Juvenile capelin (*Mallotus villosus*) off Newfoundland and Labrador in the 1990s

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Juvenile capelin, *Mallotus villosus* (Müller), were distributed primarily on the northern Grand Banks and secondarily along the northeast coast of Newfoundland during late summer, 1994–1999. In some years, distributions extended to coastal Labrador. Capelin were seldom observed over deep water of the northeast Newfoundland Shelf or in shallow water of the southern Grand Banks. There were large areas encompassing wide ranges of capelin densities measured by the IYGPT trawl where the acoustic system did not detect capelin. Mean growth rate of capelin from 0- to 2-group was represented by length (mm)=90.9 age (years)$^{0.57}$ (r^2=99%). The 1-group capelin formed discrete schools that varied significantly in fish length from 65 to 110 mm (p<0.05). Spatially, the different size groups occurred at scales of <55 km and possibly <3 km in some cases. The geographic distribution of age groups was not a simple function of cohort abundance. Capelin were distributed primarily in the middle ranges of temperature (5–8°C) and zooplankton biomass (2–4 g dry weight m^{-2}) sampled during the surveys. It is possible that interspecific competition limits the distributions of juvenile capelin, where juvenile Arctic cod (*Boreogadus saida*) and sandlance (*Ammodytes* sp.) were abundant to the north and south respectively.

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Introduction

Capelin, *Mallotus villosus* (Müller), have been managed as a single stock complex within NAFO Divisions 2J3KLNO (Carscadden *et al.*, 1997). Spawning is traditionally in June on the coastal beaches of southern Labrador and along the northeast coast of Newfoundland, as well as offshore on the southern Grand Bank (Carscadden *et al.*, 1989; Frank and Carscadden, 1989). Autumn acoustic surveys during the 1980s sampled juvenile capelin that were distributed broadly offshore (Miller and Lilly, 1991). In the 1990s capelin underwent dramatic changes in distribution, size and maturity at age, and time and duration of spawning (Frank *et al.*, 1996; Carscadden and Nakashima, 1997; Carscadden *et al.*, 1997). Together, the changes repre-

sent biological responses to a colder, less favourable environment. In autumn 1990, the offshore abundance of capelin, sampled acoustically, declined significantly, whereas inshore abundance indices and offshore bottom-trawl indices remained relatively high (Anon., 2001).

The physical environment cooled throughout the 1980s, reaching a historical minimum in 1991 (Colbourne, 2000). Since then the environment has been warming, returning to near-normal conditions by the mid-1990s, 1996 being one of the warmest years on record. Historically, there were no large-scale measures of zooplankton abundance in the waters off Newfoundland and Labrador.

The significant differences observed in capelin during the early 1990s challenge basic understanding of their
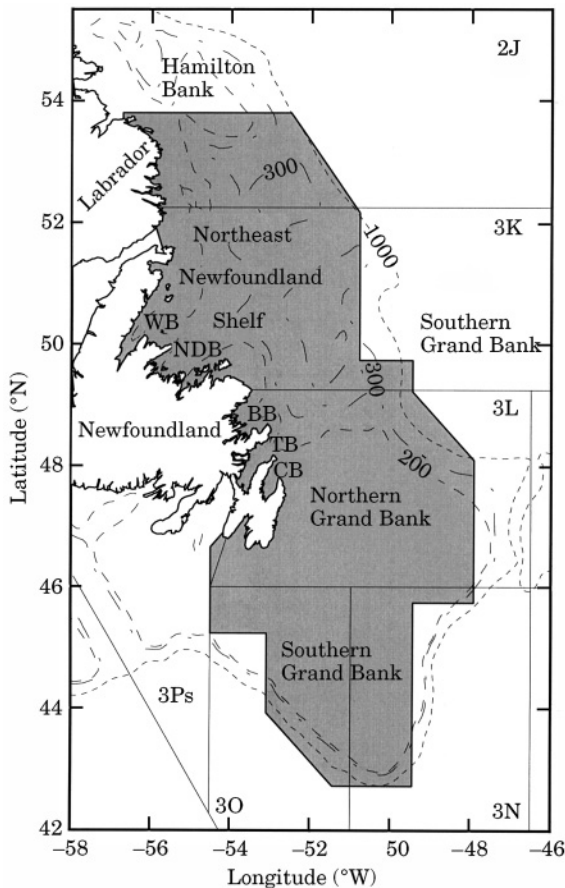
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Figure 1. Area surveyed (shaded) during annual pelagic juvenile fish surveys, 1994–1999. The inshore area of the northeast Newfoundland coast includes: WB – White Bay; NDB – Notre Dame Bay; BB – Bonavista Bay; TB – Trinity Bay; CB – Conception Bay. The dashed lines are depth contours of 200, 300, and 1000 m, and the fisheries statistical areas are shown.

Table 1. Summary of sampling dates and number of samples collected during the pelagic juvenile fish surveys, 1994–1999. IYGPT refers to the International Young Gadoids Pelagic Trawl.

Year	Dates	Middle day of year	Bongo	IYGPT
1994	22 Aug.–3 Sep.	241	99	99
1995	5–22 Sep.	257	139	139
1996	19 Aug.–6 Sep.	241	147	147
1997	11–29 Aug.	233	148	148
1998	24 Aug.–10 Sep.	244	132	132
1999	23 Aug.–19 Sep.	248	129	127

of population distribution and biology of the species during the important summer feeding period.

The purpose of this paper is to describe the summer distributions of 1- and 2-group capelin off Newfoundland and Labrador for the first time. Both midwater trawl and acoustic methods are used to describe these distributions, and results from the different measuring techniques are compared. We relate the geographic distribution of juvenile capelin to their physical and biological environment and discuss limiting factors. Such basic information is essential to building a comprehensive conceptual model of capelin life history, which in turn can contribute towards assessing the status of the population in this region.

Material and methods

Pelagic juvenile fish surveys were carried out on two ships in August and September of the years 1994–1999 (Table 1). The survey design was based on a systematic survey grid at 55 km (30 nautical miles) station spacing. At each station a CTD probe was profiled ≤500 m, measuring water temperature, salinity, and density. This was followed by a double oblique bongo tow to 100 m, and finally by a 30 min IYGPT (International Young Gadoids Pelagic Trawl) tow that sampled the 20–60 m depth stratum. For a full description of the survey design, refer to Anderson and Dalley (1997). The IYGPT trawl was towed at 1.25–1.5 m s^{-1} for 30 min, slowly fishing the headrope between 20 and 50 m deep through two complete cycles. Trawl depth and configuration were monitored using acoustic net sensors (SCANMAR). Capelin were sorted and measured at sea. When catches were large, the entire catch of capelin was weighed and then a random sample of 200 capelin was selected. The division of samples from the IYGPT into 1-year-old (1-group) and two-years-and-older (2-group) capelin was based on examination of the length frequency distributions from the IYGPT samples and age determination of samples from 1994 and 1995 (Anderson and Dalley, 1996). Ageing, based on otolith examination, demonstrated that capelin <50 mm long

biology and behaviour. This, in turn, has compromised our ability to assess the status of capelin on the basis of traditional sampling methods. In 1994, a new pelagic trawl survey was implemented to measure the distribution and abundance of plankton and nekton off Newfoundland and Labrador (Anderson et al., 1999). This survey was carried out in late summer, sampling from southern Labrador to the southern Grand Banks and including inshore bays along the northeast coast of Newfoundland (Figure 1). The survey was designed, in part, to measure the distribution and abundance of juvenile capelin during their primary feeding and growth period. Hydroacoustic sampling was added to the survey design, beginning in 1998, to measure abundance and distributions below the trawl zone as well as between trawl locations. Although the ultimate goal was to census year-class strength of 1- and 2-year-old capelin, a more fundamental goal was to understand the extent

were young of the year (0-group). Typically, there was an overlap in 1- and 2-year-old capelin within the length range 110–130 mm, half or more capelin <115 mm being 1 year old and half or more capelin >120 mm being aged 2 years. Based on these observations, 1-year-old capelin were classified as 55–120 mm and two-years-and-older capelin as >120 mm. Experience has demonstrated that strong and weak year-classes can be tracked through these size ranges.

Plankton were sampled using 0.61 m diameter bongos fitted with large (0.505 mm) and small (0.333 or 0.232 mm) Nitex mesh nets each year. The bongos were towed obliquely bewteen 0 and 100 m, depending on bottom depth, at a tow speed of 1.25–1.5 m s^{-1} and with winch payout and retrieval rates of approximately 0.8 and 0.3 m s^{-1} respectively (Smith and Richardson, 1977). The bongo sampler was instrumented with an electronic monitoring and sampling system (Applied Microsystems) that measured digital flow in each net as well as temperature, salinity, and depth during the entire tow. Samples were preserved at sea in 5% buffered formalin and returned to the laboratory for processing. Zooplankton from the small-mesh sample were split into halves using a Motoda plankton splitter. One half subsample was divided into three size-classes using a series of sieves (<1, 1–2, >2 mm), and then dried for 24 h at 55°C and subsequently weighed to the nearest milligramme.

Acoustic data were collected during surveys in 1998 and 1999 using a 38 kHz SIMRAD EK500 split-beam echosounder calibrated with a tungsten carbide standard target. In 1998, data were collected and integrated using the EK500 echo-integrator. In 1999, raw acoustic data were saved and subsequently analysed using a recently developed standard format (Simard *et al.*, 1997). Signals from capelin were distinguished on the basis of signal characteristics and information from IYGPT trawl sets, including one targeted tow on deep capelin. Acoustic data were integrated in 100 m bins along-track and scaled by target strength (TS) to give estimates of area density (capelin m^{-2}) in each 100 m bin. Mean target strengths were calculated from fishing-set length frequency data using the relationship TS = 20logL − 73.1 (Rose, 1998), where L is total length (cm). Area density estimates were grouped into larger bins corresponding to 0.05 degrees of latitude and 0.05 degrees of longitude, approximately equivalent to 5.6 × 3.7 km at 49°N.

Results

The distributions of 1-group capelin were centred offshore on the northern Grand Banks each year, as well as inshore along the northeast coast of Newfoundland (Figure 2). In four years these distributions extended to the coastal region of southern Labrador, but only in

1999 were capelin broadly distributed over the northeastern Newfoundland Shelf. When distributions extended to the southern Grand Banks in 1994 and 1999, capelin were found at the eastern boundary of the surveys, indicating their presence along the shelf break within the cold waters of the Labrador Current. The distribution of 2-group capelin was similar to that of 1-group fish, with greatest concentration on the northern Grand Banks (Figure 3). The inshore distribution of 2-group fish was more variable than those for 1-group capelin.

The 1993 and 1996 year-classes were strong, but that of 1994 was weak (Anon., 2001). However, there was no apparent simple relationship between abundance and distribution of juvenile capelin. The 1993 year-class was more broadly distributed as 1-group in 1994, but the 1996 year-class in the 1997 survey was not (Figure 2). As 2-group, only the 1996 year-class was broadly distributed (Figure 3). The 1994 year-class distribution was constrained as both 1- and 2-group. Overall, however, the centres of distribution of year-classes remained largely over the northern Grand Banks, whether strong or weak. This suggests that abundance was not the primary factor controlling distributions and implies that environmental conditions were more important.

Acoustic sampling allowed us to examine capelin distributions between trawl locations, as well as capelin that may have been below the pelagic trawl zone. Comparison of the acoustic data in 1998 and 1999 with the trawl catches demonstrated that the broad-scale distributions of juvenile capelin were similar (Figure 4). There were occasions where the acoustic system detected capelin that were not reflected in the trawl catches. However, these occasions appeared to result from small-scale distribution of capelin at scales <55 km. Inclusion of these acoustic observations would not significantly alter the distributional maps based on the trawl data. Alternately, there were a number of occasions where capelin occurred over relatively large areas in the trawl data, but their densities did not exceed thresholds for acoustic detection and recognition. This happened, for example, throughout Notre Dame Bay, Bonavista Bay, and Trinity Bay in both years (Figure 4), and also offshore, even when the trawl catches of capelin were relatively large and over extensive areas of the Grand Banks, particularly in 1998. The difference between trawl and acoustic data was less in 1999, perhaps a result of the lower acoustic thresholds and the higher precision of data collection and analysis used that year. However, the distribution of capelin based on acoustic data alone would result in incomplete distributions that would underestimate abundance.

Capelin captured by the IYGPT trawl ranged in length from 13 to 196 mm (Figure 5). The 0-group capelin (<55 mm) were most abundant in 1995 and 1999, with fewer captured in 1997 and virtually none in
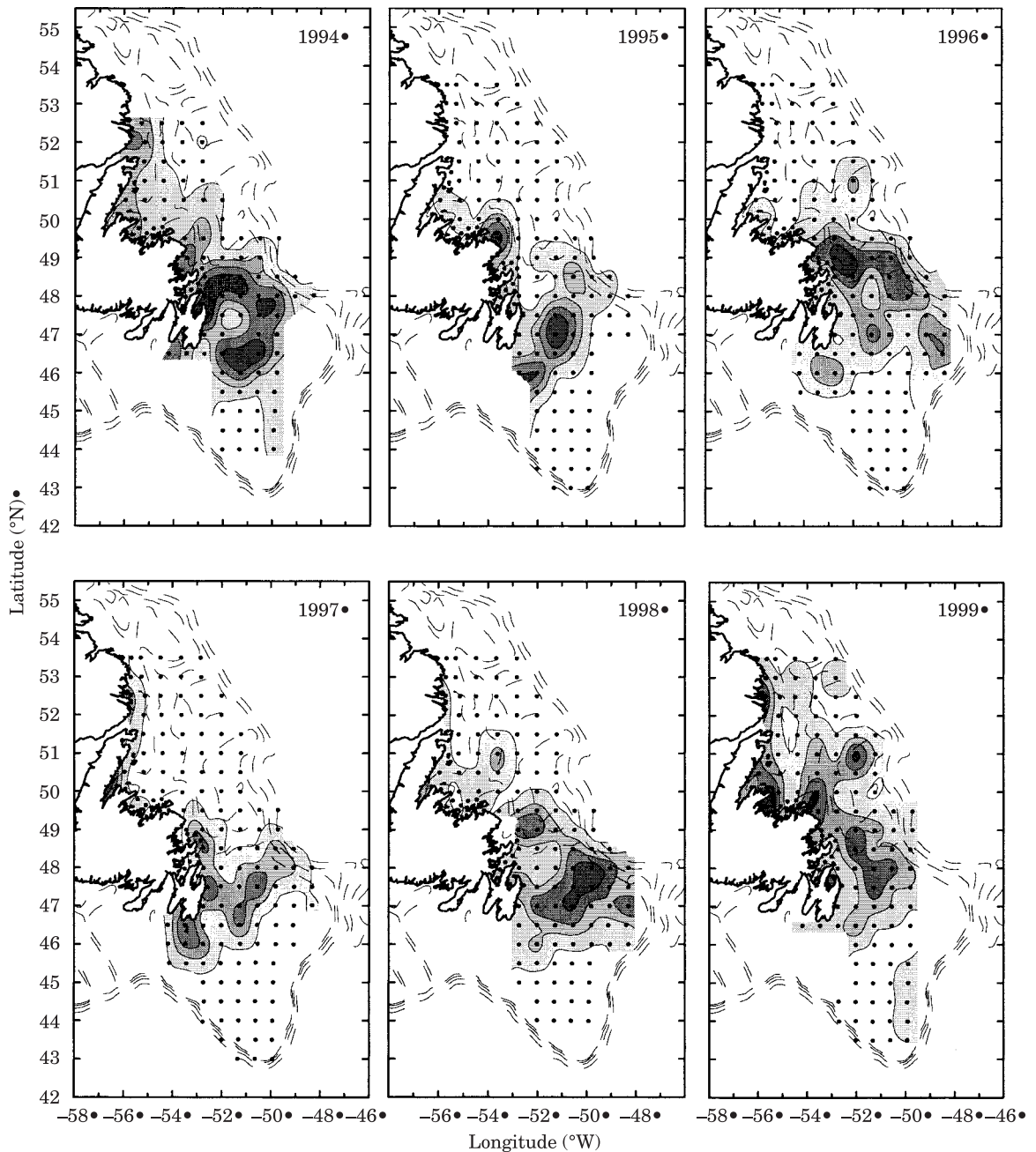
Figure 2. Distributions of 1-year-old capelin caught by the IYGPT midwater trawl ($\log_{10}$ number 10^4 m^{-3}) during surveys, 1994–1999. Abundances are displayed as four contoured intervals scaled for each survey year, where the contour intervals are even units of the $\log_{10}$ abundance values. The dots are trawl locations and blank areas represent areas where no capelin were caught. The dashed lines are the depth contours 200, 300, 500, and 1000 m.

the other two years. Mean length of 0-group capelin ranged from 28.7 mm to 37.3 mm during these three years. Capelin that were predominantly 2 years of age occurred as distinct length modes in 1996, 1997, and 1998 between approximately 120 and 160 mm length. In 1999, there was a small but distinct length mode from 140 to 180 mm; these were mainly 3-year-old capelin from the 1996 year-class. Mean lengths of capelin larvae sampled in the bongos ranged from 7.6 to 13.2 mm (Anderson *et al.*, 2001). Comparison of mean lengths-at-age demonstrated a declining growth rate with age (Figure 6). Length differences of 0-group (post-larvae)
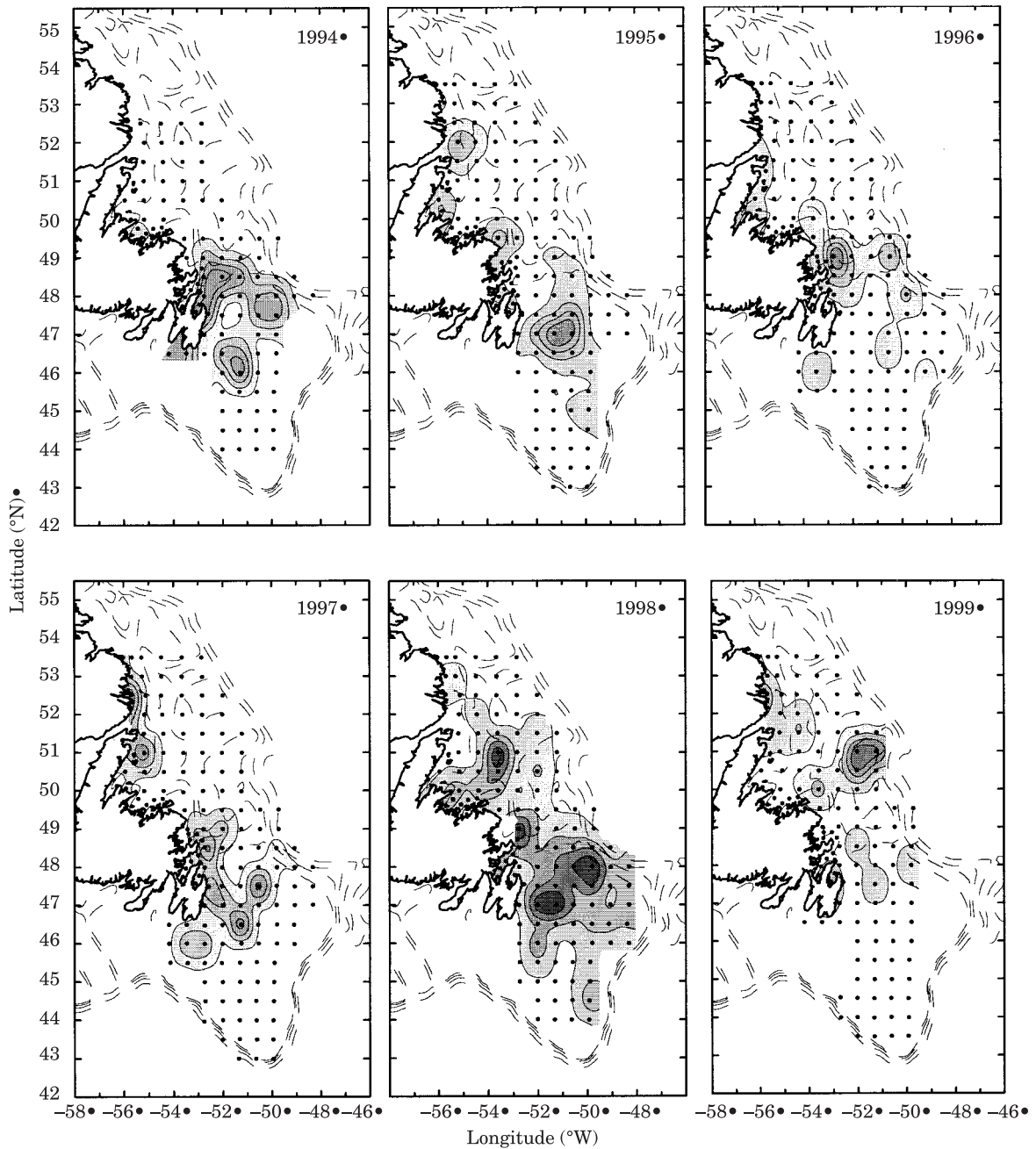
Figure 3. Distributions of primarily 2-year-old capelin caught by the IYGPT midwater trawl ($\log_{10}$ number 10^4 m^{-3}) during surveys, 1994–1999. Abundances are displayed as four contoured intervals scaled for each survey year. The dots are trawl locations and blank areas represent areas where no capelin were caught.

sampled by the IYGPT were age-offset, based on a growth rate of 0.35 mm d^{-1} (Frank and Carscadden, 1989) and larval release size of 5 mm. Lengths at ages one and two were 12 and 24 months later. Mean growth rate based on these data was described by the equation length=90.9 age$^{0.57}$, where length is in mm and age is in years (F=2032, p<0.0001, r^2=99.2%). The greatest

variability in mean size-at-age was for 1-group capelin, mean lengths ranging from 83 to 103 mm and capelin being typically abundant from 60 to 120 mm (Figure 5).

Examination of the 1-group length data demonstrated that individual trawl catches were primarily unimodal around relatively small length ranges. We extracted
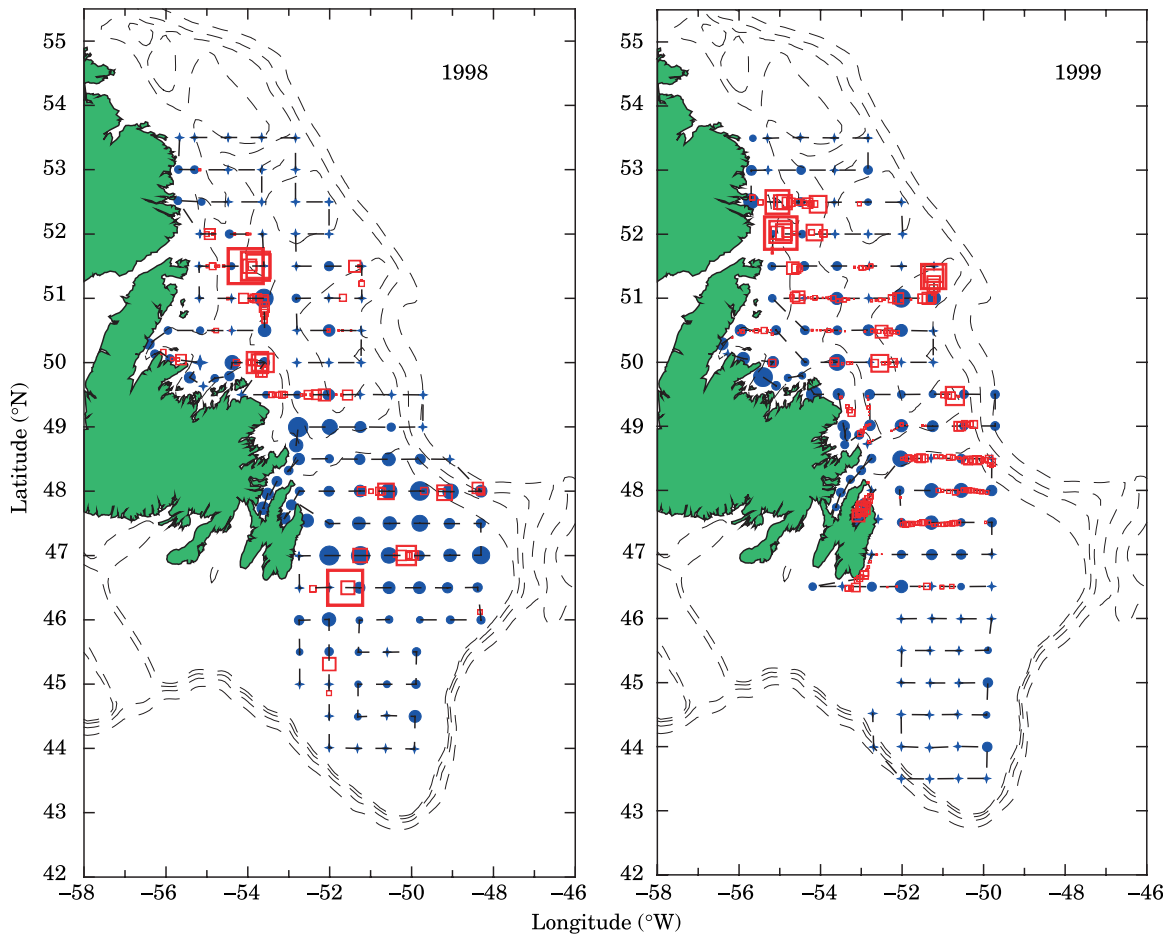
Figure 4. Distributions of capelin detected acoustically (open squares, square root of the number m^{-2}) and capelin caught by the IYGPT midwater trawl (filled circles, $\log_{10}$ number 10^4 m^{-3}) in the 1998 and 1999 surveys. Heavy dashed lines represent the ship survey tracks and the small crosses reflect no trawl catches.

unimodal length data from the trawl database, where 25 or more capelin were measured and length CV was ≤13%. The data demonstrated substantial differences in length of 1-group capelin among years (Figure 7). In four years, the ranked distribution of lengths approximated a sigmoid curve, whereas in 1997 and 1999, the distribution of lengths approached linear (Figure 7). The number of statistically different length-classes (p<0.05) ranged from two in 1998 to nine in 1996 and 1997.

Comparison of the unimodal length data among years (Table 2) demonstrated significant variation in both range and magnitude of lengths. For example, no large capelin were caught in 1994 and no small capelin were caught in 1995 and 1998. In other years, mean lengths in trawl catches ranged widely, from 65 to 117 mm. The difference within-year among mean lengths was as great as 41–45 mm, but in 1998 the difference was only 14 mm. In addition, while the biggest length-classes might represent 2-year-old capelin in some instances, there were no apparent

increases in length that would indicate a clear separation between year-classes. These ranked length distributions indicate that length-at-age was essentially continuous across annual age-classes.

The annual differences in mean lengths of 1-group capelin in single tows suggests that there was small-scale variation for groups (schools) of capelin that had experienced different growth histories. There were no apparent spatial patterns to the length-class distributions, both small and large capelin typically being found spatially in close association. Therefore, spatial scales were often <55 km for different size groups of 1-group capelin. Examination of the remaining catch data where the CV was >13% demonstrated both bi- and multimodal length distributions of 1-year-old capelin. The catches indicate that either different length groups of capelin co-occurred, or that their spatial scale of distribution was less than within a single 30-min tow (<3 km). The number of bi- and multimodal catches each year was low, ranging from none in 1995 to six in 1994.
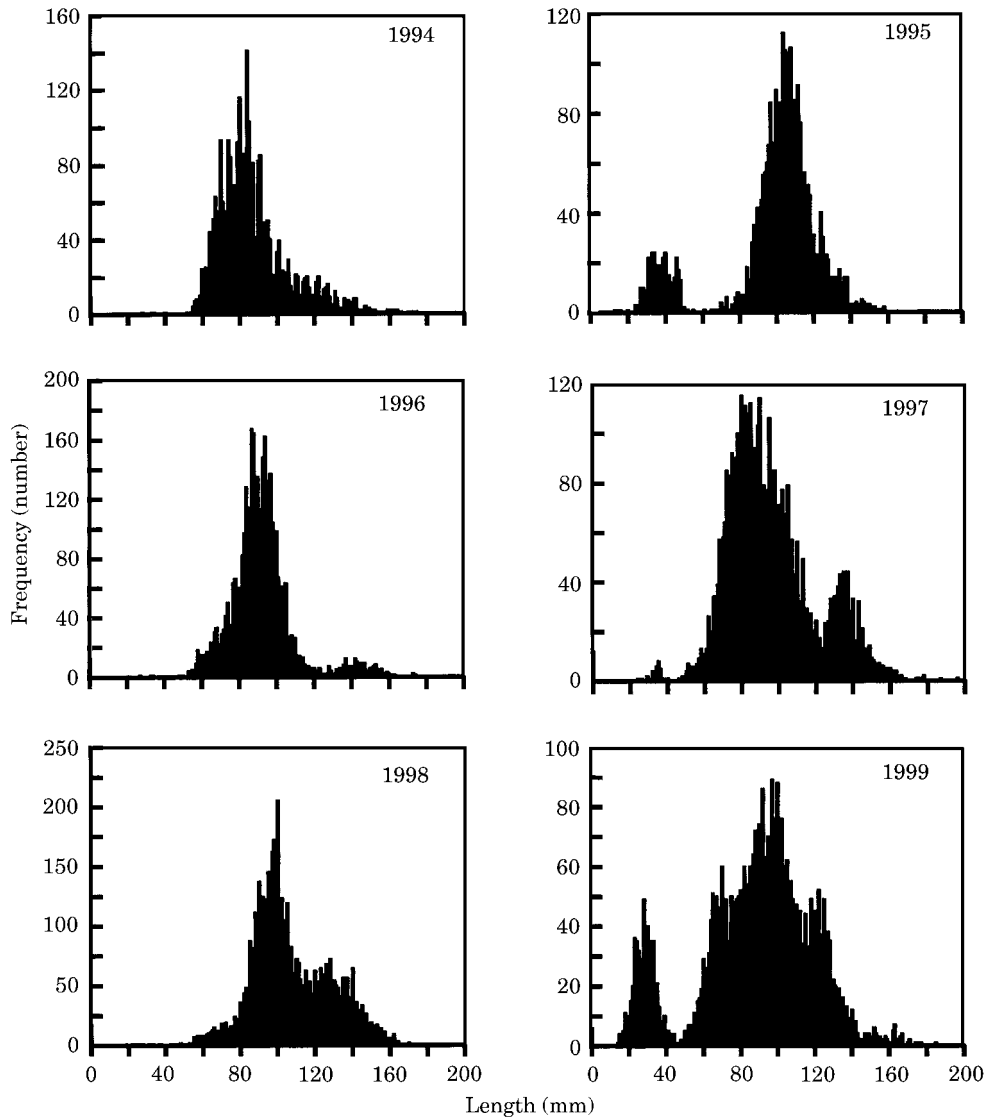
Figure 5. Length-frequency distributions of capelin measured from the IYGPT midwater trawl samples during surveys, 1994–1999. Note the differing vertical scales.

Table 2. Summary of capelin 1-group unimodal length distributions, 1994–1999. The column Length-classes refers to the number of statistically different length-classes observed each year ($p < 0.05$), the column Year-class ranking to the relative abundance of 1-year-old capelin sampled each year in the surveys, where 1 was the largest.

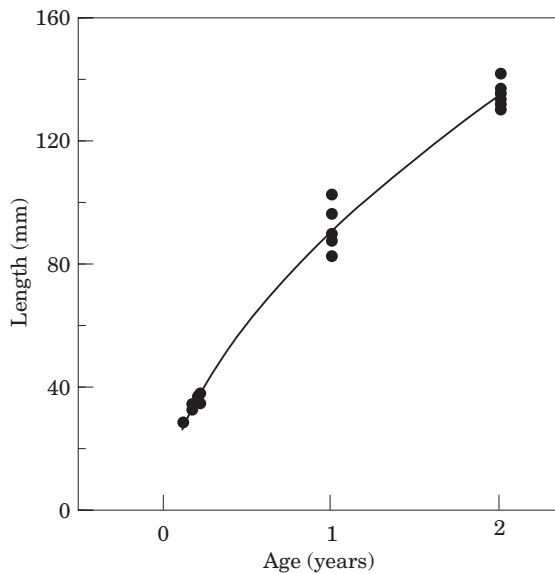| Year	Length-classes	Year-class ranking	Length range (mm)	Length difference (mm)
1994	5	2 (1993 year-class)	69–97	28.0
1995	3	6 (1994 year-class)	90–110	19.6
1996	9	4 (1995 year-class)	64–109	45.4
1997	9	1 (1996 year-class)	68–109	40.9
1998	2	5 (1997 year-class)	87–101	13.8
1999	8	3 (1998 year-class)	65–117	52.5

Figure 6. Mean lengths of capelin captured by the IYGPT midwater trawl for 0-group (<55 mm), 1-group (55–120 mm), and 2-group (120 mm) capelin captured in surveys, 1994–1999. The solid line is a power equation (ln − ln) fit to the data (see Results).

Similarly, there were no geographic patterns in their distributions.

During surveys in late summer the water was stratified around 30 m depth. The average water temperature in the upper 50 m ranged from 3°C in the north to 10°C over the southern Grand Banks (Figure 8). Water temperatures were warmer within the inshore bays along the northeast coast of Newfoundland than over adjacent shelf waters. The biomass of invertebrate zooplankton, primarily copepods, was highest over deep water in the north and lowest on the southern Grand Banks (Figure 8). Mean biomass averaged over six years was 4.1 ($\pm$0.37 95% CI) g dry weight (DW) m^{-2} offshore north of 49°N, 1.2 ($\pm$0.20 95% CI) g DW m^{-2} over the Grand Banks, and 2.9 ($\pm$0.28 95% CI) g DW m^{-2} for the inshore bays. Spatially, juvenile capelin were distributed primarily in the middle ranges of both temperature (5–8°C) and zooplankton (2–4 g DW m^{-2}). For the survey area, there were no statistical correlations between 1- or 2-group capelin and temperature ($p < 0.05$), but there were weak negative relationships with zooplankton biomass ($r = -0.25$, $p = 0.0017$ and $r = -0.24$, $p = 0.0030$ respectively).

Discussion

Comparison of the trawl and acoustic data demonstrates that pelagic trawl catches were representative of capelin distributions over their geographic range. The continuous distributions of juvenile capelin demonstrate a high degree of spatial autocorrelation at scales greater than the trawl locations (55 km). The similar distributions of 1- and 2-group capelin are consistent with their similar requirements for growth and survival. These distributions can also be remarkably stable over many years, weaker year-classes tending towards the central area of distribution. Similar observations have been made off Iceland over 11 years (Vilhjálmsson, 1994) and in the Barents Sea over 18 years (Gjøsæter, 1998).

Capelin were seldom observed acoustically below the trawl zone (>60 m); when they were, the distributions were small and within the geographical distributions sampled by the trawl. In contrast, there were large areas where capelin were not detected nor recognized by the acoustic system. This does not appear to be a simple function of capelin density threshold, because the trawl catches demonstrated significant quantities of capelin within these areas. However, it is possible that we failed to recognize capelin within the echograms. In our surveys, any surface-feeding capelin would have been missed by both trawl and acoustic systems (they did not sample depths <20 and <15 m respectively). Questions concerning the detectability of capelin in the 1990s using acoustic methods have been raised (Miller, 1996). Capelin may be missed acoustically when concentrations are below the detection threshold, when other species interfere with their recognition, when their behaviour changes and they are not recognized, or when they avoid the hull-mounted transducer. We believe that avoidance immediately below the ship may have been the problem, considering the wide range of capelin densities that were missed by the acoustic system but captured by the trawl. Surveys that rely primarily on acoustic detection and enumeration would significantly underestimate the distribution and abundance of capelin (Viljhámsson, 1994), so combining pelagic trawl and acoustic sampling methods would permit the most reliable census of the capelin population.

The distributions we observed in late summer were significantly different from those observed during autumn acoustic surveys in the 1980s. During those acoustic surveys, capelin were observed over shelf waters north of approximately 53°N, where distributions often extended north of 55°N (Miller and Lilly, 1991). In our surveys, concentrations were between 46 and 52°N, with the exception that coastal concentrations in some years extended to southern Labrador. The southward distribution of juvenile capelin in the 1990s is consistent with the significant southward shifts in distributions observed for various fish species during the same period (Frank et al., 1996; Rose et al., 2000). These southward shifts have been linked with extensive ice and cold surface water that attained extremely cold conditions in the early 1990s (Colbourne, 2000). Similarly, summer feeding distributions in the Iceland Sea (Vilhjálmsson, 1994) and the Barents Sea (Gjøsæter, 1998) are adversely
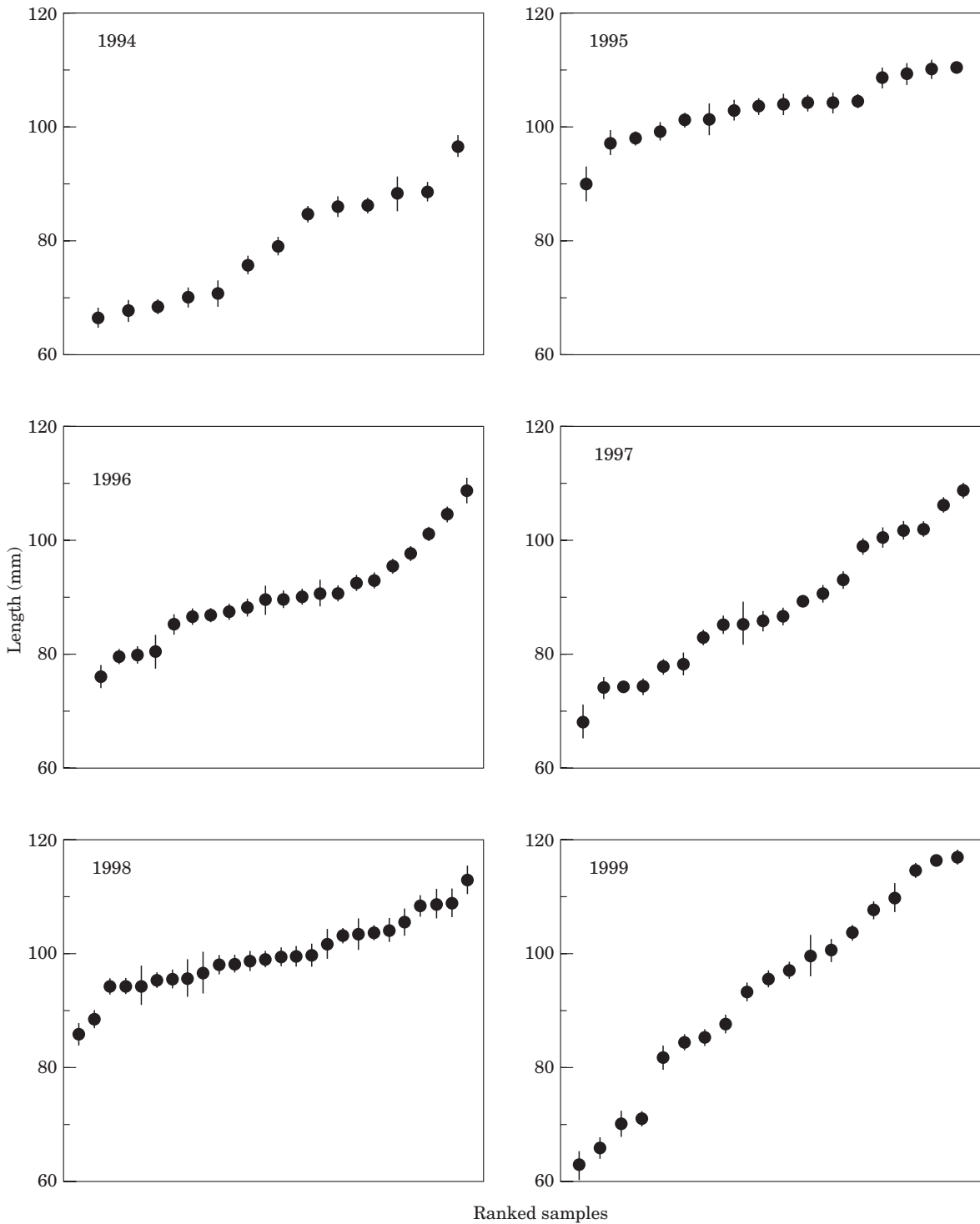
Figure 7. Ranked mean lengths (mm) of 1-group capelin from unimodal IYGPT midwater trawl catches, 1994–1999. The vertical bars are 95% confidence intervals.
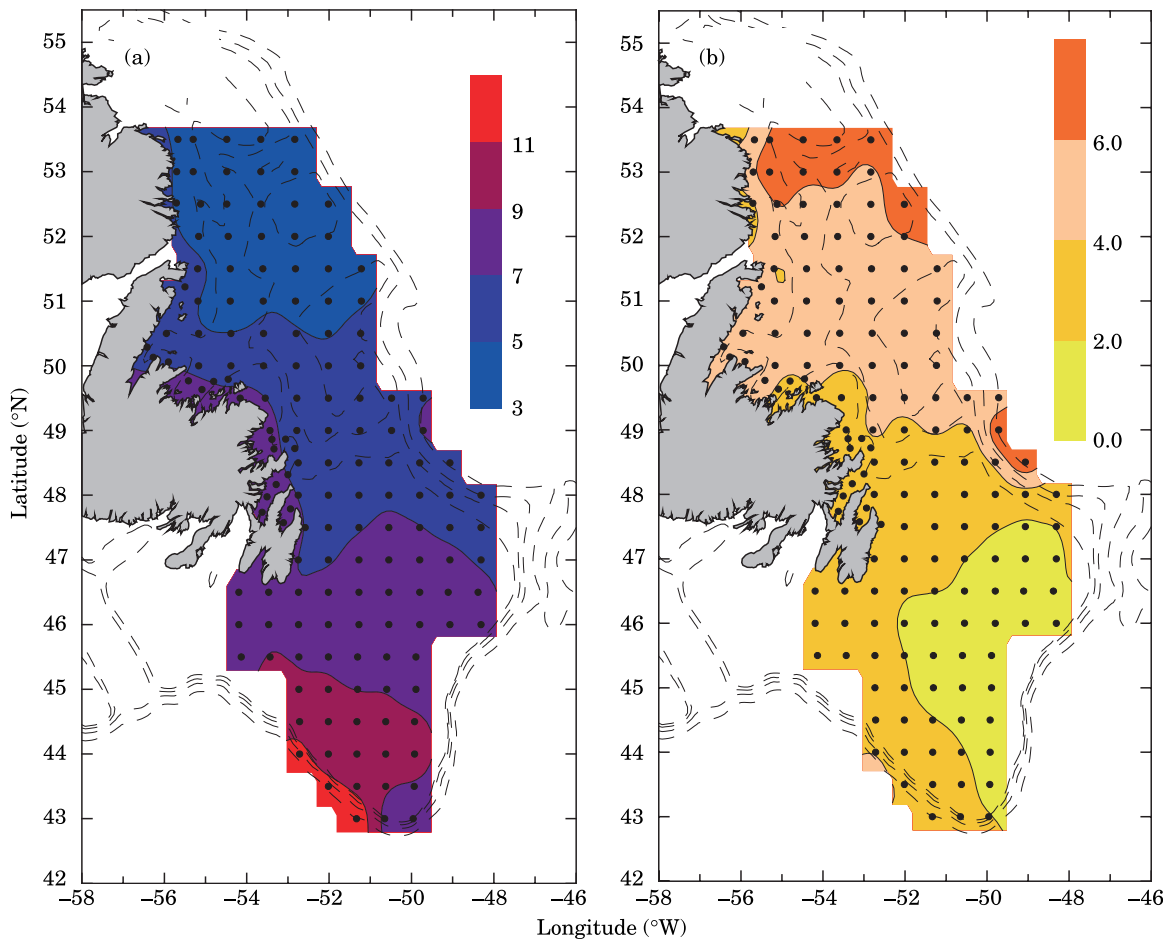
Figure 8. (a) Averaged surface water temperatures (°C) from 0 to 50 m deep, and (b) averaged zooplankton biomass ($\log_{10}$ g DW m^{-2}) at each location for the years 1994–1999.

affected by the intrusion of cold polar water. Capelin avoid cold Arctic water in which the copepod fauna is dominated by *Calanus hyperboreus* and *Metridia longa*. Conditions warmed through the 1990s, 1996 being the third warmest year on record (Colbourne, 2000). However, there appears to be a lag in the distributional response of capelin to improved environmental and feeding conditions. Unfortunately, monitoring future changes in capelin distribution in relation to the local environment will likely be impossible given the recent termination of the juvenile pelagic fish survey.

Juvenile capelin occupied the central section of the survey area, coinciding with the middle ranges of both temperature and zooplankton biomass. There was no simple density-dependent relationship between year-class strength and the distribution of capelin, suggesting that their distributions may have been primarily controlled by environmental factors. Based on the distributions observed, preferred temperatures were primarily 5–7°C and these distributions appeared to coincide with

sufficient planktonic prey to sustain feeding and growth, even though zooplankton biomass was greater to the north. However, in the northern part of the survey area, the nekton were dominated by pelagic juvenile (0-group) Arctic cod (*Boreogadus saida*), whereas over the southern Grand Banks, juvenile sandlance (*Ammodytes* sp.) dominated (Anderson *et al.*, 1999). These spatial associations suggest that interspecific competition may also be important in controlling the spatial distribution of capelin off Newfoundland and Labrador.

The growth rate of immature capelin during the first three years of life fitted a simple power relationship. Capelin sampled in our surveys were smaller as 0-group than capelin sampled in September/October surveys off Iceland, where the mean length of the 0-group was 62 mm with an annual range of 50–71 mm (Appendix II and Table II of Vilhjálmsson, 1994). In addition, we sampled significant concentrations of larvae in the bongos; their length averaged 10.4 mm (Anderson *et al.*, 2001). These sizes reflect the different spawning times.

Off Iceland, capelin spawn primarily in March with peak hatching in April (Vilhjálmsson, 1994); capelin off Newfoundland spawned primarily in July and August during the 1990s (Nakashima and Slaney, 2001). However, one year later there was a smaller difference in mean sizes, 1-group capelin averaging 92 mm in our surveys and 105 mm off Iceland. Expressed as growth, Newfoundland capelin increased in mean length by 164% on the basis of 0-group lengths and by more than 300% if larval lengths are included. This compares with a growth rate of 69% for Icelandic capelin from the 0- to the 1-group stage. The size difference between the populations is further reduced by the 2-group stage, Newfoundland capelin averaging 135 mm and Icelandic capelin 138 mm. Growth rate from 1- to 2-group was 47% off Newfoundland and 31% off Iceland. These comparisons indicate that capelin off Newfoundland were growing faster than those off Iceland during their first three years of life. Growth rate of Barents Sea capelin was also slower, the mean increase in length measured at the start of winter from the 0- to the 1-group being 73% and from the 1- to the 2-group being only 26% (Gjøsæter, 1999).

Within-year length differences of 1-group capelin were significant, ranging as high as 70–80% between small and large groups. To what degree do these lengths represent differences in growth rate rather than age since spawning? During the years 1994–1999 the spawning period averaged 32 days at a beach monitored in Trinity Bay (Nakashima and Slaney, 2001). However, 0-group capelin in our surveys averaged 34.8 mm and larvae 10.4 mm. These sizes would equate to spawning periods of approximately 70 days, assuming a growth rate of 0.35 mm d^{-1} (Frank and Carscadden, 1989). Therefore, it is possible that the large size range of 1-group capelin sampled in our surveys resulted from protracted spawning during the 1990s.

Alternatively, the observed differences in length may have resulted from different growth histories. In Icelandic waters, a small proportion of 1-year-old capelin typically grow faster and mature at age 2 (Vilhjálmsson, 1994). Maturing 1-year-old capelin can be detected as early as August, when they are approximately 18–20 months old (Vilhjálmsson, 1994). The 1-year-old capelin in our surveys were approximately 12–14 months old. We detected significant differences in maturity among years (JTA, unpublished data) that were not simply related to the ranges or magnitudes of the size groups of 1-group capelin. Our belief is that both age and growth differences within year must have contributed to the observed differences in size at age 1.

Acknowledgements

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