Response to Frank et al. 2016

Inshore capelin indices from aerial surveys and commercial catch rates (inshore traps) increased through 1980s and 1990s HANNAH

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 2001, 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 1997).

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 1997). 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 1997). 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 1996, 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 1996). 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 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, 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.

Timing of inshore spawning: Trinity Bay. Peak spawning 25 days later. Therefore acoustic survey might have been too early HANNAH, DOM

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 2015). 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 2015, 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 2015). 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 2015).

Capelin recruitment Trinity Bay larval production did not change post 1991. Therefore it is inconsistent with capelin collapse HANNAH, DOM

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 1996). 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).

References

Anon (1998) Capelin in SA2 + Div. 3KL. Book 98/63. Canadian Science Advisory Secretariat (CSAS) Research Document

Carscadden J, Nakashima BS (1997) Abundance and changes in distribution, biology, and behaviour of capelin in response to cooler waters of the 1990s. Forage fishes in marine ecosystems. Alaska Sea Grant College Program, AK-SG-97-01, Alaska Sea Grant College Program

Carscadden J, Nakashima BS, Miller DS (1994) An evaluation of trends in abundance of capelin (Mallotus villosus) from acoustics, aerial surveys and catch rates in NAFO Division 3L, 1982-89. Northw Atl Fish Sci 17:45-57

Carscadden JE, Frank KT, Leggett WC (2000) Evaluation of an environment-recruitment model for capelin (M*allotus villosus)*. ICES J Mar Sci 57:412-418

Dalley EL, Anderson JT, deYoung B (2002) Atmospheric forcing, larval drift, and recruitment of capelin ( Mallotus villosus ). ICES Journal of Marine Science 59:929-941

DFO (2001) Capelin in SA 2 + Div. 3KL during 1999. DFO Res Doc 2001/161

DFO (2015) Assessment of capelin in subarea 2 and divisions 3KL in 2015. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2015/036

Evans GT, Nakashima BS (2002) A weighted multiplicative analysis to estimate trends in year-class size of capelin. ICES Journal of Marine Science 59:1116-1119

Frank KT, Leggett WC (1981) Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 38:215-223

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

Leggett WC, Frank KT, Carscadden JE (1984) Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 41:1193-1201

Murphy HM, Pepin P, Robert D (2018) Re-visiting the drivers of capelin recruitment in Newfoundland since 1991. Fisheries Research 200:1-10

Nakashima B (1996) The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (M*allotus villosus)*. NAFO Sci Coun Studies 24:55-68

Nakashima BS (1998) Results of the 1997 aerial survey of capelin (Mallotus villosus) schools. in Anon: Capelin in SA2 + Div. 3KL. Canadian Stock Assessment Secretariat Research Document 98/63.

Nakashima BS, Mowbray F (2014) Capelin (*Mallotus villosus)* recruitment indices in NAFO Division 3KL. DFO Canadian Science Advisory Secretariat Research Document 2013/091