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Early life history of capelin (*Mallotus villosus*) in the northwest Gulf of Alaska: a historical perspective based on larval collections, October 1977–March 1979

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Analyses of ichthyoplankton samples collected in the vicinity of Kodiak Island, Alaska, during the period October 1977–March 1979 provide new information on the spawning strategy and early life history of capelin in the Gulf of Alaska. Seasonal variation in abundance, length, and distribution of capelin larvae indicates that capelin populations in this area in 1978 spawned inshore during summer and autumn, and that spawning activity peaked during June–July. Distribution patterns of capelin larvae suggest that, subsequent to hatching and emergence into the plankton, larvae are transported from the bays and coastal zone around Kodiak Island into adjacent shelf waters, probably by tidal flushing and wind-induced surface currents. Mixing processes on the shelf seawards of Kodiak Island, reflecting variable current patterns there, are likely to enhance the dispersal of larvae as indicated by the uniformity observed among distribution patterns of several length categories. A comparison of larval abundance and length between bongo and neuston samples suggests that capelin larvae >30 mm standard length actively migrate to the surface layer. The observations represent a picture of capelin early life history during a period of abundance of adult capelin that has been linked to a cold phase in the oceanographic environment of the Gulf of Alaska.

Keywords: capelin, early life history strategies, Gulf of Alaska, larvae, oceanographic regime.

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Introduction

Capelin, *Mallotus villosus* (Müller), is a boreo-arctic species of the North Atlantic and Arctic Oceans, Chukchi and Bering Seas, Gulf of Alaska, and northeastern Pacific Ocean as far south as Washington, USA. The ecological importance of the species as a forage species utilized by seabirds and marine mammals has been well documented for the Gulf of Alaska (Piatt and Anderson, 1996; Merrick *et al*., 1997), and declines in abundance of forage species, including capelin, have been observed following the dramatic change in ocean climate (regime shift) in the late 1970s (Anderson *et al*., 1997; Anderson and Piatt, 1999). The biology of capelin has been extensively studied in the North Atlantic for many years, but despite its importance in the trophic web of Alaskan coastal waters, there have been few studies of capelin early life history in the North Pacific. Kendall and Dunn (1985) reported on the abundance and distribution of capelin larvae as part of the ichthyoplankton assemblage near Kodiak Island, Alaska. Doyle *et al*. (1995) documented the occurrence of capelin

Table 1. List of cruises, dates, and numbers of stations sampled by bongo and neuston nets during UW and AFSC cruises, Kodiak Archipelago, 1977–1979.

UW bay stations			AFSC continental shelf and slope stations			
Cruise	Dates	Bongo	Cruise	Dates	Bongo	Neuston
7801	29 Mar.–8 Apr.	20	4MF77	31 Oct.–14 Nov.	59	83
7802	10–17 Apr.	20	4DI78	29 Mar.–20 Apr.	85	113
7803	21 Apr.–1 May	19	2MF78	20 Jun.–5 Jul.	88	112
7804	3–28 May	25	3MF78	9–21 Sep.	26	28
7805	31 May–6 Jun.	26	4MF78	26 Sep.–7 Oct.	66	45
7806	14–24 Jun.	25	5MF78	19 Oct.–1 Nov.	19	11
7807	28 Jun.–18 Jul.	26	1WE78	31 Oct.–14 Nov.	88	92
7808	21–29 Jul.	26	1MF79	14 Feb.–8 Mar.	88	89
7809	1–9 Aug.	26	Total number of stations		519	573
7810	15–21 Aug.	26				
7811	3–13 Nov.	25				
7901	6–16 Mar.	25				
Total number of stations		289				

larvae in spring neuston collections in the western Gulf of Alaska, and Brown *et al.* (1999) included capelin larvae in investigations of forage fish in Prince William Sound. None of these studies, however, focused exclusively on capelin.

Ichthyoplankton surveys, designed to describe the distribution and abundance of fish eggs and larvae in the Gulf of Alaska, have been conducted annually by the National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Center (AFSC) from 1977 to the present. Since 1981, sampling has been restricted to spring and early summer, when capelin larvae are relatively scarce in subsurface plankton samples (Matarese *et al.*, in press). From late 1977 to early 1979, however, research cruises were conducted seasonally by the AFSC and the University of Washington (UW) to assess potential effects of offshore oil development on Alaskan marine resources (Doyle *et al.*, in press). These cruises sampled ichthyoplankton over a 17-month period in four Kodiak Island bays and along the adjacent continental shelf and slope. The resulting data provide an opportunity to examine aspects of the early life history of capelin, in particular temporal and spatial patterns in larval abundance, during a period when abundance of adult capelin was high, prior to the observed decline in forage fish in the Gulf of Alaska.

In this study, we examine seasonal and spatial patterns in the abundance and size of capelin larvae in the water column and neuston, in the vicinity of Kodiak Island, from autumn 1977 through winter/early spring 1979. Survey details and an initial exploration of the larval capelin data are presented in Doyle *et al.* (in press). The latter report also reviews the literature, mostly grey, that includes information on the biology or early life history of capelin in the northeastern Pacific Ocean. The purpose of the present study is to use the data to describe likely capelin spawning patterns and larval dispersal in the area and to interpret the observations of capelin early life history in relation to physical and biological characteristics of the pelagic ecosystem of the northwest Gulf of Alaska.

Methods

Field collections

Ichthyoplankton were collected from 31 October 1977 to 16 March 1979 during a series of 20 AFSC and UW cruises (Doyle *et al.*, in press; Table 1). AFSC cruises primarily sampled areas on the continental shelf and slope southeast of Kodiak Island, whereas UW cruises sampled within four Kodiak Island bays (Figure 1). A neuston net (Sameoto sampler) and 60 cm bongo net, fitted with flowmeters and plankton nets and codends of 505 μm mesh, were used to collect ichthyoplankton. Tow procedures generally followed survey guidelines in Smith and Richardson (1977). Sea surface temperature and salinity data were collected at irregular intervals throughout the sampling area (Doyle *et al.*, in press). Plankton samples were preserved in a 5% formalin-seawater mixture buffered with sodium tetraborate.

Laboratory procedures and analysis

Ichthyoplankton were identified, and capelin larvae were removed, enumerated, and measured to the nearest 0.1 mm standard length (SL). Data relevant to sample collection for AFSC samples (geographic coordinates, date/time collected, gear used, etc.) were archived in a database at AFSC. Data for UW samples were obtained with the assistance of the National Oceanographic Data Center (NODC). Preliminary observations of a developmental series of young capelin (40–85 mm SL) suggest

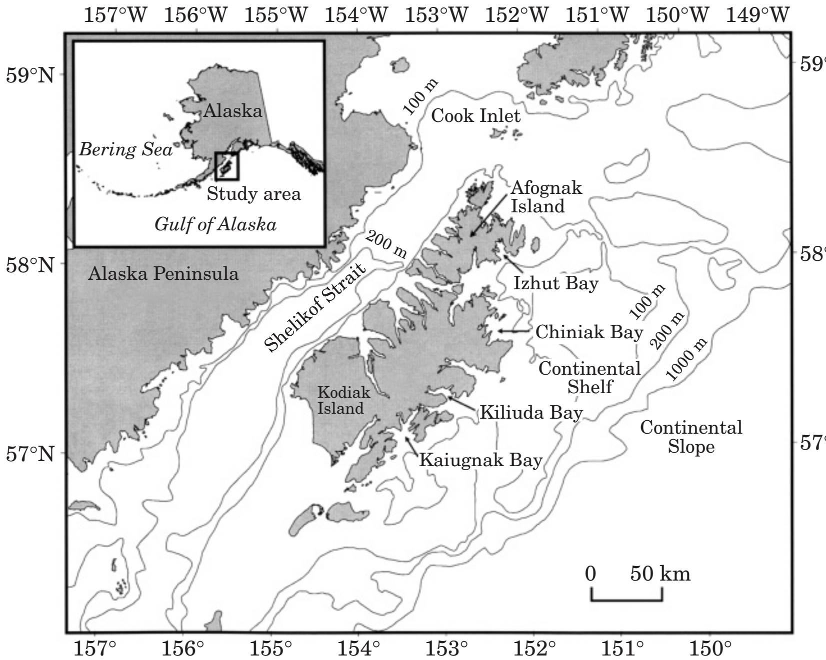

Figure 1. Map of the Kodiak Archipelago and adjacent study area.

that the juvenile stage begins at approximately 80 mm SL (Doyle *et al.*, in press), so all capelin encountered in this study are considered to have been larvae.

Numbers of larvae from each tow were standardized for bongo (number under 10 m^2 of sea surface) and neuston (number per 1000 m^3) tows on the basis of tow depth and volume filtered (Kendall and Dunn, 1985). Variation in larval abundance with season (six periods from October 1977 to March 1979) and geographic stratum (bay, continental shelf, continental slope) was examined by mapping standardized catches by season and using two-way ANOVAs. Data were fourth-root transformed prior to analyses to reduce heteroscedasticity and to increase symmetry (Downing, 1979). Growth was examined by plotting mean SL against mean date for each cruise. A regression of these data over summer and autumn 1978 provided an average change in length of the population per day. Based on data from the shelf only, length frequency distributions for larvae caught in the neuston tows were compared with those from the bongo tows.

Results

Seasonal variation in abundance and size of larvae

Seasonal variation in larval abundance for the 1977–1979 bongo collections was statistically significant ($p<0.001$); it indicates a summer peak (June–August) in abundance within the Kodiak bays (Figure 2). A peak of capelin larval abundance is apparent on the continental shelf during autumn, from September to November. Larvae are in the plankton throughout the rest of the year in low numbers, with a minimum during spring, from March to May. The data indicate a summer-autumn spawning season for capelin in the vicinity of Kodiak Island.

Seasonal variation in the mean SL of larvae in bongo samples from the Kodiak area (Figure 3) suggests a summer peak in capelin spawning activity and hatching of larvae into the plankton. Mean larval size increased from <10 mm in summer 1978 to >30 mm in winter/early spring 1979, with intermediate values for early and late autumn 1978. The mean SL of larvae caught during spring 1978 (4 larvae) was >40 mm, indicating that they were spawned during summer-autumn 1977. Larvae from late autumn 1977 were comparable in SL to late autumn 1978 specimens. Using data from summer through autumn of 1978, an average capelin larval growth rate of 0.11 mm d^{-1} (± 0.011 s.e.) was estimated from the slope of a length/time regression for this larval year-class (Figure 3). Seasonal progression in larval SL is also apparent in length frequency distributions of larvae from sampling cruises grouped into six seasonal periods from October 1977 to March 1979 (Figure 4).

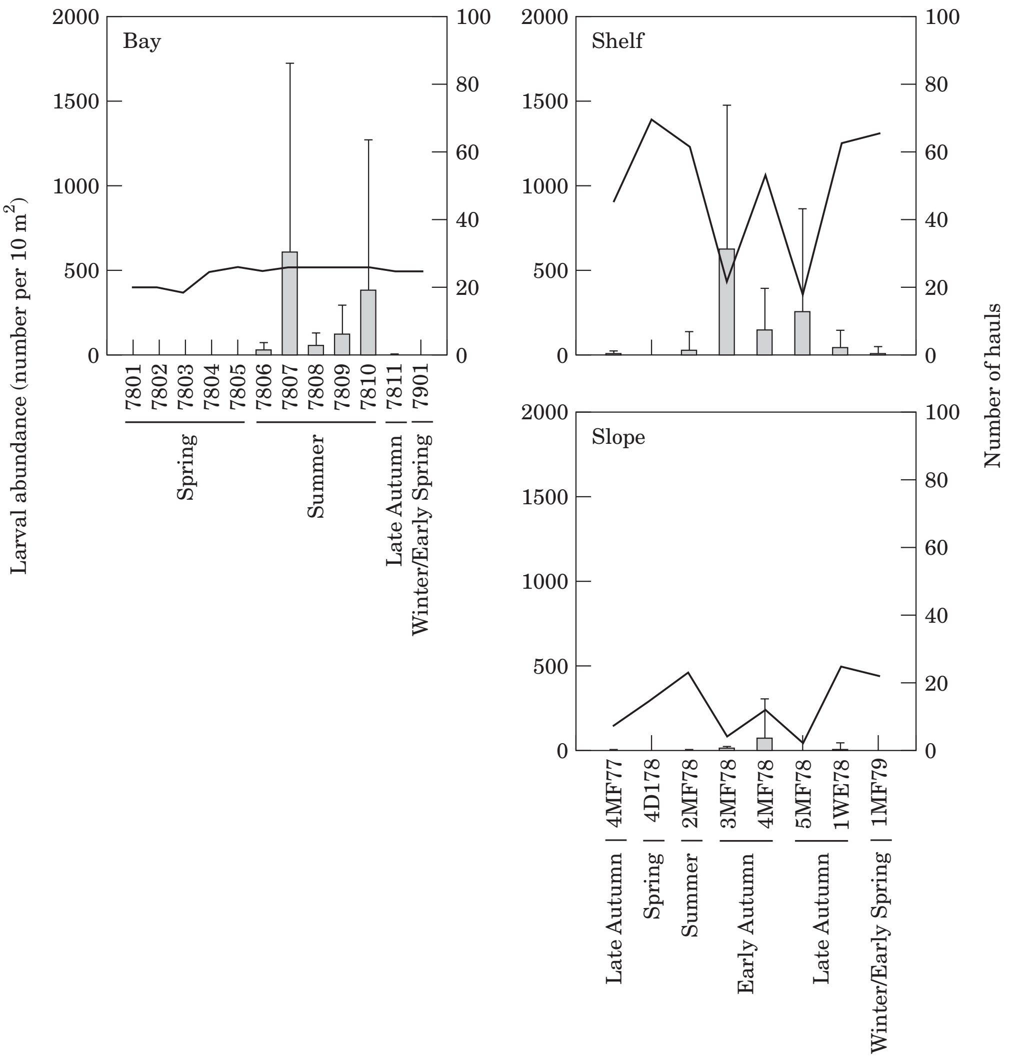

Figure 2. Seasonal variation in abundance of *Mallotus villosus* larvae (number per 10 m^2; means +s.e.), and number of bongo samples collected, in bays, on the continental shelf, and over the continental slope near Kodiak Island, October 1977–March 1979. Labels 7801, 4MF77, etc, are cruise numbers (see Table 1).

Distribution and dispersion of larvae

Seasonal variation in horizontal distribution patterns of capelin larvae caught in the bongo samples indicates that the smallest larvae (<10 mm), which were most abundant during summer 1978 (Figures 3, 4), are associated primarily with the Kodiak bays and adjacent coastal zone in water shallower than 100 m (Figure 5). During autumn 1978 and winter/early spring 1979, when larvae were mostly 10–40 mm SL, the larvae were more evenly distributed throughout the shelf zone, northeast to southwest of Kodiak Island (Figure 5), suggesting a seaward dispersal of larvae with development. A comparison of the distribution patterns of four size categories of larvae (<10, 10–20, 20–40, and >40 mm SL), for early and late autumn 1978, indicated a substantial difference only for larvae <10 mm (coastal distribution) and >10 mm SL (dispersed on the shelf; Doyle *et al.*, in press). Very few larvae were caught over the continental slope, in water >200 m deep, during any season (Figure 5).

Patterns of horizontal distribution of capelin larvae in the neuston collections mirrored those observed for the bongo collections, including the occurrence of the smallest larvae (<10 mm SL) close to the coast, as did seasonal variation in abundance of larvae (Doyle *et al.*, in press). Larvae ≤10 mm SL were equally well represented in both neuston and bongo samples, suggesting

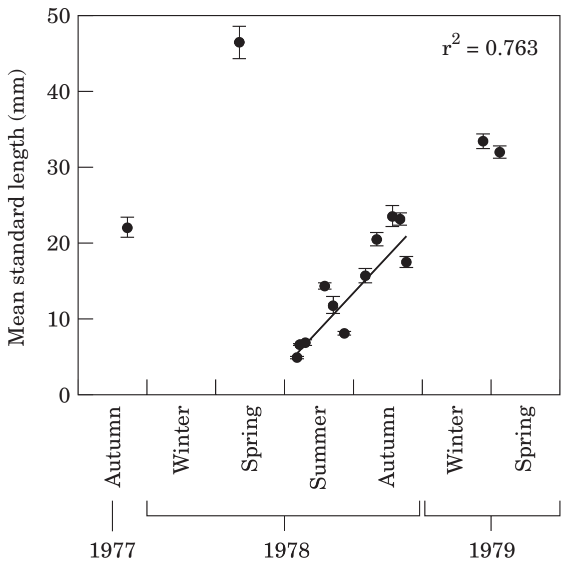

Figure 3. Seasonal variation in mean standard length (± s.e.) of *Mallotus villosus* larvae collected in bongo tows in bays, on the continental shelf, and over the continental slope near Kodiak Island, October 1977–March 1979.

that when the newly hatched larvae are in shallow coastal waters, they are as likely to be in the surface layer as deeper in the water column (Doyle *et al.*, in press). However, there was a substantial difference between the proportions of larger larvae (>30 mm SL) caught in the neuston and bongo samples. For larvae >10 mm SL, 63% of those in the neuston collections were >30 mm SL, in contrast to only 7.9% in the bongo samples.

Sea surface temperature and salinity

Temperature and salinity data for the study area and period are presented in Doyle *et al.* (in press). Mean sea surface temperature in the Kodiak bays varied seasonally, with a maximum of 9.8–10.4°C in summer, when spawning and larval hatching is most intense in the coastal zone. Mean temperature on the shelf increased from 5°C in spring 1978 to 9°C in summer 1978, but in autumn when capelin larvae were most abundant on the shelf, the mean temperature was 6.9°C. Mean salinity ranged from 31.4 to 34.2 among the Kodiak bays but remained relatively constant with season. There was a slight decrease in the mean value (maximum difference of 2.2 for Kiliuda Bay) during summer, possibly reflecting a seasonal peak in freshwater run-off. No seasonal variation in mean salinity (32.2) was apparent for the shelf.

Discussion

This study provides new information on the spawning strategy and early life history of capelin in the Northeast Pacific, specifically in the vicinity of Kodiak Island in the northwest Gulf of Alaska. Capelin populations there appear to spawn inshore during summer and autumn. A peak in spawning activity during June–July in the Kodiak bays results in a summer peak in abundance of recently hatched (<10 mm SL) capelin larvae in coastal waters and a September–October peak in abundance of well-developed larvae (10–50 mm SL) in adjacent shelf waters. This seasonal pattern in spawning activity appears consistent with beach and aerial spawning surveys in the North Pacific that found capelin spawning runs in late spring and early summer (Blackburn *et al.*, 1981; Pahlke, 1985). It is similar to the spawning season (June–July) observed for capelin in the Newfoundland–Labrador region of the Northwest Atlantic (Templeman, 1948; Carscadden *et al.*, 1997), but later than the March–April peak observed for the capelin populations of the Barents Sea and Iceland–Greenland regions of the Northeast Atlantic (Vilhjálmsson, 1997).

The dominant fish populations in the Gulf of Alaska spawn in spring, and larval abundance of most species peaks then (April–May; Matarese *et al.*, in press), coinciding with a peak in phytoplankton production in coastal and shelf waters between late April and early May (Cooney, 1986; Napp *et al.*, 1996). The contrasting, later occurrence of capelin larvae actually coincides with a summer peak in production of copepod nauplii (Cooney, 1986), suitable food for first-feeding larvae.

Carscadden *et al.* (1997) conclude that the timing of spawning of capelin off Newfoundland is related primarily to water temperature. The prespawning water temperature and the size and age structure of the adult population, however, also seem to exert significant influence on timing of spawning of capelin in the Northwest Atlantic (Carscadden *et al.*, 1997). These factors are also likely to influence capelin prespawning and spawning dynamics in the Gulf of Alaska, but we lack the data in our area, especially from the spawning beaches, to explore such a relationship. Our 1977–1979 data, however, suggest that larval hatching and emergence into the plankton is associated with water temperatures of 8–11°C.

An average daily growth rate of 0.11 mm d^{-1} estimated for the 1978 larval year-class appears low in comparison with mean rates of 0.2–0.35, 0.15–0.25, and 0.18–0.25 mm d^{-1} reported for larval capelin populations in the Gulf of St Lawrence, Icelandic waters, and Newfoundland waters respectively (Jacquaz *et al.*, 1977). Rather than expressing the true growth rate (i.e. the change of length with age) of individual larvae, however, these estimates represent the change in average length of the larval population over time, and are a function of growth, mortality, larval production, and larval transport into and out of the survey area. Furthermore, a direct comparison between our data and those from

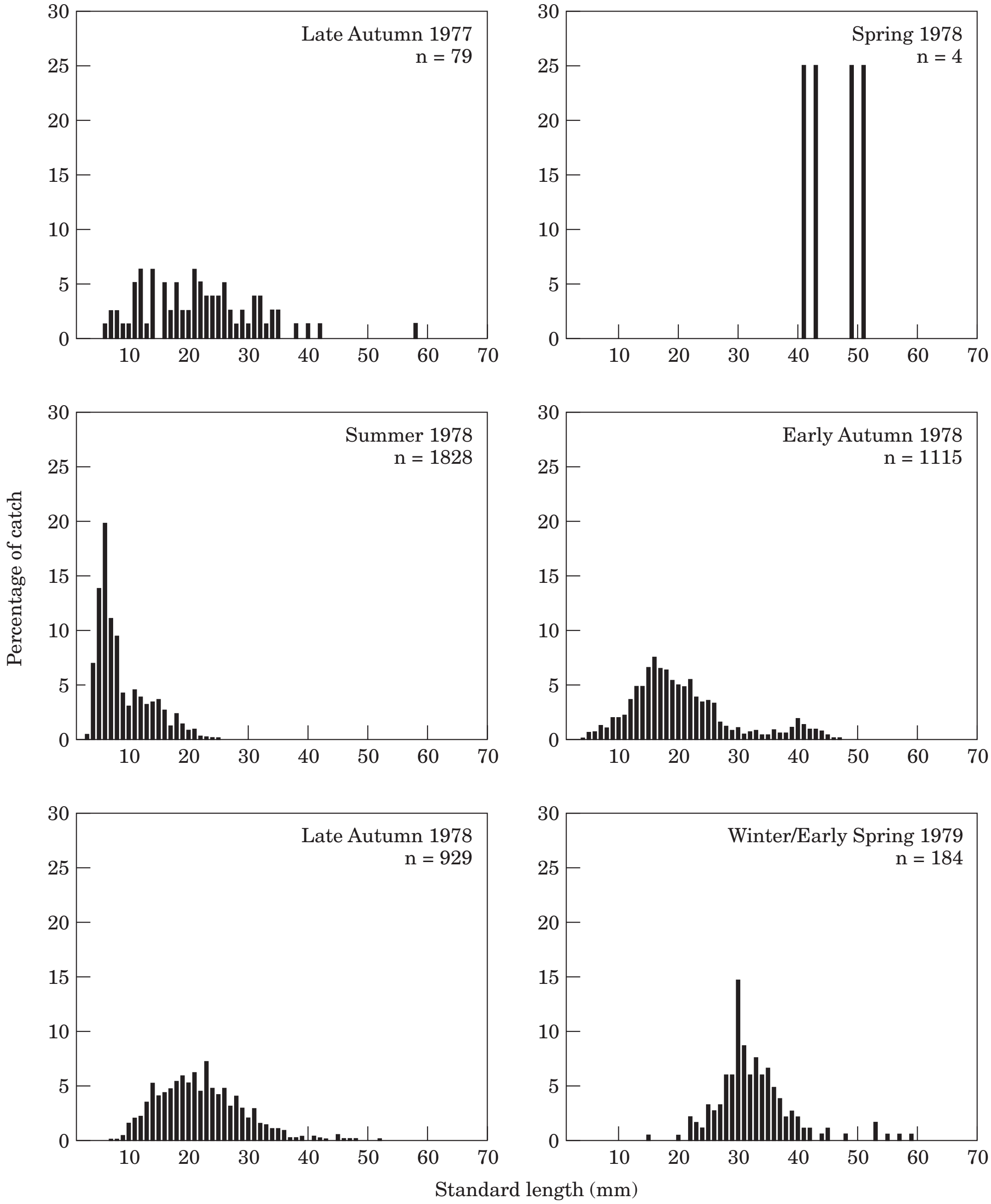

Figure 4. Seasonal variation in length (SL) frequency distributions of *Mallotus villosus* larvae in the study area based on bongo samples collected during the period October 1977–March 1979. Sampling cruises were assigned to six seasonal periods according to grouping in Figure 2.

the Atlantic Ocean seems inappropriate without further exploration of larval growth rates in relation to temperature and plankton characteristics (food conditions) of water masses containing capelin larvae, among the different ocean regions. Similarly, a more thorough investigation is needed of environmental conditions in the Gulf of Alaska pelagic ecosystem, and adjacent coastal and beach zones, where prespawning adult capelin are found, for a meaningful comparison to be made between spawning strategies and early life history of capelin here and in the Atlantic Ocean.

Our observations of capelin larval distribution patterns suggest that, subsequent to hatching and emergence into the plankton, larvae are dispersed from the

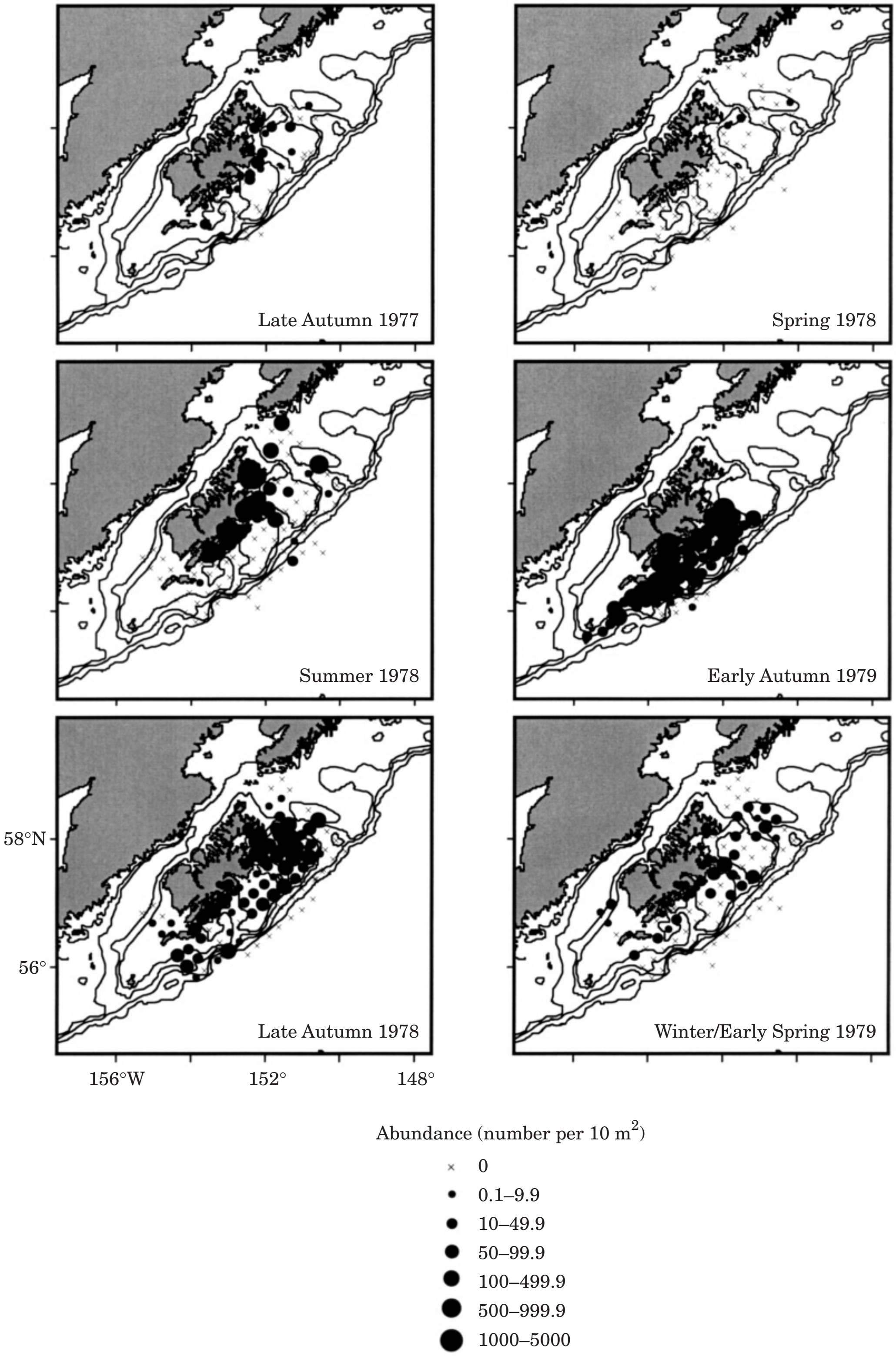

Figure 5. Seasonal variation in distribution and abundance of *Mallotus villosus* larvae in the study area based on bongo samples collected during the period October 1977–March 1979. Sampling cruises were assigned to six seasonal periods according to the grouping in Figure 2.

bays and coastal zone around Kodiak Island into adjacent shelf waters. The mechanism for seaward transport of capelin larvae in the area is unknown, but it is likely to involve both tidal flushing and wind-induced surface currents, as is the case in Newfoundland waters (Fortier and Leggett, 1982; Frank and Leggett, 1982). Salinity in the Kodiak bays was relatively homogeneous and similar to that on the shelf and slope, implying that the bays experience regular tidal flushing. As such, larvae may be transported from bays onto the shelf with tidal currents. It is likely that, subsequent to seaward drift, larvae are subject to mixing processes on the shelf. The uniformity in distribution patterns observed among four length categories of larvae >10 mm SL on the shelf outside Kodiak Island reflects such a process. Reed and Schumacher (1986) showed that current patterns in this area are variable, including onshore and offshore flow on the shelf that is likely to enhance the dispersal of larvae. Along the outer shelf and slope, the Alaska Stream flows in a steady southwesterly direction, parallel to the slope, probably contributing to the retention of larvae on the shelf and the southwesterly transport of larvae over the slope.

The high proportion of larvae >30 mm SL in the neuston samples relative to the bongo samples implies a facultative association of larger capelin larvae with the surface layer. It seems that these larger larvae are likely to migrate vertically into the neuston. Doyle *et al.* (1995) documented a high fraction (57%) of large capelin larvae (>25 mm SL) in neuston relative to bongo collections in the Gulf of Alaska during spring, and diel variation in their abundance in the neuston samples suggested that they migrate into the neuston at night. This association of large capelin (and other fish) larvae with the neuston layer is considered to be a feeding adaptation that allows large larvae to exploit a wide variety and size range of food organisms that accumulate at the surface, particularly at night (Neilson and Perry, 1990; Doyle *et al*., 1995).

Although the data analysed for the present study were collected slightly later than the 1976–1977 oceanographic regime shift documented for the Gulf of Alaska, abundance of adult capelin remained high until the early 1980s (Anderson *et al*., 1997; Anderson and Piatt, 1999). Therefore, our findings represent a picture of capelin early life history during a period of high abundance of adults that has been linked to a cold phase in the oceanographic environment of the Gulf of Alaska. Our observations could form the basis for a future comparative study of the early life history of capelin in the Gulf of Alaska during the warm-water and transitional phases of the oscillating oceanographic regime in the region. In order to investigate capelin early life history variability and population fluctuations in the Gulf of Alaska in relation to oceanographic regime shifts or other temporal changes, annual ichthyoplankton and oceanographic surveys during summer and autumn, when larvae are most abundant in the plankton, are crucial.

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