## 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).

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

Buren AD, Koen-Alonso M, Pepin P, Mowbray F, Nakashima BS, Stenson GB, Ollerhead N, Montevecchi WA (2014a) Bottom-up regulation of capelin, a keystone forage species. PLoS ONE 9:e87589

Buren AD, Koen-Alonso M, Stenson GB (2014b) The role of harp seals, fisheries and food availability in driving the dynamics of northern cod. Marine Ecology Progress Series 511:265-284

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series 352:213-220

Montevecchi WA, Myers RA (1997) Centurial and decadal oceanographic influences on changes in Northern Gannet populations and diets in the Northwest Atlantic: Implications for climate change. ICES Journal of Marine Science 54:608-614

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

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

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

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

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

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

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

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

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

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

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

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

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