## Title:

Rebuttal to Frank et al 2016

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## Abstract

## Introduction

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

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

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

## Integrated overview of NL ecosystem

## Capelin

### Offshore capelin distribution: acoustic surveys

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

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

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

### Independent indexes of inshore capelin abundance

### Demographic change of harvested inshore capelin

### Timing of inshore capelin beach spawning

### Inshore recruitment index

### Blind spot analysis

## Ecosystem response

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

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

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

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

### Harp seal population trends and diet

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

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

### Seabird population trends

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

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

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

### Zooplankton response: *Calanus finmarchicus* abundance

### Physical variability

## Revisiting the Div. 3L offshore acoustic survey

## Discussion

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