



Original Article

Bottom-up limits to Newfoundland capelin (*Mallotus villosus*) rebuilding: the euphausiid hypothesis

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Capelin (*Mallotus villosus*) is the key forage fish species in the Newfoundland and Labrador Shelf ecosystem. Capelin stocks collapsed in the early 1990s, concurrent with declines in “northern” Atlantic cod, *Gadus morhua*. Neither has fully recovered yet. Changes in growth, condition, and behaviour accompanied capelin declines on the northern Grand Banks (NGB), and remain two decades later. Feeding, growth, and condition of NGB capelin were all lower when compared with capelin from the eastern Scotian Shelf (ESS), where abundance increased following predator declines. For age 2–5 capelin of both sexes, all but one of five comparable age–sex groups were significantly larger on the ESS (e.g. age 3 females average 169 mm on the ESS and 151 mm on the NGB). Neither temperature nor density-dependence explain these differences. However, dietary differences were prominent. ESS capelin had higher total fullness indices (*TFI*s) than NGB fish at all sizes [mean $TFI_{ESS} = 1.43 (\pm 1.14)$, mean $TFI_{NGB} = 0.48 (\pm 0.70)$]. Euphausiids (especially *Thysanoessa* spp.) were a main dietary component on the ESS but not on the NGB. Stable isotope analyses ($\delta^{15}N$ and $\delta^{13}C$) for NGB capelin also indicated few dietary euphausiids. Trophic fractionation of $\delta^{15}N$ was 4.74^{0}_{00} , suggesting NGB capelin were food limited. Capelin recovery on the Newfoundland and Labrador Shelf appears limited by bottom-up forcing, in particular lack of euphausiid prey.

Keywords: capelin, diet, euphausiids, Grand Banks, *Mallotus villosus*, Newfoundland, Scotian Shelf, stable isotopes.

Introduction

Capelin (*Mallotus villosus*) are a key forage fish for seabirds, marine mammals, and fish in shelf ecosystems throughout the North Atlantic. Capelin population dynamics are known to influence the dynamics of their predators, in particular Atlantic cod (*Gadus morhua*) in the Barents Sea (Nakken, 2008) and Icelandic waters (Vilhjálmsen, 2002). On the Newfoundland and Labrador Shelf, the collapse of capelin coincided with the collapse of the northern cod stock (NAFO Divisions 2J + 3KL). In 1991, the spring acoustic biomass estimate for northern Grand Banks (NGB) capelin was <5% of estimates for the 1980s and has remained at low levels (<10%) for over two decades (DFO, 2013). Northern cod biomass

declined precipitously in the early 1990s to the lowest levels in 500 years and has remained low since (Rose, 2004; Brattey *et al.*, 2010). These parallel declines and lack of recovery, coupled with evidence of poor condition in cod, led Rose and O'Driscoll (2002) to predict that the northern cod would not rebuild without recovery of capelin, their chief and irreplaceable prey in this ecosystem.

The population dynamics of capelin on the NGB contrasts with that on the eastern Scotian Shelf (ESS). On the ESS, capelin were never the dominant pelagic species as on the NGB, but their biomass (along with that of other forage fish) increased in the late 1980s to early 1990s following the collapse of key local predators (Frank *et al.*, 2011). On the NGB there is no evidence of predation

release; capelin abundance did not increase following the drastic declines in predator abundance (Carscadden et al., 2013; DFO, 2013). Further, NGB capelin abundance has remained at low levels since their collapse. Nevertheless, based solely on life-history traits, a relatively rapid population recovery might have been expected, as capelin have short generation times, are fast growing, and have high dispersal ability (Vilhjálmsen, 1994; Frank et al., 1996; Rose, 2005). However, environmental and ecological conditions must also remain favourable for population recovery. Shifts in capelin distribution, growth, and behaviour, which coincided with the 1990s collapse, are symptomatic of the unfavourable conditions for capelin on the Newfoundland and Labrador Shelf that have persisted for the past two decades.

Historically, spring (April–May) was a period of intense feeding by capelin in the Newfoundland region (Winters, 1970). Newfoundland capelin (NAFO 2J + 3KL stock) migrated south from the Labrador Shelf to the NGB, fed heavily on zooplankton prey, and then migrated inshore to spawn in bays on the northeast coast of Newfoundland (Gerasimova, 1994; Carscadden et al., 2013). Major changes in Newfoundland capelin biology that began in the early 1990s included distributions shifting south and east towards the shelf edge (Frank et al., 1996; Carscadden et al., 2002; DFO, 2013), reduced or erratic vertical migrations (Mowbray, 2002), lower growth and somatic condition (Nakashima, 1996; Carscadden and Frank, 2002; DFO, 2013), and spawning that occurred up to four weeks later than historical norms (Carscadden et al., 2002; DFO, 2013), with increased proportions of younger age classes spawning (DFO, 2013).

Capelin growth has been linked to both temperature and zooplankton availability, with slower growth associated with low water temperatures (Winters, 1982; Gjøsæter and Loeng, 1987; Hedeholm et al., 2010) and low zooplankton production (Gjøsæter et al., 2002) or the absence of key zooplankton (e.g. *Calanus* copepods and *Thysanoessa* euphausiids; Gerasimova, 1994; Orlova et al., 2010; Hedeholm et al., 2012). While decreased growth and altered behaviour of Newfoundland capelin coincided with record low water temperatures (Nakashima, 1996), these changes have persisted despite a return to warmer water temperatures on the Newfoundland and Labrador Shelf since the mid-1990s (Colbourne et al., 2012; DFO, 2013). Based on the concurrent changes in capelin growth, somatic condition, and presumed feeding behaviour, previous researchers hypothesized that capelin recovery is being limited by the availability of their zooplankton prey on the Newfoundland and Labrador Shelf (O'Driscoll et al., 2001; Carscadden and Frank, 2002; Mowbray, 2002).

Stomach content analysis of Newfoundland capelin collected prior to their collapse indicated that while copepods were the most common prey item across all size classes, euphausiids accounted for a larger proportion of stomach contents weight among mature fish (Gerasimova, 1994). Following the collapse, copepods remained the numerically dominant prey item, but euphausiid contribution to capelin diets has been minimal, either measured as per cent occurrence (O'Driscoll et al., 2001) or as prey mass (Dalpadado and Mowbray, 2013). In contrast, euphausiids were the most important prey type, as measured by mass, among capelin stomachs collected from the ESS between 1999 and 2005 (Cook and Bundy, 2010). Comparisons of spring capelin diets between the two regions lead to the hypothesis that the difference in euphausiid prey consumed may explain the area-based differences in capelin dynamics. However, such regional comparisons require multiple stomach content indices to distinguish an absence of key prey in the diet from an overall reduction in feeding intensity,

and therefore potential food limitation (e.g. Carruthers et al., 2005). Moreover, stomach content analyses only provide a snapshot of feeding at the time of capture. Tissue stable isotope ratios reflect both current and previous diet, as isotope signature turnover takes place over months (Maruyama et al., 2001) to longer than a year, depending on growth rate (Hesslein et al., 1993).

In this paper, the spring feeding and growth of capelin on the NGB is investigated and compared with that of capelin from the ESS to determine if spring feeding (particularly of euphausiids) can explain the changes in growth, condition, and therefore capelin productivity in the regions. The objectives were to test the euphausiid hypothesis by: (i) describing spring feeding of NGB capelin using multiple stomach content indices and stable isotope analyses; and (ii) comparing spring diets, feeding intensity, growth, and condition factors between the NGB and ESS capelin, which have experienced markedly different capelin population dynamics during the past two decades.

Methods

Sample collection

In the spring of 2004, capelin were collected from the NGB and ESS (Figure 1). NGB capelin were collected with a Campelen 1800 trawl, during both day and night, during the annual Fisheries and Oceans Canada (DFO) stratified acoustic survey (11–28 May) for capelin (see Mowbray, 2012). Samples were taken from 24 of the 36 sets that captured capelin, with the largest samples from sets with greater capelin numbers. ESS capelin were collected opportunistically with a shrimp trawl during the daytime DFO spring shrimp survey (1–4 June) and frozen at sea. During each survey, the widest possible range of sizes, with a maximum of 100 fish per 10 mm size group, was collected for stomach content analysis ($n = 499$ for NGB, $n = 299$ for ESS). Additionally, during the NGB survey, up to 4 capelin per 10 mm length group were frozen at -20°C for stable isotope analysis ($n = 34$). Fish were considered to be independent samples under this design, without regard to set. All capelin used for stomach content analysis were measured for total length (parallel to the lateral axis, from the tip of the snout to the upper lobe of the caudal fin) (± 1 mm). Fresh lengths were obtained for frozen ESS capelin by multiplying thawed length by 1.03 (Winters, 1982). Total body weight (± 0.1 g), gonad weight (± 0.1 g), and stomach weight (± 0.01 g) were recorded. Stomachs were preserved in 5% formalin made with sodium borate-buffered seawater; NGB stomach samples were preserved at sea, while ESS stomach samples were preserved after thawing. Gonads were examined to determine sex and maturity. Maturing capelin were identified by the presence of eggs or sperm but were considered immature if the gonads were small and eggs or sperm were not free-flowing. Capelin otoliths were removed for ageing, and surface readings of seasonal bands were used to estimate age (e.g. Winters, 1982).

Zooplankton samples for stable isotope analysis were collected concurrently at seven of 45 stations (Figure 1). Bongo nets (63 cm in diameter, mesh size 505 μm) were towed vertically from 20 m above the bottom to the surface. Large euphausiids (*Meganyctiphanes norvegica*) were collected from the trawlnet, as euphausiids were rare in the bongo nets. Zooplankton samples were sorted at sea into prey groups (e.g. Copepoda, Euphausiacea, and fish larvae) and frozen at -20°C .

Capelin growth

Regional differences in capelin length-at-age and condition were compared only within capelin of the same maturity stage and sex,

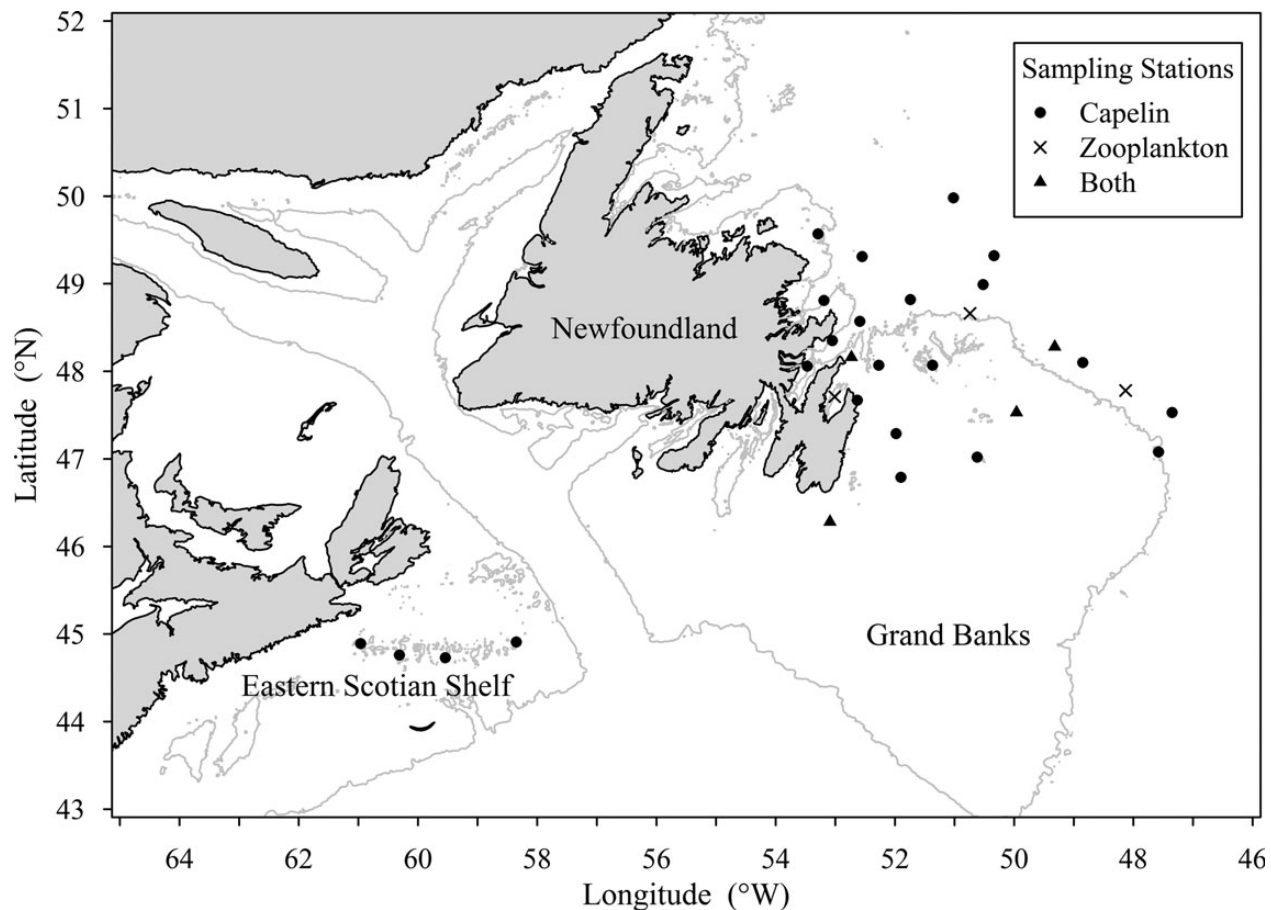


Figure 1. Locations where capelin, zooplankton, or both were collected during spring 2004 from the northern Grand Banks and eastern Scotian Shelf. Light grey depth contour is 200 m.

as differences in life-history characteristics are evident within and between regions (e.g. Winters, 1982). Thus, only mean length-at-age of maturing capelin for each sex was compared across regions to assess differences in growth. Fulton's K was used to assess condition factor of maturing capelin. Gonad weight can account for a large portion of the total body weight in maturing capelin (Carscadden and Frank, 2002); Fulton's K represents the gonad-corrected somatic condition factor of fish i and was calculated as:

$$K_i = \left((WB_i - WG_i) / L_{Ti}^3 \right) \times 10^3, \quad (1)$$

where WB is total body weight (g), WG is gonad weight (g), and L_T is the total length (cm) of fish i . Differences in the condition factor across the regions were assessed for each sex. Capelin condition factor generally increases with length (Carscadden and Frank, 2002); therefore, length was included as a covariate when assessing regional differences in condition. Capelin missing gonad weight or age data were excluded from the condition ($n = 5$) and length-at-age ($n = 2$) analyses.

Stomach content and stable isotope analysis

Stomach contents, from formalin-preserved stomachs, were washed and examined under a dissecting microscope. Prey items were identified to species, sorted into categories based on major taxonomic level (class or order), and wet weight was determined for each category. Prey categories were used for subsequent analyses. Stomach

content analyses, including frequency of occurrence (FR), total and partial fullness indices (TFI , PFI), per cent body weight ($\%BW$), and per cent of empty stomachs, were used to describe the diet similarity among capelin, relative importance of different prey items, and overall feeding intensity. For each prey type j , frequency of occurrence was calculated as:

$$FR_j = (N_j / N) \times 10^2, \quad (2)$$

where N_j is the number of stomachs containing prey type j and N is the total number of stomachs collected. Total fullness index is a measure of stomach contents weight relative to fish length and was calculated as:

$$TFI_i = (WS_i / L_{Ti}^3) \times 10^4, \quad (3)$$

where WS is the total stomach contents weight (g) for fish i . Partial fullness indices are a measure of the weight of a given prey type relative to fish length. Mean fullness indices are calculated from the sum of $TFIs$ (or PFI s) divided by the number of individual fish (Lilly and Fleming, 1981). TFI and PFI were calculated for each 10-mm length class of capelin. Per cent body weight was calculated as:

$$\%BW_i = (WS / (WB_i - WS_i)) \times 10^2, \quad (4)$$

and is a comparable measure to fullness index, which enabled comparisons with capelin feeding levels reported for other regions (e.g.

Vesin et al., 1981; Wilson et al., 2006). The proportion of empty stomachs indicates the level of feeding activity within the sampled population. Overall fullness indices and fullness indices of key prey items were compared between regions and across capelin size classes. If interaction terms indicated a relationship between fish size and region, then shifts in fullness indices were tested both within region across fish length and between regions for all 10-mm length classes with sufficient data.

Frozen capelin and zooplankton collected during the NGB survey were used for stable isotope analysis. While stomach content analyses provide information on dietary composition and feeding intensity when stomachs were collected, stable isotope ratios for carbon ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$ or $\delta^{15}\text{N}$) indicate feeding patterns over a longer period and cover the full spectrum of the diet for that period, which may not be seen in stomach contents. Sample preparation for stable isotope analysis followed Sherwood and Rose (2005) for the capelin ($n = 34$) and zooplankton species [$n = 3$ for all species except *Thysanoessa inermis* ($n = 1$), *Parathemisto libellula* ($n = 12$), and small hyperiids ($n = 2$)]. As $\sim 1\text{--}2$ g of material was required for each sample, stable isotope samples for the following zooplankton contained multiple individuals: *Thysanoessa raschii*, *P. libellula*, small hyperiids, *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, and *Metridia longa*.

Stable isotope signatures can be used to quantify foodweb relationships (e.g. assigning trophic position). Calculating foodweb parameters, like trophic position, requires a measure of trophic fractionation, which is how the stable isotope signatures change from the prey to their consumers (Vander Zanden and Rasmussen, 2001). Original *in situ* trophic fractionation factors were calculated for the changes in the stable isotope ratios (carbon and nitrogen) between capelin and their zooplankton prey. Trophic fractionation values for $\delta^{13}\text{C}$ ($\Delta\delta^{13}\text{C}$) and $\delta^{15}\text{N}$ ($\Delta\delta^{15}\text{N}$) for capelin ($n = 499$) were calculated based on dietary proportions (by weight) of prey items and their respective stable isotope signatures (Sherwood and Rose, 2005; Obradovich, 2008). Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with capelin length were tested, as an indicator of ontogenetic dietary shifts among NGB capelin. Trophic fractionation factors were not calculated for the ESS because zooplankton samples were not collected during the shrimp survey. Further, spatial or temporal differences in isotopic signatures from the base of the foodweb can limit regional comparisons (e.g. Hedeholm et al., 2012).

Results

Capelin growth

Maturing capelin collected from the NGB were smaller-at-age than those collected from the ESS. Almost all of the 299 capelin (length

range: 106–195 mm) collected from the ESS were maturing ($n = 295$), whereas only half of the 499 capelin (length range: 70–179 mm) collected from the NGB were maturing ($n = 285$). Length-at-age was significantly less among maturing female capelin aged 2, 3 and 4 collected from the NGB than the ESS (Table 1). Similarly, age 2 males collected from the NGB were significantly smaller than those from the ESS (Table 1). Length-at-age of 3-year-old males was not significantly different between regions (Table 1). The condition factor for NGB capelin was significantly lower than for ESS capelin in both males (ANCOVA, $F_{1,294} = 225.7$, $p < 0.001$) and females (ANCOVA, $F_{1,275} = 254.5$, $p < 0.001$) (Figure 2).

Stomach contents

Common prey items differed between the two regions, as indicated by prey frequency of occurrence. Copepods were the most common prey type in NGB capelin stomachs but rare in ESS stomachs (NGB $FR_{\text{copepods}} = 65\%$; ESS $FR_{\text{copepods}} = 2\%$). By contrast, euphausiids were the most common prey type in ESS capelin stomachs, occurring in more than three-quarters of stomachs (ESS $FR_{\text{euphausiids}} = 78\%$). Almost no NGB capelin stomachs contained euphausiids (NGB $FR_{\text{euphausiids}} < 1\%$). Copepods did not replace euphausiids in the diets of NGB capelin; although common, their lower weight led to fullness indices in NGB capelin that were considerably lower than on the ESS (Figure 3).

Fullness indices and proportion of empty stomachs indicated lower feeding levels on the NGB, in addition to a shift in common prey items. NGB capelin had lower total fullness indices than did ESS capelin [Figure 3; mean $TFI_{\text{NGB}} = 0.48$ (± 0.70), mean $TFI_{\text{ESS}} = 1.43$ (± 1.14)] with a significant interaction between region and fish length (ANCOVA, $F_{3,794} = 86.32$, $p < 0.001$). No ontogenetic shift in fullness indices was evident for fish collected from the ESS (Figure 3; TFI_{ESS} , $F_{1,297} = 1.22$, $p = 0.27$). In contrast, larger capelin collected from the NGB had higher fullness indices than did smaller capelin (Figure 3; TFI_{NGB} , $F_{1,497} = 61.54$, $p < 0.001$). NGB capelin stomachs also showed an ontogenetic shift in the amount of prey with higher copepod and amphipod fullness indices among the larger fish (PFI_{copepods} , $F_{1,497} = 45.74$, $p < 0.001$; $PFI_{\text{amphipods}}$, $F_{1,497} = 17.69$, $p < 0.001$).

Overall feeding levels, as indicated by per cent body weight, were lower in NGB than ESS capelin (NGB $\%BW = 1.18 \pm 0.07$; ESS $\%BW = 2.74 \pm 0.13$). This regional difference in fullness indices holds even when the indices are based only on feeding capelin (NGB $\%BW = 1.49 \pm 0.08$, $n = 395$; ESS $\%BW = 2.89 \pm 0.13$, $n = 283$). Feeding levels, as indicated by total fullness indices, were lower in capelin stomachs collected from the NGB for all

Table 1. Mean length-at-age (mm \pm standard error) of maturing capelin collected from the northern Grand Banks (NGB) and eastern Scotian Shelf (ESS) during spring 2004.

Age	Region	Males				Females			
		<i>n</i>	Mean	s.e.	<i>p</i>	<i>n</i>	Mean	s.e.	<i>p</i>
2	NGB	64	153	1.3	<0.001	69	134	1.4	<0.001
	ESS	151	161	0.9		82	150	0.9	
3	NGB	71	167	0.7	0.16	48	151	2.7	<0.001
	ESS	11	162	3.1		10	169	1.2	
4	NGB	2	177	2.0	–	30	164	0.9	<0.001
	ESS	–	–	–		35	180	0.9	
5	NGB	–	–	–	–	1	165	–	–
	ESS	–	–	–		4	187	2.3	

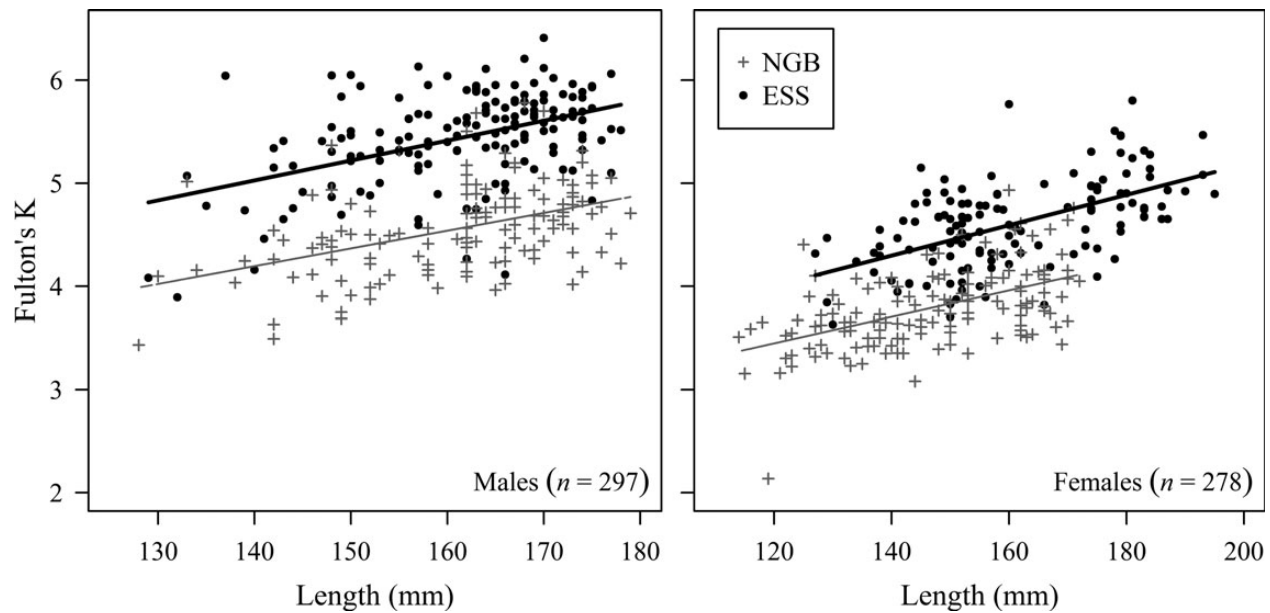


Figure 2. Fulton's K condition factor for maturing male and maturing female capelin collected from the northern Grand Banks (cross; NGB) and eastern Scotian Shelf (filled circle; ESS) in the spring of 2004. Regression lines fitted for NGB males ($y = 0.02x + 1.78$), ESS males ($y = 0.02x + 2.32$), NGB females ($y = 0.01x + 1.91$), and ESS females ($y = 0.01x + 2.23$).

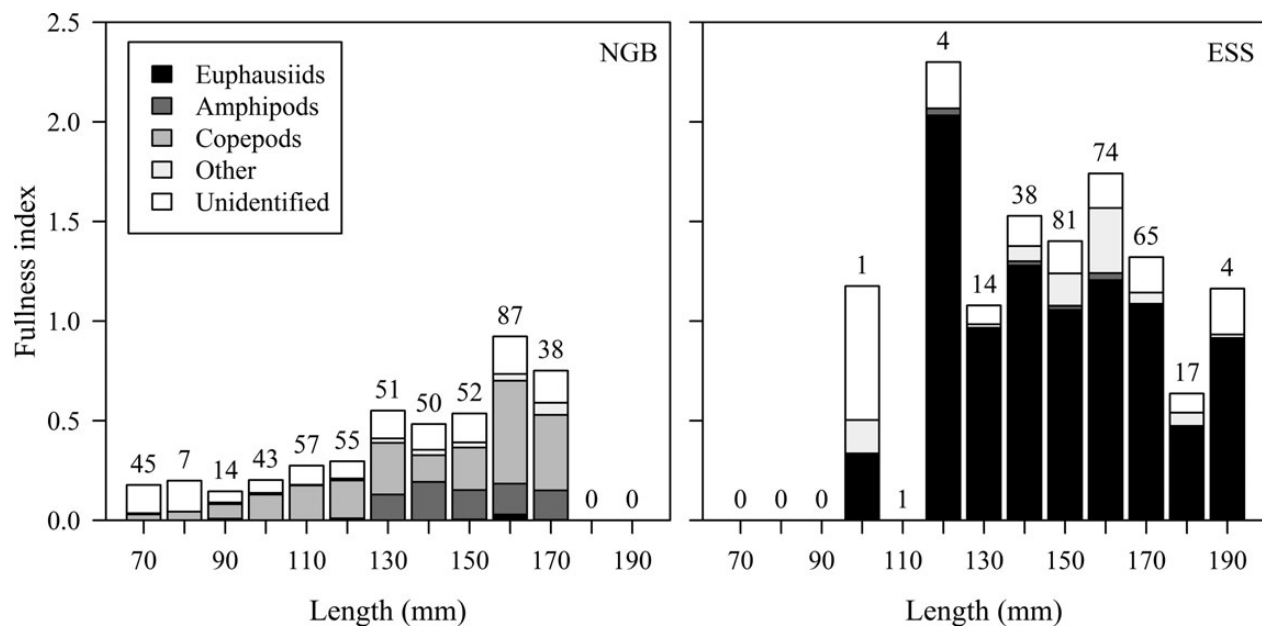


Figure 3. Fullness indices for capelin stomachs collected from the northern Grand Banks (NGB) and the eastern Scotian Shelf (ESS). Partial fullness indices for each major prey type sum to mean total fullness indices for each 10-mm length class. Sample size for each length class is shown above the bars.

common length classes (Figure 3; 140 mm: $t = -5.91$, $p < 0.001$; 150 mm: $t = -5.12$, $p < 0.001$; 160 mm: $t = -4.34$, $p < 0.001$; 170 mm: $t = -3.37$, $p < 0.001$). Moreover, fewer NGB capelin were feeding as evidenced by higher occurrence of empty stomachs (NGB 21% empty; ESS 5% empty).

Stable isotopes

The stable isotope signatures for NGB capelin were consistent with the dietary composition derived from stomach content analyses.

Capelin $\delta^{13}\text{C}$ signatures were similar to those of the common NGB copepod and amphipod species analysed from the zooplankton tows (Figure 4). $\delta^{15}\text{N}$ signatures of NGB capelin did not change with length ($F_{1,32} = 0.44$, $p = 0.51$), which is consistent with the lack of a length-based dietary shift from lower $\delta^{15}\text{N}$ signature copepods to higher $\delta^{15}\text{N}$ signature euphausiids. The capelin $\delta^{13}\text{C}$ signatures increased with length ($F_{1,32} = 11.66$, $p = 0.002$), which suggests increased contribution of larger amphipods and copepods (*P. libellula* (pl), *C. hyperboreus* (ch); Figure 4). Trophic

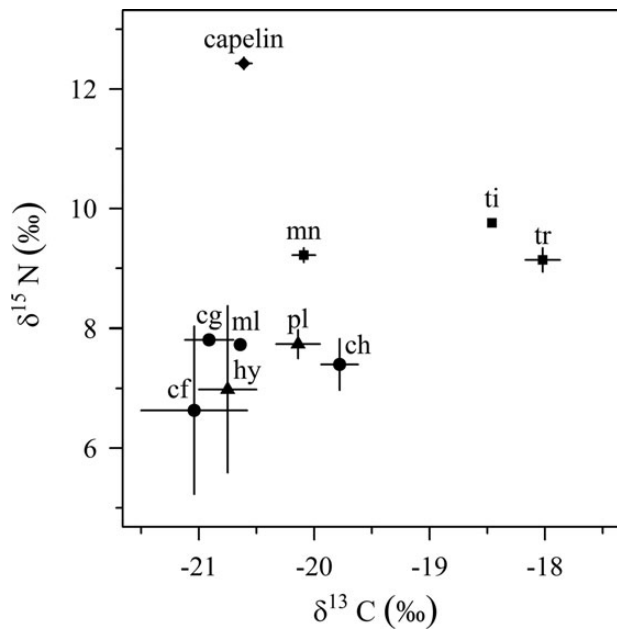


Figure 4. Mean stable isotope signatures (± 1 s.e.) for northern Grand Banks capelin and their dominant prey: the euphausiids (filled squares) [*M. norvegica* (mn), *T. raschii* (tr), and *T. inermis* (ti)]; the amphipods (filled triangles) [*P. libellula* (pl), small hyperiids (hy)]; and the copepods (filled circles) [*C. hyperboreus* (ch), *C. glacialis* (cg), *C. finmarchicus* (cf), and *M. longa* (ml)].

fractionation values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were 4.74‰ ($\Delta\delta^{15}\text{N}$) and -0.12‰ ($\Delta\delta^{13}\text{C}$), respectively.

Discussion

The data indicate that in the early 2000s, NGB capelin experienced poorer feeding conditions than did ESS capelin. Not only did fewer NGB capelin stomachs contain food, but the amount consumed was lower across the full range of size classes. The difference in feeding intensity appears to result primarily from an absence of euphausiids in the diet of NGB capelin, in contrast to their relative abundance in the diet of ESS capelin (Figure 3). Isotope analyses were consistent with a lack of euphausiids in the diet of NGB capelin over longer time-scales. Growth of NGB capelin was poorer than that of ESS capelin; NGB capelin were in poorer condition and smaller-at-age (for females and 2-year-old males) than those from the ESS. Although ESS capelin samples were limited to bycatch from a shrimp survey, euphausiid feeding was dominant among them and the maximum length of individuals exceeded that of the larger sample from the NGB capelin survey.

Regional differences in capelin feeding and growth occur across the species' range, with higher indices where euphausiids are the key prey (e.g. Orlova et al., 2002, 2009; Hedeholm et al., 2012). For example, along the West Greenland coast capelin growth rates and energy densities are highest where euphausiid consumption and stomach fullness are highest (Hedeholm et al., 2010, 2012). In the present study, length-at-age and condition indices, and therefore growth, were higher among ESS capelin where euphausiids dominated the stomach contents and where fullness indices were higher. The stomach contents are consistent with those from larger multiple year studies on the ESS (Cook and Bundy, 2010) and NGB (Dalpadado and Mowbray, 2013), as are the measures of

mean length-at-age for NGB capelin (Mowbray, 2012). The anomalously low fullness indices of NGB capelin in 2004 are also apparent in comparisons of capelin feeding in other systems. For example, fullness indices for NGB capelin ($\%BW = 1.18$) were even lower than those reported under "poor" feeding levels for the Barents Sea ($\%BW < 1.75$; Orlova et al., 2010), whereas fullness indices for ESS capelin ($\%BW = 2.74$) were higher but still considerably less than the high feeding intensities found in the Barents Sea ($\%BW = 11.2$; Orlova et al., 2010). Despite the broader sampling programme on the NGB compared with the ESS, both spatially and temporally, NGB capelin were nowhere in good condition. NGB capelin were in poorer condition than those reported from the region during the late 1980s (Carscadden and Frank, 2002), whereas somatic condition indices of ESS capelin were comparable with those reported from the NGB prior to the collapse of the Newfoundland capelin. Moreover, very low capelin feeding on euphausiids was evident in NGB capelin stomachs. Euphausiids appeared in only 1% of non-empty stomachs, a lower occurrence than the 11–44% reported in Newfoundland capelin dietary studies conducted prior to 1991 (Kovalyov and Kudrin, 1973; Gerasimova, 1994).

Capelin diets typically show an ontogenetic shift to larger prey items, namely euphausiids. Although the magnitude and timing of the shift differs between regions and between seasons within regions (e.g. Vesin et al., 1981; Gerasimova, 1994; Gjøsæter et al., 2002; Orlova et al., 2010; Hedeholm et al., 2012), the growth of older capelin in the Barents Sea is correlated with the abundance of large zooplankton including large Arctic copepods, euphausiids and amphipods (Gjøsæter et al., 2002). However, even among smaller capelin euphausiids may be the preferred prey; small capelin (mean length 84 mm) in the Gulf of Alaska preferentially select euphausiids when present, while in euphausiid-poor locations their stomachs are mostly empty (Wilson et al., 2006). Ontogenetic dietary shifts were not observed within either sampling region reported here. ESS capelin of all lengths fed on euphausiids, but most (>90%) were larger than 140 mm, the size at which Vesin et al. (1981) reported a shift to euphausiid prey among Gulf of St Lawrence capelin. Among NGB capelin there was no shift to euphausiid prey, even though almost half of the capelin collected were larger than 140 mm. The lack of ontogenetic dietary shift among NGB capelin was not limited to the short period covered by the stomach contents; $\delta^{15}\text{N}$ signatures did not increase with length, indicating no increase in prey trophic level.

Stable isotope analyses provided strong evidence that NGB capelin had not recently fed on euphausiids. Together with the stomach content analyses, they indicate that the absence of euphausiids from NGB capelin diets was not due to short-term shifts in behaviour, such as daily feeding chronologies. Capelin $\delta^{13}\text{C}$ signatures were similar to those of the common NGB copepods and amphipods analysed but not to those of *Thysanoessa* euphausiids, previously identified as the chief euphausiid prey in Newfoundland waters (Gerasimova, 1994; O'Driscoll et al., 2001; Dalpadado and Mowbray, 2013) and elsewhere (e.g. Vesin et al., 1981; Wilson et al., 2006; Dalpadado and Mowbray, 2013). Although the $\delta^{13}\text{C}$ signature of the euphausiid *M. norvegica* was similar to that of NGB capelin, it likely did not contribute much to the capelin diet; it has historically been a minor dietary component on the NGB compared with the *Thysanoessa* spp. (Gerasimova, 1994). Moreover, *M. norvegica* did not appear in any of the 499 capelin stomachs from the NGB, including those collected from the same trawl sets as the *M. norvegica* samples used in stable isotope determinations. Among ESS capelin stomachs containing euphausiids, *M. norvegica*

was present in <8%, whereas 68% contained *Thysanoessa* spp.; the remaining stomachs contained only euphausiids that could not be identified due to digestion. The $\delta^{15}\text{N}$ trophic fractionation for Grand Banks capelin was $4.74^{+0.00}_{-0.00}$, which exceeded the global average of $3.4^{+0.00}_{-0.00}$ enrichment of a predator over its diet, reported from field-based stable isotope studies (Vander Zanden and Rasmussen, 2001). The high value for $\delta^{15}\text{N}$ enrichment in NGB capelin could reflect more than just the expected change between trophic levels. An elevated $\Delta\delta^{15}\text{N}$ may reflect a poor nutritional state in capelin, as starvation and fasting can lead to catabolism of body proteins and an elevation in tissue $\delta^{15}\text{N}$ (Hobson *et al.*, 1993; Sherwood and Rose, 2005). These data suggest that NGB capelin were food limited as a direct consequence of the absence of euphausiids, particularly *Thysanoessa* spp.

The absence of euphausiids in NGB capelin stomachs likely reflects a decline in abundance in the Newfoundland and Labrador Shelf ecosystem. Continuous plankton recorder (CPR) data showing long-term trends in plankton abundance have been collected along transits of the NGB since the 1960s. Unfortunately CPR data were not collected during the critical period of ecosystem changes between 1979 and 1990, and were less frequent prior to 1979 than after 1990 (Head and Pepin, 2010). Nonetheless, CPR data from the NGB show euphausiid abundance was lowest from 2000–2006 (Head and Pepin, 2010), when capelin samples were collected for this study, than during earlier periods of higher capelin abundance such as the 1970s. Marine predator diets on the Newfoundland Shelf also show a decline in euphausiid consumption, particularly in *Thysanoessa* spp., since the 1980s. *Thysanoessa* euphausiids were absent from murre (*Uria* spp.) stomachs collected during the late 1990s but had been the dominant invertebrate prey a decade earlier (Rowe *et al.*, 2000). Similarly, *Thysanoessa* euphausiids were absent from Leach's storm petrel (*Oceanodroma leucorhoa*) stomachs collected in the early 2000s, although present in the late 1980s (Hedd *et al.*, 2009). Euphausiids have been largely absent from capelin stomachs collected from the Newfoundland and Labrador Shelf since the 1990s: including those collected in 1999 (O'Driscoll *et al.*, 2001), 2004 (this study), and 2004/2005, 2007/2008 (Dalpadado and Mowbray, 2013).

On the NGB, the weight of the evidence suggests that reduced spring feeding is limiting capelin growth and somatic condition. Poor spring feeding may lead to reduced survival among mature fish, and therefore, to the ongoing absence of older NGB capelin. The age structure of the spawning population of Newfoundland capelin is truncated, with increased proportions of younger age classes spawning (e.g. 37–79% of 2-year-olds maturing in recent years vs. <5% in the 1980s; DFO, 2013). While a higher proportion of 2-year-olds spawning could be an indication of better conditions for growth leading to early maturation (e.g. Orlova *et al.*, 2002), this does not appear to be the case as somatic condition of all NGB capelin is poorer than in the 1980s and older capelin are smaller than in the 1980s. Because the rate of capelin gonad development increases during the spring prespawning period when feeding is intense but fat stores diminish, Winters (1970) suggested that energy stored from feeding the previous year (e.g. autumn) is used in gonad development. Building on this, Gerasimova (1994) hypothesized that spring feeding intensity contributes to post-spawning survival, because survival rates and muscle fat stores are correlated. Post-spawning survival rates differ among regions and years (Flynn *et al.*, 2001), with higher survival rates among females, beach spawning habitats, and capelin with higher fat stores (Gerasimova, 1994; Flynn *et al.*, 2001; Christiansen *et al.*, 2008).

The consequences of low survival rates and a truncated age structure due to poor feeding are twofold. First, among Newfoundland and Labrador capelin, older repeat spawners have higher fecundities (Winters, 1971; Flynn *et al.*, 2001). Second, a truncated age structure contributes to reduced life history diversity among Newfoundland and Labrador capelin, and therefore increased vulnerability to ecological and environmental change (Christiansen *et al.*, 2008; Schindler *et al.*, 2010). If post-spawning survival depends upon spring feeding intensity, then rebuilding a broad spawning stock age structure may require multiple years of high euphausiid abundance.

Alternative mechanisms, such as size-selective losses due to fishing or predation, could lead to the observed regional differences in length-at-age among NGB and ESS capelin and the truncated age structure in NGB capelin. However, size-selective losses do not account for the continued poor somatic condition among NGB capelin. Moreover, there have been drastic reductions in the abundance of major predators and of fishing pressures for Newfoundland capelin: northern cod autumn biomass estimates declined from 1 183 809 t in 1990 (Brattey *et al.*, 2008) to 143 151 t in 2009 (Brattey *et al.*, 2010) and combined landings of NAFO 2J + 3KL capelin declined from at least 140 300 t in 1990 to < 30 000 t for the past decade (data from the Northwest Atlantic Fisheries Organization database, available online at <http://www.nafo.int>). Nonetheless, continued research on the links between feeding, reproduction, recruitment, and the fishery is needed in capelin, as this species is key to the ecosystem dynamics of the Newfoundland and Labrador Shelf (Rose and O'Driscoll, 2002; Carscadden *et al.*, 2013). Additional sampling by site (by capture set) is needed (e.g. Picquelle and Mier, 2011), as field observations and experimental studies indicate that the timing of feeding and growth may differ among capelin sexes and maturity stages (Flynn *et al.*, 2001; Christiansen *et al.*, 2008). In addition, better knowledge of prey availability, feeding, growth, and reproductive development of capelin throughout the year would assist in linking their dynamics with changing ecological conditions.

In conclusion, the data suggest that NGB capelin recovery is limited by bottom-up forcing of euphausiid prey abundance. Snow crab (*Chionoecetes opilio*) and, recently, pandalid shrimp in this region are also believed to be influenced primarily by bottom-up forcing, and not by top-down influences of groundfish predator abundance (e.g. Dawe *et al.*, 2012). In the present study, NGB capelin showed reduced feeding intensity, low euphausiid consumption, slower growth, and poorer somatic condition, suggesting bottom-up effects of food limitation not experienced by their ESS counterparts. For example, given that the average weight of 2- and 3-year-old ESS capelin was almost double that of NGB capelin (20.5 g and 11.4 g respectively), NGB capelin biomass would be half that of the ESS for populations of similar abundance. The combination of reduced capelin abundance and growth argues against any density-dependent influences, and together restricts the availability of the key prey species to many predators in Newfoundland and Labrador marine ecosystems. For example, Rose and O'Driscoll (2002) argued that rebuilding and recovery of northern cod populations was unlikely without increased abundance of capelin, historically their main prey. Poor condition (liver index), maturation at younger ages, and smaller maximum sizes of northern cod have been linked to the poor availability of capelin (Sherwood *et al.*, 2007). For capelin, *Thysanoessa* euphausiids appear to be the missing key prey. We predict that a full recovery of capelin is unlikely to occur unless maturing capelin are once again feeding

heavily on euphausiids in Newfoundland and Labrador Shelf waters. What is limiting euphausiid abundance remains unknown.

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