

# Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland

Frances K. Mowbray

Mowbray, F. 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. – ICES Journal of Marine Science, 59: 942–949.

Vertical distribution patterns of capelin were examined using data from spring and autumn acoustic surveys off northeastern Newfoundland in the years 1988–2000. Until 1991, capelin typically underwent diel vertical migrations from 50 to 150 m. Since 1991, vertical migrations have been reduced or have become erratic, with capelin commonly located deeper in the water column (200+m) and closer to the seabed. Changes in vertical distribution initially coincided with the onset of a severe cold period, but distributions failed to return to normal as waters warmed. Vertical distribution was examined with regard to potential habitat-selection factors, including capelin density, water temperature, fish size, maturity stage, and proximity of predators. Of these, only fish density and predator (Atlantic cod) presence were significant. Capelin occupied more of the water column when their density was high than when it was low, and they were found farther from the seabed in areas with cod than without. Results indicate that, during the 1990s, capelin should have been able to optimize vertical distribution and feeding. This is not consistent with reports of poorer capelin condition and size-at-age in the 1990s, suggesting that vertical distributions are likely a result of changes in other factors, such as prey availability.

Crown Copyright © 2002 Published by Elsevier Science Ltd on behalf of International Council for the Exploration of the Sea. All rights reserved.

Keywords: capelin, habitat selection, hydroacoustics, Newfoundland, vertical distribution.

Received 13 August 2001; accepted 7 April 2002.

F. K. Mowbray: Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland, Canada A1C 5X1; tel: +1 709 7725542; fax: +1 709 7724188; e-mail: [mowbrayf@dfo-mpo.gc.ca](mailto:mowbrayf@dfo-mpo.gc.ca).

## Introduction

Abrupt changes in horizontal distribution and migration pattern of capelin, *Mallotus villosus* (Müller), in response to changing oceanographic conditions have been observed in a number of stocks (Vilhjálmsson, 1994; Gjosaeter, 1999). In the Northwest Atlantic (Figure 1), capelin distribution, abundance, and biological characteristics (size at maturity and spawning time) underwent considerable change during the 1990s, many of which were initially thought to be linked with oceanographic variation (Frank *et al.*, 1996; Nakashima, 1996; Carscadden and Nakashima, 1997). Starting in the 1960s, the waters of the Northwest Atlantic underwent a cooling period heightened by severe cold ocean conditions in 1984/85 and from 1989 to 1993. By 1991, this resulted in record ice coverage and the expansion of the sub-zero cold intermediate layer (CIL; Petrie *et al.*, 1988; Figure 2). However, since 1996, Newfoundland waters

have been warming (Colbourne, 2001), but many of the changes in capelin biology and distribution persist.

Until 1991, capelin in offshore Newfoundland waters were typically found throughout NAFO Divisions 2J3KL (Figure 1). In autumn most fish fed in the north, moving southwards along the shelf break during early spring before crossing the Grand Banks and coming inshore to spawn in bays along the northeast Newfoundland coast during June (Carscadden *et al.*, 1994). Vertical distributions of these capelin included diel migrations characterized by the fish moving up and dispersing in the water column at night and descending to aggregate at greater depths during the day (Dragesund and Monstad, 1973; Kovalyov and Kudrin, 1973; Bailey *et al.*, 1977; O'Driscoll and Rose, 1999). However, since 1991 capelin surveyed in spring have been aggregating deeper in the water column and exhibiting a reduced vertical migration (Shackell *et al.*, 1994).

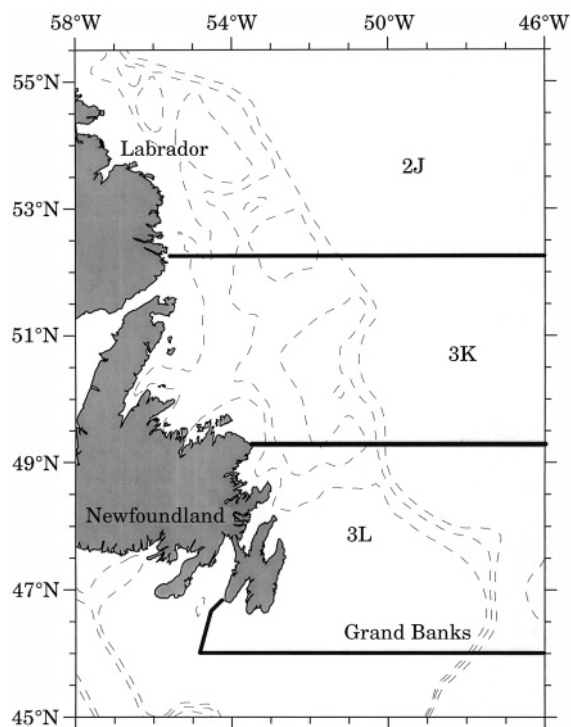


Figure 1. Map of the northeastern Newfoundland shelf showing locations of NAFO Divisions 2J, 3K, and 3L. Dashed lines give locations of 200, 300, and 500 m depth contours.

Vertical distribution is a good example of mesoscale habitat selection. As capelin can traverse depths rapidly, it is likely that the depth at which they are usually found is one that represents, for that given point in time and space, the most advantageous combination of temperature, food supply, competition, and predation risk. Unlike other osmerids, capelin do not produce antifreeze proteins. They can, however, super-cool and have been caught in water as cold as  $-1.5^{\circ}\text{C}$ ; nearly a degree below the freezing point of their body fluids ( $-0.4$  to  $-0.8^{\circ}\text{C}$ ). Nonetheless, capelin coming in contact with sea ice or temperatures below  $-1.9^{\circ}\text{C}$  will die, so these conditions must be avoided (Raymond and Hassel, 2000). Consequently an expanded CIL with a minimum temperature between  $-1.6$  and  $-1.8^{\circ}\text{C}$  could act to constrain capelin vertical distribution and migration. However, so may other factors such as capelin maturity state, body size, capelin density, or predatory or prey fields; many of these factors have also varied during the study period. With this in mind, this study strives to (a) document the extent of spatial and temporal changes in vertical distribution of capelin during a period of changing environmental conditions, and (b) examine potential causes of these changes in light of some common assumptions regarding habitat selection.

## Methods

Information on the distribution and abundance of capelin in northeast Newfoundland waters has been collected during acoustic surveys since the early 1980s. This study uses data collected during spring (May) surveys of NAFO Division 3L (1988–1994, 1996, 1999, 2000) and autumn (October) surveys in Divisions 2J3K (1989–1994; Figure 1). All surveys were conducted around the clock, and despite minor changes in vessels and design (zigzag or parallel transects), the timing and spatial coverage (coastline eastwards to the 500 m contour along the shelf break) of the surveys has been largely unchanged (Miller, 1985; Carscadden *et al.*, 1994; Mowbray, 2000).

Biological samples were collected from trawl sets conducted at a minimum rate of one every 12 h, as required to interpret acoustic records. Either midwater (Diamond IX or IYGPT) or bottom trawls (Campelen 1800 or Engels-145) were used, depending on the vertical distribution of the acoustic backscatter encountered. A random sample of approximately 200 capelin was collected from each set, and the total length (mm), sex, and maturity was recorded for each fish. Expendable bathythermograph (XBT) or conductivity, temperature, and depth profiler (CTD) casts were made at most fishing sites and the resultant temperature data averaged in 1 m vertical bins. Binned data were then used to calculate the height of bottom water (waters contiguous with bottom) with temperatures  $\geq 0^{\circ}\text{C}$ .

Four different echosounder system configurations were used during the course of the study (Table 1), each calibrated prior to surveying. With systems A–C the transducer was towed astern of the vessel; system D used a hull-mounted transducer. Once near-field and noise-zone data were discarded, useable acoustic measurements were available for an average of 13–500 m depth for systems A–C and 16–500 m for system D. Backscatter measures (voltage [20 Log R] or volume backscatter [Sv]) were edited to isolate signals containing capelin using a visual editing program. Backscatter measurements were then integrated to give backscatter area estimates (Sa) for 10 m surface-referenced layers, and the whole water column (WWC), over approximately 3 km segments (bins) of survey track. Integrations were performed with a 50 mV threshold for systems A–C, and a  $-85$  dB Sv threshold for system D. When trawling indicated that backscatter signals contained a mix of species, Sa was partitioned according to the species composition in the catch. Sa attributed to capelin was then scaled by a constant target strength of  $-34$  dB  $\text{kg}^{-1}$  (Miller, 1985) to give capelin densities ( $\text{g m}^{-2}$ ).

## Vertical distribution

Variables describing vertical distribution of capelin were derived from the relative amplitude and placement of

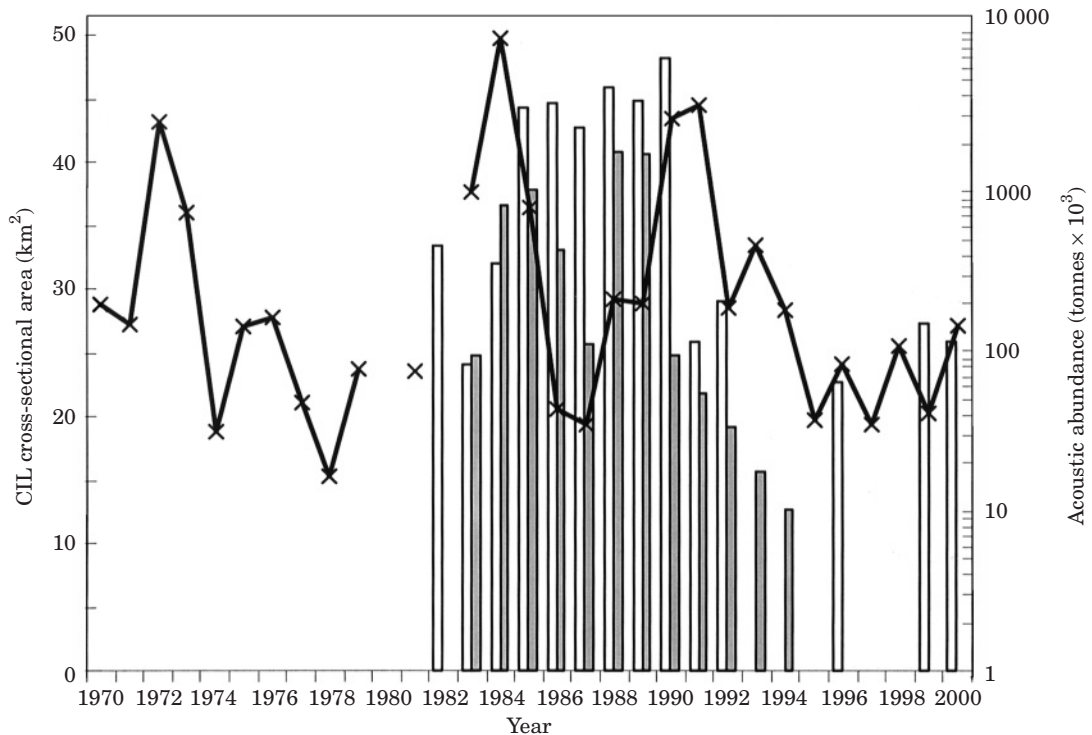


Figure 2. Annual acoustic estimates of offshore capelin biomass during spring (clear bars) and autumn (shaded bars) surveys, and the cross-sectional area of the cold intermediate layer along the Bonavista transect (NAFO Divisions 2J3KL) in summer, after Colbourne (2001; line). No CIL data points were available for 1980 and 1982.

Table 1. Echo-sounder system configurations used during offshore capelin acoustic surveys 1988–2000. All surveys 1988–1994 were on the RV “Gadus Atlantica” and 1996–2000 on the RV “Teleost”.

System	Period	Echo-sounder	Digitizer/recorder	Transducer depth (m)	Frequency (kHz)	Pulse length (ms)	Band-width (kHz)	Time-varied gain
A	1988–1990	EK400	HYDAS <sup>a</sup>	6–10	49	0.6	3.3	Analogue
B	1991–1993	EK400	HDPS <sup>b</sup>	6–10	49	0.6	3.3	Analogue
C	1994–1996	ES2000	HDPS	6–10	38	0.8	2.5	Analogue
D	1999–2000	EK500	CH1 <sup>c</sup>	6	38	1.0	3.8	Digital

<sup>a</sup>Custom built system – Hydroacoustics Data Acquisition System (Stevens, 1986).

<sup>b</sup>FEMTO electronics product.

<sup>c</sup>Canadian National Hydroacoustics Program Data Analysis Tool.

backscatter in the water column, and consequently should not be unduly influenced by inter-survey changes in equipment. Using relative densities of capelin among 10 m depth layers, three variables describing various aspects of vertical distribution were derived. These were: (a) the depth layer at which capelin densities peaked (DPD); (b) the distance of that peak density layer from the bottom (POB); and (c) the height of the water column occupied by capelin (maximum depth – minimum depth; RANGE). Variations in DPD, POB, and RANGE across time and space were then examined by

calculating the mean value of each variable for the time period and/or area of interest, weighted by the WWC capelin density for the same period/area.

In the first portion of the analysis, mean (weighted) variables (DPD, POB, and RANGE) were used to document change over time, by season, using all available data. Subsequent analysis focused on examining relationships between various vertical distribution patterns and such potential habitat-selection pressures as WWC capelin density, water temperature, biological characteristics (maturity status or length), and the

presence/absence of predators, e.g. Atlantic cod (*Gadus morhua*). Owing to differences in sampling scales and frequency between and among acoustic and non-acoustic data, the various effects were examined individually. In particular, investigations of the effects of biological characteristics and water temperature were limited to fishing-set locations and used only the acoustic data from the 3 km bin directly preceding the set.

Many variables (DPD, POB, WWC density, and cod density) were not normally distributed and could not be rendered normal through transformation. Consequently, a non-parametric statistical technique (Spearman's ranked correlation) was used to investigate relationships among: (a) WWC capelin density, DPD, and RANGE (whole data set); (b) depth of capture, mean length, and the proportion of maturing capelin caught (set locations only); (c) RANGE of capelin at set locations and the height of bottom water above 0°C.

Log-transformed catch rates of cod (number tow<sup>-1</sup>) from bottom-trawl surveys conducted 2–4 weeks subsequent to the acoustic surveys were used to examine potential effects of predators on vertical distribution of capelin. Those surveys were conducted as part of annual random-stratified surveys designed to assess the biomass of demersal fish in NAFO Divisions 3LNO in spring, and 2J3KL in autumn (Anon., 2001a). During the study period, two types of bottom trawl (Engels-145 and Campelen 1800) were employed, using slightly different fishing methods. For this analysis all Engels catch rates were converted to "Campelen equivalents" using information secured from comparative trawling of the two gears (Warren, 1997). To mitigate problems related to possible fish movement between the acoustic (capelin) and bottom-trawl (cod) surveys, data from both surveys were averaged over 0.5° latitude by 1.0° longitude blocks and a Spearman correlation analysis performed using block averages. A Kruskal–Wallis test was used to examine differences in vertical distribution of capelin in the presence and absence of cod.

## Results

From 1988 to 1990, spring and autumn capelin aggregations exhibited a typical diurnal pattern of migration, rising to near 50 m at dusk and descending to around 150 m during the day. However, since 1991, capelin have failed to undergo regular diel migrations (Figure 3). In spring, capelin tended to stay at depth around the clock, remaining below the CIL. In autumn, vertical migrations were erratic, and although capelin were generally deeper in the water column, they sometimes spanned a greater vertical distance than during the 1980s (Figure 4). Since 1991, capelin in both seasons were closer to the seabed, and in areas of greater bottom

depth (Figure 5). Though possible, it is not likely that the observed changes in capelin distribution are due to the greater (+3 m) minimum detection depth of the acoustic system used in 1999 and 2000. Capelin were rarely detected in the upper 50 m in either of those years (Figure 4), and no capelin were caught during spot checks (trawls) of the waters above the detectable zone (<16 m).

Changes in capelin vertical distribution coincided with a marked decline in acoustic estimates of abundance offshore in spring, although changes in vertical distribution during the autumn survey lagged declines in abundance by a year (Figure 2). Correlations between WWC density and DPD were statistically significant in both seasons (spring,  $r=0.05$ ,  $n=10\ 636$ ,  $p<0.001$ ; autumn,  $r=0.26$ ,  $n=8110$ ,  $p<0.001$ ), although the explanatory power was weak. RANGE, however, was positively correlated with WWC density in spring ( $r=0.35$ ,  $n=10\ 636$ ,  $p<0.001$ ), and autumn ( $r=0.52$ ,  $n=8110$ ,  $p<0.001$ ). The proportion of sexually mature capelin caught was loosely, but positively, correlated with fishing depth in both seasons, though again the explanatory power of the relationships was weak and of questionable biological significance (spring,  $r=0.15$ ,  $n=364$ ,  $p=0.004$ ; autumn,  $r=0.32$ ,  $n=68$ ,  $p=0.007$ ). Capelin length was not correlated with depth fished in spring ( $p=0.41$ ) nor autumn ( $p=0.27$ ).

Water-column temperature profiles taken at set locations failed to reveal any biologically significant link between the RANGE occupied by capelin and the height of above-zero bottom water. Temperature profiles did reveal a tendency for capelin to be taken in warmer waters in the 1990s than during previous years (Figure 6). Capelin DPD was significantly closer to the seabed when cod were absent from a block than when these demersal predators were present (Kruskal–Wallis,  $D=4.5$ ,  $d.f.=1$ ,  $p<0.05$ ). Similarly, the distance of peak capelin density from bottom (POB) was positively correlated with the log-transformed catch per tow of cod during spring surveys ( $r=0.48$ ,  $n=139$ ,  $p<0.001$ ), though not during autumn (Figure 7).

## Discussion

It is clear from this study that capelin have undergone a major shift in habitat usage, one that persists through both spring and autumn and the entire study area. Given that these changes continued into 2000, when water temperatures were once again similar to those of the late 1980s, it is unlikely that temperature was the direct cause. In fact the deeper distributions in the 1990s resulted in capelin experiencing overall warmer water temperatures. Given that warmer waters (0.5–2.0°C) have been associated with improved growth of capelin in the Barents Sea (Gjosæter, 1999), one might assume



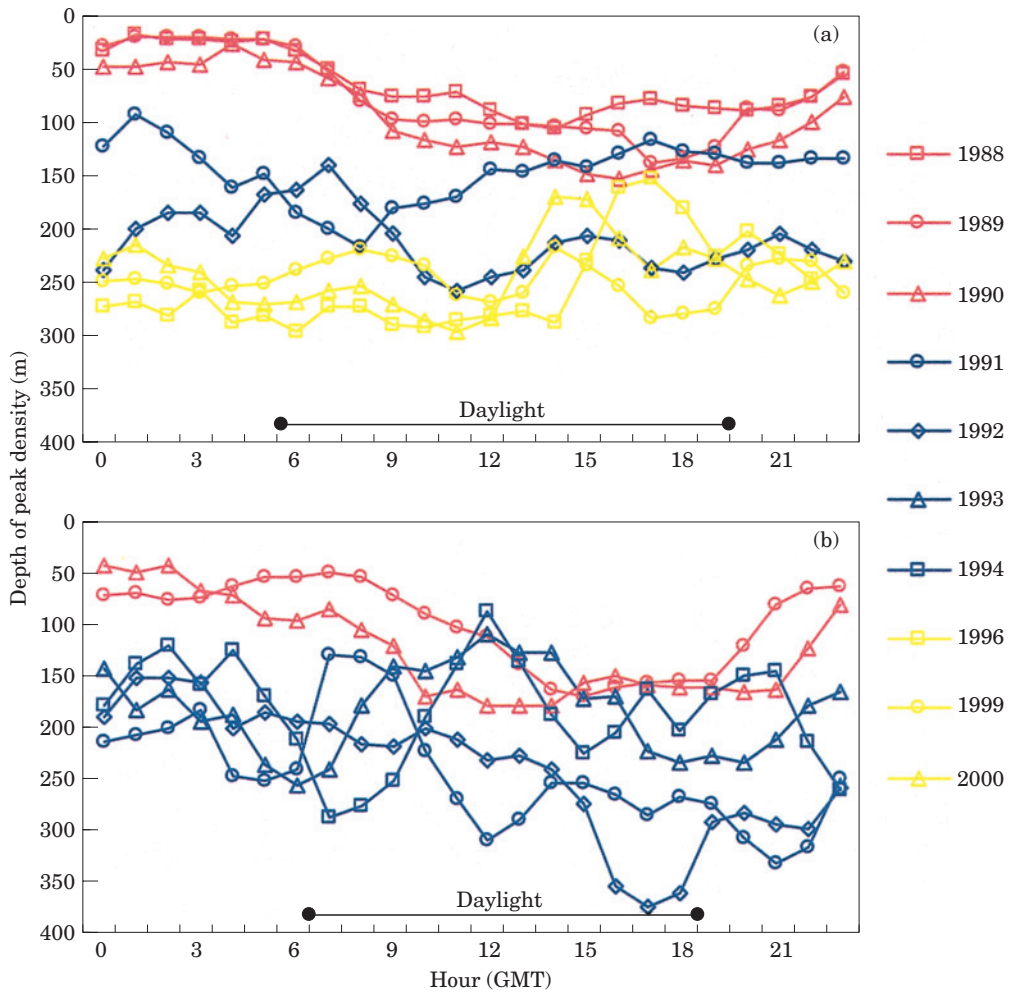


Figure 3. Hourly mean depth of peak capelin density from spring 3L (upper) and autumn 2J3K (lower) during the cooling period (red), extreme cold years (dark blue), and recent warming period (yellow).

that they would also be beneficial to northwest Atlantic capelin. However, capelin off Newfoundland do not appear to have reaped any benefit from remaining in warm bottom waters. On the contrary, body condition and size-at-age in the 1990s declined from their status in the previous decade (Nakashima, 1997; Carscadden and Frank, 2002). The question is, therefore, why have capelin moved into these deeper, warmer waters?

Habitat selection by pelagic fish is probably the culmination of many factors, one of the most studied of which is fish density (Maravelias, 1999). In a typically density-dependent manner, Barents Sea capelin remain to feed in warmer southerly waters when stock sizes are small, expanding their range northwards into colder waters only when numbers increase or local food supply is inadequate (Gjosæter, 1999). A similar model could work for vertical distribution in Northwest Atlantic capelin. Vertical range of capelin was loosely associated

with density. If upwards dispersal resulted from intra-specific competition (increased density), then one would expect that, at low density, vertical distribution would be minimized, as in the 1990s. However, one would also expect that, if there was little intra-specific competition, capelin size and condition would be equal or better than in previous years.

Predator evasion is one mechanism by which a species may be forced out of optimal feeding habitat. Predation on capelin comes from all directions. Until the 1990s, Atlantic cod was the most important consumer of capelin, but capelin are also an important prey item for other demersal species, such as Greenland halibut (*Reinhardtius hippoglossoides*), in addition to seabirds and marine mammals (Carscadden *et al.*, 2001). Vertical dispersion by capelin may be a useful way of reducing predation risk, particularly when capelin density is high. Rose and Leggett (1989) suggested that water

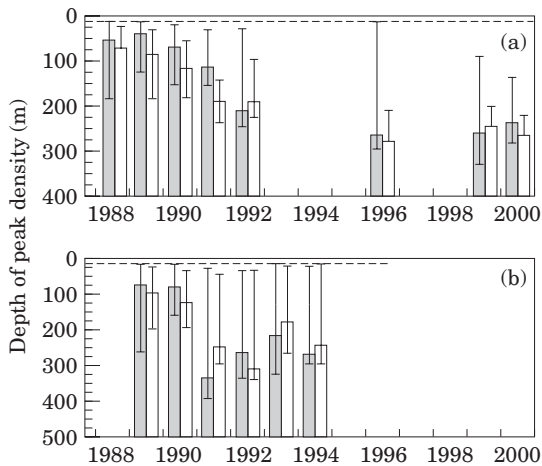


Figure 4. Mean depth of peak capelin density during dark (shaded bars) and daylight (clear bars) of (a) spring 3L and (b) autumn 2J3K surveys, 1988–2000. Vertical lines indicate RANGE of capelin during each photoperiod. The dashed line indicates minimum detection depth.

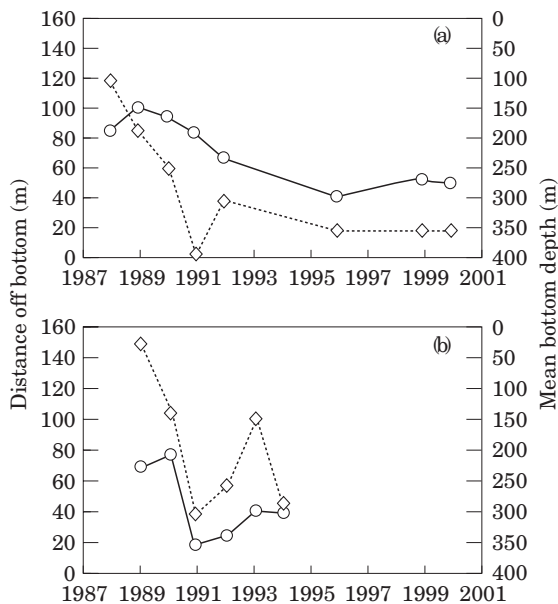


Figure 5. Distance of peak capelin density from bottom (diamonds) and mean bottom depth of occupied areas (circles) during (a) spring and (b) autumn acoustic surveys, 1988–2000.

temperatures less than  $-0.5^{\circ}\text{C}$  and greater than  $8.5^{\circ}\text{C}$  can form refuges from cod predation, so capelin in the 1980s might have been dispersing into the CIL in order to reduce cod predation. This could explain why capelin are deeper in the water column now, and closer to the seabed than in the past. However, it is an unlikely explanation for changes in diel vertical migration pattern because the height of these migrations in the past far exceeded that required to escape cod. Also, the study

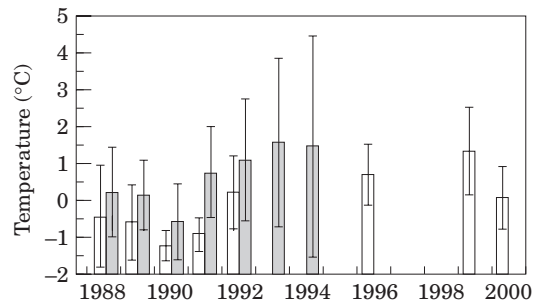


Figure 6. Mean water temperature at which capelin were caught in fishing sets during spring 3L (clear) and autumn 2J3K (shaded) acoustic surveys, 1988–2000. Vertical lines give standard deviation.

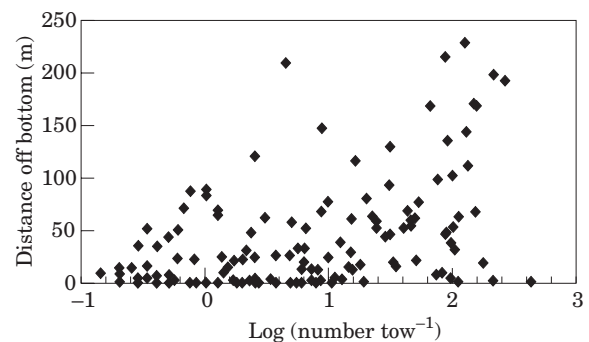


Figure 7. Log of the mean number of cod per tow during spring 3L bottom-trawl surveys, and the distance off-bottom of peak capelin density during spring 3L acoustic surveys, 1988–2000.

failed to find correlations between cod density and capelin POB in autumn, even though cod were present and feeding on capelin in both seasons.

Given that cod density in the 1990s was as much as an order of magnitude lower than during the 1980s (Anon., 2001a), and that the numbers of harp seals (*Phoca groenlandica*) have increased, it might be argued that capelin are distributing themselves deeper to avoid predation from above. This, however, is unlikely; harp seals can dive to depths in excess of 500 m (G. Stenson, unpublished data), so capelin in the 1990s would still be accessible to seals. Also, capelin have exhibited changes in vertical distribution in autumn as well as spring, but harp seals are not present offshore in 2J3KL during the autumn survey period (Stenson and Sjare, 1997).

Condition and size of capelin in the 1990s was poor despite circumstances that should have permitted the fish to occupy optimal feeding habitat. At the same time, capelin vertical distribution changed, fish being virtually absent from surface waters and distributed deeper in the water column. Taken together, these findings seem to suggest a major shift in prey availability and feeding. Our knowledge of zooplankton composition and abundance in the study area is unfortunately very limited.

The only long-term zooplankton abundance data come from Continuous Plankton Recorder (CPR) readings (1959–1986, 1991–1998) and are not available for the late 1980s. Nonetheless, the CPR does suggest that the abundance of zooplankton (copepods and euphausiids) in the 1990s was less than that of the previous period, whereas phytoplankton densities were greater (Sameoto, 2000).

Preliminary results from the analysis of stomachs collected during spring surveys in 1999 and 2000 indicated that, although most food items consumed by capelin were similar to those taken in the 1980s, one item (euphausiids) was considerably less frequent (Kovalyov and Kudrin, 1973; Gerasimova, 1994). The most prominent euphausiid in the diet of mature capelin off Newfoundland (*Thysanoessa raschii*) undertakes diel vertical migrations and is usually found in relatively shallow water (<150 m; Berkes, 1976). If euphausiids are no longer available, it might explain capelin moving into deeper water and altering their vertical migration pattern. The primary prey species of capelin, *Calanus finmarchicus*, overwinters in water >200 m deep, but in spring it ascends and reproduces near the surface (Gerasimova, 1994). The timing of this ascent depends on the warming of surface water temperatures. Hence, in cooler years, the timing and the intensity of feeding on this copepod by capelin may be delayed, leading to changes in capelin vertical distribution (Gerasimova, 1994).

Understanding vertical distribution and how it reflects ecosystem change is important. For instance, in the face of uncertain stock status (Anon., 2001b), smaller sizes and poorer condition of capelin in the 1990s have been used to make a case for density-dependence and a strong stock (Carscadden *et al.*, 2001). However, the same observations, coupled with changes in vertical and horizontal distribution and sexual maturation at smaller sizes (Carscadden *et al.*, 1997), suggest that the stock may be stressed. Changes in vertical distribution are an immediate response to a condition(s) that may take longer to be recognized in time-series of abundance or biological characteristics. Accordingly such shifts may provide warning of things to come. However, until a good comprehensive model of vertical habitat selection is available, interpretation of such changes will be difficult.

## Acknowledgements

Without the many years of meticulous data collection and analysis performed by past and present colleagues, this paper would not have been possible. Accordingly, I acknowledge with thanks the excellent work of Dan Miller, the NAWFC hydroacoustics support group, our pelagic research technicians, and the captains and crews of the two research vessels. I am also indebted for the

many thoughtful suggestions and comments on the manuscript provided by J. E. Carscadden, B. S. Nakashima, C. Lang, J. Wheeler, G. K. Davoren, and J. T. Anderson.

## References

- Anon. 2001a. Northern (2J+3KL) cod. Canadian Stock Assessment Secretariat Science Stock Status Report, A2-01. 16 pp.
- Anon. 2001b. Capelin in sub-area 2+Div. 3KL – Update. Canadian Stock Assessment Secretariat Science Stock Status Report, B2-02. 5 pp.
- Bailey, R. F. J., Able, K. W., and Leggett, W. C. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St Lawrence Estuary and western Gulf of St Lawrence. *Journal of the Fisheries Research Board of Canada*, 34: 2030–2040.
- Berkes, F. 1976. Ecology of euphausiids in the Gulf of St Lawrence. *Journal of the Fisheries Research Board of Canada*, 33: 1894–1905.
- Carscadden, J. E., and Frank, K. T. 2002. Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. *ICES Journal of Marine Science*, 59: 950–958.
- Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2001. Ecosystem changes and effects on capelin (*Mallotus villosus*), a major forage species. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 73–85.
- Carscadden, J., and Nakashima, B. S. 1997. Abundance and changes in distribution, biology, and behaviour of capelin in response to cooler waters of the 1990s. *In* Forage Fishes in Marine Ecosystems, pp. 457–468. Lowell Wakefield Fisheries Symposium Series, 14.
- Carscadden, J., Nakashima, B., and Miller, D. S. 1994. An evaluation of trends in abundance of capelin (*Mallotus villosus*) from acoustics, aerial surveys and catch rates in NAFO Division 3L, 1982–89. *Journal of Northwest Atlantic Fisheries Science*, 17: 45–57.
- Colbourne, E. 2001. Physical oceanographic conditions on the Newfoundland and Labrador shelves during 2000. Canadian Stock Assessment Secretariat Atlantic Fisheries Research Document, 2001/018b. 58 pp.
- Dragesund, O., and Monstad, T. 1973. Observations on capelin, *Mallotus villosus*, in Newfoundland waters. International Commission for the Northwest Atlantic Fisheries Organisation Research Document, 73/33. 14 pp.
- Frank, K. T., Carscadden, J. E., and Simon, J. E. 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.
- Gerasimova, O. V. 1994. Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987–90. *Journal of Northwest Atlantic Fisheries Science*, 17: 59–67.
- Gjosæter, H. 1999. Studies on the Barents Sea capelin (*Mallotus villosus* Müller). Ph.D. thesis, Institute of Fisheries and Marine Biology, University of Bergen, Norway. 160 pp.
- Kovalyov, S. M., and Kudrin, B. D. 1973. Soviet investigations on capelin in the Northwest Atlantic in 1972. International Commission for the Northwest Atlantic Fisheries Research Document, 73/26. 5 pp.
- Maravelias, C. D. 1999. Habitat selection and clustering of a pelagic fish: effect of topography and bathymetry on species

- dynamics. Canadian Journal of Fisheries and Aquatic Sciences, 56: 437–450.
- Miller, D. S. 1985. The use of hydroacoustic surveys to estimate capelin biomass in NAFO Divisions 2J+3KLNO. Northwest Atlantic Fisheries Organisation Science Council Research Document, 85/105. 18 pp.
- Mowbray, F. 2000. Distribution and biological characteristics of capelin in northeastern Newfoundland waters during May 1999. In Capelin in SA2+Div. 3KL, pp. 53–74. Canadian Stock Assessment Secretariat Research Document, 2000/71.
- Nakashima, B. S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). Northwest Atlantic Fisheries Organisation Science Council Studies, 24: 55–68.
- Nakashima, B. S. 1997. The inshore fishery for capelin (*Mallotus villosus*) in NAFO Div. 3KL in 1996. In Capelin in SA2+Div. 3KL, pp. 42–62. Canadian Stock Assessment Secretariat Research Document, 97/29. 188 pp.
- O'Driscoll, R., and Rose, G. A. 1999. Seasonal changes in abundance, distribution, and vertical migration of capelin in Placentia Bay. In Capelin in SA2+Div. 3KL, pp. 182–195. Canadian Stock Assessment Secretariat Research Document, 99/206. 195 pp.
- Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and northeast Newfoundland shelves, 1978–1986. Northwest Atlantic Fisheries Organisation Science Council Studies, 12: 57–69.
- Raymond, J. A., and Hassel, A. 2000. Some characteristics of freezing avoidance in two osmerids, rainbow smelts and capelin. Journal of Fish Biology, 57(Supplement A): 1–7.
- Rose, G. A., and Leggett, W. C. 1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distribution of a marine predator, Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 46: 1904–1913.
- Sameoto, D. 2000. Decadal plankton changes on the eastern Nova Scotian shelf and western North Atlantic. ICES CM 2000/M: 18, 19 pp.
- Shackell, N. L., Carscadden, J. E., and Miller, D. S. 1994. Diel vertical migration of capelin (*Mallotus villosus*) and its effect on acoustic estimates of density. In Capelin in SA2+Div. 3KL, pp. 109–126. Canadian Stock Assessment Secretariat Research Document, 94/18.
- Stenson, G. B., and Sjare, B. 1997. Seasonal distribution of harp seals, *Phoca groenlandica*, in the Northwest Atlantic. ICES CM 1997/CC: 10, 23 pp.
- Stevens, C. R. 1986. A hydroacoustic data acquisition system (HYDAS) for the collection of acoustic data from fish stocks. Canadian Technical Report of Fisheries and Aquatic Sciences, 1520. 73 pp.
- Warren, W. G. 1997. Report on the comparative fishing trial between the “Gadus Atlantica” and “Teleost”. Northwest Atlantic Fisheries Organisation Science Council Studies, 29: 81–92.
- Vilhjálmsón, H. 1994. The Icelandic capelin. Journal of the Marine Research Institute of Reykjavik, 13: 281 pp.