# The collapse of a keystone forage species: A response to Frank et al. 2016

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## Abstract

According to acoustic monitoring surveys conducted by Canada and the USSR, the Newfoundland (NAFO Division 2J3KL) capelin stock suffered an order of magnitude decline in biomass during the early 1990s. This collapse was concomitant with drastic changes in the ecosystem during the late 1980s and early 1990s, and was considered a key signal in the identification of a regime shift that occurred in the early 1990s. While more than a dozen studies have provided evidence supporting a capelin stock collapse, Frank et al. (2016) disputed this conclusion. They instead concluded that the apparent capelin collapse was due to either (1) the stock changing its migratory patterns with the timing of the acoustic survey remaining constant, leading to a spatio-temporal mismatch between the survey and the stock, or (2) capelin becoming less migratory and remaining inshore year round, therefore being largely underestimated by the offshore surveys. We tested these hypotheses using multiple independent datasets, which included both fishery-dependent (inshore commercial catch) and fishery-independent (spring acoustic and fall bottom trawl surveys, oceanography cruises, capelin larval indices, aerial surveys, predator diet and behaviour, and diverse statistical methods) data. The hypothesis of a non-collapse of the capelin stock was rejected by our analyses. The weight of evidence approach led us to conclude that the Newfoundland capelin stock suffered a population collapse in 1991 with minimal recovery over the subsequent 25 years.

## Introduction

Forage fish play crucial roles in many ecosystems, transferring the bulk of energy from lower trophic levels to large vertebrate predators. Typically, they are small shoaling species that are characterized by short life expectancy and rapid but variable growth driven by environmental factors. Forage fish species often exhibit “boom and bust” population 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, 2014). Forage fish species can experience prolonged periods of ‘bust’ dynamics. For example, the Norwegian spring-spawning herring (*Clupea harengus*) stock collapsed in the late 1960s after a pulse of overfishing and remained at very low levels until the late 1980s (Toresen & Østvedt 2000, Skagseth et al. 2015); while sardine (*Sardinops sagax*) and anchovy (*Engraulis* spp.) 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 (*Mallotus villosus*) 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 the coast of Iceland, and along the Newfoundland and Labrador (Canada) continental shelf. The Barents Sea capelin stock experienced four collapses over the past 4 decades: the mid- to late-1980s, the mid-1990s, the mid-2000s, and the mid-2010s. The size of the stock fluctuated between 3 and 7 million tonnes during the boom phase and around 200 thousand tonnes during 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 over the past 4 decades: the early 1980s, the early 1990s, and most of the 2000s. The size of the stock was around 1.5-2 million tonnes during the boom phase and between 100-500 thousand tonnes during bust phases (ICES 2017). The first two bust phases were due to a combination of poor recruitment and the stock being easily available to the fishing fleet, while the most recent bust phase was likely associated with a climate-related shift in distribution (Pálsson et al. 2012, Carscadden et al. 2013).

Fisheries and Oceans Canada (DFO) is responsible for the assessment of the Newfoundland and Labrador (NL) capelin stock. DFO concluded that the stock experienced an order of magnitude decline in the early 1990s with minimal recovery during the past two decades (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015) DFO 2018. The size of the stock fluctuated between 2 and 6 million tonnes before 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 (deYoung & Rose 1993, Gomes et al. 1995, Montevecchi and Myers 1997, Lilly et al. 2000, Rice 2002, Rose 2007, Koen-Alonso et al. 2010, Hammill et al. 2011, Pedersen et al. 2017), including major changes in the biology and ecology of capelin, such as delayed and protracted spawning, changes in their geographical and vertical distribution, and declines in somatic condition and size and age at maturity (Frank et al. 1996, Carscadden & Nakashima 1997, Carscadden et al. 2001, Mowbray 2002, Nakashima & Wheeler 2002, DFO 2010). The collapse of capelin was a key signal in the identification of regime shift such as occurred in the early 1990s (Rose 2005, Buren et al. 2014a,b).. *Capelin ( Mallotus villosus ) distribution and climate: a sea “canary” for marine ecosystem change. G.A. Rose, ICES Journal of Marine Science, Volume 62, Issue 7, 1 January 2005, Pages 1524–1530, https://doi.org/10.1016/j.icesjms.2005.05.008*

Frank et al. (2016) argued that the capelin stock off NL did not collapse; alternatively, they argued that the offshore surveys have failed to detect large capelin aggregations since 1991 because of spatio-temporal mismatch between the surveys and the stock. Specifically, they hypothesized that post-1991 either (1) capelin changed their migratory patterns while the timing of the acoustic survey remained constant, leading to a spatio-temporal mismatch between the survey and the stock or (2) capelin suddenly became less migratory and now remains inshore, and are therefore undetected by the offshore surveys. Support for the hypothesis of non-collapse of capelin was based on changes in the biology of capelin post-1991 (e.g., 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, Atlantic cod (*Gadus morhua*), seabirds, seals] to the large-scale changes that have occurred since the early 1990s (Frank et al. 2016). The objective of the present paper is to assess the empirical support for the hypothesis of stock collapse (DFO 2015) vs that of non-collapse (Frank et al. 2016) using all available data.

**Methods**

To test the hypotheses of collapse and non-collapse of the capelin stock in NAFO Divisions 2J3KL (hereafter Div. 2J3KL; Fig. 1), we applied the weight of evidence approach using multiple, independent data sets and diverse statistical methods (e.g., triangulation, sensu Munafò & Davey Smith 2018). To do this, we constructed the present study following the structure of Frank et al. (2016) (hereafter Frank et al.). Each section of the present study opens with a statement presenting how the main conclusion(s) from the analyses presented in Frank et al. contrast with the consensus from the primary and government literature. In some sections, new data and analyses were presented to test alternative hypotheses. Each section concludes by weighting evidence in support for each alternative hypothesis. Once this was completed for all sections, the weight of evidence approach was used to determine which hypothesis was best supported by the combination of previously-published results and additional analyses based on independent data sets.

## Capelin

### Offshore capelin distribution: acoustic surveys

Frank et al. contended that Canada and the USSR offshore acoustic surveys found low capelin biomasses in the fall of 1991 and 1992 in Div. 2J3KL because capelin became non-migratory from the fall of 1990. The alternative hypothesis presented in the literature is that the fall acoustic surveys detected a sudden decrease in capelin biomass in Div. 2J3KL in 1990 (e.g., Miller & Lilly 1991, Bakanev 1992, Miller 1992, 1993, 1994, Mowbray 2014), and, while capelin changed their distribution offshore post-1991 [southern shift in distribution (e.g., Miller & Lilly 1991, Miller 1992)], they did not become non-migratory.

From 1977 to 1992, Canada conducted fall (October) acoustic surveys for capelin in Div. 2J3K (Fig. 2) (e.g., Miller and Carscadden 1984, Miller and Lilly 1991). The fall acoustic surveys targeted the maturing portion of the stock during winter feeding migrations to provide estimates of the size and number of maturing fish being recruited to the fishery the following year (Mowbray 2014). The capelin stock in Div. 2J3K was also acoustically surveyed by the former USSR in November from 1972-1992 although the USSR acoustic survey covered a more restricted geographic area compared to the Canadian acoustic survey as it did not go as far into the inshore area (Bakanev 1992; Fig. 2). The USSR fall acoustic surveys were conducted later than the Canadian surveys and consistently estimated higher capelin abundances, which may have been due to timing, as capelin start aggregating into large overwintering shoals in November (Winters 1995). In 1990, the Canadian fall acoustic survey reported a very low capelin biomass while the USSR acoustic survey reported the smallest biomass since 1984 (Winters 1995). Both the USSR and Canadian acoustic surveys reported record low biomasses in the fall of 1991 and 1992 (Winters 1995). The decrease in capelin biomass in both surveys corresponded with very few capelin being detected off the coast of Labrador and a southward shift in stock distribution to the southern portion of Div. 3K and northern portion of Div. 3L (Miller & Lilly 1991, Miller 1992). A Canadian expanded fall survey (Div. 2J3KL) in 1993-94 was conducted to determine if the ‘missing’ capelin could be located. However, the expanded fall acoustic survey confirmed the findings of the 1991-92 fall surveys that offshore capelin biomass was low and characterized by a southward change in distribution (Miller 1994, 1995).

Frank et al. based their hypothesis of an inshore, non-migratory capelin stock post-1991 on high densities of overwintering maturing capelin and large schools of immature capelin observed during winter surveys conducted in Trinity Bay in 1967-68 (Winters 1970), suggesting that capelin can survive inshore through the winter. Fisheries and Oceans Canada tested the hypothesis of year-round residency of capelin in the inshore by conducting seasonal acoustic surveys in Trinity Bay (September and October 2003; January, June and September 2004-05) and expanding the annual offshore spring acoustic survey into Trinity Bay (1999-2005, 2007-13, 2017) ([Fig. 3](#Ref514161259) a; see supplementary section for details on methods). Seasonally, capelin densities were low in Trinity Bay in January and May, and the maximum mean density of capelin was observed in June (10,000 kg km-2), which corresponded with the start of the spawning period when capelin were highly aggregated inshore ([Fig. 3](#Ref514161259) a). In September and October, capelin densities were low once again (Fig. 3 a). There was also a distinct seasonal pattern in the age and maturity composition inshore. In January, overwintering fish were composed of ~70% immature age-1 and age-2 fish ([Fig. 3](#Ref514161271) b, c); the relative contribution of older fish increased through the spring as maturing age-2 and age-3 fish migrated into Trinity Bay ([Fig. 3](#Ref514161271) b, c); and by October, immature age-1 fish dominated the inshore area, strongly suggesting that spent mature fish either died or left the bay (Fig. 3 b). The seasonal surveys found no evidence of a large inshore, non-migratory capelin stock. In agreement with this finding, an inshore acoustic survey in January 2000 for overwintering cod from Conception to Notre Dame Bay found concentrations of juvenile capelin (e.g., O’Driscoll and Rose 2001) but few older fish (G.A. Rose, unpublished data). *In situ acoustic target strength of juvenile capelin. Richard L. O'Driscoll George A. Rose. ICES Journal of Marine Science, Volume 58, Issue 1, 1 January 2001, Pages 342–345, https://doi.org/10.1006/jmsc.2000.1015*

In the majority of years, the biomass of capelin surveyed in Trinity Bay during the spring acoustic survey was less than 10% of the capelin biomass surveyed offshore (Fig. 4). However, in three years (2000, 2001 and 2010) when the offshore capelin biomass was low, there was increased capelin biomass inshore in Trinity Bay (Fig. 4). Such changes in spatial distribution may be linked to temperature-driven interannual variability in migration routes, as observed in the Icelandic capelin stock (Olafsdottir & Rose 2012). However, while capelin biomass was relatively higher inshore in these three years, it was far from the ‘missing’ 3-6 million tonnes of capelin from the offshore since 1991.

In summary, while the fall acoustic surveys in Div. 2J3KL cannot refute the hypothesis that capelin are non-migratory post-1991 as inshore areas were not systematically surveyed, the lack of significant inshore aggregations of capelin outside of the peak spawning period during seasonal and annual spring acoustic surveys provides additional support for the hypothesis of a capelin stock collapse post-1991. Furthermore, capelin stocks in other regions did not become non-migratory in response to changes in stock abundance and environmental conditions but rather demonstrated changes in spatial distribution and migration routes (Olafsdottir & Rose 2012, Carscadden et al. 2013), and these changes were best documented for the fall feeding periods of these stocks (Ingvaldsen & Gjøsæter 2013).

**Offshore capelin distribution: annual multi-species bottom-trawl surveys**

Frank et al. hypothesized that there was an abrupt change in capelin migration patterns post-1991, with capelin now remaining inshore year round. The fall bottom trawl survey (FBTS) data were used to point to a westerly, inshore shift in the centre of capelin concentration in 1996-2010 compared to 1985-1995 (Frank et al. 2016). Alternatively, the use of bottom-trawl gear with low catchability of pelagic species has limited usefulness as an abundance index (O’Driscoll et al. 2002) and is likely to produce biased estimates on the demographic trends of these species (Jech and McQuinn 2016). In the NL region, the trawl gear on the FBTS was changed in 1995 from an Engels otter trawl (1978-1994) to a Campelen 1800 shrimp trawl (1995-2016). Counting capelin: a comparison of acoustic density and trawl catchability

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Frank et al.’s annual mapping of the centre of concentration of capelin using the FBTS presence/absence data aligns with the high degree of inter-annual 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). This variability is likely related to the poor catchability of capelin in the Engel otter trawl, which was designed for commercial ground fish (ref). A similar centre of gravity analysis using only post-1995 FBTS data, which corresponded with the time period of improved catchability of capelin with the use of a Campelen 1800 shrimp trawl, showed a southerly shift in capelin distribution with a recent shift to the northwest in 2011-14 (DFO 2015). Neither of these analyses accounted for inter-annual changes in capelin spatial distribution due to FBTS sampling effort or uncertain catchability of capelin in bottom trawls.

Nevertheless, Frank et al.’s hypothesis of a shoreward shift in capelin centre of distribution post-1991 was tested using FBTS data and the center of gravity approach described in Thorson et al. (2016). Specifically, the VAST package in R (Thorson & Barnett 2017) was used to fit a geostatistical delta-generalized linear mixed model to estimate the spatial and temporal distribution of capelin. The main advantages of this approach is that it accounts for inter-annual changes in the spatial distribution of sampling effort and offers a means of estimating the standard error of the centre of gravity metric, which provides perspective on the significance of distributional shifts. Like DFO (2015), we focused on the post-1995 period when the catchability of capelin improved with the use of a Campelen 1800 shrimp trawl. Our geostatistical analysis did not support the hypothesis that capelin shifted their distribution towards the inshore post-1995 and there is no evidence of an easterly or westerly movement in the center of gravity of capelin ([Fig. 5](#Ref514161325)). Instead, the center of gravity of capelin remains > 100 km offshore and demonstrates pronounced shifts in the north-south axis ([Fig. 5](#Ref514161325)).

Other analyses using the FBTS data indicate that it is unrealistic to assume that the 3 to 6 Mt of capelin that are ‘missing’ in the offshore surveys are now residing in the inshore. Even though the inshore strata are inconsistently covered by the annual FBTS with an inshore area of ~35,000 to ~71,000 km2 remaining unsurveyed each year, the minimum density for 3 to 6 Mt of capelin hiding in these inshore waters would have to be between ~41,000 to ~170,000 kg km-2, uniformly distributed throughout the unsurveyed area. In contrast, the maximum mean density of capelin observed in the Trinity Bay survey strata in June was 10,000 kg km-2, and the maximum mean density of capelin observed outside the spawning period was only 40 kg km-2 (Fig. 3 a). This analysis indicates it is unlikely that the capelin stock is currently non-migratory and has remained inshore since 1991.

In summary, recognizing the bias in catchability of pelagic fish in the Engel vs Campelen trawls, we only used FBTS data from 1995 onwards, which precludes the FBTS centre of gravity analysis from providing support for the non-collapse hypothesis. When we looked at other sources of capelin distribution data during this time period (sensu Jech & McQuinn 2016) the juvenile capelin surveys using an IGYPT trawl in the northeastern bays and the offshore from 1994-99 also found a southward distribution of capelin juveniles compared to the 1980s with centers of distribution on the northern Grand Bank and along the northeast coast, but not in the bays, of Newfoundland (Anderson et al. 2002). These two independent datasets and corresponding analyses suggest that capelin were not residing in the bays of Newfoundland post-1991.

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

Frank et al. have not considered the previously-described change in capelin diel vertical migrations (DVM) post-1991 to support or refute the capelin collapse hypothesis. The change in capelin DVM post-1991 required dedicated experiments in 1995 and 1999 to address the potential impact of DVM changes on the availability of capelin to the acoustic surveys (Mowbray 2002). The proportion of capelin biomass in the trawl zone (bottom 4 m of the water column) increased post-1991 (Mowbray 2002), likely a response to a decline in the risk of predation by Atlantic cod which may drive capelin into the pelagic zone (Rose 1993). Furthermore, when capelin densities were low, capelin were found in closer association with the bottom and DVM was less pronounced compared to when capelin densities were high (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 ([Fig. 4](#Ref514161310)).

In summary, while the DVM experiments were performed to improve acoustic estimates, they also demonstrate how capelin were more available to the FBTS post-1991 and, along with a change in trawl gear in 1995, introduced a bias in the pelagic data obtained from the FBTS. The change in DVM behavior of capelin post-1991 suggests that the population has declined and supports the capelin collapse hypothesis.

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

Frank et al. hypothesized that delays in the timing of capelin spawning post-1991 led to a mismatch in capelin availability to the spring acoustic survey, which has resulted in the spring acoustic survey severely underestimating the capelin biomass offshore. Alternatively, the Canadian regional stock assessment process concluded that the stock experienced an order of magnitude decline in the early 1990s and has remained at historic lows for the past 25 years based on the offshore fall and spring acoustic surveys (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015, 2018).

Since 1991, capelin spawning has been persistently delayed on average by four weeks (DFO 2018). Meanwhile the spring acoustic survey has been fixed spatially and temporally since the 1980s, implying changes in how the spring acoustic survey perceives migrating capelin post-1991. However, it is important to note that the spring acoustic survey, which encompasses a capelin nursery area, was primarily designed to survey the non-migratory, immature portion of the stock, rather than the spawning migration (Mowbray 2014). Specifically, the spring acoustic survey provides an index of abundance of the age-2 portion of the stock. While other age classes are encountered in the spring acoustic survey, they are not fully recruited to the survey, either due to their poor recruitment to the trawling gear and their weak acoustic signal (age-1 or younger) or due to their behaviour (ages-3+) (e.g., more northerly distribution of older fish and highly aggregated shoals for a spawning migration). All age classes acoustically surveyed are included in the annual index of capelin abundance, but the spring acoustic survey does not target capelin spawning migrations, and, therefore, cannot be used to derive a proxy for spawning stock biomass.

While the delay in spawning time should not have a direct effect on the acoustic abundance index derived from the spring acoustic survey, the earlier observed maturation of capelin post-1991 may have an effect on the capelin abundance index. The age-2 portion of the stock is the main component being surveyed and the proportion of maturing age-2 capelin has increased since 1991 (4% pre-1991 compared to 37-79% post-1991) (Mowbray 2014; DFO 2018). Earlier maturation could alter the internal structure of the stock with inter-annual variability in the proportion of age-2s starting their adult migration patterns and are, therefore, unavailable to the survey. However, there has been high internal consistency in the spring acoustic survey, with the index of abundance for the age-3 cohort being strongly correlated with the index of abundance of the age-2 cohort from the previous year (DFO 2018), which implies that the spring acoustic survey can meaningfully capture relative changes in the overall stock, regardless of migration/non-migration fractions.

In summary neither the persistent delay in spawning time nor earlier maturation of capelin post-1991 seem to significantly affect the ability of the spring acoustic survey to provide a relative index of capelin abundance. Data from the spring acoustic survey support the capelin collapse hypothesis.

### Independent indices of inshore capelin abundance

Frank et al. postulated that strong correlations among independent inshore indices of capelin abundance post-1991, and the little changes in these indices between the late 1980s and the early 1990s is supportive of a stable stock. In contrast, the offshore fall and spring acoustic surveys indicated a stock collapse (Miller 1994, 1997, DFO 2008, 2010, 2013, 2015, 2018, Mowbray 2014).

The inshore indices that Frank et al. considered in their review involved an aerial abundance index and inshore commercial catch rates. The aerial survey was designed to estimate capelin spawning stock biomass based on the area of capelin schools near spawning beaches in Div. 3L (Nakashima 1997). The aerial survey commenced in 1982, and initially followed four defined survey tracks in Conception and Trinity Bays during a fixed period of mid-June to early July (Carscadden et al. 1994). Protracted spawning post-1991 violated a key assumption of the aerial surveys, that all schools must arrive at the same time in each bay to form a single spawning peak. Protracted spawning from early July to mid-August in 1991-93 resulted in multimodal capelin spawning peaks that were covered with variable success by the aerial survey (Nakashima 1996). 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 1996, aerial coverage was at its lowest since 1991 due to poor weather and technical problems (Nakashima 1997). 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). Six of the eight years of aerial data post-1991 did not adequately cover peak spawning times (1991-93), had poor weather and technical difficulties (1996), and had reduced geographical coverage (1997-98). The aerial survey was discontinued in 1999.

The inclusion of inshore catch rate data after 1993 in the analysis presented in Figure 6 in Frank et al. is misleading and not reflective of capelin inshore abundance. Due to the small sizes of spawning capelin post-1991, management regulations introduced a size criterion of 50 count/kg to reduce dumping of undersized capelin (Carscadden & Nakashima 1997). This size criterion effectively closed the fishery in 1994 and 1995. From 1996, the size criterion was removed but management regulations to reduce discarding of small, unmarketable capelin resulted in fishing effort being concentrated to a few days when capelin were highly available (Anon 1998). Post-1991, the inter-annual variability in participation in the fishery due to fish quality and market forces in combination with high catch rates in a short period rendered the inshore catch rate index useless as an indicator of stock abundance (Anon 1998).

In summary, due to changes in capelin biology and management measures post-1991, neither of the inshore indices provide reliable data on spawning stock biomass. These indices cannot be used to support or refute either hypothesis.

### Demographic change of both inshore and offshore capelin

Frank et al. argued that the truncation in capelin age structure and reductions in condition, growth, and maturation timing post-1991, are in agreement with the dynamics of a non-migrating stock post-1991. However, earlier maturation is also consistent with the hypothesis that age at maturity will decline in stressed and depleted fish populations ( Shuter 1990, Trippel 1995). Rapid changes in age at maturity occur in response to changes 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).

Unlike Frank et al., we used the annual age composition data from both the inshore commercial catch and the spring acoustic survey to test the migration hypothesis. If capelin were no longer migrating, we would expect to see a higher proportion of age-2 fish caught in the inshore post-1991 (e.g. fish that are vulnerable to the fishing gear, but are immature). The alternative hypothesis, based on the spring acoustic data, is that capelin were still migrating post-1991. We predicted that the proportion of age-2 fish in the offshore is similar pre and post-1991 as capelin were still maturing offshore before their spawning migration. There were large shifts in capelin age compositions from 1980-2016. For the inshore commercial fishery pre-1991, age-2 capelin were a negligible component of the fishery (< 5% of total catch; DFO 2018). Post-1991, the contribution of age-2 capelin increased to almost half of commercial inshore catches (DFO 2018), which supports the hypothesis of non-migratory fish maturing early. However, the population demographics from catches offshore refute the non-migratory hypothesis as the proportion of age-2 and age-3 fish sampled offshore has remained constant pre- and post-1991 at ~60% and ~28% of the catch, respectively (DFO 2018). Furthermore, post-1991, the increased proportion of maturing age-2 fish offshore provides an explanation for the increased catch rate of mature age-2 fish inshore (DFO 2018).

In summary, the inshore commercial catch data alone provided support for the hypothesis that the capelin stock is no longer migratory, but once coupled with the demographic composition of capelin obtained from the offshore acoustic survey, the body of data available rather support the hypothesis that capelin still perform a spawning migration. As such, the increased proportion of mature age-2 fish in the inshore post-1991 can be explained by the increase in proportion of age-2 fish maturing offshore and undergoing a spawning migration, rather than an absence of migration per se.

### Timing of inshore capelin beach spawning

Frank et al. hypothesized that the late spawning of capelin produced a temporal mismatch with the spring acoustic survey, as they postulated that persistently late spawning post-1991 has delayed the timing of arrival of high concentrations of capelin to the offshore acoustic survey area. However, as noted earlier, the spring acoustic survey in Div. 3L targets the immature, non-migratory portion of the stock. Moreover, if mature capelin are present in the surveyed area in May, the dense, highly aggregated shoals of migrating fish are difficult to quantify because shoals are relatively sparse in terms of both the spatial (e.g., transect lines are ~10 to 30+ km apart) and the temporal coverage (e.g., each line is only surveyed once) of the spring acoustic survey program. This is in contrast to immature capelin that were characterized by broadly distributed shoals of feeding fish that are non-migratory. Indeed, capelin surveys in the Barents Sea are timed to avoid spawning migrations (Gjøsæter 1998). In Iceland, if capelin are not detected in surveys during the fall feeding period due to shifting stock distribution, follow-up surveys during spawning migrations are required using coordinated effort from numerous vessels to find the highly aggregated migrating shoals (reviewed in Carscadden et al. 2013). In summary, the delay in spawning post-1991 does not explain the sudden, and persistent, decrease in capelin abundance offshore post-1991.

### Inshore recruitment index

Frank et al. argued that since larval production in Trinity Bay did not decrease appreciably post-1991, capelin biomass did not collapse. However, post-1991, a larval index from Trinity Bay was related to the age-2 abundance index from the spring acoustic survey, which suggests that the spring acoustic survey is providing a valid index of capelin abundance (Murphy et al. 2018).

DFO collects two larval indices in Trinity Bay: an emergent larval index (3-10 mm SL) in a nearshore area and a late-larval index (10-30 mm SL, see Nakashima & Mowbray 2014 for more details). Late-larval abundance data were collected both pre- and post-1991. While Frank et al. compared the late-larval index in August for both datasets, the persistently-late capelin spawning since 1991 has resulted in smaller and younger larvae observed in August 2008-12 compared to August 1982-86, and a better comparison would have to be made between August in years pre-1991, and September in years post-1991 (Nakashima & Mowbray 2014). The average late-larval density in Trinity Bay in September 2002-15 was 30.9 m-2 (SD: 26.9, range 6.73-96.95 m-2), which is considerably lower than the August 1982-86 estimate (48.8 m-2, SD: 15.1, range 33.2-73.6 m-2). The trend in the 2000s is for lower and more variable late-larval densities compared to the 1980s; for example, in 12 of the 14 years in the 2000s, average late-larval densities in September were below the average August larval densities in the 1980s.

If the bulk of capelin biomass was residing inshore year-round and was not available to the annual offshore spring acoustic survey, then we would expect an absence of relationship between larval production and the age-2 abundance index from the spring acoustic survey. However, post-1991, the emergent larval index was related to the age-2 abundance index from the spring acoustic survey (Murphy et al. 2018), which suggests that the offshore acoustic survey tracks inshore productivity. There is currently no relationship between the late-larval index in Trinity Bay and the age-2 abundance index (Murphy et al. 2018). This could be due to changes in the survey design post-1991 including a spatio- temporal contraction of sampling with 19 of the original 52 stations sampled in 1 week in September from 2003-07 and 1 week in both August and September from 2008-15. Such reduction in sampling effort may have resulted in a temporal mismatch between capelin spawning times and the late-larval survey, with capelin larvae either being too small for the gear in August or already advected away from the surveyed area in September.

In summary, while the appreciable decrease in the late-larval productivity index post-1991 supports the capelin collapse hypothesis, the spatio-temporal contraction of the survey post-1991 reduces our ability to directly compare larval productivity between the two periods. The positive, significant relationship between the emergent larval index and the offshore age-2 abundance index post-1991 supports previous research that identified early larval survival as an important driver of recruitment (Frank & Leggett 1982, Leggett et al. 1984, Dalley et al. 2002). This significant relationship between two fishery-independent inshore and offshore indices post-1991 provides support for the capelin collapse hypothesis.

**Ecosystem response**

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

Frank et al. contend that since Atlantic cod weight at age and liver condition indices post-collapse were not spatially homogenous then capelin did not collapse. Alternatively, Atlantic cod weight at age and liver condition indices were never spatially homogenous due to the species complex inhabiting distinct ecosystem production units in NAFO Div. 2J3KLNO (e.g., Lilly 2005, Koen-Alonso et al. 2013, Morgan et al. 2017) on the Labrador and northeast Newfoundland Shelf and Grand Bank. These units are characterized by distinct marine communities and food web systems (Pepin et al. 2010, 2012, 2014, Koen-Alonso et al. 2013, NAFO 2014). Hence the non-homogenous traits of Atlantic cod from Labrador (2J) to the southern Grand Bank (3NO) are typical of this stock. Furthermore, post-1991 changes in spatial overlap between the collapsed stocks of Atlantic cod and capelin may have exacerbated spatial differences in Atlantic cod condition indices (Rose et al. 2000).

The existence of spatial structure in traits of Atlantic cod in NAFO 2J3KL (also known as Northern cod) is well known historically (e.g., Lilly 2005, Neville et al. 2018, Rose & Rowe 2018), with gradients from north to south in growth (length at age) and condition indices (liver, gutted and total body mass) (Buren et al. 2014b, Morgan et al. 2017). Historically, Atlantic cod was a dominant fish predator on the NL Shelf, with capelin being its primary prey (Winters & Carscadden 1978, Lilly 1987, Lilly 1991). During and post-1991, capelin shifted its fall distribution from having two distinct aggregations, one in the northwest (NAFO Div. 2J3K) and one in the southeast (NAFO Div. 3L, at the northern slope of the Grand Bank) to having only one in the southeast (Lilly & Davis 1993, Miller 1994), with records of excursions onto the Flemish Cap and the Scotian Shelf (Frank et al. 1996). Coincidently, Atlantic cod moved southward on the northeast Newfoundland Shelf in the late 1980s/early 1990s and aggregated within a small area on the north of the Grand Bank and in the Bonavista Corridor by the early 1990s (Rose 1993, Rose et al. 2000). One hypothesis by Rose et al. (2000) to explain this shift in Atlantic cod distribution is that they moved in response to the distribution of capelin. Atlantic cod’s weight at age and liver condition worsened in northerly areas where there was no spatial overlap between Atlantic cod and capelin, and remained relatively stable in southerly areas, where the collapsed Atlantic cod stock overlapped with capelin.

In summary, the spatial structure of Atlantic cod condition indices is explained by the distinct ecosystem production units this stock complex inhabits. Since 1991, Atlantic cod condition worsened in northerly areas where there was no spatial overlap with capelin, and remained relatively stable in southerly areas, where the collapsed Atlantic cod stock overlapped with the remaining capelin. The observed change in Atlantic cod distribution and condition indices post-1991 supports the capelin collapse hypothesis.

**Harp seal population trends and diet**

Frank et al. argued that the absence of an obvious response in Northwest Atlantic harp seals (*Pagophilus groenlandicus*), specifically large number of starving harp seals as observed following the collapse of capelin in the Barents Sea (Haug & Nilssen 1995), supports their contention that the capelin stock did not collapse. However, there are significant differences to note between the two regions. In the Barents Sea, the collapse of capelin during the mid-1980s occurred when the stock of other important forage fish, namely Atlantic herring and Arctic cod (*Boreogadus saida*), were severely depleted (Hamre 1994, Hop & Gjøsæter 2013). Therefore the effects of the capelin collapse were amplified and reached several taxa including seals, seabirds and Atlantic cod (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 alternative prey (Atlantic herring and Arctic cod, Nilssen et al. 1998). In the Northwest Atlantic, however, alternate prey were still available during the early 1990s as evidenced by a harp seal diet shift from capelin towards Arctic cod and Atlantic herring (Stenson 2012).

While Northwest Atlantic harp seals did not show catastrophic mortalities post-1991, they have been impacted by the decline in capelin. Since the 1980s, pregnancy rates of harp seals declined while inter-annual variability in pregnancy rates increased, ranging from ~20% to 75% over the past 3 decades (Stenson et al. 2014, 2016). Also, since 1987, harp seals have shown indications of late term abortions. Stenson et al. (2016) found that while the general decline in fecundity reflects 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 in pregnancy rates. Changes in the abortion rates, in turn, were found to be 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 reflect changes in environmental conditions that influence many prey species. While, as pointed out by Frank et al., 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, particularly since commercial catches have declined over the past decade and there has not been a concomitant increase in harp seal population abundance.

In summary, the absence of an obvious response in Northwest Atlantic harp seals does not support the hypothesis of a collapsed capelin stock as there were alternative forage fish available for harp seals post-1991. Increased inter-annual variability in pregnancy rates of harp seals post-1991, which was related to capelin biomass, suggests a dependency of harp seals on capelin availability and supports the hypothesis of stock collapse.

### Seabird population trends and diets

Frank et al. (Figure 11B) considered that the post-1990 trend in abundance of common murres (*Uria aalge*) on Funk Island (NAFO Div. 3K) does not reflect an order of magnitude decrease in their primary prey. In doing so, Frank et al. 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.). 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 with major reductions in adult mortality due to the coincident closure of the Atlantic cod fishery. The removal of thousands of gillnets from inshore areas during the 1990s and 2000s resulted in a significant reduction in bycatch mortality (Regular et al. 2013). As well, reductions in adult mortality associated with ship-sourced oil pollution and hunting also decreased during this same period (Wilhelm et al. 2009). The cumulative effects of these reductions in adult mortality would have overweighed negative population effects associated with bottom-up prey base reductions. Along these 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-mentionned cumulative effects.

Frank et al. contend that the fact that throughout the 1990s common murre chicks on Funk Island were fed almost exclusively capelin during rearing represents support for the non-collapse hypothesis. However, maintaining a high percentage of capelin in parental deliveries resulted from an increased abundance of capelin at spawning sites within seabird foraging ranges of breeding colonies (Davoren et al. 2012). These spawning sites are persistent and predictable interannually (Davoren 2013), which explains the persistent high percentage of capelin in the diet. However, if the timing of the diet sampling does not overlap with the timing of capelin spawning, the percentage of gravid capelin (energy rich prey) in the diets of murres decreases greatly (Davoren et al. 2012). Frank et al. also questioned why the northern gannets’ consumption of capelin is considerably higher from 1990-2004 (20 – 100 %) than it was before 1990 (<12%, Montevecchi 2007), yet they ignored the primary contention that the cold water regime shift precluded the gannet’s preferred large pelagic warm-water prey (mackerel *Scomber scombrus*, Atlantic saury *Scomberesox saurus* and short-finned squid *Illex illecebrosus*) from moving into the region which facilitated a prey switch to capelin (Montevecchi & Myers 1997, Montevecchi 2007). Moreover, the contribution of capelin to the gannets’ diet is highly dependent on the timing of diet sampling and whether diet sampling temporally overlaps with capelin spawning (Davoren et al. 2012). In addition, the pulse of incoming spawning capelin into the inshore is reflected in a reduction of the dietary niche breadth of seabird and cetacean predators (Gulka et al. 2017).

In summary, the trends in seabird abundance do not provide support for either the collapse or non-collapse hypothesis as other variables, such as removal of gill nets in the inshore area, had a larger impact on seabird survival. However, seasonal seabird dietary information does support the hypothesis of capelin collapse as it refutes the hypothesis of capelin as an inshore year-round resident.

### Zooplankton response: *Calanus finmarchicus* abundance

Given the magnitude of the capelin collapse, Frank et al. expected a significant increase in their main copepod prey, *Calanus finmarchicus (Dalpadado & Mowbray 2013)*. They used the continuous plankton recorder (CPR) data to estimate *C. finmarchicus* abundance pre- and post-1991 in the NL region. However, the usefulness of CPR data for the Northwest Atlantic has been questioned. Head and Pepin (2010) noted that only two years between 1960-1978 had more than 8 months of observations over the Grand Banks sections of the CPR sampling (corresponding to Area E9 used by Frank et al.), and inconsistencies in the course of the survey tracks from ships-of-opportunity resulted in uneven sampling of different water masses (Pepin et al. 2011). Furthermore, there was a substantial reduction in CPR mileage towed in the 1980s with a contraction of monitoring to 20° W in the eastern Atlantic (Reid et al. 2003). During this decade, monitoring science fell out of favour (Reid et al. 2003). Other researchers have looked at the CPR data as a potential source for productivity levels in the NL region, but the large CPR data gap in the region from 1979-1990 precluded its use in a recent capelin study (Mullowney et al. 2016).

Since 1999, Fisheries and Oceans Canada has run the Atlantic Zonal Monitoring Program (AZMP) in three regions in eastern Canada: Scotian Shelf, Gulf of St. Lawrence, and NL. The AZMP program collects physical, chemical and biological data at stations along 14 oceanographic transects during offshore spring and fall cruises (see Pepin et al. 2015 for details).The yearly changes in densities of *C. finmarchicus* based on AZMP surveys are highly significant for the four main sections across the Newfoundland Shelf, and range from 3 to 70-fold changes in abundance from 1999-2015 (Pepin et al. 2017). Interestingly, there has been an observed decrease in *C.* *finmarchicus* biomass in the AZMP survey since 2013, which was paralleled by a decrease in the spring acoustic index of capelin biomass in recent years (DFO 2018).

In summary, neither the CPR nor AZMP data can be used directly to support or reject the hypothesis of a capelin stock collapse. The AZMP data does, however, support the hypothesis that bottom-up processes are driving capelin survival in the NL region (Buren et al. 2014a, Obradovich et al. 2014, Murphy et al. 2018).

**Physical variability**

Frank et al. argued that their analysis of ocean climate showed a change in conditions ~ 5 years after the proposed capelin collapse and, therefore, the physical evidence was weak for an environmental driver of capelin collapse. They contend that the transition from cold to warm conditions in 1996 is the distinguishing signal of their PC1 analysis. However, elsewhere in the literature, 1991, not 1996, has been identified as climatologically important due to its strong cold anomaly (e.g., Drinkwater 1996, Colbourne et al. 2014, 2015, 2016) and biologically important due to the dramatic regime shift in the North Atlantic ecosystem in 1991 with the collapse of Atlantic cod, capelin and other finfish species and an increase in shellfish biomass (Gomes et al. 1995, Lilly et al. 2000, Rice 2002, Koen-Alonso et al. 2010, Hammill et al. 2011, Buren et al. 2014a, Pedersen et al. 2017); seabird dietary shifts from warm- to cold-water pelagic prey (Montevecchi & Myers 1992, Montevecchi & Myers 1997, Montevecchi 2007); and shifts in groundfish diet (Dawe et al. 2012).

In summary, based on the extensive published literature on the regime shift in the Northwest Atlantic (e.g., Drinkwater 1996, Buren et al. 2014a, Pedersen et al. 2017), the weight of evidence approach suggests that the cold-water anomaly of the early 1990s was the physical driver of capelin collapse.

## Discussion

Numerous sources of primary and government literature have concluded that the NL capelin stock suffered an order of magnitude decline in the early 1990s (DFO 1994, Miller 1994, 1997, Rose & O'Driscoll 2002, Davoren & Montevecchi 2003, Rose 2007, DFO 2008, 2010, 2013, Buren et al. 2014a, Mullowney & Rose 2014, DFO 2015, Murphy et al. 2018). In contrast, Frank et al. postulated that the capelin stock did not suffer a collapse but rather experienced a dramatic change in phenology post-1991 and became non-migratory. We used the weight of evidence approach to evaluate the empirical support for the hypothesis of a capelin stock collapse using multiple, independent lines of enquiry with diverse statistical methods (e.g., triangulation, sensu Munafò & Davey Smith 2018). The weight of evidence approach led us to conclude that the Div. 2J3KL capelin stock suffered a bottom-up, climate-driven population collapse in 1991 with minimal recovery in the subsequent 25 years.

Frank et al. proposed two alternative explanations for their hypothesis of non-collapse: (1) a spatio-temporal mismatch between the spring acoustic survey and capelin phenology; and (2) a change in biology of capelin from a highly migratory stock to one that resides inshore year-round. The first hypothesis was rejected by both Frank et al. and our analyses. While the spring acoustic survey surveys all age classes (age-1 to age-3+), it primarily targets the younger, 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. The positive significant relationship between an inshore larval index and the offshore age-2 abundance index also supports the ability of the spring acoustic survey to produce an index of age-2 capelin abundance (Murphy et al. 2018). Therefore, we argue that the spring acoustic survey provides a valid index of a currently depressed capelin stock in the offshore.

Frank et al.’s second hypothesis was that the capelin stock has become less migratory and stayed inshore year round post-1991. We tested this hypothesis using multiple independent datasets, which included both fishery-dependent (inshore commercial catch) and fishery-independent (spring acoustic survey, FBTS, AZMP oceanography cruises, larval indices, predator diet, predator behaviour) data. Using the FBTS data and the center of gravity approach described in Thorson et al. (2016), we found no evidence of inter-annual longitudinal movements of capelin post-1995, but rather that the stock’s centre of gravity moved latitudinally depending on abundance. In years with low capelin abundance, capelin were distributed further south. This southerly distribution of capelin post-1991 was also found for juvenile capelin (Anderson et al. 2002) and in fall acoustic surveys (Miller & Lilly 1991, Miller 1992, 1993, 1994). However, the FBTS surveys a limited number of inshore strata. If we considered all of the inshore strata not surveyed by the FBTS, there would need to be a minimum of 41,000 kg km-2 of capelin uniformly distributed in these inshore strata to compensate for the ‘missing’ 3-6 Mt capelin from the offshore. Seasonal acoustic surveys in Trinity bay found a maximum of 10,000 kg km-2 in June, and the inshore capelin densities were a fraction of this outside of the peak spawning period. The lack of adult capelin in the inshore area outside of the spawning period was also corroborated with predator diet and behavior data. Atlantic cod inshore diet data from 1996-2003 found that consumption of capelin was highly prevalent in June compared to January (Sherwood et al. 2007); murres exhibited a temporal shift towards later breeding in the late 1990s, which corresponded with the later inshore arrivals of capelin in the murres’ foraging range (Davoren & Montevecchi 2003); dietary shifts in four seabird species (great shearwater *Ardenna* *gravis*, sooty shearwater *Ardenna grisea*, herring gull *Larus argentatus*, great black-backed gull *Larus marinus*) and humpback whale (*Megaptera novaeangliae*) throughout the summer was associated with dramatic shifts in inshore capelin abundance associated with the spawning migration (Gulka et al. 2017). Furthermore, it is highly unlikely that 3-6 Mt of capelin inshore would have been missed by both DFO and harvesters since 1991, given the presence of hundreds of active inshore fishing vessels equipped with echosounders over much of the northeast coast of NL.

Using the weight of evidence approach, the majority of the independent data sources examined support the hypothesis of a collapsed capelin stock. Therefore, we consider that the spring acoustic survey provides a robust index of abundance and biomass of the capelin stock. Given the survey design, the survey is considered to yield minimum biomass estimates, but all data sources examined indicate that the spring acoustic survey captures trends in the capelin population, which collapsed in the early 1990s.

## Figure captions

Fig. 1. Capelin stock area in NAFO Divisions 2J3KL including the embayments of Newfoundland, Canada.

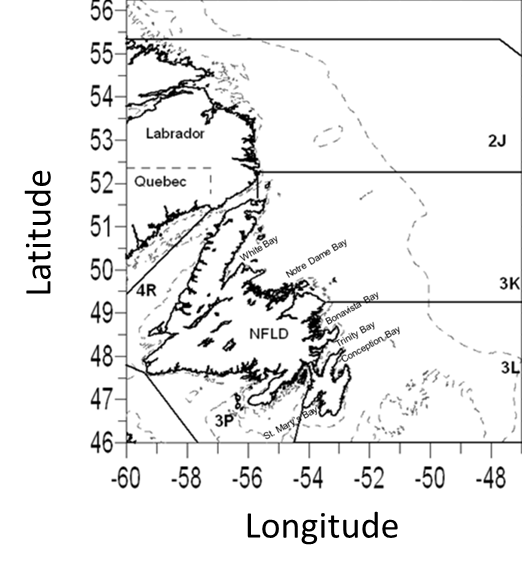
Fig. 2. The fall acoustic survey track in NAFO Div. 2J3K for capelin of (a) Canada in October 1983 (see Miller and Carscadden 1983 for more details) and (b) USSR in November 1991 (see Bakanev 1992 for more details).

Fig. 3. (a) Capelin biomass estimated from the seasonal inshore acoustic survey. The May values are for the main portion of Trinity Bay only, while the other months surveyed the entire bay, including the arms and headland (note the log scale); and (b) capelin maturity stage composition (n = 5319) and (c) capelin age composition (n=864) sampled in the seasonal inshore acoustic surveys in Trinity Bay in 2003-05. S/R is spent/recovering, Mat. is maturing, and Imm. is immature.

Fig. 4. Spring (May) acoustic index of capelin in NAFO Div. 3L (black circles) (1988-1992, 1996, 1999-2005, 2007-2015, 2017) and Trinity Bay May inshore acoustic index (grey triangles) (1999-2005, 2007-2013, 2017). Black and grey vertical lines indicate 95% confidence intervals. Note the log scale.

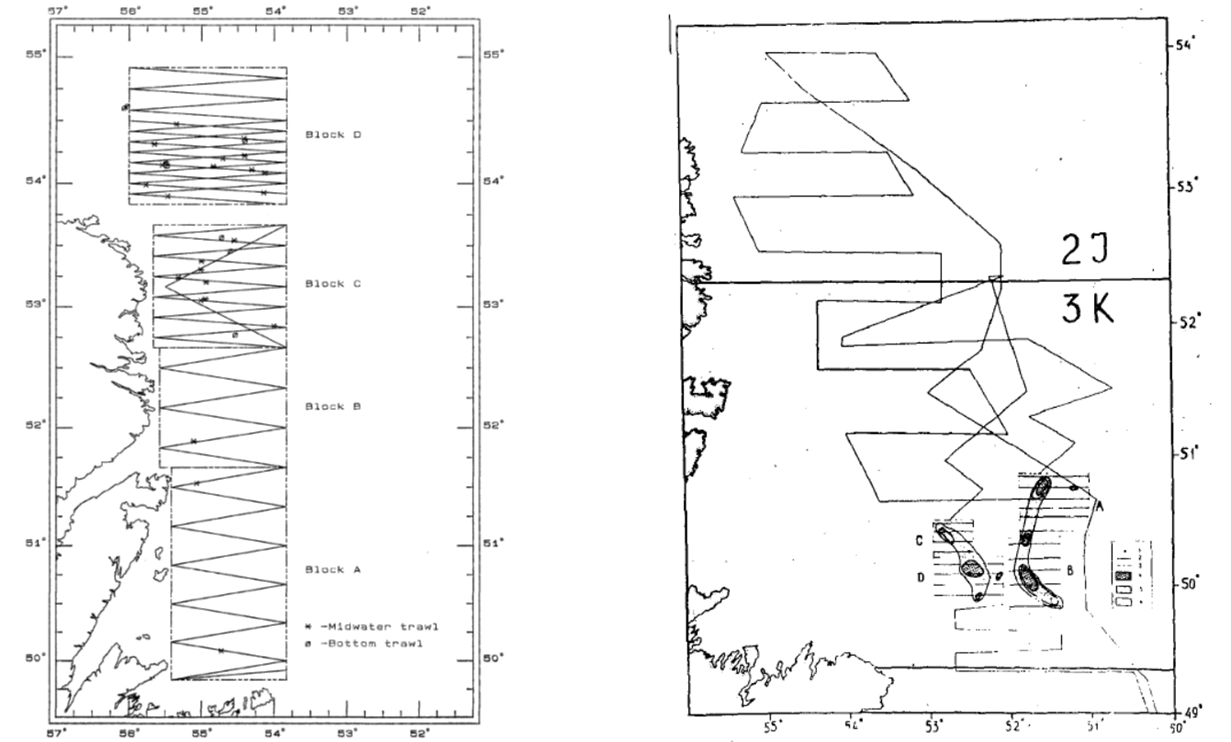
Fig. 5. Center of gravity analysis using the VAST package in R (Thorson et al. 2016, Thorson & Barnett 2017) using data from the fall bottom-trawl survey (1995-2017) to fit a geostatistical delta-generalized linear mixed model to estimate the spatial and temporal distribution of capelin. Annual center of gravity estimates are connected by lines through time, where cooler colors (blue) indicate earlier years and warmer colors (red) indicate more recent years. The red area indicates areas not covered by the survey and the light pink (cream) area indicates inshore strata that are poorly covered by the fall bottom-trawl survey.

**Fig. 1**

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**Fig. 2**

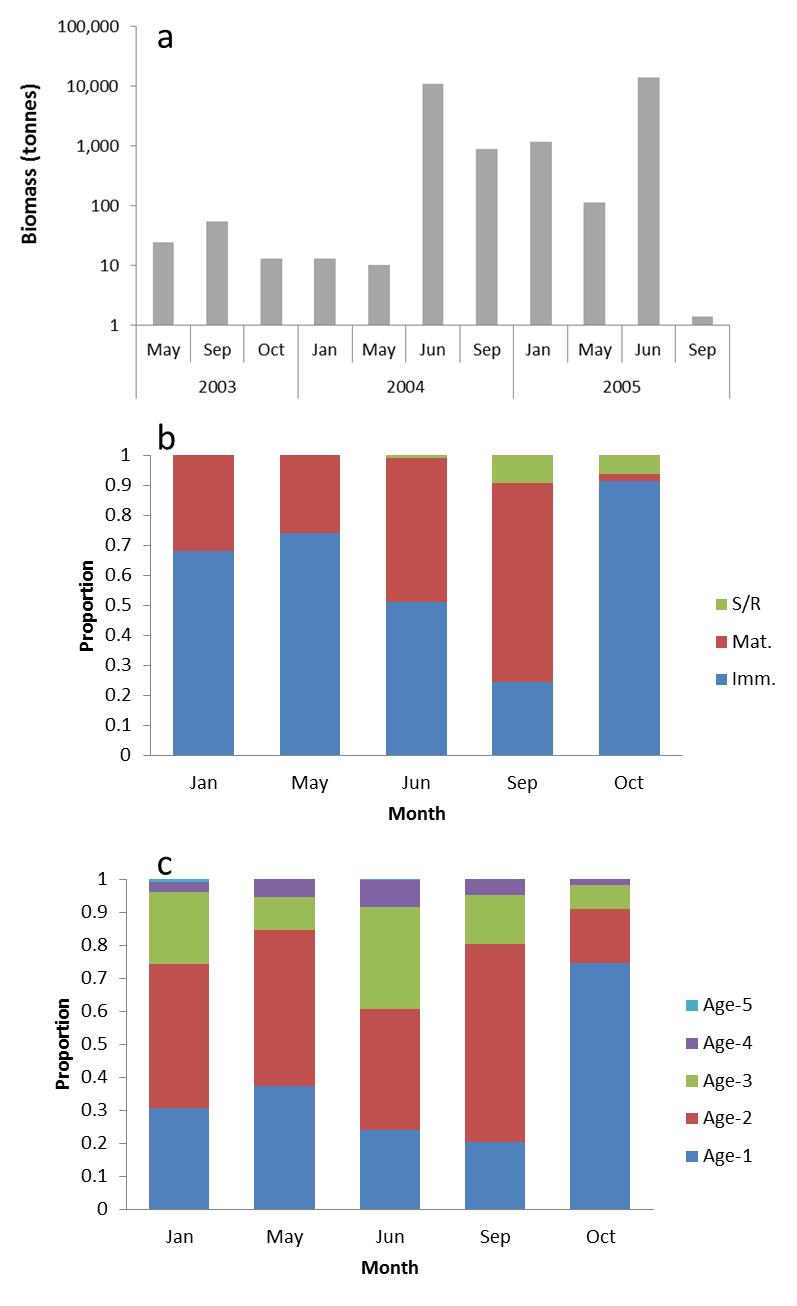
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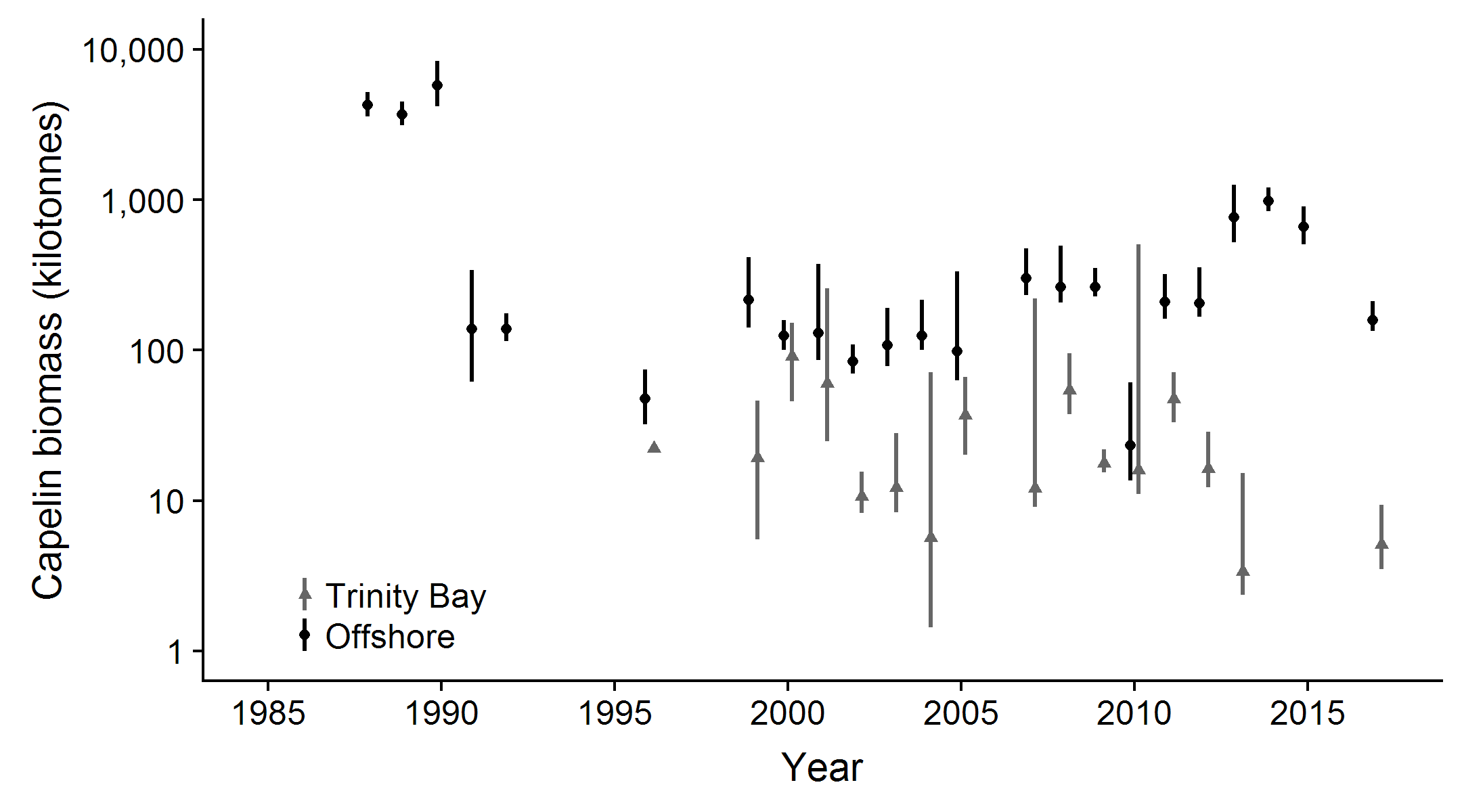
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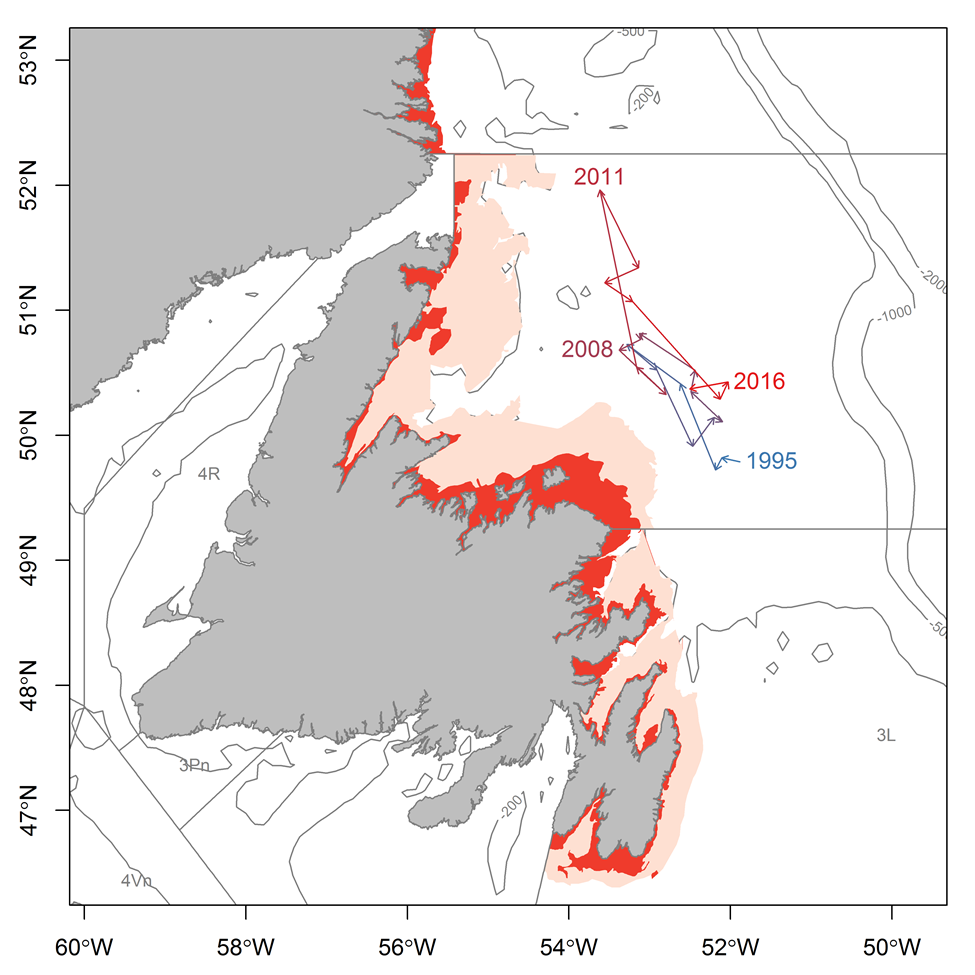
**Fig. 3**

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**Fig. 4**

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**Fig. 5**

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## Supplementary material

### Trinity Bay seasonal inshore acoustic surveys (2003-2005)

Inshore seasonal acoustic surveys (January, June, September) in Trinity Bay were conducted from a 23 m inshore research vessel (CCGS Shamook) using a calibrated EK500 echo-sounder with a towed 38 kHz transducer. Surveys followed a fixed transect design and covered both the main portions and the four arms of Trinity Bay (Suppl. Fig 1). When acoustic targets were encountered, sampling was conducted using bottom and midwater trawls to target the portion of the water column where the acoustic signal occurred. The lack of fishable aggregations of capelin during the seasonal surveys precluded extensive sampling but samples were obtained from most aggregations. Length, sex and maturity stage were recorded for all fish sampled and ages determined for two fish per sex per 0.5 cm interval.

Spatial patterns in age composition were similar to those patterns reported by Winters (1970) with older larger capelin overwintering in the main portion of the bay while juvenile capelin were more prevalent in the inner arms. In all months except June, capelin were aggregated along the sides of the trench around 200 m depth, whereas in June they present in the arms and in shallower water closer to shore at the bottom of the bay (Suppl. Fig. 2).

The spring acoustic surveys have opportunistically surveyed other northeastern bays of Newfoundland including Conception Bay (XXXX), Notre Dame Bay (1999) and Bonavista Bay (XXXX) (Fig. 1). These surveys did not produce a biomass estimate due to low densities of capelin surveyed.

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