## Title:

Rebuttal to Frank et al 2016

## Authors:

NAFC1Montevecchi WA2  
Robert D3  
Davoren GK4  
Rose G5?

## Affiliations:

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

## Abstract

## Introduction

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

Fisheries and Oceans Canada is responsible for the assessment of the Newfoundland and Labrador capelin stock; it has concluded that there was an order of magnitude decline in the stock in the early 1990s, and that capelin abundance declined to less than 1% of historic levels in 2010 (DFO 1994, Miller 1994, 1997, DFO 2008, 2010, 2013, 2015b). 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 2015b).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 1997b, 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 1996b, Carscadden & Nakashima 1997b, Carscadden et al. 2001, DFO 2001b). And while this discordance resulted in the exclusion of the offshore acoustic survey as an input into the capelin multiplicative year-class model, this model still had large statistical uncertainties ((Evans & Nakashima 2002), suggesting that the inshore indices alone did not explain capelin year class variability. This model is no longer in use as the number of inshore indices collected has been reduced over time (DFO 2000). Since 1999, the offshore acoustic survey is considered the best method to obtain an index of the immature capelin biomass in NL (O'Driscoll et al. 2002, Mowbray 2014), which is in accordance with Iceland and the Barents Sea (e.g. Gjøsæter et al. 2009, ICES 2017). In Frank et al. (2016), support for the non-collapse of capelin was based on changes in biology of capelin post-1991 (i.e. distribution and demography), re-analysis of the offshore research surveys (multi-species bottom trawl and acoustic), and the response of various components of the ecosystem (e.g., zooplankton, northern cod, birds, seals) to the large scale changes that occurred during the early 1990s. These authors postulated that the reported collapse was not real and proposed two hypotheses to interpret why the offshore spring acoustic surveys have failed to detect 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 2015b) 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 (Inshore capelin indices title in summary document)

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

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

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

### Demographic change of harvested inshore capelin

### Timing of inshore capelin beach spawning

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

### Inshore recruitment index (capelin recruitment title in summary document)

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

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

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

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

### 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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