

# **The collapse and continued low productivity of a keystone forage fish species**

Buren, A.D.<sup>1</sup>§, Murphy, H.M.<sup>1\*</sup>§, Adamack, A.T.<sup>1</sup>, Davoren, G. K.<sup>2</sup>, Koen-Alonso, M.<sup>1</sup>,  
Montevecchi W.A.<sup>3</sup>, Mowbray, F. K.<sup>1</sup>, Pepin, P.<sup>1</sup>, Regular, P.<sup>1</sup>, Robert, D.<sup>4</sup>, Rose, G.A.<sup>5</sup>,  
Stenson, G.<sup>1</sup>, Varkey, D.<sup>1</sup>

Affiliations:

1. Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, NL, Canada

2. Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada

3. Cognitive and Behavioural Ecology Programme, Departments of Biology and Psychology,  
Memorial University of Newfoundland, St. John's, NL, Canada

4. Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada

5. Institute for the Oceans and Fisheries, UBC, Vancouver, BC, Canada.

\*corresponding author: Tel: +1 709 772 4925; Fax: + 1 709 772 4138; e-mail:  
Hannah.Murphy@dfo-mpo.gc.ca

§ A.D.B and H.M.M. contributed equally to this paper and others have contributed equally.  
Authors have been listed in alphabetical order for each contribution level.

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## Abstract

Capelin are a focal forage species of the Northwest Atlantic ecosystem as they act as an energy conduit from lower to higher trophic levels. According to acoustic monitoring surveys conducted by Canada and the former USSR, the Newfoundland capelin stock (NAFO Divisions 2J3KL) suffered an order of magnitude decline in biomass in 1990-91. This collapse was concomitant with drastic changes observed in the ecosystem during the late 1980s and early 1990s. However, while the results of more than a dozen studies have supported a capelin stock collapse, there is also literature suggesting that the capelin stock has not collapsed during that period. The non-collapse hypothesis purports that rather than collapsing in 1990-91, the capelin stock either (1) changed its migratory patterns while the timing of the spring acoustic survey remained constant, leading to a spatio-temporal mismatch between the survey and the stock, or (2) became less migratory and remained inshore year round, therefore being largely underestimated by the offshore acoustic surveys. We tested the collapse and non-collapse hypotheses using multiple independent datasets, which included both fishery-dependent (inshore commercial catch) and fishery-independent (spring and fall acoustic and fall bottom trawl surveys, oceanography cruises, capelin larval indices, aerial surveys, predator diet and behavior) data, and diverse statistical methods. 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 1990-91 with minimal recovery over the subsequent 25 years.

Keywords: capelin, *Mallotus villosus*, acoustic survey, regime shift, Newfoundland

## Introduction

Forage fish play crucial roles in many ecosystems, transferring the bulk of the energy from lower trophic levels to high trophic level predators. Typically, forage fish are small shoaling species that are characterized by short life expectancy and rapid, but variable, somatic 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 or extremely low abundances (Soutar & Issacs 1969, Schwartzlose et al. 1999, Chavez et al. 2003, Pikitch et al. 2012, 2014). Each of these phases can last for prolonged periods. For example, the Norwegian spring-spawning Atlantic 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, Dragesund et al. 2008, 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, Barange et al. 2009).

Capelin (*Mallotus villosus*) is the focal forage fish species in ecosystems of the North Atlantic Ocean (Templeman 1948, Jangaard 1974, Vilhjálmsson 1994, Lavigne 1996, 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 6 million tonnes (Mt) during the “boom” phase and around 200 thousand tonnes during the “bust” phase. There is general agreement that ecosystem changes (i.e. bottom-up forces) were behind these “boom-bust” 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 Mt during the “boom” phase and between 100-500 thousand tonnes during “bust” phase (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 associated with poor recruitment attributed to an increase in the inflow of Atlantic water north of Iceland and a climate-related shift in distribution (Vilhjálmsón 2002, Pálsson et al. 2012, Carscadden et al. 2013).

Fisheries and Oceans Canada (DFO) is responsible for the assessment of the NAFO Divisions 2J3KL (Newfoundland) capelin stock (hereafter Div. 2J3KL capelin stock). DFO concluded that the stock experienced an order of magnitude decline in 1990 with minimal recovery during the past two decades (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015, 2018). The size of the stock fluctuated between 2-6 Mt from 1982 and 1990, and between 25-900 thousand tonnes during the ensuing period (DFO 2015). The decline in capelin biomass was concomitant with drastic changes in the ecosystem during the late 1980s and early 1990s (deYoung & Rose 1993, Gomes et al. 1995, Montevecchi & 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 and minimal recovery of capelin since 1990-91 is hypothesized to have been due to bottom-up processes that affected the recruitment and survival of capelin (Buren et al. 2014a, Obradovich et al. 2014, Murphy et al. 2018).

Some authors do not feel that the Div. 2J3KL capelin stock collapsed in the 1990s (Frank et al. 2016). This non-collapse hypothesis postulates that the stock did not collapse in 1990-91 but rather that the offshore acoustic surveys have failed to detect large capelin aggregations since 1990 because of a spatio-temporal mismatch between the surveys and the stock (Frank et al. 2016). Specifically, the hypothesis states that post-1990 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 became non-migratory in 1990 and are therefore undetected by the offshore surveys. Support for the non-collapse hypothesis 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 current paper is to assess the empirical support for the hypothesis of capelin stock collapse (DFO 2015) versus that of non-collapse (Frank et al. 2016) using all available data.

## **Methods and Results**

To test the hypotheses of collapse and non-collapse of the Div. 2J3KL capelin stock (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). We organized our paper into sections that address similar lines of evidence as Frank et al. (2016). 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, overall, which hypothesis was best supported by the combination of previously-published results and additional analyses based on independent data sets.

### **Capelin**

#### **Offshore capelin abundance: acoustic surveys**

The capelin collapse hypothesis is supported by the fall and spring offshore acoustic surveys conducted by Canada and the former USSR that found a sudden decrease in capelin biomass in the fall of 1990 in Div. 2J3KL (e.g., Miller & Lilly 1991, Bakanev 1992, Miller 1992, 1993, 1994, Mowbray 2014). The non-collapse hypothesis purports that Canada and the USSR offshore acoustic surveys found low capelin biomasses in the fall of 1991 and 1992 in Div. 2J3KL because capelin did not migrate offshore starting in the fall of 1990 (Frank et al. 2016).

From 1982 to 1992, Canada conducted fall (October) acoustic surveys for capelin in Div. 2J3K (Fig. 1) (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 1982-1992 (Bakanev 1992; Fig. 1). The USSR fall acoustic surveys were conducted approximately a month 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 (96 thousand tonnes, < 5% of the biomass surveyed in 1989) while the USSR acoustic survey reported the smallest biomass since 1984 (631 thousand tonnes) (Winters 1995) (Fig. 2). Both the USSR and Canadian acoustic surveys reported record low capelin biomass in the fall of 1991 and 1992 (16-55 thousand tonnes) (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).

Consistent with the fall acoustic surveys, both the Canadian (Div. 3L; 1988-1993, 1996, 1999-2005, 2007-2015, 2017) and the USSR (Div. 3LNO; 1975-1994) spring offshore acoustic surveys reported record low capelin biomass in 1991 (Bakanev 1992, Mowbray 2014) (Figs. 1, 2). In the Canadian spring acoustic survey, capelin biomass decreased an order of magnitude from a high of 6 million tonnes in the late 1980s to 23,000 tonnes in 2010 (Mowbray 2014) (Fig. 2). While there has been an increase in capelin biomass in recent years in the Canadian spring acoustic survey, capelin biomass overall has remained persistently low since 1990-91 (DFO 2018). Post-1991, capelin is only acoustically surveyed in the spring in Div. 3L by Canada with

the discontinuation of the other three acoustic surveys in the early 1990s (Canada fall acoustic survey in 1994; USSR fall and spring acoustic surveys in 1992 and 1994, respectively).

While the offshore acoustic surveys provided strong evidence of a capelin collapse, they did not survey the inshore area. The non-collapse hypothesis uses qualitatively estimated densities of overwintering maturing capelin and large schools of immature capelin observed during winter surveys conducted in Trinity Bay in 1967-68 (Winters 1970) as evidence that significant densities of capelin can inhabit the inshore year-round. DFO 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. 1; 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 ( $10,000 \text{ kg km}^{-2}$ ), which corresponded with the start of the spawning period when capelin were highly aggregated inshore (Fig. 3 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 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 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). In agreement with this finding, an inshore acoustic survey in January 2000 for overwintering cod from Conception Bay to Notre Dame Bay found concentrations of juvenile capelin (O'Driscoll & Rose 2001) but few older fish (G.A. Rose, unpublished data). These seasonal surveys found no evidence of a large inshore, non-migratory capelin stock.



We also tested the capelin non-collapse hypothesis by investigating the spatial distribution of capelin in years when the annual offshore May acoustic survey included an inshore component (1999-2005, 2007-13, 2017) (Fig. 2). Capelin biomass inshore and offshore in May was weakly negatively correlated but non-significant (Pearson Correlation:  $t = -0.83$ ,  $df = 14$ ,  $p = 0.42$ ,  $R = -0.22$ ). In the majority of years,  $> 90\%$  of surveyed capelin biomass was offshore (Fig. 2). In four of the 14 years (2000, 2001, 2005, and 2010), 27 - 42% of the total capelin biomass surveyed was inshore (Fig. 2). A significant portion of the capelin population inshore in some years provides support for the non-collapse hypothesis. However, simple back-of-the-envelope calculations indicate that it is unrealistic to assume that the 3-6 Mt of capelin that are “missing” in the offshore surveys since 1990 are now residing in the inshore. The minimum density for 3 to 6 Mt of capelin undetected in up to  $\sim 71,000 \text{ km}^2$  of un-surveyed inshore waters would have to be between  $\sim 41,000$  to  $\sim 170,000 \text{ kg km}^{-2}$ , uniformly distributed throughout the un-surveyed area. The maximum mean density of capelin observed in the Trinity Bay seasonal acoustic survey was  $10,000 \text{ kg km}^{-2}$  in June, and the maximum mean density of capelin inshore outside of the spawning period, including the inshore May acoustic survey, was only  $120 \text{ kg km}^{-2}$  (Fig. 3 a). Overall, these analyses indicate it is unlikely that the capelin stock became non-migratory and has remained inshore since 1990.

In summary, while the fall and spring acoustic surveys in NAFO Divs. 2J3KLNO support the collapse of the capelin stock, they cannot refute the hypothesis that capelin are non-migratory post-1990 as inshore areas were not systematically surveyed. However, the lack of significant inshore aggregations of capelin outside of the peak spawning period during seasonal and annual spring acoustic surveys, and the impossibility of the “missing” 3-6 Mt of capelin (up to  $170,000 \text{ kg km}^{-2}$ , uniformly distributed throughout the un-surveyed area) remaining undetected in the

inshore strata since 1990 by DFO and hundreds of fishing vessels equipped with echosounders on the water, is inconsistent with a hypothesis that capelin are present inshore in large numbers and, therefore, provides strong support for the capelin collapse hypothesis.

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

The fall bottom trawl survey (FBTS) data was analyzed by Frank et al. (2016) and they concluded that there was a westerly, inshore shift in the center of capelin concentration in 1996-2010 compared to 1985-1995. They interpreted this to indicate that the stock had not collapsed. However, the center of concentration of capelin using the FBTS presence/absence data from 1985-1995 found inshore distributions occurred in three high abundance years (1986-1988, Fig S2 in Frank et al. 2016). This variability may be related to the poor catchability of capelin in the Engel otter trawl (used from 1978-1994), which was designed for harvesting commercial groundfish like flatfish and Atlantic cod. In 1995, the gear used for sampling in the FBTS was changed to a Campelen 1800 shrimp trawl, which improved the catchability of capelin in the survey. A similar center of gravity analysis using only post-1995 FBTS data showed a southerly shift in capelin distribution with a recent shift to the northwest in 2011-14 (DFO 2015). However, neither of these analyses accounted for inter-annual changes in capelin spatial distribution due to FBTS sampling effort nor considered the uncertainty around the center of gravity estimates.

To address the abovementioned issues and to test the hypothesis of a shoreward shift in capelin distribution post-1991, we revisited the center of gravity analysis of the FBTS data using the approach described in Thorson et al. (2016). 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 (Thorson et al. 2016). The advantages of this approach are

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 center of gravity metric, which provides perspective on the significance of distributional shifts. Like DFO (2015), we had to focus on the post-1995 period due to the poor catchability of capelin in the Engel otter trawl, so the data considered in our analysis was collected using only one gear type with a consistent catchability of capelin (i.e. Campelen 1800 shrimp trawl). Our geostatistical analysis does not support the hypothesis that capelin shifted their distribution towards the inshore in 1990-91 and remained inshore for the subsequent two decades. There is no evidence of an easterly or westerly movement in the center of gravity of capelin post-1995; instead, the center of gravity of capelin remains > 100 km offshore and demonstrates pronounced shifts in the north-south axis (Fig. 4). Like the acoustic surveys, the FBTS has poor survey coverage of the inshore. It is, therefore, possible that significant aggregations of capelin could go undetected. However, if significant capelin aggregations were present inshore, then the center of gravity would be oriented towards the inshore during years when more inshore strata were surveyed (1996-1998, 2000-2002, 2004-2006, 2010, 2013), which it is not (Fig. 4).

There has been a bias for increased catches of capelin in the FBTS post-1995 not only due to a change in sampling gear but also due to the increased proportion of capelin biomass in the trawl zone (bottom 4 m of the water column) post-1991 (Mowbray 2002), possibly in response to a decline in the risk of groundfish (e.g., Atlantic cod) predation that may drive capelin into the pelagic zone (Rose 1993, McQuinn 2009). Furthermore, post-1991, when capelin densities are low, capelin are found in closer association with the bottom and diel vertical migration is less pronounced compared to when capelin densities are high (Mowbray 2002). Due to the inherent biases in the FBTS data, we also considered other data sources to investigate the

center of distribution of capelin post-1991 (sensu Jech & McQuinn 2016). Juvenile capelin surveys using an International Young Gadoid Pelagic Trawl (IYGPT) in the northeastern bays and the offshore from 1994-99 found centers of distribution of capelin juveniles on the northern Grand Banks and along the northeast coast, but not in the bays, of Newfoundland (Anderson et al. 2002). This is consistent with capelin migrating to their nursery areas in the offshore. Thus, this independent study of juvenile capelin distribution supports our center of gravity analysis using the FBTS data.

In summary, capelin distribution moved in the north-south rather than east-west axis post-1995 based on a center of gravity of analysis that accounts for both the inter-annual changes in the spatial distribution of sampling effort and the uncertainty around the center of gravity estimates. The center of gravity analysis does not support the hypothesis of inshore residence of capelin since 1990, and, in combination with our analysis that up to 170,000 kg km<sup>-2</sup> of capelin uniformly distributed throughout the un-surveyed inshore waters is required to make up for the “missing” 3-6 Mt of capelin since 1990, supports the capelin collapse hypothesis.

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

The hypothesis that capelin did not collapse assumes that the delay 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 capelin biomass offshore (Frank et al. 2016). 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, which raises the possibility that the spring acoustic survey may not monitor migrating capelin consistently 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). 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, should not be considered as a proxy for spawning stock biomass.

While a delay in the timing of spawning should not have a direct impact on the acoustic abundance index derived from the spring acoustic survey, the earlier observed maturation of capelin post-1991 could affect the population fractions sampled by the spring acoustic survey. 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 age structure of the stock with inter-annual variability in the proportion of age-2s starting their adult migration patterns and would, therefore, be 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 for 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 the proportion of migrating/non-migrating fractions.

If there was a significant inshore capelin population post-1991, we would expect to see this change in population demographics reflected in both the offshore acoustic survey and the inshore commercial catch. Prior to 1991, mature age-2 capelin were a negligible component of the inshore commercial fishery (< 5% of total catch) (DFO 2018). Post-1991, the contribution of mature age-2 capelin increased to almost half of commercial inshore catches (DFO 2018), which supports the hypothesis of inshore residence and early maturation of capelin proposed by Frank et al. (2016). However, the age structure of offshore catches are not consistent with the non-

migratory hypothesis as the proportion of age-2 and age-3 fish sampled offshore has remained constant pre- to post-1991 at ~60% and ~28% of the catch, respectively (DFO 2018). Furthermore, the increased proportion of mature age-2 fish in the inshore catch 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.

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

#### **Independent indices of inshore capelin abundance**

The non-collapse hypothesis implied that strong correlations among independent inshore indices of capelin abundance post-1991 in addition to no obvious decrease in these indices between the late 1980s and the early 1990s was supportive of a stable stock (Carscadden and Nakashima 1997, Frank et al. 2016).

The two inshore indices collected by DFO during the 1980s and 1990s were 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: all spawning fish 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 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 (Anon 1998). Five of the eight years of aerial data post-1991 did not adequately cover peak spawning times (1991-93) and had reduced geographical coverage (1997-98). The aerial survey was discontinued in 1999 due to lack of funding.

Although considered an index of capelin spawning stock biomass during the 1980s, the inshore commercial catch rate data have not been included in the capelin stock assessment process since 1993 due to changes in management regulations post-1991. As a consequence of the small sizes of spawning capelin post-1991, management regulations introduced a size criterion of 50 capelin/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 large capelin were available (Anon 1998). Post-1991, the inter-annual variability in participation in the fishery due to fish quality and market forces resulted in overall fishing effort being reduced and concentrated to when capelin were available resulting in high catch rates which 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. Therefore, these indices cannot be used to support or refute either hypothesis.

#### **Inshore recruitment index**

Capelin larval production in August in Trinity Bay did not decrease appreciably post-1991, which was used as support for the non-collapse hypothesis (Frank et al. 2016). 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) collected in the middle of the Bay (see Nakashima & Mowbray 2014 for more details). Given the persistently later capelin spawning since 1991, it is appropriate to compare late-larval densities in August in years pre-1991 to September in years post-1991 (Nakashima & Mowbray 2014). Late-larval densities during the 2000s were consistently lower and more variable than during the 1980s: average late-larval density in Trinity Bay in September 2002-15 was  $30.9 \text{ m}^{-2}$  (SD: 26.9, range 6.73-96.95  $\text{m}^{-2}$ ) while in August 1982-86 was  $48.8 \text{ m}^{-2}$  (SD: 15.1, range 33.2-73.6  $\text{m}^{-2}$ ). There has been a substantial decrease in larval productivity post-1991, which is consistent with the capelin collapse hypothesis.

Post-1991, the emergent larval index (2001-2015) was related to the age-2 abundance index from the spring acoustic survey, which was lagged by 2 years in order to compare survival in the same cohort (Murphy et al. 2018). The positive, significant relationship between two fishery-independent inshore and offshore indices post-1991 supports previous research that identified early larval survival as an important driver of capelin recruitment (Frank & Leggett 1982, Leggett et al. 1984, Dalley et al. 2002). This result suggests that the offshore acoustic survey tracks inshore larval productivity, supporting the capelin collapse hypothesis. While it is possible that the offshore age-2 capelin abundance index reflects an overflow or spillover of age-



2 capelin in proportion to inshore productivity, the inshore acoustic seasonal surveys did not find a significant inshore population of capelin outside of the spawning period.

In summary, the significant relationship between two fishery-independent inshore and offshore indices post-1991 concurs with the collapse hypothesis.

## **Ecosystem response**

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

From the early 1980s to the late 1990s, the condition and weight at age of Atlantic cod in Div. 2J3KL (also known as ‘Northern’ cod) declined markedly in the northern portion of its range (Div. 2J) with a similar declining trend in Div. 3K. Condition indices remained relatively unchanged in the southern portion of Atlantic cod’s range (Div. 3L). Weight at age of 4- and 5-year old Atlantic cod actually increased slightly in the mid-1990s in Div. 3L but later declined to the post-1991 average (Frank et al. 2016). This increase in weight-at-age in Div. 3L during the mid-1990s was considered as support for the non-collapse hypothesis (Frank et al. 2016).

The increase in Atlantic cod weight at age and condition in Div. 3L in the mid-1990s may have been due to a shift in spatial distribution of both capelin and Atlantic cod. During and post-1991, capelin shifted its fall distribution from having two distinct aggregations, one in the northwest (Div. 2J3K) and one in the southeast (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 of capelin onto the Flemish Cap and the Scotian Shelf (Frank et al. 1996).

Coincidentally, Atlantic cod moved southward on the northeast Newfoundland Shelf in the late 1980s and early 1990s and aggregated within a small area on the northern Grand Banks and in the Bonavista Corridor (Rose 1993, Rose et al. 2000). Rose et al. (2000) hypothesized that the observed shift in Atlantic cod distribution was a response to the southerly distribution of capelin

observed post-1991. 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.

The existence of spatial structure in condition traits of Atlantic cod is not unique to the early 1990s and has been documented extensively in the scientific literature (e.g., Lilly et al. 2005, Neville et al. 2018, Rose & Rowe 2018), with historical latitudinal gradients in growth (length at age) and condition indices (liver, gutted and total body mass) (Buren et al. 2014b, Morgan et al. 2017). Atlantic cod weight at age and liver condition indices have never been spatially homogenous due to the species complex inhabiting distinct ecosystem production units in NAFO Divs. 2J3KLNO (e.g., Lilly 2005, Koen-Alonso et al. 2013, Morgan et al. 2017). 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). Therefore, the non-homogenous traits of Atlantic cod from Labrador (Div. 2J) to the southern Grand Banks (Div. 3NO) are typical of this stock complex and cannot be used to support the non-collapse hypothesis.

In summary, the lack of change in Atlantic cod condition in Div. 3L in the 1990s does not support the non-collapse hypothesis as Atlantic cod condition is associated with the contraction of the capelin population south into Div. 3L. In northerly areas, Atlantic cod condition worsened where there was no spatial overlap with capelin.

### **Harp seal population trends and diet**

Large numbers of starving harp seals (*Pagophilus groenlandicus*) were observed following the collapse of capelin in the Barents Sea in the mid-1980s (Haug & Nilssen 1995). The absence of an obvious response in Northwest Atlantic harp seal populations to the proposed collapse of the capelin stock in 1991 was considered support for the non-collapse hypothesis

(Frank et al. 2016). However, there are significant differences between the two regions and populations of predators may be expected to respond differently in the two areas. In the Barents Sea, the collapse of capelin during the mid-1980s occurred when the stocks of other energy rich forage fish, including 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 declined in 1992-93 without a similar ‘invasion’ of starving seals which was likely due to the availability of alternative prey (Atlantic herring and Arctic cod, Nilssen et al. 1998). In the Northwest Atlantic, alternate prey were available during the early 1990s (Lilly et al. 1994, Bourne et al. 2015, DFO 2017), as indicated by the large increase in the presence of Arctic cod and Atlantic herring in diet of harp seals in the early 1990s (Stenson 2012).

While Northwest Atlantic harp seals did not show catastrophic mortalities post-1991, they have been impacted by the decline in capelin. Until the late 1970s, pregnancy rates were consistently around 85%. Since then, pregnancy rates have been highly variable (ranging from ~20% to 75%) with an overall declining trend (Stenson et al. 2014, 2016). In addition, late-term abortions have become a regular occurrence since the late 1980s (Stenson et al. 2016). Stenson et al. (2016) found that while the general decline in harp seal fecundity reflected density-dependent processes associated with increased population size, including the late-term abortion rates in 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 associated with ice conditions, suggesting that late January ice conditions reflect changes in environmental

conditions that influence many prey species. While higher catches in the Canadian commercial seal hunt from 1996-2008 contributed to reductions in the rate of harp seal population growth, lower pregnancy rates also had a major impact on the dynamics of this population. This is evident in the past decade where the commercial catches have declined but there has not been a concomitant increase in harp seal population abundance.

In summary, we cannot conclude that the absence of starving seals post-1991 indicates that capelin biomass remained stable and did not collapse. However, a declining trend in pregnancy rates and an increase in late-term abortions, which was related to capelin abundance, suggest a change in capelin abundance has been a limiting factor in harp seals fecundity during the past three decades.

#### **Seabird population trends and diets**

Populations of common murre (*Uria aalge*), Atlantic puffins (*Fratercula arctica*) and northern gannets (*Morus bassanus*) off eastern Newfoundland increased in the 1990s (e.g., Chardine et al. 2003, 2013, Wilhelm et al. 2015). Given that capelin is an important prey item for these predators, particularly during the breeding season, increases in their populations are considered to be inconsistent with a collapse in the capelin stock (Frank et al. 2016).

Fish stocks in general and pelagic stocks in particular contract their geographic range during periods of rapid population decline (Winters & Wheeler 1985, Worm & Tettensor 2011, Burgess et al. 2017). This pattern has been described for several finfish and shellfish populations (Prince et al. 2008, Wilberg et al. 2009), including Atlantic cod (Rose & Kulka 1999) and Northwest Atlantic herring stocks (Winters & Wheeler 1985). Capelin's center of distribution moved southward during the early 1990s, i.e. closer to the vicinity of seabird colonies along Newfoundland's northeast coast. Throughout the 1990s, common murre on Funk Island almost

exclusively fed capelin to their chicks during the breeding season (Davoren and Montevecchi 2003). Consistently high local abundances of capelin at annually persistent spawning sites within seabird foraging ranges allowed for the high percentage of capelin in parental deliveries (Davoren et al. 2012, Davoren 2013). Therefore, a higher proportion of capelin in common murre's diet post-1991 is not inconsistent with the collapse hypothesis, whereby the range of the collapsed capelin stock overlapped with the foraging range of seabird breeding colonies.

Capelin also represented significant proportions of northern gannet's diet from 1990-2012 (20 – 100 %) in contrast to pre-1990 (<12%, Montevecchi 2007, Bennett et al. 2013). This change in northern gannet diet was proposed as support for the non-collapse hypothesis (Frank et al. 2016). However, this change in diet occurred at the same time as a cold water intrusion that occurred during the 1990s which was associated with a decline in the abundance of northern gannet's preferred large pelagic prey (mackerel *Scomber scombrus*, Atlantic saury *Scomberesox saurus* and short-finned squid *Illex illecebrosus*) which are found in warm waters (Montevecchi & Myers 1997, Montevecchi 2007). For example, when mackerel and saury were more abundant in the region in 2005 and 2006 when waters were warmer and the percentage of capelin in the gannets' prey landings fell to 13% and 2%, respectively (Montevecchi 2007). As well, capelin was a minor prey item in seabird diets during the 1990s in Labrador (Bryant & Jones 1999, Baillie & Jones 2004) which is inconsistent with the hypothesis of a non-collapsed capelin stock.

The population increase of common murre post-1991 has been associated with major reductions in adult mortality due to the coincident closure of the Atlantic salmon (*Salmo salar*) and Atlantic cod gillnet fisheries (Regular et al. 2013). They considered the removal of thousands of gillnets from inshore areas during the 1990s and 2000s resulted in a significant reduction in bycatch mortality of breeding adult diving seabirds. Reductions in common murre

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 common murre adult mortality may have been more important for survival than negative population effects associated with bottom-up prey base reductions. Increases in the populations of Atlantic puffins and northern gannets in the 1990s and 2000s were associated with the same cumulative effects.

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 breeding adult seabird survival. Seabird dietary information does not provide support for either hypothesis, but seabird diet did reflect the late inshore arrival of capelin post-1991 (Davoren & Montevecchi 2003, Gulka et al. 2017) and is consistent with changes in local abundance of various prey.

#### **Zooplankton response: *Calanus finmarchicus* abundance**

Given the magnitude of the capelin collapse, a significant increase in their main copepod prey, *Calanus finmarchicus*, might have been expected (Frank et al. 2016). To test this hypothesis, the continuous plankton recorder (CPR) data were used to estimate *C. finmarchicus* densities pre- and post-1991 in the NL region (Frank et al. 2016). No significant difference in *C. finmarchicus* densities pre- and post-1991 was found. 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, which was the section used to test the collapse hypothesis (Frank et al. 2016), 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 favor (Reid et al. 2003). Other researchers have assessed the CPR data as a potential data source for historical productivity in the NL region, but the large gap in CPR data from 1979-1990 precluded its use in a recent capelin study (Mullowney et al. 2016). In summary, CPR data cannot be used to support either hypothesis.

### **Physical variability**

The non-collapse hypothesis used an analysis of ocean climate to show a change in environmental conditions ~ 5 years after the proposed capelin collapse and concluded that the physical evidence was weak for an environmental driver of capelin collapse (Frank et al. 2016). The authors contend that the transition from cold to warm conditions in 1996 is the distinguishing signal of their PC1 analysis (Frank et al. 2016). Elsewhere in the literature, 1991, not 1996, has been identified as climatologically important decadal signal 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 the early 1990s with the collapse of Atlantic cod, capelin and other finfish species and correspondent 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 published literature and our analyses here, the weight of evidence approach suggests that cold environmental conditions were an important driver of the regime shift observed in the Northwest Atlantic in the late 1980s and early 1990s, and the cold-

516 water anomaly of the early 1990s emerges as a likely critical tipping point in triggering the  
517 capelin collapse.

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## Discussion

The weight of evidence led us to conclude that the Div. 2J3KL capelin stock suffered a bottom-up, climate-driven population collapse in 1990-91 with minimal recovery in the subsequent 25+ years. We found strong internal and external consistency in trends across multiple independent sources of data (Table 1). In particular, the spring acoustic survey effectively tracked capelin year classes and was strongly correlated to an independent inshore larval abundance survey. Moreover, we found strong agreement across independent acoustic surveys conducted in offshore waters. These acoustic surveys supported the scenario of a capelin stock collapse in the early 1990s, and subsequent surveys and data examined were not consistent with the possibility that millions of tonnes of capelin have been residing along the northeast coast of NL for almost three decades. Our conclusion is thus consistent with that of numerous past studies that 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. (2016) postulated that the capelin stock did not suffer a collapse but instead experienced a dramatic change in phenology post-1991, which reduced their vulnerability to existing surveys. They provided two alternative explanations for their non-collapse hypothesis: (1) a spatio-temporal mismatch between the spring acoustic survey and capelin phenology; and (2) a change in the ecology of capelin from a highly migratory stock to one that resides year-round within poorly-surveyed inshore waters. The first hypothesis was rejected both by Frank et al. (2016) and our analyses. From our test of the second hypothesis proposing the inshore residence of 3-6 Mt of capelin, we concluded that there would have to be a minimum average capelin biomass of 41,000 kg km<sup>-2</sup> evenly distributed throughout the un-

544 surveyed inshore area over much of the past 25 years to compensate for the “missing” offshore  
545 fish. Instead, seasonal inshore acoustic surveys in Trinity Bay revealed a maximum capelin  
546 biomass of 10,000 kg km<sup>-2</sup> in June, and much lower densities outside of the peak spawning  
547 period. Most importantly, we conclude it is not plausible that 3-6 Mt of capelin distributed  
548 inshore would have gone unnoticed for more than 25 years by both by DFO and the hundreds of  
549 harvesters based in the numerous fishing communities that span the northeast coast of NL.

550

551

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554    None of the authors have a conflict of interest to declare.

555 **Tables**

556 Table 1. Summary of the differing degrees of support that each line of evidence provides for the  
 557 capelin collapse and non-collapse hypotheses. Degrees of support have been categorized into 5  
 558 classes; see key in the footnote

559

Evidence	collapse hypothesis	non-collapse hypothesis
Fall Canada Acoustic Survey (Div. 2J3K)	↑	↓
Fall USSR Acoustic Survey (Div. 2J3K)	↑	↓
Spring Canada Acoustic Survey (Div. 3L)	↑	↓
Spring USSR Acoustic Survey (Div. 3LNO)	↑	↓
Trinity Bay Acoustic Survey (inshore Div. 3L)	↑	↓
Seasonal age and maturity composition of stock	↑	↓
Analysis of 'missing' capelin distributed inshore	↑	↓
Offshore distribution - Fall Bottom trawl survey	↑	↓
Juvenile capelin surveys - IYGPT trawl	↑	↓
Timing of capelin offshore residence	↑	—
Aerial inshore abundance index	—	—
Inshore commercial catch rate index	—	—

Inshore recruitment index	↑	↓
Relationship between larval index and age 2 abundance	↑	↓
Spatial structure in cod weight at age and condition	—	—
Spatial overlap of cod and capelin post 1991	↑	↓
Harp seal population trend	—	—
Harp seal reproductive rates	↑	↓
Seabird population trends	—	—
Seabird diets	↑	↑
<i>Calanus finmarchicus</i> abundance	—	—
Physical variability	↑	↓

- 560    ↑ Support in favor of hypothesis  
561    ↑ Consistent with hypothesis  
562    — Equivocal support or the evidence cannot be used to test the hypotheses  
563    ↓ Inconsistent with hypothesis  
564    ↓ Support against hypothesis  
565

## Figure captions

Fig. 1. Capelin stock area in NAFO Divisions 2J3KL including the embayments of Newfoundland, Canada. Included are the acoustic survey tracks conducted in Div. 3L (offshore) and Trinity Bay (inshore) in May 2018 by Canada (DFO, unpublished data); Div. 3LNO in June 1991 by the former USSR (see Bakanev 1992 for more details); Div. 2J3K in October 1983 by Canada (see Miller and Carscadden 1983 for more details); and Div. 2J3K in November 1991 by the former USSR (see Bakanev 1992 for more details).

Fig. 2. Trends in five acoustic survey indices: Div. 2J3K Fall Canada (1982-92), Div. 2J3K Fall USSR (1982-92), Div. 3L Spring Canada (1988-92, 1996, 1999-2005, 2007-15, 2017), Div. 3LNO Spring USSR (1975-94), and Trinity Bay (inshore Div. 3L; 1999-2005, 2007-13, 2017). The vertical lines indicate 95% confidence intervals of the index. Note the log scale.

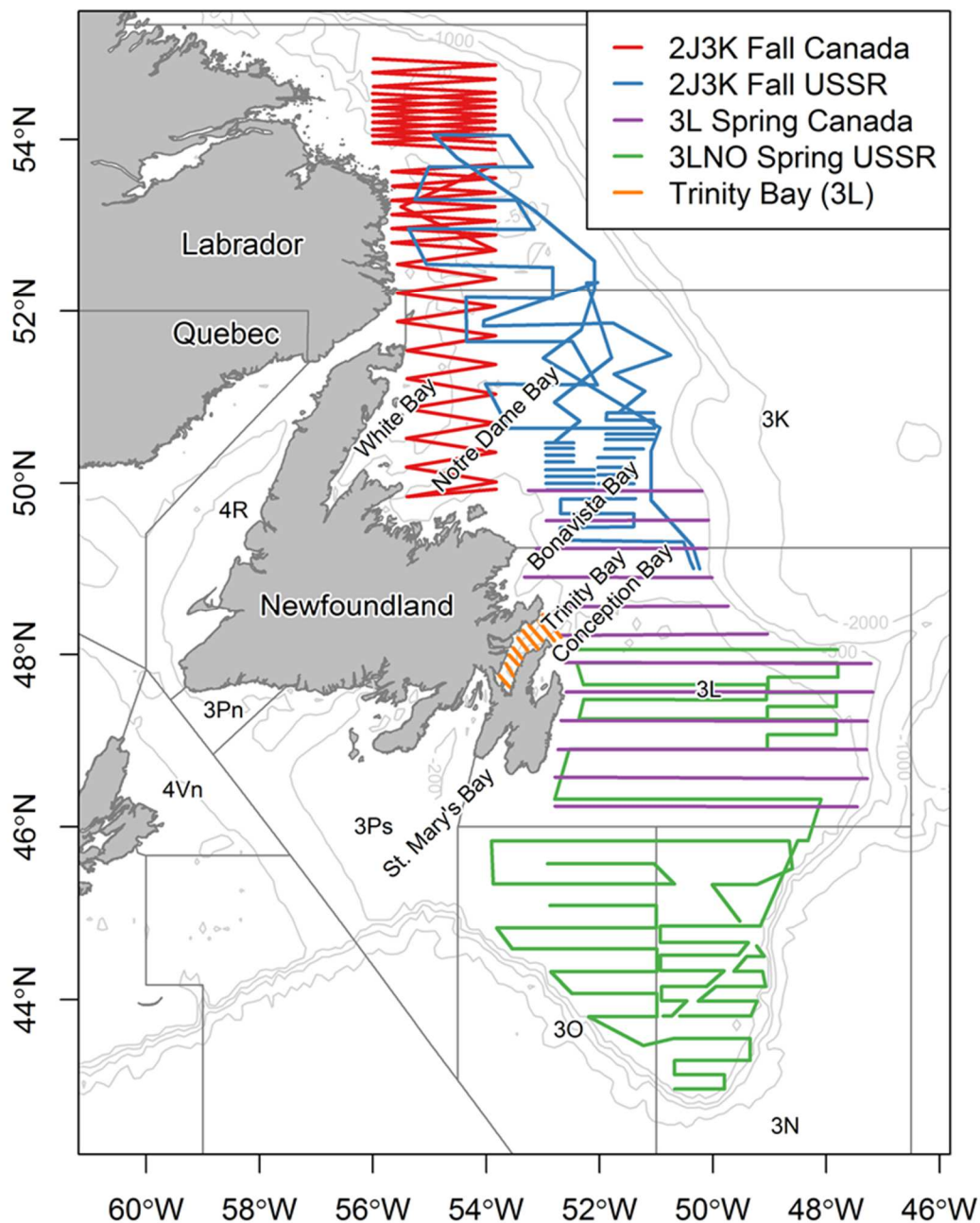
Fig. 3. (a) Capelin biomass ( $\text{kg}/\text{km}^2$ ) estimated from the seasonal inshore acoustic survey in Trinity Bay, NL, Canada. The May values are for the main portion of Trinity Bay only, while the other months surveyed the entire bay, including the arms and headland (note the log scale); and (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. 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 in NAFO Divisions 2J3KL (Newfoundland and Labrador, Canada; 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, and approximate 95% confidence intervals around these estimates are indicated by the dotted black line. The red area indicates areas not

589 covered by the survey and the light pink (cream) area indicates inshore strata that are poorly  
590 covered by the fall bottom-trawl survey.

591

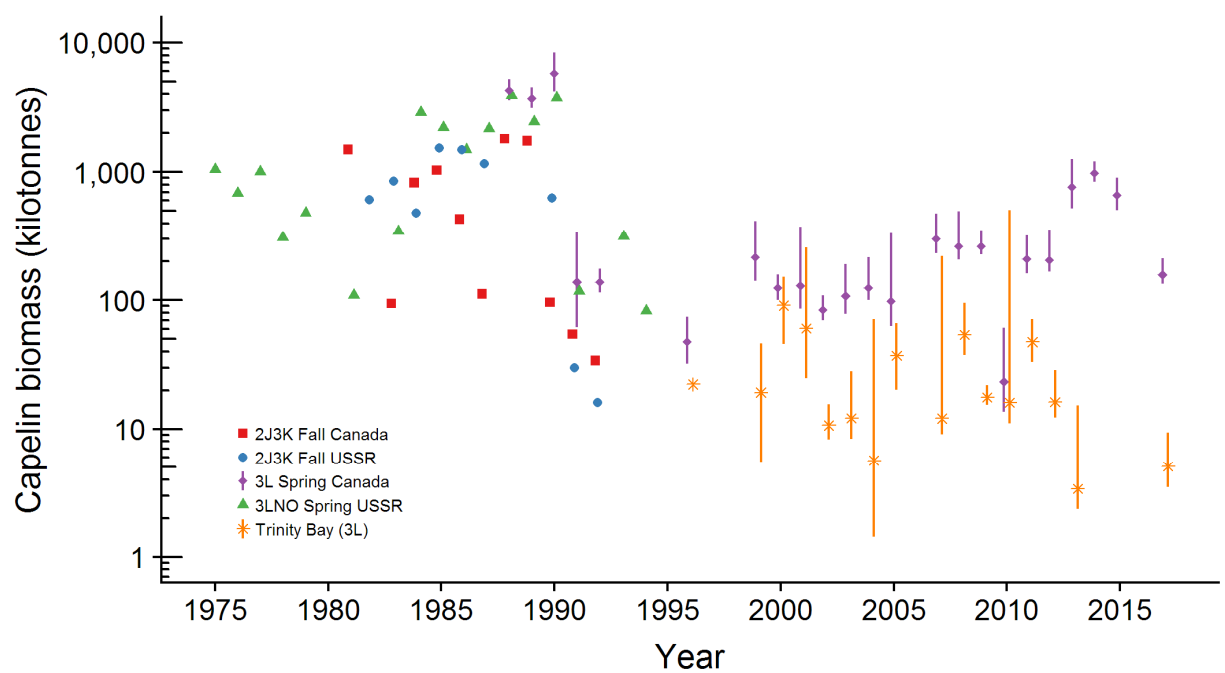
592 Fig. 1

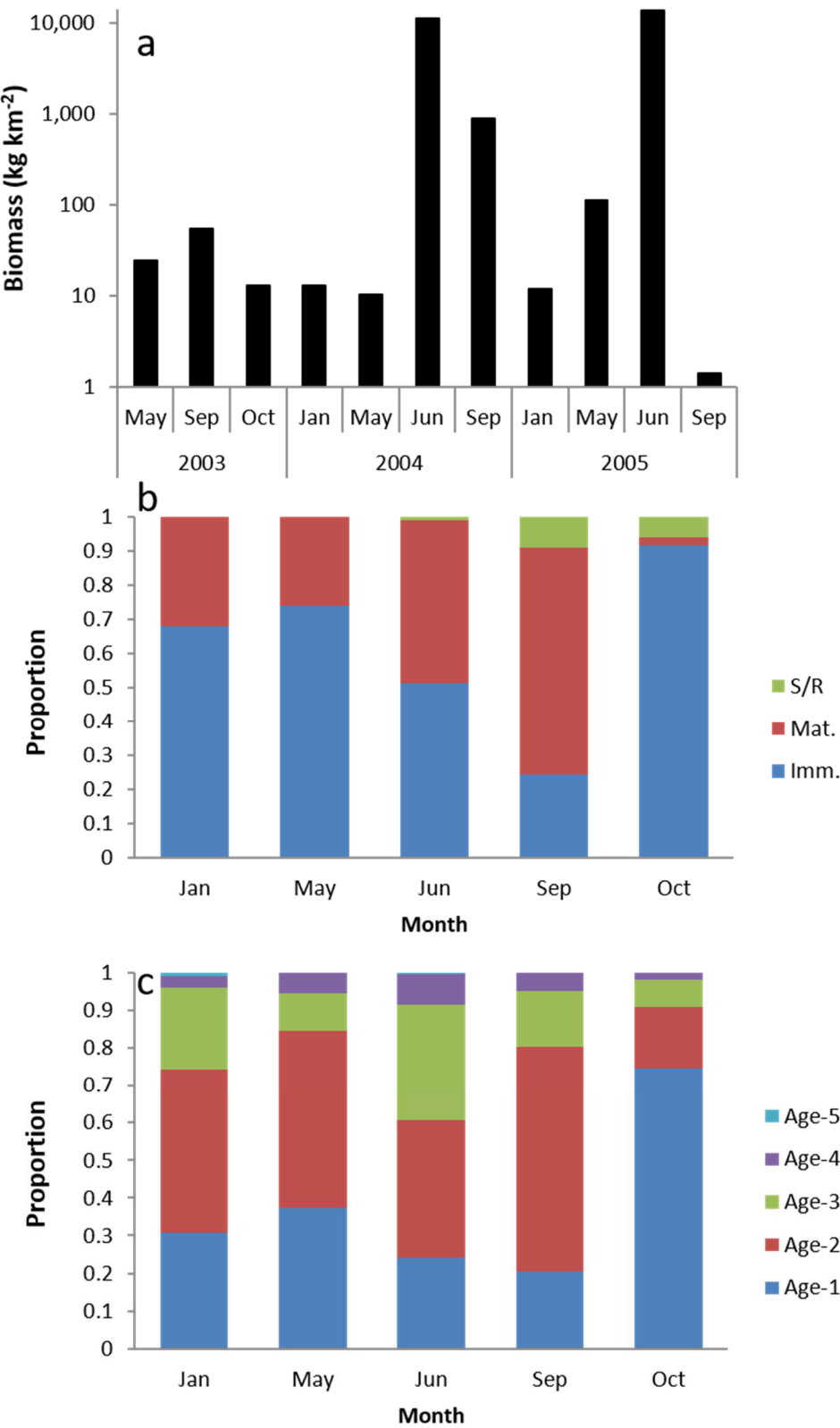


593

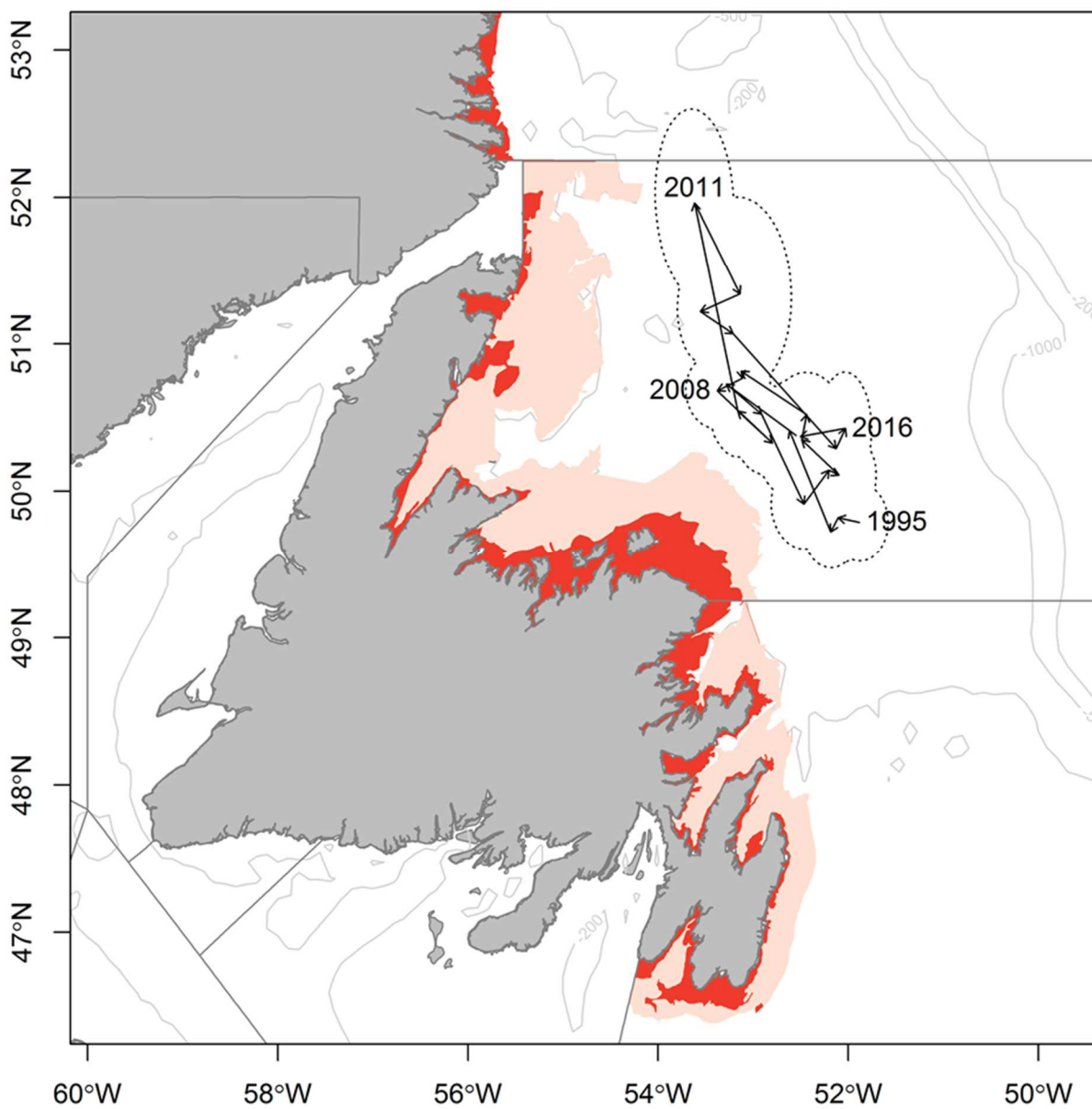


594 **Fig. 2**





602 **Fig. 4**



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