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Seasonal abundance and vertical distribution of capelin (*Mallotus villosus*) in relation to water temperature at a coastal site off eastern Newfoundland

David A. Methven and John F. Piatt

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The seasonal abundance and vertical distribution of capelin in relation to water temperature have been investigated by conducting repeated hydroacoustic surveys at a coastal site off eastern Newfoundland. Water temperatures were warmer in 1983 than in 1984 as indicated by the earlier appearance and greater depth of the seasonal thermocline. Correspondingly, schools of capelin appeared earlier, were more abundant, and extended deeper in the water column in 1983 than in 1984. Most capelin were found between the surface and the 5°C isotherm. In both years, initial peaks of capelin abundance occurred when nearshore water temperatures increased from about 0–1°C to above 6°C and, at or near, periods of maximum tidal oscillation. Short-term variations in the depth of the 5°C isotherm were related to nearshore wind-induced upwelling events. Annual variations corresponded to the volume of cold (<0°C) water and sea-ice transported south by the Labrador Current.

David A. Methven: Ocean Sciences Centre, Memorial University of Newfoundland, St John's, Newfoundland, A1C 5S7 Canada. John F. Piatt: Alaska Fish and Wildlife Research Center, US Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, Alaska, 99503 USA.

Introduction

Capelin (*Mallotus villosus*, Müller) is a pelagic fish species that migrates inshore during summer to spawn on beaches along the east coast of Newfoundland (Templeman, 1948). Many predators, including Atlantic cod, *Gadus morhua* (Templeman, 1965; Lilly, 1987; Methven and Piatt, 1989), baleen whales (Piatt *et al.*, 1989), and seabirds (Piatt, 1987) also occur inshore at this time and feed extensively on dense schools of capelin. Capelin are also caught in nearshore purse-seine and trap fisheries (Jangaard, 1974; Nakashima, 1987).

Little is known about factors that influence the vertical distribution of capelin. Bailey *et al.* (1977) and Atkinson and Carscadden (1979) observed most capelin at depths less than 50 m, generally above the cold (0°C) water layer in the Gulf of St Lawrence and off Newfoundland. How the vertical distribution of capelin varies from year to year and whether it is related to changes in water temperature is unknown. Variation in the vertical distribution of capelin may be of considerable importance to predators that exploit capelin at different depths in the water column (Templeman, 1965, 1966; Whitehead, 1981; Piatt and Nettleship, 1985).

In this paper, we describe the vertical distribution and seasonal abundance of capelin in relation to water temperatures, tides, and the depth of the seasonal thermocline at a coastal site off eastern Newfoundland during two successive summers (1983 and 1984). We discuss some factors that influence water temperature and the availability of capelin to predators.

Methods

The abundance and vertical distribution of capelin were recorded on 54 standardized hydroacoustic surveys in Witless Bay, Newfoundland (Fig. 1) from 27 May to 15 August in 1983 (n = 29 surveys) and from 9 May to 30 August in 1984 (n = 25 surveys) using a Kelvin-Hughes acoustic sounder (Mark 2, 48 kHz). Surveys were conducted between 0600 and 1200 h (Newfoundland Standard Time) along a 30-km transect route requiring about 2.0–2.5 h to complete. All surveys began in Bay Bulls and ended at hydrographic station 2 on the west side of Gull Island (Fig. 1). We report results for each entire hydroacoustic survey conducted along the route shown in Figure 1. Additional hydroacoustic surveys conducted in 1982 and 1985 are not included here because of differences in survey methodology and transect route (see Schneider and Piatt, 1986; Piatt *et al.*, 1989).

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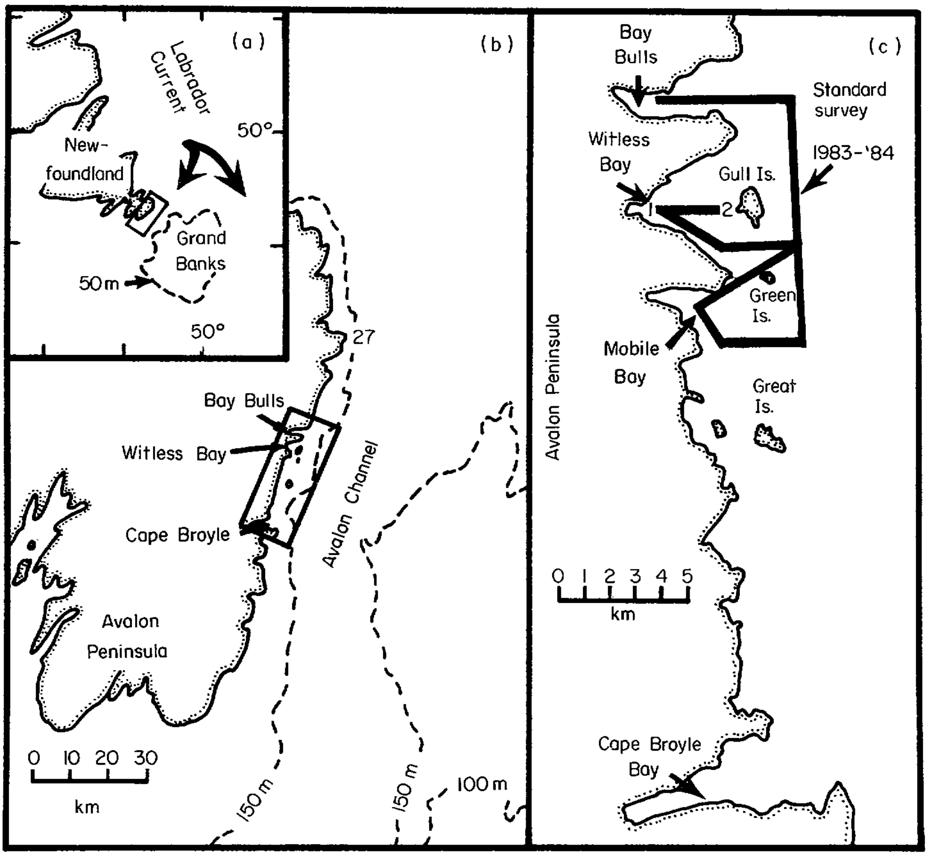

Figure 1. (a) Map of Newfoundland showing the Labrador Current. (b) Location of the study area on the Avalon Peninsula and hydrographic station 27. (c) Hydroacoustic survey route and hydrographic stations 1 and 2 in Witless Bay.

The method used to quantify relative capelin abundance has been reported in detail by Piatt (1987, 1990). Briefly, each hydroacoustic echogram was partitioned into blocks of time (1–2 min intervals) and depth (10 m intervals). The registration intensity of fish schools within each block was graded visually on a scale of 0–9. This grade was squared to make it proportional to fish abundance (Forbes and Nakken, 1972). Mean capelin abundance was calculated for each survey and for each 10 m depth interval within each survey. Mean abundance was calculated by dividing the sum of the squared abundance grades by the total number of blocks (including zeros) in each survey and for each depth interval within a survey, respectively.

The technique of visually grading echograms to obtain estimates of relative fish abundance has been used in a variety of studies (Forbes and Nakken, 1972; Whitehead *et al.*, 1980; Safina and Burger, 1985). However, estimates of abundance at deeper depths are biased when echograms are visually graded due to spreading of the echosounder beam with depth. We believe this is a minor source of error in our study because: (i) the vast majority of capelin were recorded near the surface (<20–30 m), thus reducing the spreading effect of the echosounder beam to a minimum, and (ii) we are more interested in defining the limits of vertical distribution (presence–absence of capelin) in relation to temperature than in determining the absolute abundance by depth interval.

Traces of schooling fish were most dense and abundant in late June and early July – the time of year that capelin typically migrate inshore and spawn along the east coast of Newfoundland (Templeman, 1948, 1966; Campbell and Winters, 1973). We believe that the vast majority of fish traces recorded on survey echograms were capelin because: (i) echogram traces were typical of small pelagic schooling fish (Forbes and Nakken, 1972) and similar to those reported by Atkinson and Carscadden (1979) and Whitehead (1981) for capelin schools off eastern Newfoundland, (ii) no fish other than capelin were caught in small mesh gillnets suspended near the surface in Witless Bay in July 1984, (iii) capelin were the only pelagic fish caught and sampled from nearby capelin traps of the commercial fishery in June and July, 1983 and 1984, (iv) capelin were the overwhelmingly dominant food of cod (Methven and Piatt, 1989) and seabirds (Piatt, 1987) during the summers of 1983 and 1984 at Witless Bay, and (v) other schooling nekton (e.g. herring and squid) either do not appear in the area in any abundance, or appear only after mid-July (Dawe, 1988; Schneider, 1989).

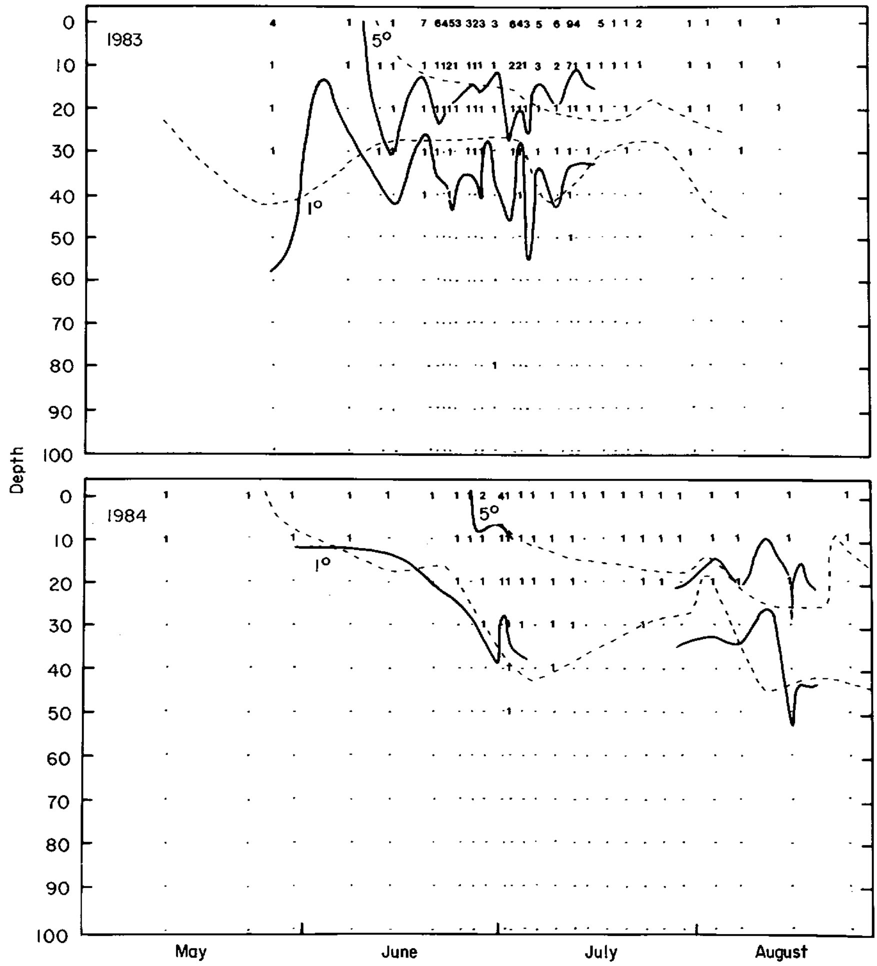

Figure 2. Relative mean abundance of capelin by 10 m depth intervals (scale 0–9) for each entire hydroacoustic survey in relation to water temperature. Solid lines represent the 5°C and 1°C isotherms at hydrographic station 2. Dashed lines represent the 5°C and 1°C isotherms at station 27. Dots indicate no capelin present.

Vertical profiles of water temperature were obtained near the beach of Witless Bay (station 1, maximum depth 5 m; Fig. 1) and west of Gull Island (station 2, maximum depth 65 m; Fig. 1) using an Applied Microsystems conductivity-temperature-depth probe. A continuously recording thermograph moored at 5 m depth near station 1 was also used to record water temperatures in 1984 (Schneider and Methven, 1988). Water temperature was not collected at station 2 after mid-July 1983 and for most of July 1984. Additional hydrographic data were obtained for May–August, 1983–1984, from ocean climate station 27 (47°32′50″N, 52°35′10″W); located about 35 km northeast of Witless Bay (Fig. 1) in 173 m of water (Akenhead, 1983).

Tide information was extracted from Canadian Tide and Current Tables published annually by the Government of Canada, Fisheries and Oceans, Scientific Information and Publications Branch, Ottawa, for the reference port of St John's, about 40 km north of Witless Bay.

Results

The 5°C isotherm formed earlier and extended deeper in 1983 than in 1984, indicating that 1983 was the warmer of the two years (Fig. 2). The maximum depth of the 5°C isotherm was 20–30 m in 1983 and only 10–20 m in 1984. Capelin were concentrated in the warm surface layer above the 5°C isotherm in both years (Fig. 2). Capelin were abundant (mean values ≥ 2 relative units, r.u.) between the surface and 20 m for weeks in 1983, and between the surface and 10 m for only 2 days in 1984. The lower depth limit for capelin generally corresponded with the depth of the 1°C isotherm (Fig. 2).

The annual (May–June) index of capelin abundance declined significantly (Kolmogorov–Smirnov [K–S] test, $Z = 12.5$, $p < 0.001$) from 0.83 ± 0.05 r.u. (mean $\pm$ s.e.) in 1983 to 0.11 ± 0.02 r.u. in 1984.

Two peaks of capelin abundance were observed in late June and early July 1983, and a single peak in early July

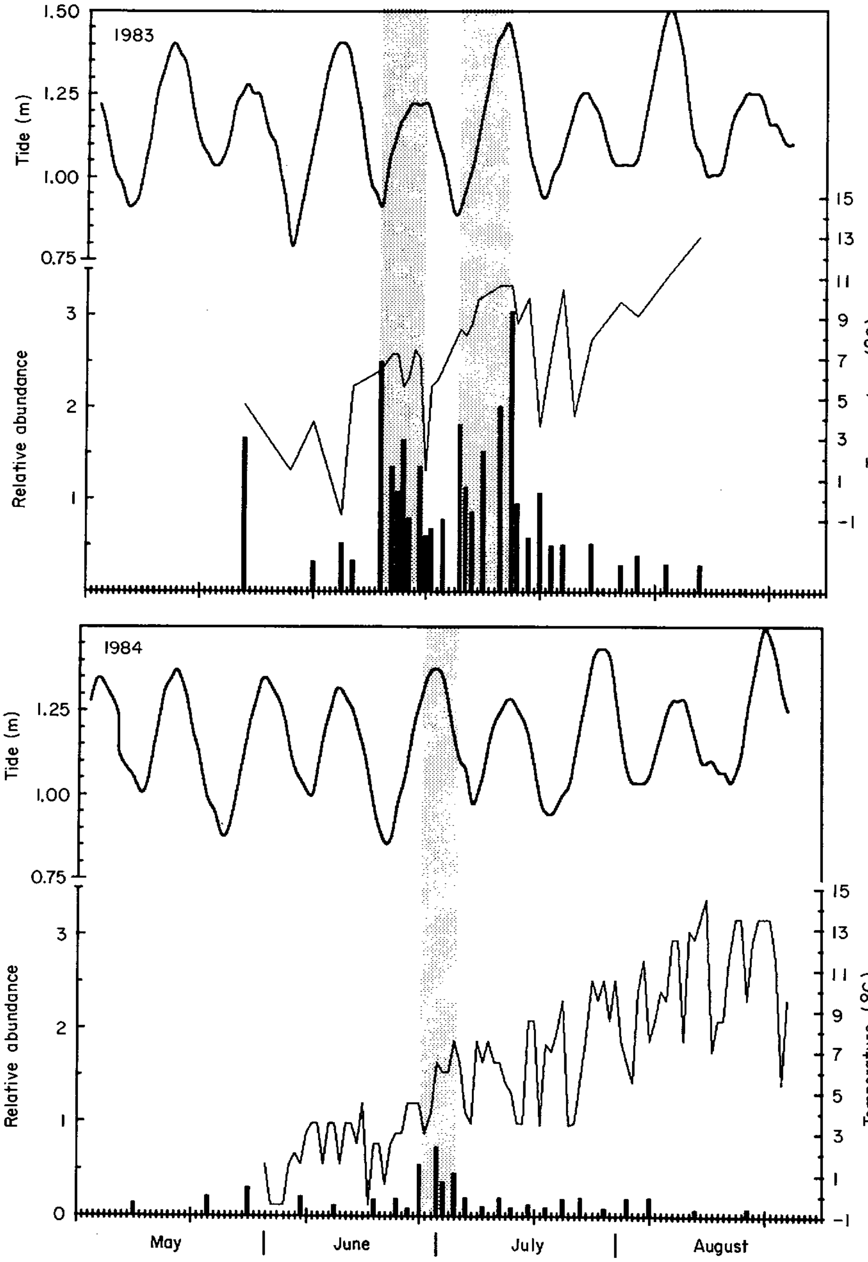

Figure 3. Relation between capelin abundance (relative units, r.u.; bar graph), water temperature (°C), and tides (m). Water temperature is from hydrographic station 1 (5 m depth). The two peaks of capelin abundance in 1983 and the single peak of abundance in 1984 are highlighted.

1984 (Fig. 3). After mid- to late July, abundance decreased in both years to levels observed prior to spawning (May and early June). Periods of peak abundance were associated with rapidly increasing water temperatures and with maximum tide oscillations (Fig. 3). For example, capelin abundance increased markedly as water temperature increased from less than 0°C on 13 June to greater than 6°C on 25 June 1983. The trough between the two periods of peak abundance in 1983 was associated with a drop in water temperature. In 1984, a single peak of abundance occurred when tidal oscillations were maximal and when water temperature increased from less than 1°C on 22 June to 6.5°C on 1 July (Fig. 3).

Discussion

Repeated hydroacoustic surveys in the Witless Bay area indicated that the seasonal abundance and the vertical distribution of capelin during the spawning season were influenced by water temperatures in the upper 20–30 m of the water column. In both years, capelin abundance initially peaked 1–2 weeks after water temperature increased from about 0–1°C to greater than 6°C. Templeman (1948) has shown that capelin are usually not abundant near the beach and that beach spawning activities rarely occur until water temperatures reach approximately 5°C (see also review by Stergiou, 1989). Historically, spawning has usually taken place in the second half of June and in July off eastern Newfoundland (Templeman, 1948, 1966; Campbell and Winters, 1973), which is the time of year when the 5°C isotherm usually first forms (Drinkwater and Trites, 1986).

This study, and subsequent studies conducted at Witless Bay (Schneider and Methven, 1988; Schneider, 1989) indicate that water temperatures can vary over periods of days and from year to year. At least two mechanisms may be responsible for these short- and long-term variations in water temperature. Schneider and Methven (1988) showed that longshore winds were coherent with thermal fluctuations in the upper water column over periods of about 4–6 days. Theoretical calculations and empirical measurements indicated that moderate to strong southwest winds resulted in coastal upwelling of cold water with a concomitant decrease in surface temperature and a raising of the thermocline to the surface (Schneider and Methven, 1988). These short-term fluctuations have an important effect on the schooling behaviour and vertical distribution of capelin. Elevation of the thermocline, for example, could result in a substantial thinning of the warm surface layer and may have the effect of concentrating capelin near the surface.

Annual variation in the depth of the thermocline corresponds with variations in the volume of cold water and sea-ice transported south in the Labrador Current (Petrie *et al.*, 1988). This cold current, the inshore branch of which flows past Witless Bay (Fig. 1), had a larger cross-sectional area of cold (<0°C) intermediate water associated with it off Cape Bonavista, Newfoundland in 1984 than in 1983 (Petrie *et al.*, 1988, Fig. 8). This resulted in the coldest (0–175 m) water temperatures during the last 40 years at station 27. The anomalously cold temperatures of 1984 may also be related to the amount of sea-ice present in the Newfoundland region. Surface ice coverage south of 55°N off Newfoundland in the spring of 1984 was twice that reported for 1983, which was itself a year of cold water temperatures with extensive ice coverage (Petrie *et al.*, 1988).

As a result of the above factors, it appears that the volume of water suitable for occupation by schools of capelin was reduced in 1984. This may account, in part, for the lower abundance of capelin in Witless Bay in 1984 relative to 1983. This lower abundance of capelin occurred with a decreased abundance of baleen whales, an important capelin predator (Piatt *et al.*, 1989), and a diminished amount of capelin taken by cod and seabirds (Piatt, 1987; Methven and Piatt, 1989). In contrast, hydroacoustic surveys conducted offshore on the Grand Bank indicated that the abundance of capelin increased there between 1983 and 1984 (Miller, 1985). Migration of capelin from offshore overwintering sites to inshore spawning grounds is known to be affected by cold water temperatures (Carscadden, 1978; Luka, 1979; Loeng, 1989). Furthermore, growth and maturation rates of overwintering capelin are reduced in cold water (Winters and Campbell, 1974; Gjøsæter and Loeng, 1987). Feeding areas and spawning sites for Barents Sea capelin have also been shown to vary as a result of differences in annual temperatures (Ozhigin and Luka, 1985; Loeng, 1989). Thus, it is possible that many capelin remained offshore in 1984 rather than migrating inshore.

Non-standardized hydroacoustic surveys conducted in Witless Bay in 1982 and 1985 (Piatt, 1987; Piatt *et al.*, 1989) also support the results from 1983 and 1984. For example, Petrie *et al.* (1988) indicate that 1982 was warmer than either 1983 or 1984; there being a substantially lower cross-sectional area of cold (<0°C) water off Cape Bonavista and higher water temperatures at station 27. In addition, the extent of ice coverage south of 55°N was also considerably less in 1982 than in either 1983 or 1984 (Petrie *et al.*, 1988). Capelin appear to have responded to these warmer conditions by being more abundant inshore (mean abundance = 2.3 r.u.) and by extending deeper into the water column (>70 m on all surveys) in 1982 (Piatt, 1987; Piatt *et al.*, 1989).

Most studies reporting on the abundance or spawning activities of capelin in relation to tides have been conducted at capelin beach spawning sites. Frank and Leggett (1981) reported spawning at or near maximum tide oscillations. This corresponds with our observations of increased capelin abundance several kilometres offshore at maximum tide oscillations. It appears that beach spawning capelin may prefer to spawn at maximal tides. Egg development rates are fastest, median time to hatching lowest, and mortality of eggs is less at high tide locations relative to low tide locations (Frank and Leggett, 1981). Tidal oscillations may therefore be an important cue for capelin gathering in pre-spawning aggregations offshore.

Variations in vertical distribution and abundance of capelin schools have important implications for capelin predators. Baleen whales and diving seabirds, like common murres (*Uria aalge*) and Atlantic puffins (*Fratercula arctica*), require high density aggregations of capelin for profitable foraging at different depths in the water column (Whitehead, 1981; Piatt and Nettleship, 1985; Piatt *et al.*, 1989). The availability of capelin as prey for demersal or pelagic feeding cod also depends on the vertical distribution of capelin schools (dos Santos and Falk-Petersen, 1989). Thus, the foraging success of capelin predators in Newfoundland appears to be indirectly influenced by several physical factors operating over differing spatial and temporal scales, including wind strength and direction, current transport volume, sea ice, and tidal oscillations.

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Note added in proof

Water temperatures in 1991, (mean = 5.9°C), from 19 June to 15 July, were 1.4°C to 3.3°C colder than any of the three preceding years at a capelin spawning beach 45 km north of Witless Bay, Newfoundland. The initiation of spawning was delayed by 20–29 days and the nearshore abundance of capelin was low. The cold water temperatures, reduced abundance and late arrival of capelin coincided with low catches of cod (*Gadus morhua*) in the inshore commercial trap fishery and relatively low numbers of baleen whales in the Witless Bay area.

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