results in consistently smaller capelin across age-classes (Carscadden et al. 2001) and has an additional effect of reducing the number of eggs that an individual female can produce as the number of eggs produced is related to mass with capelin that have higher masses producing more eggs than capelin with lower masses (Penton & Davoren 2013). These factors are likely to result in a reduction in capelin biomass.

*Trophic cascade*

A decrease in groundfish biomass, specifically northern cod, in 1991 should have resulted in a rapid increase in capelin biomass due to a trophic cascade(Frank et al. 2005). In regions where there was a rapid increase in capelin biomass in response to a decline in cod biomass (Frank et al. 2016), the decline in cod biomass was due to overfishing rather than a broader ecosystem effect. In these cases, it is quite straightforward that a decline in predator biomass leads to an increase in prey biomass. This was not the case in the 1990-1991 collapse of capelin, cod and a number of other finfish species in the NL region. Several species were simultaneously negatively affected by a common environmental factor. As Frank et al. (2016) note, “it is possible that capelin availability had not declined relative to the diminished cod biomass” suggesting capelin in NL in 1990-1991 did not experience a predation release. On the other hand, shellfish biomass increased post-1991, likely due to a release from predation and favourable environmental conditions following the finfish collapse (Lilly et al. 2000, Worm & Myers 2003).

To investigate the effect of northern cod decline on capelin mortality, we developed an index of total mortality from the spring acoustic survey from 1982-2015. Annual estimates of abundance by age-class were rearranged to create a time series of abundance estimates for cohorts that were spawned from 1977 to 2013. For each cohort, we solved the exponential decay function

for *Z*, an index of the total mortality between subsequent estimates of abundance (~1 year), for each pair of consecutive age-classes within a cohort. *Z* is an index of the total mortality rate rather than an estimate of total mortality as not all age-classes are fully recruited to the acoustic survey. Furthermore, differences in spatial coverage and trawling effort between surveys and differences in spatial overlap between the area surveyed and the spatial distributions of the different age-classes of capelin are not accounted for. Other variables in the equation were *N*, the abundance of capelin in an age-class; *a* the age-class of interest; and *a* + 1 is the subsequent age-class. The indices of total mortality for cohorts over time were then rearranged in order to produce time-series plots of the index of total mortality over time by transition group (e.g., age-2 to age-3, age-3 to age-4) (Figure). The data were aligned so that the indices of total mortality are shown for the year in which the *a* + 1 age-class was surveyed. The age-1 to age-2 transition group is not shown as age-1 capelin are not fully recruited to the trawl. The indices of total mortality for 2010 and 2011 are suspect as most extant cohorts at that time had very low abundances in 2010 and much higher abundances in 2011 resulting in high index of total mortality values in 2010 and very low index of total mortality values for 2011. Hence, , the total mortality index values were grouped for the periods 1983-1990, 2000-2005 and 2008-2015, excluding 2010 and 2011 (Table XX). The mean value for the index of total mortality for each transition group was higher for the 2000-2005 and 2008-2015 time periods than it was for the pre-1991 time period (TableXX). This suggests that rather than experiencing a predator release post-1991, capelin experienced higher mortality since the collapse of one of its main predators. There are at least four potential non-exclusive explanations as to why the index of total mortality has increased over time. First, while capelin biomass has declined an order of magnitude, the inshore commercial catch of capelin has declined by xx% which would result in an increase in the fishing mortality experienced by capelin. Second, capelin post-1991 are smaller than capelin pre-1991, and in general, smaller fish experience higher predation mortality rates than larger fish (Sogard 1997, Gislason et al. 2010). Third, with an earlier age at maturation, younger age classes of capelin are experiencing higher rates of mortality due to mortality associated with reproduction (Huse 1998). Fourth, there may have been a shift in the spatial distribution of capelin that has resulted in a systematic increase in the index of total mortality (e.g., Frank et al. 2016). Therefore the patterns of variation in the rates of natural mortality of capelin do not support the hypothesis of non-collapse.

### Offshore capelin distribution: annual bottom-trawl surveys

Fall multispecies bottom trawl surveys (FBTS) have been conducted in NAFO Div. 2J3KL from 1978. The FBTS is a random depth-stratified sampling design with trawls of fixed duration and speed. From 1978-1994, trawls were conducted using an Engel otter trawl. In 1995, the FBTS switched to using the smaller mesh size Campelen 1800 shrimp trawl, and the trawls were adjusted to a slower speed and shorter duration to account for larger catches. The change in trawls in 1995 increased the catchability of small fish species, like capelin, in the FBTS. With the cancellation of the fall acoustic survey, the FBTS is the only source of data on the distribution and presence/absence of maturing capelin in the fall in NAFO Div. 2J3KL. There is a concordance in the multi-year trends of age-dependent capelin distributions in the FBTS and the spring acoustic survey (Figure FM2), with a latitudinal cline in age composition in the FBTS with the youngest capelin in the south (Div. 3L) and the older ages more prevalent in the north (Div.2J3K).

In addition to changes in the trawl in 1995, ecosystem and behavioural changes in capelin post-1991 improved capelin’s catchability in the FBTS. Capelin were sampled closer to the seabed when cod were not present, and as cod abundance declined in the late 1980s, the proportion of capelin biomass in the trawl zone (bottom 4 m of the water column) increased(Mowbray 2002). Furthermore, when capelin densities were low, capelin were found in closer association with the bottom and displayed less vertical behaviour compared to when capelin densities were high (Mowbray 2002). This change in a pelagic fish’s vertical behaviour was also seen in Atlantic herring in the Gulf of St. Lawrence where in the absence of Atlantic cod predation, Atlantic herring moved into the suprabenthic zone and increased their availability to the bottom trawl despite declines in abundance (McQuinn 2009). These changes in vertical distribution are a cause for concern for acoustic surveys, as acoustic surveys are unable to resolve targets on or near the seabed, also known as the bottom deadzone (Ona & Mitson 1996). The height of the deadzone is a function of the pulse length and frequency of the acoustic system used, and the bottom deadzone was approximately 0.75 m for the capelin spring acoustic surveys. In order to address the potential impact of vertical distribution changes on the availability of capelin to the acoustic surveys, dedicated experiments were carried out in 1995 and 1999 (Mowbray 2002). The range of values for diel changes in capelin detectability obtained from these experiments were used in the calculation of confidence estimates for each survey since 1988 using a Monte Carlo simulation. Confidence estimates indicate a significant decline in capelin biomass between the late 1980s and 1991 (Figure FM-9).

*Capelin stock is non-migratory and inshore post-1991*

Frank et al. (2016) hypothesized that there was an abrupt change in capelin migration patterns post-1991, with capelin now remaining inshore year round. Frank et al. (2016) used the FBTS data to point to a westerly, inshore shift in the center of capelin concentration in 1996-2010 compared to 1985-1995. However, their own annual mapping demonstrates the high degree of interannual variability in capelin abundance within the earlier period (1985-1995), with inshore distributions occurring in three high abundance years (1986-1988, Fig S2 in Frank et al. 2016). To test this migration hypothesis using the FBTS data, we used the center of gravity approach described in Thorson et al. (2016). Specifically, we used the VAST package in R (Thorson & Barnett 2017) to fit a geostatistical delta-generalized linear mixed model to estimate the spatial and temporal distribution of capelin. The main advantage of this approach is that it accounts for changes in the spatial distribution of sampling effort from one year to the next. This method also provides a means of estimating the standard error of the center of gravity metric, which provides a perspective on the significance of distributional shifts. This geostatistical analysis did not support the hypothesis that capelin have shifted their distribution towards the inshore post-1991 with no evidence of an easterly or westerly movement in the centre of gravity of capelin (Figure x). Instead, the center of gravity of capelin shifts northward as abundance increases and southwards as abundance decreases (Figure x). Other analyses also indicate that it is unrealistic that 3 to 6 Mt of capelin are residing in the inshore. The ‘blind-spot’ of the FBTS is between ~35,000 to ~71,000 km2, depending on whether the inshore strata are counted or not. The minimum density of 3 to 6 Mt of capelin in these inshore waters would have to be between ~41,000 to ~170,000 kg / km2, uniformly distributed throughout the blind area. The maximum mean density of capelin observed in Trinity Bay survey strata in June, which corresponds with the start of the spawning period when capelin are highly aggregated inshore, was 10,000 kg / km2 (Table X). Maximum mean density of capelin observed outside the spawning period was only 40 kg / km2 (Table X). Neither observation can account for the required amount of capelin hypothesised to be residing inshore if there was no collapse of capelin in the NL region. Therefore, the FBTS supports the capelin collapse hypothesis.

### Inshore fishery-dependent catch data

*Capelin stock is non-migratory and inshore post-1991*

Annual age composition data from the spring acoustic survey and the inshore commercial capelin fishery using all fishing gears (purse, beach and tuck seines, and traps) in NAFO Div. 3KL were used to test Frank et al. (2016)’s hypothesis that capelin are no longer migratory post-1991. If capelin had stopped migrating offshore in the fall, we would expect to see fewer, older capelin in offshore waters compared to inshore waters. We found that there were large shifts in capelin age compositions from 1980-2016. Prior to 1991, ~97% of the spring acoustic survey catches were composed of ages 2, 3, 4. Post-1991, contributions of ages-2, 3 have remained consistent at ~60% and ~28% of the catch, respectively, while age-1 capelin has gone from being 1% of the catch to ~10% of the catch and contributions of ages-4, 5, 6 have declined. In the inshore commercial fishery pre-1991, ~96-99% of the catches in NAFO Div. 3KL consisted of ages 3, 4, 5 with age-2 capelin comprising 0.6 - 3.4% of total catch. Post-1991, the 3 oldest age-classes of capelin (ages 4, 5 and 6) experienced severe declines with the 2 oldest age-classes effectively disappearing from the inshore commercial fishery. Age-2 capelin averaged 32% (60-fold increase) of the catch in Div. 3K and 42% (12-fold increase) of the catch in Div. 3L, while the contribution of age-3 fish to commercial inshore catches has been relatively unchanged.

The decrease in numbers of older capelin being caught in the spring acoustic survey supports Frank et al. (2016)’s migration hypothesis. However, the lack of a corresponding increase in the numbers of older capelin caught in the inshore commercial fishery, where their numbers have actually decreased both in absolute terms and as a proportion of the overall catch, supports the rejection of the migration hypothesis. The truncation of the age-structure of capelin in both inshore and offshore waters and a subsequent shift to younger age-classes does support Fisheries and Oceans Canada findings that the capelin population in NAFO Div. 2J3KL has collapsed relative to the 1980s and has not yet recovered.

### Independent indices of inshore capelin abundance

In the 1990s, the inshore indices from aerials surveys and commercial catch rates from inshore traps were similar or increased compared to the 1980s while the acoustic survey found low abundance of capelin offshore (DFO 2001a, Evans & Nakashima 2002). The discordance between the offshore and inshore indices in the 1990s has never been explained. However, it is hypothesized that the severe environmental conditions post-1991 and resulting changes in biology and behaviour of capelin had an impact on the effectiveness of the acoustic survey in providing a capelin stock abundance index (Carscadden & Nakashima 1997).

We postulate that changes in capelin biology and behaviour post-1991 negatively impacted the effectiveness of the aerial and inshore catch-rate indices in providing estimates of capelin abundance. Capelin traps are a passive gear type that intercepts capelin as they move into the nearshore area to spawn. Because of changes in the biology and behaviour of capelin post-1991, fishing behaviour and management regulations changed. Due to the small sizes of spawning capelin, management regulations included a size criterion to reduce dumping of undersized capelin (Carscadden & Nakashima 1997). This size criterion effectively closed the fishery in 1994 and 1995. From 1996, management regulations to reduce discarding of small, unmarketable capelin effectively concentrated fishing effort to a few days when capelin was highly available (Anon 1998). The inter-annual variability in participation in the fishery due to quality of fish and market forces in combination with high catch rates in a short period of time rendered the inshore catch rate index useless as an indicator of stock abundance (Anon 1998). In the year-class multiplicative model, the inshore catch rate index was only used for the years 1981-1993 (Evans & Nakashima 2002). Three years of inshore catch rate data post-1991 does not provide support for either a collapse or non-collapse of capelin. The inclusion of inshore catch rate data after 1993 in the analysis presented in Figure 6 in Frank et al. (2016) is misleading and is not reflective of capelin inshore abundance.

Post-1991, the late, protracted spawning of capelin introduced logistic difficulties and uncertainties in estimating spawning stock size using the aerial survey (Carscadden & Nakashima 1997). The aerial survey commenced in 1982, and initially followed four defined survey tracks in Conception and Trinity Bays during a fixed time period of mid-June to early July (Carscadden et al. 1994). Images of capelin schools obtained using film (1982-89), Compact Airborne Spectrographic Imager (CASI) (1990-1996), and video (1997-1998) were identified by their greyish colour and distinctive shapes, and school surface area was calculated for each completed survey track (Carscadden et al. 1994, Nakashima 1996, Nakashima 1998). An annual relative abundance index was calculated by summing the highest total capelin surface area from each of the transects (Carscadden et al. 1994). Protracted spawning post-1991 violated a key assumption of the aerial surveys: all schools arrive at the same time in each bay to form one single spawning peak (Nakashima 1996). Protracted spawning from early July to mid-August in 1991, 1992, and 1993 resulted in multimodal capelin spawning peaks that were covered with variable success by the aerial survey. For example, in 1993, the peak spawning period was adequately surveyed in Conception Bay, but two spawning peaks in Trinity Bay, based on the egg deposition index, were missed (Nakashima 1996). In 1997, the geographical coverage of the aerial survey was reduced to two transects in the inner areas of Trinity and Conception Bays (Anon 1998). While the estimated aerial abundance index in 1997 was fourth highest in the series, there were concerns that the limited geographical coverage of the aerial survey did not accurately reflect the status of the stock, especially when harvester opinion surveys indicated that stock abundance was changing at different rates within the stock area (e.g., bays vs headlands) (Anon 1998) . Five of the eight years of aerial data post-1991 either did not adequately cover peak spawning times (1991-1993) or had reduced geographical coverage (1997-1998). Due to the reduced ability of the aerial survey to estimate capelin stock abundance post-1991, this index should be used with caution and does not unequivocally support the hypothesis of a non-collapse of capelin.

### Demographic change of harvested inshore capelin

### Timing of inshore capelin beach spawning

The later timing of inshore spawning post-1991 does not explain the persistently low capelin biomass surveyed by the May spring acoustic survey in NAFO Div. 3L (Frank et al. 2016). The probability of the acoustic survey missing peak offshore capelin biomass in 25 successive years was 22% (Frank et al. 2016). Furthermore, the acoustic survey of the immature portion of the stock has picked up on trends seen in both the larval indices (Nakashima & Mowbray 2014, Murphy et al. 2018) and the fall multi-species bottom trawl surveys (DFO 2015). There was an increase in the larval index in the mid- 2000s as well as in 2011-13, and these increases in recruitment were detected in the acoustic survey (DFO 2015, Murphy et al. 2018). In the fall multi-species bottom trawl surveys, there were changes in the distribution of capelin in the years 2006-2007 and 2011-2014 when capelin were distributed further north (DFO 2015). This change in distribution was similar to capelin distribution in the fall in the 1980s, when capelin biomass was much higher. This change in distribution reflected a higher biomass of capelin detected in the acoustic survey in those years (DFO 2015).

### Inshore recruitment index

Since the NL capelin stock does not follow a stock-recruit relationship (Carscadden et al. 2000), low capelin biomass can be related to high capelin larval productivity and vice versa, as survival in the larval stage, rather than the egg stage, is related to recruitment (Frank & Leggett 1981, Leggett et al. 1984, Dalley et al. 2002, Murphy et al. 2018). Three indices of capelin larval densities in Trinity Bay have been collected since 1990 by Fisheries and Oceans Canada. From 1990-2012 (except 1997), beach emergent larval densities [< 6 days old; yolk sac is absorbed on average at 5.5 d (range: 3.2 – 8.5 d); Frank and Leggett 1982] were sampled every 1-2 days during high tide in the intertidal zone using a 165 µm mesh plankton net towed parallel to Bellevue beach for a distance of 40 m from the start of emergence to the end of emergence (July-August) (Nakashima & Mowbray 2014). From 2001-2015, surface tows of 10 min duration at 2.1 knots sampled capelin larval densities (< 1 week to 2 weeks old) at five stations in the nearshore area of Bellevue Beach (0.5 – 1 nm from the beach; 20 m depth) using a 270 µm mesh ring net (Nakashima & Mowbray 2014). Larval sources in the nearshore area were from one large and four small spawning beaches and two demersal sites (Nakashima & Mowbray 2014). Like the beach larval tows, surface tows were conducted every 1-2 days from the start of emergence to the end of emergence in July and August (Nakashima & Mowbray 2014). From 2002-2015, late-stage larval (< 30 days old; 10 – 25 mm SL) capelin densities were sampled using bongo tows of 333 µm mesh nets at 52 stations in Trinity Bay in September and October 2002, and 19 stations in the middle of Trinity Bay in August and/or September 2003-2015 (Nakashima & Mowbray 2014) (Table 1). The late-stage larval sampling protocol is based on Dalley et al. (2002). While there was concordance among these three larval indices and the age-2 recruitment index obtained from the acoustic survey from 2002 until 2011, there has been an unexplained divergence in recent years (Nakashima & Mowbray 2014, Murphy et al. 2018).

Two of the three larval indices allow for a comparison of larval densities pre- and post-1991. The beach larval index in 1990 is relatively high, and there is a dramatic reduction in the index in 1991 (Table 1). From 1992 onwards, the beach larval index is variable and larval densities in some years are as high as 1990 (Table 1). However, the beach larval index is reflective of productivity at one section of a main spawning beach and may not be reflective of productivity at other beaches, bays and/or regions. This index was useful for determining peak spawning and emergence timing and was incorporated into the year-class multiplicative model (Evans & Nakashima 2002), but its limited spatial coverage precludes its use as an indicator of capelin collapse or non-collapse. The beach and surface tow indices tracked each other in most years (Table 1; Nakashima & Mowbray 2014), but the relationship is not significant, which may be a reflection of the surface tow index sampling older larvae that have experienced mortality processes in the nearshore area as well as including contributions from demersal sources of larvae. The importance of nearshore demersal sources of larvae to recruitment is currently unknown.

Frank et al. (2016) argued that since late-stage larval production did not decrease appreciably post-1991, capelin biomass did not collapse. Late-stage larval abundance estimations pre- and post-1991 were sourced from Dalley et al. (2002) (1982-86) and Nakashima and Mowbray (2014) (2008-2012). While Frank et al. (2016) compared August in both decades, the persistently late spawning in capelin since 1991 has resulted in smaller and younger larvae in August 2008-12 compared to August 1982-86, and a better comparison would be between August pre-1991 and September post-1991 (Nakashima & Mowbray 2014). The average larval densities in Trinity Bay in September 2002-2015 is 30.9 m-2 (SD: 26.9, range 6.73-96.95 m-2), which is considerably lower than the August 1982-1986 estimate (48.8 m-2, SD: 15.1, range 33.2-73.6 m-2) (Table 1). The trend in the 2000s is for lower and more variable larval densities compared to the 1980s; for example, in 12 of the 14 years in the 2000s, average larval densities in September were less than the average August larval densities in the 1980s (Table 1).

The decrease in capelin late-stage larval productivity post-1991 does not support the hypothesis of a collapse of capelin biomass, as there is no relationship between the late-stage larval and age-2 recruitment indices post-1991 (Murphy et al. 2018). In the 1980s, the relationship between the late-stage larval abundance index, which was based on sampling at 52 stations in July and August in Trinity Bay, explained 82% of the variation in year class strength (Dalley et al. 2002). Post-1991, the late-stage larval index is not providing a quantitative index of capelin larval abundance in Trinity Bay likely due to the spatial and temporal contraction of the sampling protocol since 2003 (19 of the original 52 stations sampled in 1 week in September from 2003-2007 and 1 week in both August and September from 2008-2015). Instead the surface tow index explains ~40% of variance in the age-2 recruitment index (Murphy et al. 2018). While the surface tow index is spatially restricted to one inshore area of Trinity Bay, widespread hydrology and meteorological forcing has been linked to the synchronous release of emergent larvae at various sites across eastern NL, which supports the use of Bellevue beach inshore area as a proxy for larval emergence in NAFO Div. 3L (Frank & Leggett 1981, Nakashima 1996). Furthermore, the high intensity temporal sampling of surface tows (every 1-2 d for 4-6 weeks) produces a robust quantitative larval index. The positive, significant relationship between two fishery-independent inshore and offshore indices provides support for the capelin collapse hypothesis. If the majority of capelin biomass was in the inshore area and was not available to the annual offshore spring acoustic survey, then no relationship would be expected between larval productivity and the age-2 recruitment index. Moreover, with less than half of the variability in recruitment explained by the surface tow index, the continued sampling of late-stage larvae is important as the remaining 60% of unexplained variability in age-2 recruitment may be explained by characteristics of the late-stage larvae, such as growth and diet (Murphy et al. 2018).

## Ecosystem response

### Temporal dynamics of cod weight at age and condition

Frank et al. (2016) contend that the fact that cod’s response in weight at age and liver condition was not spatially homogenous represents support for the hypothesis of non-collapse of capelin. There is spatial structure (i.e. gradient in the magnitude of the changes from north to south) in cod’s growth (length at age), condition (liver, gutted and total body mass), and variability in condition indices (Buren et al. 2014b, Morgan et al. 2017). Inconsistent patterns in liver and body condition are common in cod (Foster et al. 1993, Marshall et al. 2004, Pardoe et al. 2008, Pardoe & Marteinsdóttir 2009, Morgan et al. 2010), and these respond quickly to changes in food abundance (Lambert & Dutil 1997a, b, Morgan et al. 2017).

The existence of spatial structure in traits of northern cod is not surprising, given that the term refers to a complex of cod populations. These have been defined by a north-south cline in size at age and spawning time, and a change in vertebral counts at approximately the north slope of Grand Bank (ICES 2005). In addition, northern and southern components of the stock inhabit different ecosystem production units, i.e. northeast Newfoundland Shelf (subareas 2J3K), and the Grand Banks (subareas 3LNO). These units are characterized by distinct productivity and reasonably well defined major marine communities and food web systems (Pepin et al. 2010, Pepin et al. 2012, Pepin et al. 2014).

During 1991 and following years, capelin shifted its fall distribution from having two distinct aggregations, one in the northwest of the area (NAFO Div 2J3K) and one in the southeast (NAFO Div 3L, at the northern slope of the Grand Banks) to having only one in the southeast (Lilly & Davis 1993, Miller 1994), with records of excursions into the Flemish Cap and the Scotian Shelf (Frank et al. 1996). Coincidently, cod moved southward on the northeast Newfoundland Shelf in the late 1980s and early 1990s, and became aggregated within a small area on the north of the Grand Bank and in the Bonavista corridor by the early 1990s (Rose et al. 2000). One of the hypotheses proposed by Rose et al. (2000) to explain this shift in the distribution of cod is that they did so in response to the distribution of capelin. Therefore, weight at age and liver condition of cod worsened in northerly areas where there was no spatial overlap between cod and capelin, and remained relatively stable in southerly areas, where the collapsed cod stock overlapped with capelin. This, we argue, supports the hypothesis of a collapsed capelin stock.

### Harp seal population trends and diet

Frank et al. (2016) argue that the absence of an obvious response in northwest Atlantic harp seals supports their contention that the capelin stocks off NL did not collapse. One of their arguments is that a large number of starving harp seals were observed following the collapse of capelin in the Barents Sea (Haug & Nilssen 1995) while there were no reports of similar sightings in the NW Atlantic. However, there are significant differences between the two situations. In the Barents Sea, the collapse of capelin during the mid-1980s happened at a time when the stock of other important forage fish, namely Atlantic herring, was severely depleted (Hamre 1994). The Barents Sea Atlantic herring stock collapsed in 1969, and did not see any signs of recovery until the late 1980s, and therefore the effects of the capelin collapse were amplified and reached several taxa such as seals, seabirds and Atlantic cod (*Gadus morhua*) (Hamre 1994). Barents Sea capelin also declined between 1992 and 1993 without a similar ‘invasion’ of starving seals. This was likely due to the availability of alternate prey (Atlantic herring and polar cod, *Boreogadus saida*) for the seals (Nilssen et al. 1998). As Frank et al. (2016) indicate, ‘starving’ harp seals were not reported in Newfoundland waters during the early 1990s, when capelin biomass declined. During this period, however, alternate prey, particularly *B. saida* and Atlantic herring were still available (Lilly et al. 1994, Bourne et al. 2015) and were consumed by harp seals (Stenson 2012). Also, total consumption of capelin declined during the 1990s due primarily to the significant decline in the Atlantic cod (Carscadden et al. 2001). Therefore, it is possible that this may have caused an increase in relative abundance of capelin available to harp seals.

While the harp seals did not show catastrophic mortalities, they have been impacted by the decline in capelin. Since the 1980s, pregnancy rates of harp seals have declined while inter-annual variability has increased, ranging from ~20% to 75% over the past 3 decades (Stenson et al. 2014, Stenson et al. 2016). Also, beginning in 1987, harp seals have shown indications of late term abortions. Stenson et al. (2016) found that while the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, including the late term abortion rates into their model allowed them to explain the large inter-annual variability. Changes in the abortion rates, in turn, are influenced by ice cover in late January and capelin biomass. Buren et al. (2014a) showed that capelin abundance is correlated with ice conditions suggesting that late January ice conditions also reflect changes in environmental conditions that influence a number of prey species. Abundance of Northwest Atlantic harp seals has been relatively stable for the past decade. While, as pointed out by Frank et al. (2016), higher catches in the Canadian commercial hunt between 1996 and 2008 contributed to reductions in the rate of population growth, these lower pregnancy rates have also had a major impact on the population dynamics of this population (Hammill et al. 2015).

### Seabird population trends

Frank et al. (2016; Figure 11B) consider the population of common murres *Uria aalge* on Funk Island (NAFO Div. 3K) since 1990 is contrary to expectation given the purported order of magnitude decrease in their primary prey (Montevecchi 2000, Davoren & Montevecchi 2003). In doing so, Frank et al. (2016) misinterpreted the murre abundance graph from Figure 3 in Davoren and Montevecchi (2003) as an indication of population increase on Funk Island (mislabeled as Fogo Island in Figure 1 of Frank et al. 2016). Figure 3 in Davoren and Montevecchi (2003) depicts the numbers of breeding murres present during August and documents a temporal shift toward later breeding in the late 1990s. This shift in breeding corresponds with the later inshore arrivals of capelin in the murres’ foraging range. Yet the population of murres on Funk Island did increase during the 2000s (Chardine et al. 2003), though it is in no way paradoxical with reduced capelin biomass. Much of this population increase is associated major reductions in adult mortality with the coincident closure of the northern cod fishery and the removal of thousands of gillnets from inshore areas during the 1990s and 2000s and consequent bycatch mortality (Regular et al. 2013). As well, reductions in adult mortality associated with ship-source oil pollution and with hunting have also decreased during this same period (Robertson et al. 2008), and the cumulative effects of these reductions in adult mortality would have overweighed negative population effects associated with bottom-up prey base reductions. Along the same lines the population growth of Atlantic puffins *Fratercula arctica* and northern gannets *Morus bassanus* also increased over this period (Chardine et al. 2003), and these increases are associated with the above cumulative effects.

While the overall abundance of capelin is well below 33% long-term stock biomass assumed to be a critical threshold for seabird production (Cury et al. 2011), it appears that the distribution and density of the forage fish within the seabird foraging around Funk Island is robust representing a hotspot in an otherwise very sparse overall distribution [Gail; Mowbray]. Interestingly, the common murres’ largest colony is on Funk Island, perhaps as a consequence of these conditions.

Frank et al. (2016) also questioned why the northern gannets’ consumption of capelin is considerably higher from 1990- 2004 (20 – 100 %) than it is before 1990 (<12%; Montevecchi 2007), yet they ignore our primary contention that the cold water regime shift precluded the gannet’s preferred large pelagic warm-water prey from moving into the region hence facilitating ther prey switch to capelin (Montevecchi & Myers 1997, Montevecchi 2007).

### Zooplankton response: *Calanus finmarchicus* abundance

### Physical variability

## Discussion

Fisheries and Oceans Canada has concluded that the Newfoundland and Labrador capelin stock suffered an order of magnitude decline in the early 1990s (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015). Frank et al. (2016) disputed this conclusion and postulated that the capelin stock did not suffer a collapse. Here we weighted the empirical support for the hypotheses of stock collapse vs non-collapse, using multiple, independent lines of enquiry using diverse statistical methods (i.e. triangulation, sensu Munafò & Davey Smith 2018). The weight of the evidence led us to conclude that the 2J3KL capelin stock suffered a population collapse.

Frank et al. (2016) proposed two explanations for their hypothesis of non-collapse: (1) there was a spatio-temporal mismatch between the spring acoustic survey and capelin phenology; and (2) there was a change in biology of capelin from a highly migratory stock to one that inhabits the inshore. The first explanation was rejected by both Frank et al. (2016) and our analyses. The spring acoustic survey targets the immature portion of the stock that is not migrating, so late spawning post-1991 would not affect the abundance index of the immature portion of the stock. Furthermore, repeat surveys in June 1992 and 2003 did not find an increase in capelin biomass (Mowbray 2014), and the probability that the acoustic survey would miss the immature capelin biomass every year for the past 25 years was 22% (Frank et al. 2016). The positive significant relationship between an inshore larval index and the age-2 recruitment index also provides strong support for the ability of the spring acoustic survey to provide an index of immature capelin abundance (Murphy et al. 2018). Therefore, the spring acoustic survey is providing us with a real index of a currently depressed capelin stock in the offshore.

Frank et al. (2016)’s second explanation for their contention of no collapse is that the stock has become less migratory and stays inshore year round. . We tested this hypotheses using multiple independent datasets, which included both fishery-dependent (inshore commercial catch) and fishery-independent (spring acoustic survey, FBTS, AZMP oceanography cruises, three larval indices, aerial surveys, predator diet data, predator behaviour data) data. Using the FBTS data and the center of gravity approach described in (Thorson et al. 2016), we found no evidence of capelin moving either east or west inter-annually, but rather capelin’s centre of gravity moved either north or south depending on abundance. In years with high capelin abundance, capelin were distributed further north. However, the FBTS surveys a limited number of inshore strata. If we considered all of the inshore area not surveyed by the FBTS (‘the blind spot’), there would need to be a minimum of 41,000 kg/km2 uniformly distributed of capelin in the inshore strata to compensate for the ‘missing’ 3-6 mt capelin from the offshore. It is highly unlikely that this amount of capelin would have been missed for over 25 years, given that there are active inshore fisheries for capelin, Atlantic herring, snow crab and northern cod. Furthermore, year round inshore acoustic surveys have found a maximum of 10,000 kg/km2 in Trinity Bay in June, and the inshore densities are a fraction of this outside of the peak spawning period. Since the FBTS has few inshore strata, we do not have much diet data of fish predators in the nearshore. However, murres have had a temporal shift towards later breeding in the late 1990s, which corresponds with the later inshore arrivals of capelin in the murres’ foraging range (Davoren & Montevecchi 2003). This would not be expected if capelin resided year round in the bays. These two independent lines of enquiry suggest that the ‘missing’ capelin are not in the inshore.

Capelin experienced profound changes in their biology post-1991. One of these changes is earlier maturation. Frank et al. (2016) postulated that earlier maturation is due to non-migratory behaviour exhibited by capelin. We used capelin maturity data from the acoustic offshore survey and the age composition data from the inshore commercial catch to test this hypothesis. We would expect to see fewer older, mature fish in the offshore compared to the inshore if capelin are now residing in the inshore. There were large differences in maturity and age composition of catches pre- and post-1991, but there were no substantial differences in age composition and maturity between the offshore and inshore data post-1991. This data provides equivocal support for the collapse hypothesis as earlier maturation in both the inshore and offshore is also consistent with the collapse hypothesis where age at maturity declines in fish populations that have undergone a reduction in population size (Shuter 1990) and are stressed (Trippel 1995).

We used both northern cod (predator diet) and a total mortality index from the acoustic survey to investigate predator release on capelin post-1991. If capelin moved into the inshore with no reduction in biomass in post-1991, then the reduced population of northern cod should have high condition while capelin total mortality should be low. Instead we have evidence of northern cod aggregated within a small area north of the Grand Bank and in the Bonavista corridor by the early 1990s (Rose et al. 2000), which was hypothesized to be in response to the change in distribution of capelin (Rose et al. 2000), and northern cod condition was low where there was no spatial overlap between cod and capelin. However, even with a decrease in northern cod predation pressure, capelin has experienced higher total mortality since 1991. With the increase in the total mortality index over time, it seems quite plausible that capelin numbers have remained low since 1990-1991 due to a combination of several factors: (1) capelin have not experienced a release from predation mortality following the collapse of northern cod because the decrease in cod biomass is in proportion to their own decrease in biomass (Frank et al. 2016); (2) predation pressure from species other than northern cod, like seabirds, harp seals, and whales, has remained either unchanged or increased since 1991 (reference); (3) environmental conditions are driving a bottom-up control on capelin biomass (Pepin reference)(Buren et al. 2014a); (4) and there is a commercial fishery for capelin, which is managed using the precautionary approach but there are no reference points for capelin. For capelin biomass to return to its historic levels, reductions in natural and fishing mortality as well as improved ocean conditions may be required.

All relevant and informative data sources examined support the hypothesis of a collapsed capelin stock. While some data sources provide equivocal support for the non-collapse hypothesis, the effectiveness or adequacy of these is questionable. Market fluctuations have made the inshore catch rate index useless as an indicator of stock abundance (Anon 1998), violation of key assumptions of aerial surveys have made that index unreliable, and the comparison of the magnitude of the late larval index without accounting for changes in spawning phenology Frank et al. (2016) carried out is misleading. Evidence from all other sources; , the offshore acoustic survey, the fall multi-species survey, primary and secondary productivity (?), and cod, seabirds, and harp seal data support the collapse hypothesis. The spring acoustic survey carried out by Fisheries and Oceans Canada provides robust indices of abundance and biomass of the 2J3KL capelin stock. Given the survey design, these are minimum estimates, but all data sources examined indicate that the survey captures trends in the capelin population.

## References

Alheit J, Roy C, Kifani S (2009) Decadal-scale variability in populations. In: Checkley D, Alheit J, Oozeki Y, Roy C (eds) Climate Change and Small Pelagic Fish. Cambridge University Press, Cambridge, UK

Anon (1998) Capelin in SA2 + Div. 3KL. Book 98/63. Canadian Science Advisory Secretariat (CSAS) Research Document

Bourne C, Mowbray F, Squires B, Croft J (2015) An assessment framework and review of Newfoundland east and south coast Atlantic herring (*Clupea harengus*) stocks to the spring of 2013. Canadian Science Advisory Secretariat (CSAS) Research Document 2015/029

Buren AD, Koen-Alonso M, Pepin P, Mowbray F, Nakashima BS, Stenson GB, Ollerhead N, Montevecchi WA (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. Marine Ecology Progress Series 511:265-284

Campbell JS, Winters GH (1973) Some biological characteristics of capelin, *Mallotus villosus*, in the Newfoundland area. International Commission for the Northwest Atlantic Fisheries Research Document 73/90

Carscadden J, Nakashima BS, Miller DS (1994) An evaluation of trends in abundance of capelin (Mallotus villosus) from acoustics, aerial surveys and catch rates in NAFO Division 3L, 1982-89. Northw Atl Fish Sci 17:45-57

Carscadden JE, Frank KT, Leggett WC (2000) Evaluation of an environment-recruitment model for capelin (M*allotus villosus)*. ICES J Mar Sci 57:412-418

Carscadden JE, Frank KT, Leggett WC (2001) Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences 58:73-85

Carscadden JE, Gjøsæter H, Vilhjálmsson H (2013) A comparison of recent changes in distribution of capelin (*Mallotus villosus)* in the Barents Sea, around Iceland and in the Northwest Atlantic. Progress in Oceanography

Carscadden JE, Nakashima BS (1997) Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s. Forage fishes in marine ecosystems Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems Alaska Sea Grant College Program Rep No AK-SG-97-01. University of Alaska Fairbanks, Fairbanks, Alaska

Chardine JW, Robertson GJ, Ryan PC, Turner B (2003) Abundance and distribution of common murres breeding at Funk Island, Newfoundland in 1972 and 2000. Canadian Wildlife Service Technical Report Series Atlantic Region:iv + 15

Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen MC (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217-221

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L, Sydeman WJ (2011) Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. Science 334:1703

Dalley EL, Anderson JT, deYoung B (2002) Atmospheric forcing, larval drift, and recruitment of capelin ( Mallotus villosus ). ICES Journal of Marine Science 59:929-941

Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. Marine Ecology Progress Series 258:253-261

DFO (1994) Report on the status of pelagic fishes (capelin off Newfoundland and in the Gulf of St. Lawrence, and herring off the East, Southeast and South coasts off Newfoundland). DFO Atlantic Fisheries Stock Status Report 1994/3

DFO (2000) Capelin in Subarea 2 + Div. 3KL. DFO Science Stock Status Report B2-02 (2000):1-6

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

DFO (2001b) Capelin in Subarea 2 + Div. 3KL - Update. DFO Science Stock Status Report B2-02 (2001):1-5

DFO (2008) Assessment of capelin in SA2+Div. 3KL in 2008. DFO Canadian Science Advisory Secretariat Science Advisory Report 2008/054

DFO (2010) Assessment of Capelin in SA 2 + Div. 3KL in 2010. DFO Canadian Science Advisory Secretariat Science Advisory Report 2010/090

DFO (2013) Assessment of capelin in SA2 + Div. 3KL in 2013. DFO Canadian Science Advisory Secretariat Science Advisory Report 2013/11

DFO (2015) Assessment of capelin in Subarea 2 and Divisions 3KL in 2015. DFO Canadian Science Advisory Secretariat Science Advisory Report 2015/036

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

Foster AR, Houlihan DF, Hall SI (1993) Effects of Nutritional Regime on Correlates of Growth Rate in Juvenile Atlantic Cod (Gadus morhua): Comparison of Morphological and Biochemical Measurements. Canadian Journal of Fisheries and Aquatic Sciences 50:502-512

Frank KT, Carscadden JE, Simon JE (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences 53:1473-1486

Frank KT, Leggett WC (1981) Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 38:215-223

Frank KT, Petrie B, Boyce D, Leggett WC (2016) Anomalous ecosystem dynamics following the apparent collapse of a keystone forage species. Marine Ecology Progress Series 553:185-202

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic Cascades in a Formerly Cod-Dominated Ecosystem. Science 308:1621

Gislason H, Daan N, Rice Jake C, Pope John G (2010) Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries 11:149-158

Gjøsæter H (1998) The population biology and exploitation of capelin (Mallotus villosus) in the barents sea. Sarsia 83:453-496

Gjøsæter H, Bogstad B, Tjelmeland S (2009) Ecosystem effects of the three capelin stock collapses in the Barents Sea. Marine Biology Research 5:40-53

Gomes MdC, Haedrich RL, Villagarcia MG (1995) Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991. Fisheries Oceanography 4:85-101

Hammill MO, Stenson GB, Doniol-Valcroze T, Mosnier A (2011) Northwest Atlantic harp seals population trends, 1952-2012. DFO Canadian Science Advisory Secretariat Research Document 2011/099

Hammill MO, Stenson GB, Doniol-Valcroze T, Mosnier A (2015) Conservation of northwest Atlantic harp seals: Past success, future uncertainty? Biological Conservation 192:181-191

Hamre J (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. Biodiversity & Conservation 3:473-492

Haug T, Nilssen K (1995) Ecological implications of harp seals *Phoca groenlandica* invasions in northern Norway. In: Schytte Blix A, Walløe L, Ulltang Ø (eds) Whales, seals, fish and man. Elsevier Science

Huse G (1998) Sex-specific life history strategies in capelin (*Mallotus villosus*)? Canadian Journal of Fisheries and Aquatic Sciences 55:631-638

Hutchings JA, Myers RA (1994) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 51:2126-2146

ICES (2005) Spawning and life history information for North Atlantic cod stocks. In: Brander KM (ed) ICES Cooperative Research Report, Book 274. ICES, Copenhagen, Denmark

ICES (2017) Report of the North Western Working Group (NWWG). Copenhagen, Denmark

Jangaard PM (1974) The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition. Bulletin of the Fisheries Research Board of Canada 186:1-70

Koen-Alonso M, Pepin P, Mowbray F (2010) Exploring the role of environmental and anthropogenic drivers in the trajectories of core fish species of the Newfoundland-Labrador marine community.

Lambert Y, Dutil J-D (1997a) Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Sciences 54:104-112

Lambert Y, Dutil J-D (1997b) Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences 54:2388-2400

Leggett WC, Frank KT, Carscadden JE (1984) Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 41:1193-1201

Lilly GR, Davis DJ (1993) Changes in the distribution of capelin in Divisions 2J, 3K and 3L in the autumns of recent years, as inferred from bottom-trawl by-catches and cod stomachs examinations. NAFO SCR Doc 93/54

Lilly GR, Hop H, Stansbury DE, Bishop CA (1994) Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. ICES CM 0:6

Lilly GR, Parsons DG, Kulka DW (2000) Was the increase in shrimp biomass on the northeast Newfoundland shelf a consequence of a release in predation pressure from cod? Journal of Northwest Atlantic Fishery Science 27:45-61

Marshall CT, Needle CL, Yaragina NA, Ajiad AM, Gusev E (2004) Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Canadian Journal of Fisheries and Aquatic Sciences 61:1900-1917

McQuinn IH (2009) Pelagic fish outburst or suprabenthic habitat occupation: legacy of the Atlantic cod (*Gadus morhua*) collapse in eastern Canada. Canadian Journal of Fisheries and Aquatic Sciences 66:2256-2262

Melvin GD, Fife FJ, Sochasky JB, Power MJ, Stephenson RL (1995) The 1995 Update on Georges Bank 5Z Herring Stock. DFO Atlantic Fisheries Research Document 95/86

Miller DS (1994) Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 2J3KL in the autumn of 1993. Capelin in SA2 + Div 3KL DFO Atlantic Fisheries Research Document 94/18

Miller DS (1997) Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 3KL in the spring of 1996. Capelin in SA2 + Div 3KL DFO Atlantic Fisheries Research Document 97/29

Misra RK, Carscadden J (1984) Stock discrimination of capelin (*Mallotus villosus*) in the Northwest Atlantic. Journal of Northwest Atlantic Fishery Science 5:199-205

Montevecchi WA (2000) Seabirds. In: Bundy A, Lilly GR, Shelton PA (eds) A Mass Balance Model of the Newfoundland-Labrador Shelf

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series 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 Journal of Marine Science 54:608-614

Morgan MJ, Koen-Alonso M, Rideout RM, Buren AD, Maddock Parsons D (2017) Growth and condition in relation to the lack of recovery of northern cod. ICES Journal of Marine Science:fsx166-fsx166

Morgan MJ, Rideout RM, Colbourne EB (2010) Impact of environmental temperature on Atlantic cod Gadus morhua energy allocation to growth, condition and reproduction. Marine Ecology Progress Series 404:185-195

Mowbray F (2002) Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. ICES Journal of Marine Science 59:942-949

Mowbray F (2014) Recent spring offshore acoustic survey results for capelin, *Mallotus villosus*, in NAFO Division 3L. DFO Canadian Science Advisory Secretariat Research Document 2013/040

Munafò MR, Davey Smith G (2018) Robust research needs many lines of evidence. Nature 553:399-401

Murphy HM, Pepin P, Robert D (2018) Re-visiting the drivers of capelin recruitment in Newfoundland since 1991. Fisheries Research 200:1-10

Nakashima B (1996) The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (M*allotus villosus)*. NAFO Sci Coun Studies 24:55-68

Nakashima BS (1992) Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 49:2423-2429

Nakashima BS (1998) Results of the 1997 aerial survey of capelin (Mallotus villosus) schools. in Anon: Capelin in SA2 + Div. 3KL. Canadian Stock Assessment Secretariat Research Document 98/63.

Nakashima BS, Mowbray F (2014) Capelin (*Mallotus villosus)* recruitment indices in NAFO Division 3KL. DFO Canadian Science Advisory Secretariat Research Document 2013/091

Nakashima BS, Wheeler JP (2002) Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters - the interaction between beach and demersal spawning. ICES Journal of Marine Science 59:909-916

Nilssen KT, Haug T, Øritsland T, Lindblom L, Kjellqwist SA (1998) Invasions of harp seals Phoca groenlandica Erxleben to coastal waters of nor way in 1995: Ecological and demographic implications. Sarsia 83:337-345

O'Driscoll RL, Rose GA, Anderson JT (2002) Counting capelin: a comparison of acoustic density and trawl catchability. ICES Journal of Marine Science 59:1062-1071

Obradovich SG, Carruthers EH, Rose GA (2014) Bottom-up limits to Newfoundland capelin (Mallotus villosus) rebuilding: the euphausiid hypothesis. ICES Journal of Marine Science 71:775-783

Ona E, Mitson RB (1996) Acoustic sampling and signal processing near the seabed: the deadzone revisited. ICES Journal of Marine Science 53:677-690

Pálsson ÓK, Gislason A, Guðfinnsson HG, Gunnarsson B, Ólafsdóttir SR, Petursdottir H, Sveinbjörnsson S, Thorisson K, Valdimarsson H (2012) Ecosystem structure in the Iceland Sea and recent changes to the capelin (Mallotus villosus) population. ICES Journal of Marine Science 69:1242-1254

Pardoe H, Marteinsdóttir G (2009) Contrasting trends in two condition indices: bathymetric and spatial variation in autumn condition of Icelandic cod Gadus morhua. Journal of Fish Biology 75:282-289

Pardoe H, Thórdarson G, Marteinsdóttir G (2008) Spatial and temporal trends in condition of Atlantic cod Gadus morhua on the Icelandic shelf. Marine Ecology Progress Series 362:261-277

Pedersen EJ, Thompson PL, Ball RA, Fortin M-J, Gouhier TC, Link H, Moritz C, Nenzen H, Stanley RRE, Taranu ZE, Gonzalez A, Guichard F, Pepin P (2017) Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. Royal Society Open Science 4

Penton PM, Davoren GK (2013) Capelin (*Mallotus villosus*) fecundity in post-1990s coastal Newfoundland. Marine Biology 160:1625-1632

Pepin P, Cuff A, Koen-Alonso M, Ollerhead N (2010) Preliminary Analysis for the Delineation of Marine Ecoregions on the NL Shelves. NAFO SCR Doc 10/72

Pepin P, Higdon J, Koen-Alonso M, Fogarty M, Ollerhead N (2014) Application of ecoregion analysis to the identification of Ecosystem Production Units (EPUs) in the NAFO Convention Area. NAFO SCR Doc 14/069

Pepin P, Koen-Alonso M, Higdon J, Ollerhead N (2012) Robustness in the delineation of ecoregions on the Newfoundland and Labrador continental shelf. NAFO SCR Doc 12/067

Pikitch EK, Boersma PD, Boyd IL, Conover DO, Cury PM, Essington TE, Heppell SS, Houde ED, Mangel M, Pauly D, Plagányi E, Sainsbury KJ, Steneck RS (2012) Little fish: big impact: managing a crucial link in ocean food webs. Lenfest Ocean Program, Washington, DC

Regular P, Montevecchi W, Hedd A, Robertson G, Wilhelm S (2013) Canadian fishery closures provide a large-scale test of the impact of gillnet bycatch on seabird populations. Biology Letters 9

Rice J (2002) Changes to the large marine ecosystem of the Newfoundland-Labrador shelf. In: Sherman K, Skjoldal HR (eds) Large marine ecosystems of the North Atlantic. Elsevier Science B.V.

Rose GA, deYoung B, Kulka DW, Goddard SV, Fletcher GL (2000) Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences 57:644-663

Schwartzlose RA, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, Lluch-Belda D, Lluch-Cota SE, MacCall AD, Matsuura Y, Névarez-Martínez MO, Parrish RH, Roy C, Serra R, Shust KV, Ward MN, Zuzunaga JZ (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21:289-347

Shuter BJ (1990) Population level indicators of stress. In: Adams SM (ed) Biological indicators of stress in fish. American Fisheries Society Symposium 8

Skagseth Ø, Slotte A, Stenevik EK, Nash RDM (2015) Characteristics of the Norwegian Coastal Current during Years with High Recruitment of Norwegian Spring Spawning Herring (Clupea harengus L.). PLOS ONE 10:e0144117

Sogard SM (1997) Size-Selective Mortality in the Juvenile Stage of Teleost Fishes: A Review. Bulletin of Marine Science 60:1129-1157

Soutar A, Issacs JD (1969) History of fish populations inferred from fish scales in anaerobic sediments off California. CalCOFI Reports 13:63-70

Stenson GB (2012) Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL. Canadian Science Advisory Secretariat (CSAS) Research Document 2012/156

Stenson GB, Buren AD, Koen-Alonso M (2016) The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal, Pagophilus groenlandicus. ICES Journal of Marine Science: Journal du Conseil 73:250-262

Stenson GB, Wakeham D, Buren AD, Koen-Alonso M (2014) Density-dependent and density-independent factors influencing reproductive rates in Northwest Atlantic harp seals, *Pagophilus groenlandicus*. DFO Canadian Science Advisory Secretariat Research Document 2014/058

Templeman W (1948) The life history of the caplin (*Mallotus villosus* O. F. Müller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory 17:1-151

Thorson J, T., Pinsky M, L., Ward E, J., Gimenez O (2016) Model‐based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods in Ecology and Evolution 7:990-1002

Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. ICES Journal of Marine Science 74:1311-1321

Toresen R, Østvedt OJ (2000) Variation in abundance of Norwegian spring-spawning herring (Clupea harengus, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries 1:231-256

Trippel EA (1995) Age at Maturity as a Stress Indicator in Fisheries: Biological processes related to reproduction in northwest Atlantic groundfish populations that have undergone declines. BioScience 45:759-771

Vilhjálmsson H (1994) The Icelandic capelin stock. Rit Fiskideildar 13:1-281

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