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**Aspects of the 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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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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ABSTRACT

Analyses of historical ichthyoplankton data collected in the vicinity of Kodiak Island, Gulf of Alaska, provide new information on the spawning strategy and early life history characteristics of capelin (*Mallotus villosus*) in the northeast Pacific. Ichthyoplankton surveys have been conducted by the Alaska Fisheries Science Center (AFSC) in the northwest Gulf of Alaska from 1977 to the present, primarily during spring. Time series data (1977-98) from these cruises indicate that a peak in capelin larval abundance occurs in late summer and early autumn (September-October) on the continental shelf. Capelin larvae occur in the plankton throughout the rest of the year in low numbers, with a minimum observed from March-May. The most intensive seasonal collections of larvae were made during a 17-month period from 1977 to 1979, within four Kodiak Island bays and over the adjacent continental shelf and slope. More extensive analyses of these data concur with observed long-term seasonal patterns of abundance on the shelf and also indicate a summer peak (July-August) in larval abundance in Kodiak Island bays. Seasonal variation in abundance, length, and distribution of capelin larvae from the 1977-79 collections indicates that in 1978, capelin populations in this area spawned during the summer and autumn in inshore waters, with a peak in spawning activity during June-July. The distribution patterns for these years 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 seaward of Kodiak Island, reflecting variable current patterns in this area, are likely to enhance the dispersal of larvae as indicated by the uniformity observed among distribution patterns of several length categories of larvae. A comparison of larval abundance and lengths between bongo and neuston samples suggests that capelin larvae, mostly greater than 30 mm standard length, actively migrate to the surface layer. Although enhanced net avoidance by the larvae during daylight hours is a confounding factor, the observed diel variation in abundance of capelin larvae in the neuston implies that the migration to the surface layer is largely nocturnal. Our observations represent a picture of capelin early life history during a period of high adult abundance that has been linked to a cold phase in the oceanographic environment of the Gulf of Alaska.

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INTRODUCTION

Capelin (*Mallotus villosus*) is a boreoarctic member of the smelt family (Osmeridae) that occurs in the North Atlantic and Arctic Oceans, Chukchi and Bering Seas, Gulf of Alaska, and northeast Pacific Ocean as far south as the waters off Washington State. They are known to spawn throughout most of their range (Hart 1973, Garrison and Miller 1982). The ecological importance of capelin as a forage species utilized by marine birds and mammals has been well documented in 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 a dramatic change in ocean climate (regime shift) that occurred in the late 1970s (Anderson et al. 1997, Anderson and Piatt 1999). Warner and Shafford (1978), Blackburn et al. (1981) and Pahlke (1985) give preliminary information on the spawning biology of capelin in Alaskan waters based on aerial and beach spawning surveys conducted in the eastern Bering Sea and Gulf of Alaska. 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 pertaining to capelin early life history in the North Pacific. Capelin larvae have been observed in the ichthyoplankton of the eastern Bering Sea shelf (Waldron 1981), and Kendall and Dunn (1985) reported on the abundance and distribution of capelin larvae as part of the ichthyoplankton assemblage near Kodiak Island. Doyle et al. (1995) documented the occurrence of capelin larvae in spring neuston collections in the western Gulf of Alaska, and Norcross and Fransden (1996) and Brown et al. (1999) included capelin larvae in investigations of forage fishes in Prince William Sound. None of these early life history studies, however, focused exclusively on capelin.

Ichthyoplankton surveys, designed to describe aspects of 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) and its predecessor agencies from 1977 to the present. Since 1981, sampling has been restricted to spring and early summer months when capelin larvae are relatively scarce in sub-surface plankton samples (Matarese et al., in press). From late 1977 to early 1979, however, a series of research cruises supported primarily by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) was conducted seasonally by the AFSC and the University of Washington's (UW) Fisheries Research Institute to assess potential effects of offshore oil development on Alaskan marine resources (Rogers et al. 1979, Kendall et al. 1980, Kendall and Dunn 1985). 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 provided 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 adult capelin abundance was high, prior to the observed decline in forage fishes 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, Alaska, from autumn 1977 through winter/early spring 1979. The purpose of this study is to use these data to describe likely capelin spawning patterns and larval dispersal in this area and also to interpret our 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 (Table 1). AFSC cruises primarily sampled areas on the continental shelf and slope southeast of Kodiak Island while UW cruises sampled within four Kodiak Island bays (Fig. 1). A neuston net (Sameoto sampler; Sameoto and Jaroszynski 1969) and a 60 cm bongo net (Posgay and Marak 1980) fitted with flowmeters and 505 μm mesh plankton nets and cod ends, were used to collect ichthyoplankton samples. 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. Plankton samples were preserved in a 5% formalin-seawater mixture buffered with sodium tetraborate. Conductivity, temperature, and bottom depth (CTD) data were collected using a Seabird CTD profiler.

Laboratory Procedures

Ichthyoplankton were identified and *Mallotus villosus* larvae were removed, enumerated, and measured to the nearest 0.1 mm standard length (SL). At the time of initial examination of the larvae, smaller individuals with incomplete fin ray development, particularly pectoral-fin rays, were identified at the family level (Osmeridae). Larger individuals with complete complements of fin rays were identified as *M. villosus*. After identification, larvae were transferred to 70% ethanol and stored in the University of Washington Larval Fish Collection (UWLFC). Data relevant to sample collection for AFSC samples (e.g., geographic coordinates, date/time collected, gear used) were archived in a database (ICHBASE) at AFSC. Data for UW samples were obtained with the assistance of the National Oceanographic Data Center (NODC). We examined and reidentified a subset of small larvae, by comparing our specimens with descriptions of taxonomic characters of other osmerid species from Hearne (1983, 1984), Young (1984), and Moser (1996) that were not available at the time of original sorting, to determine whether larvae historically characterized and archived as "Osmeridae" were *M. villosus*. In addition, we compiled and compared published data on adult distributions, early life history, and spawning habitat characteristics of other osmerid fishes reported to occur in the Gulf of Alaska with capelin. We also differentially cleared and stained a developmental series of 24 capelin specimens 4.8-90.0 mm SL using the method of Potthoff (1984) to determine length ranges for each developmental stage and identify developmental landmarks as reported by Kendall et al. (1984).

Analytical Methods

Numbers of larvae from each tow were standardized for bongo (number per 10 m^2) and neuston (number per $1,000\text{ m}^3$) tows using tow depth and volume filtered (Kendall and Dunn 1985). Variation in larval abundance with season (six periods from October 1977 through March 1979) and geographic strata (bay, continental shelf, continental slope) was examined by mapping standardized catches by season and by using two-way ANOVAs. Data were fourth-root transformed prior to analyses to reduce heteroscedasticity and increase symmetry (Downing 1979).

Length-frequency histograms were created for each sampling gear and season to examine seasonal variation in larval size and to compare length distributions between gears. Data were included from the shelf strata only because there were no larval lengths measured from the neuston samples in the bays and there were very few larvae caught by either gear in the slope strata. Spatial variation in the distribution patterns of different sizes of larvae was investigated for autumn 1978 by plotting on maps the abundance of four length categories of larvae; less than 10 mm standard length (SL) (newly hatched and preflexion), 10-20 mm SL (flexion), 20-40 mm SL (post flexion), and greater than 40 mm SL (late larvae/transformation). Placement in developmental categories is based on data for sequence of fin formation from Fahay (1983). Growth was examined by plotting mean standard length 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.

Diel variation in abundance of larvae in the bongo and neuston samples was investigated by examining data from five AFSC cruises (4MF77, 4DI78, 2MF78, 1WE78 and 1MF79) that included both day and night samples. Diel catch data were combined for these cruises to calculate a stratified mean larval abundance, and standard deviation, in one hour intervals. Cruise 4DI78 was omitted from the bongo calculations and cruise 2MF78 from the neuston calculations due to the absence or scarcity of larvae in the samples from these cruises.

For cruises when CTDs were not deployed, temperature-salinity-depth profiles were obtained from the online, 20+ year EPIC database developed by NOAA's Pacific Marine Environmental Laboratory. In these cases, profiles were obtained for cruises carried out in the same geographic region and time period. In several cases, however, no CTD data from the appropriate time and location were available (i.e., Cruises 3MF78, 4MF78, 5MF78, 1MF79). The CTD data were more limited for the UW cruises. Surface temperatures and salinities measured at each station were pooled to provide information on the seasonal characteristics of each Kodiak bay and the shelf area east of Kodiak Island.

RESULTS

Larval Identification and Development

Examination of a subset of small larvae (prior to attainment of a full complement of fin rays) initially identified and archived as "Osmeridae" led us to conclude that these larvae were, in all likelihood, *Mallotus villosus*. Comparison of published information on adult distributions and spawning times and habitat characteristics of other osmerid fishes likely to occur in the Gulf of Alaska (Table 2) supported this conclusion. Six other osmerid fishes reported to occur in Alaskan waters spawn in different habitats at different times of year with minimal overlap (Table 2). Three species are reported as being uncommon or rare and are unlikely to spawn in the study area. Consequently, data for these two taxa (Osmeridae and *Mallotus villosus*) were pooled for analyses in this study.

From our cleared and stained developmental series of capelin larvae (Table 3), we determined that notochord flexion begins at 8.5 mm SL and is complete at 25.5 mm SL. Transformation from the postflexion to juvenile stage begins at approximately 60.0 mm SL when ossification of vertebrae and fins is complete. The juvenile stage begins between 75.0 and 80.0 mm SL when the cranium, pterygiophores and bones supporting fins are ossified, lateral line scales begin to form, palatine teeth are present, and the skin has a silvery sheen characteristic of adult coloration. Using these criteria and developmental landmarks, all capelin collected for this study are considered larvae.

Seasonal Variation in Abundance and Size of Larvae

Based on an extensive set of bongo samples collected throughout the Gulf of Alaska from 1977 through 1998 (sampling coverage and methodology described in Matarese et al., in press), Figure 2 illustrates the general pattern of monthly variation in mean abundance and percent occurrence of capelin larvae in this region. Lack of sampling in January, August, and December, and the concentration of sampling during spring means that observed seasonal patterns in abundance in this region is incomplete. Nevertheless, a peak in abundance appears to occur during late summer-early autumn. Larvae occur in the plankton throughout the rest of the year in low numbers, with a minimum in March-May. The proportion of samples yielding capelin larvae was highest (40-45%) in September-October and lowest (< 3%) in April-May.

Seasonal variation in larval abundance for the 1977-79 collections was statistically significant (bongo, $P < 0.001$; neuston, $P < 0.05$) and these data concur with but expand on the above general seasonal pattern. Figure 3 shows the monthly patterns by geographic strata and sampling gear. Within the bays, the peak abundance of larvae occurred in the summer months. A peak in larval abundance was apparent on the continental shelf during autumn, September-November 1977 and 1978, whereas abundance was at a minimum during spring 1978, March-May, in all geographic strata. These data indicate a summer-autumn spawning season for capelin in the vicinity of Kodiak Island.

Seasonal variation in mean standard length of larvae in bongo and neuston samples from the Kodiak area also suggests a summer peak in capelin spawning activity and hatching of larvae into the plankton (Fig. 4). Mean larval size increased from less than 10 mm SL in the summer of 1978 to greater than 30 mm SL in the winter/early spring of 1979, with intermediate values for early and late autumn of 1978. The mean standard length of the few larvae caught in bongo and neuston tows during spring of 1978 was greater than 40 mm SL indicating that they were

spawned during summer-autumn of 1977. During autumn cruises when capelin larvae are most abundant in continental shelf samples, mean larval size was consistently greater in neuston than in bongo samples (Fig. 4). Using data from bongo collections in the summer through autumn of 1978, the rate of change in the average length of the larval population was 0.11 mm per day (\pm 0.011 SE). This was estimated from the slope of a length/time regression for this larval year class and can be considered as a proxy for larval growth rate (Fig. 4). Seasonal progression in larval standard length is also apparent in length-frequency distributions of larvae from sampling cruises grouped into six seasonal periods from October 1977 through March 1979 (Figs. 5 and 7).

Distribution and Dispersal of Larvae

The statistical comparison of larval abundance between bays, shelf, and slope yielded a significant difference among the three geographic strata (bongo and neuston $P < 0.001$), as well as the significant effect of season mentioned previously (bongo $P < 0.001$, neuston $P < 0.05$) on capelin abundance for both sampling gears. A significant interaction between the two factors (geographic strata and season) was also detected (bongo and neuston $P < 0.001$).

Seasonal variation in horizontal patterns of distribution of capelin larvae collected in the bongo tows indicates that the smallest larvae (< 10 mm SL), that were most abundant during summer 1978 (Figs. 3 and 4), are associated primarily with the Kodiak bays and adjacent coastal zone in water less than 100 m deep (Figs. 6 and 8). During autumn of 1978 and winter/early spring of 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 (Figs. 6 and 8), 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 when larval size range was greatest, indicated a substantial difference only between larvae less than 10 mm SL (coastal distribution) and those greater than 10 mm SL (dispersed on the shelf) in early autumn (Figs. 9-12). Very few larvae were caught over the continental slope, in water greater than 200 m deep, during any season (Figs. 6 and 8).

Neustonic Occurrence and Diel Variation in Catches of Larvae

As stated above, seasonal variation in abundance and 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 in summer (Figs. 4-12). Larvae less than or equal to 10 mm SL were equally well represented in both the neuston and bongo samples (Fig. 13) suggesting that when the newly hatched larvae are in shallow coastal waters, they are as likely to occur in the surface layer as deeper in the water column. A substantial difference between proportions of larger larvae (> 30 mm SL) in the neuston and bongo samples, however, was observed (Fig. 13). For larvae greater than 10 mm SL, 63% of those in the neuston samples were greater than 30 mm SL in contrast to only 7.9% in the bongo samples.

Diel catch data were combined to calculate a stratified mean larval abundance in one-hour intervals for each sampling gear (Fig. 14). For both bongo and neuston samples a reduction in catches of capelin larvae was apparent during most of the daylight hours, suggesting enhanced gear avoidance during the day. In addition, larvae were absent from the neuston tows during six

of the daylight hours implying that diel variation in catches at the surface was influenced by diel vertical migration of larvae. The high level of variance (illustrated by the standard error values) for the stratified hourly abundance values, especially for the bongo samples, however, prevents an accurate estimate of the actual level of reduction in catches during daylight.

Sea Surface Temperature and Salinity

Temperature and salinity data for the study area and period are presented in Table 4. Mean sea surface temperatures in the Kodiak bays varied seasonally with a recorded maximum of 9.4°-10.4° C in the summer when spawning and larval hatching are most intense in the coastal zone. Summertime mean temperature was slightly lower (8.2° C) on the shelf, and in autumn when capelin larvae were most abundant on the shelf, the mean temperature was 6.9° C. Mean salinities ranged from 31.4 to 34.2 psu among the Kodiak bays but remained relatively constant with season. A slight decrease in the mean value (maximum difference of 2.2 psu for Kiliuda Bay) was observed during summer, possibly reflecting a seasonal peak in fresh water runoff. No seasonal variation in mean salinity (32.2 psu) was apparent for the shelf.

DISCUSSION

This study provides new information on the early life history characteristics of capelin in the northeast Pacific, specifically in the vicinity of Kodiak Island in the northeast Gulf of Alaska.

Although we have provided new information on length at stage of development and associated osteological and morphological landmarks in capelin, identification of osmerid larvae from the Gulf of Alaska remains difficult. Of the six anadromous and marine species reported to occur in Alaskan waters (Table 2), only larvae of *Mallotus villosus* have been described at all stages of development (Templeman 1948, Fahay 1983). These descriptions, however, are based on specimens from the Atlantic Ocean. Unfortunately, larval stages of the other five species have been incompletely described and few illustrations are available (Barraclough 1964, Fahay 1983, Hearne 1983, Young 1984, Moser 1996). Larvae of the Alaskan osmerids are slender bodied and have long guts (approx. 75% SL) with rows of melanophores on the dorsal and/or ventral margins. One to several post-anal ventral melanophores are also present in all species. Because the osmerid larval stages currently known are so strikingly similar in appearance, future taxonomic studies of this group would greatly benefit from genetic analyses. Ichthyoplankton sampling in nearshore areas of the northeast Pacific will be needed to collect larvae of these anadromous and beach spawning osmerids.

In the vicinity of Kodiak Island, it appears that capelin populations spawn during the summer and autumn in inshore waters. 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 which found that capelin spawning runs occurred 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 in the Barents Sea and Iceland-Greenland regions of the northeast Atlantic (Vilhjalmsson 1997).

The dominant fish populations in the Gulf of Alaska are spring spawners and a spring peak (April-May) in larval abundance is observed for most species (Matarese et al. in press), coinciding with a late April to early May peak in phytoplankton production in coastal and shelf waters (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), a suitable food for first-feeding larvae.

Carscadden et al. (1997) conclude that the timing of capelin spawning in the Newfoundland region is related primarily to water temperature. The pre-spawning water temperature and size and age structure of the adult capelin population, however, also seem to exert significant influence on timing of spawning in the northwest Atlantic (Carscadden et al. 1997). These factors are also likely to influence capelin pre-spawning and spawning dynamics in the Gulf of Alaska but we lack the data in this area, especially from the spawning beaches, to explore such a relationship. Our 1977-79 data, however, suggest that larval hatching and emergence into the plankton occurred in water temperatures ranging approximately from 8° to 11° C.

An average daily growth rate of 0.11 mm per day 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 per day 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), 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 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 these different ocean regions. Similarly, a more thorough investigation of environmental conditions is needed in the Gulf of Alaska pelagic ecosystem, and adjacent coastal and beach zones where pre-spawning adult capelin occur, for a meaningful comparison to be made between spawning strategies and early life history characteristics 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 bays and coastal zone around Kodiak Island into adjacent shelf waters. The mechanism for seaward transport of capelin larvae in this area is unknown but is likely to involve both tidal flushing and wind-induced surface currents as is the case in Newfoundland waters (Frank and Leggett 1982, Fortier and Leggett 1982). Salinities in the Kodiak bays were relatively homogeneous and similar to those 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 greater than 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 greater than 30 mm SL in the neuston samples relative to the bongo samples implies a facultative association of larger capelin larvae with the surface layer. Given the absence or scarcity of capelin larvae in samples taken during daylight hours, it seems that these larger larvae are likely to migrate vertically into the neuston at night. The confounding factor of enhanced gear avoidance by the larvae during daylight hours, as indicated by a reduction in larval abundance in daytime bongo samples, must also be taken into consideration in the interpretation of these results. Nevertheless, Doyle et al. (1995) documented a high fraction (57%) of large capelin larvae (> 25 mm SL) in the 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. In addition, Haldorson et al. (1993) report that osmerid larvae in Auke Bay, southeast Alaska, spent most of their time in the mixed layer, rising to the surface at night and returning to shallow depths during the day. This association of large capelin, and other fish larvae, with the neustonic layer is considered to be a feeding adaptation that allows the 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 analyzed for our study were collected slightly later than the 1976-77 oceanographic regime shift documented in the Gulf of Alaska, adult capelin abundance remained high until the early 1980s (Anderson et al. 1997, Anderson and Piatt 1999). Thus, our findings represent a picture of capelin early life history during the period of high adult abundance 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 early life history characteristics of capelin in the Gulf of Alaska during the warm water and transitional phases of the oscillating oceanographic regime in this region. In order to investigate capelin population

fluctuations and early life history variability in the Gulf of Alaska, relative to oceanographic regime shifts or other temporal changes, annual ichthyoplankton and oceanographic surveys are crucial during summer and autumn months when capelin larvae are most abundant in the plankton.

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Table 1. List of cruises, dates, and numbers of stations sampled by bongo and neuston nets for University of Washington (UW) Alaska Fisheries Science Center (AFSC) OCSEAP and other cruises, Kodiak Archipelago. 1977-79.

UW OCSEAP bay stations					AFSC OCSEAP continental shelf and slope stations				
Cruise	Dates	Bongo	Neuston		Cruise	Dates	Bongo	Neuston	
7801	Mar 29-Apr 8	20	21		4MF77	Oct 31-Nov 14	59	83	
7802	Apr 10-Apr 17	20	22		4DI78	Mar 29-Apr 20	85	113	
7803	Apr 21-May 1	19	22		2MF78	Jun 20-July 5	88	112	
7804	May 3-May 28	25	27		3MF78*	Sep 9-21	26	28	
7805	May 31-Jun 6	26	28		4MF78*	Sep 26-Oct 7	66	45	
7806	Jun 14-Jun 24	25	28		5MF78*	Oct 19-Nov 1	19	11	
7807	Jun 28-Jul 18	26	27		1WE78	Oct 31-Nov 14	88	92	
7808	Jul 21-Jul 29	26	28		1MF79	Feb 14-Mar 8	88	89	
7809	Aug 1-Aug 9	26	28		totals		519	573	
7810	Aug 15-Aug 21	26	28						
7811	Nov 3-Nov 13	25	27						
7901	Mar 6-Mar 16	25	27						
totals		289	313						

*Not OCSEAP grid stations, occupied as piggyback on AFSC groundfish surveys.

Table 2. Summary of published information on environment, spawning habitat, and spawning season for the osmerid fishes of Alaska. Sources: Hart (1973), Morrow (1980), Mecklenburg et al. (2002).

Taxon	Environment	Spawning habitat	Spawning season
<i>Hypomesus olidus</i>	freshwater	ponds or streams	Jun
<i>Hypomesus pretiosus</i>	marine	beaches	Mar-May
<i>Mallotus villosus</i>	marine	beaches (small gravel), offshore? ¹	late May-Oct
<i>Osmerus mordax</i> ²	anadromous	lakes, rivers, streams, estuaries	early spring
<i>Spirinchnus starksi</i> ²	marine	beaches	May
<i>Spirinchnus thaelichthys</i> ²	anadromous	lakes, rivers, streams	Oct-Dec
<i>Thaelichthys pacificus</i>	anadromous	rivers, tributaries of large river systems	Mar-May

¹Carscadden et al. (1989) northwest Atlantic, undetermined in Pacific.

²Uncommon or rare and unlikely to spawn in study area.

Table 3. Developmental landmarks of capelin (*Mallotus villosus*) determined from examination of a cleared and stained developmental series 4.8-90.0 mm standard length (SL).

Length (mm SL)	Stage	Landmarks
4.0-5.0	Yolksac	Hatch
7.0-8.0	Preflexion	Yolk absorbed
8.5	Flexion	Notochord flexion begins.
25.5	Postflexion	Notochord flexion ends.
60.0	Transforming	All vertebrae and fin rays ossified.
75.0-80.0	Juvenile	Entire cranium, pterygiophores, and bones supporting fins ossified. Palatine teeth present, lateral line scales beginning to form, skin exhibits a silvery sheen similar to adults.

Table 4. Mean sea surface temperatures and salinities (\pm SD) for stations sampled from within bays around Kodiak Island (1977-79) in spring (March-May), summer (June-August), and autumn (November), and from the shelf seaward of Kodiak Island in spring (March-April), summer (June-July) and autumn (September-November).

Location	Spring	Summer	Autumn
Izhut Bay	4.8°C (\pm 1.3)	9.8°C (\pm 1.3)	6.2°C
	33.6 psu (\pm 1.1)	33.4 psu (\pm 0.1)	33.9 psu
Chiniak Bay	4.5°C (\pm 1.4)	9.4°C (\pm 1.6)	6.0°C
	33.6 psu (\pm 0.8)	33.3 psu (\pm 0.2)	34.2 psu
Kiliuda Bay	5.0°C (\pm 1.8)	10.4°C (\pm 1.6)	6.1°C
	33.0 psu (\pm 1.3)	31.4 psu (\pm 0.9)	33.6 psu
Kaiagnak Bay	5.2°C (\pm 1.5)	9.8°C (\pm 2.2)	5.8°C
	33.5 psu (\pm 0.7)	33.0 psu (\pm 0.4)	33.9 psu
Kodiak Shelf	3.9°C (\pm 0.9)	8.2°C (\pm 0.7)	6.9°C (\pm 0.6)
	32.2 psu (\pm 0.3)	32.2 psu (\pm 0.3)	32.2 psu (\pm 0.4)

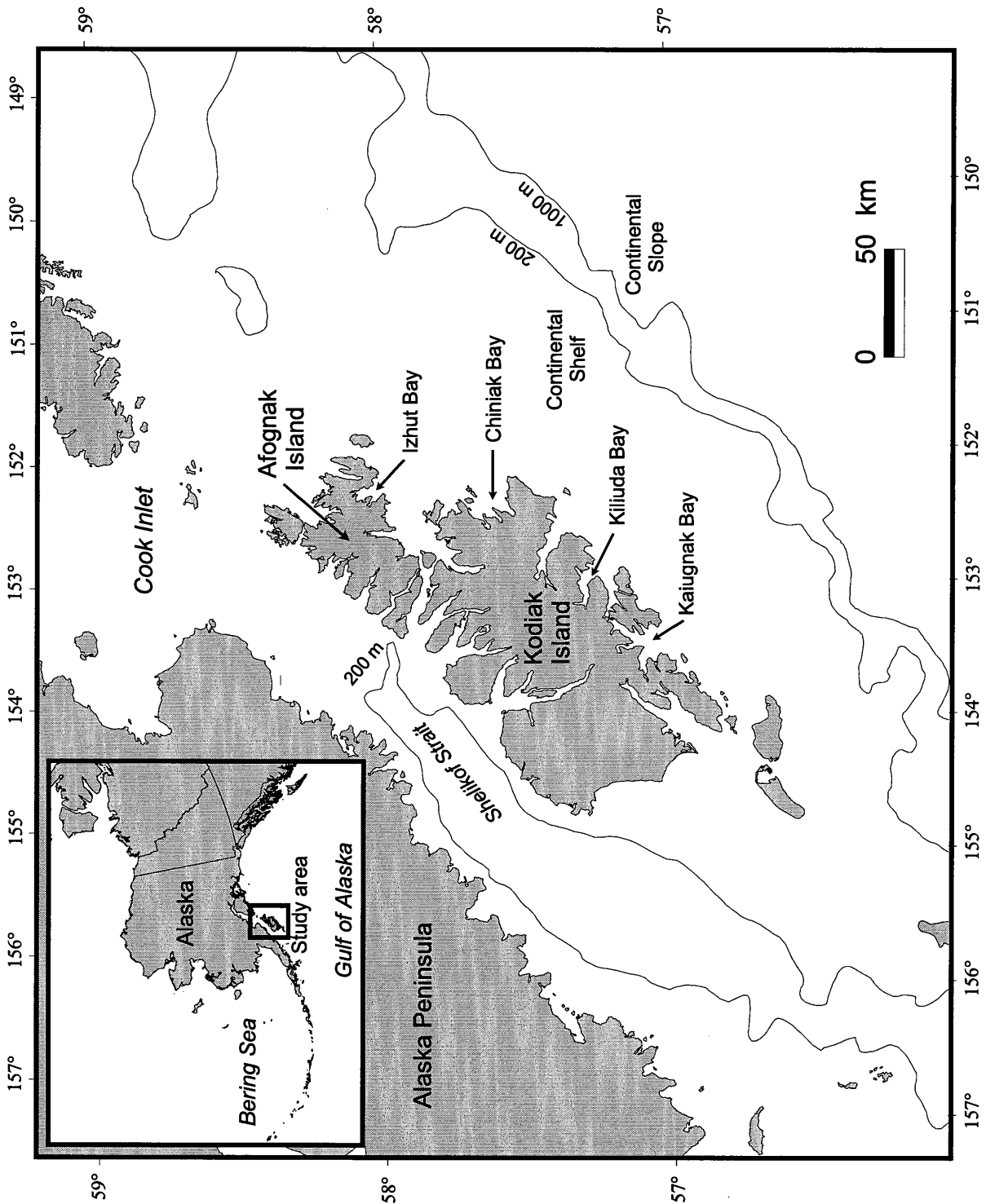


Figure 1. --- Map of the Kodiak Archipelago and adjacent study area.

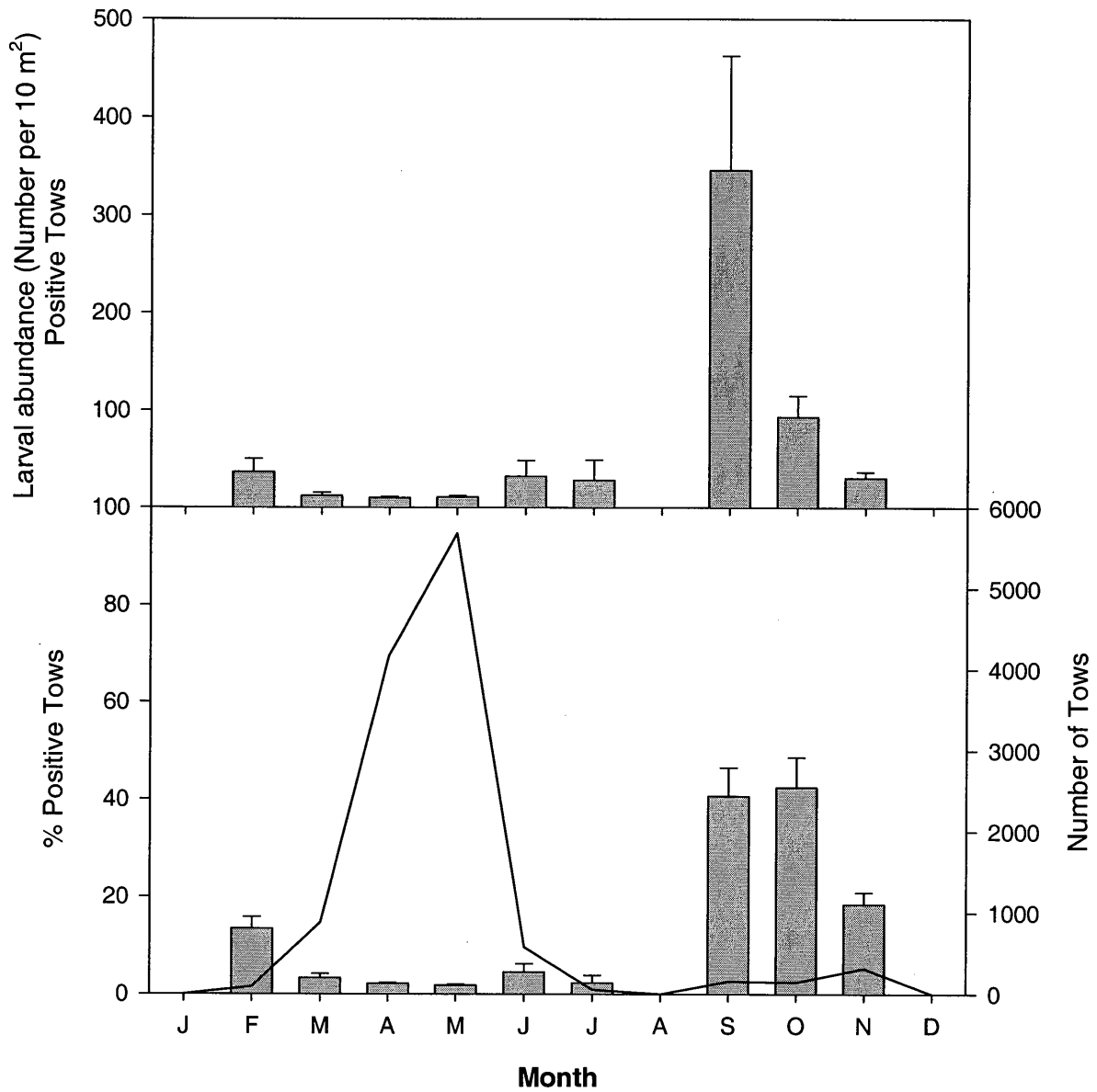


Figure 2. -- Seasonal variation in mean abundance (+SE) (top panel), and sampling effort and percent occurrence (bottom panel) of *Mallotus villosus* larvae in bongo samples collected in the Gulf of Alaska 1977-98.

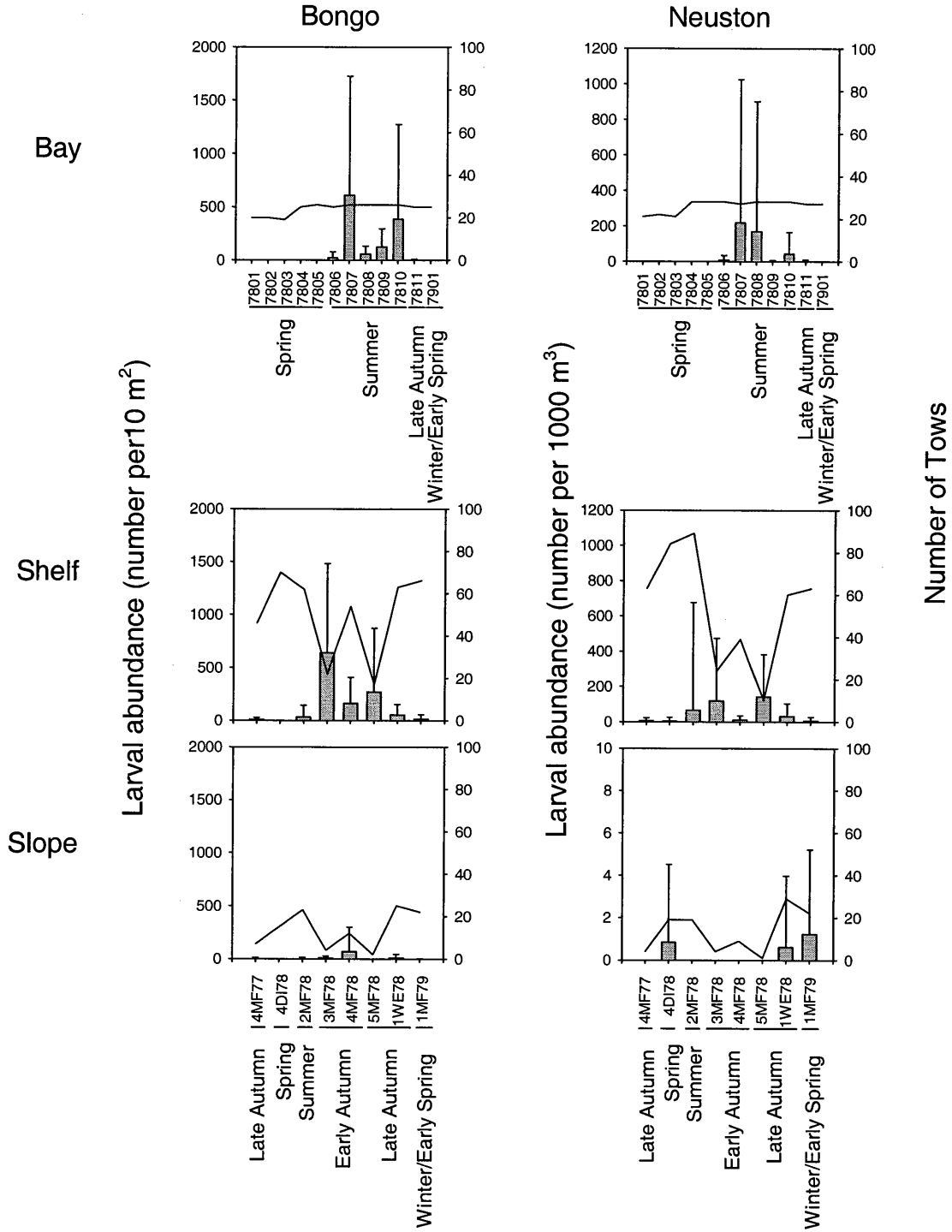


Figure 3. -- Seasonal variation in sampling effort and mean abundance (+SE) of *Mallotus villosus* larvae in bongo and neuston samples collected in bays and over the continental shelf and slope near Kodiak Island, October 1977 - March 1979. Labels 7801, 4MF77 etc. are cruise numbers (see Table 1).

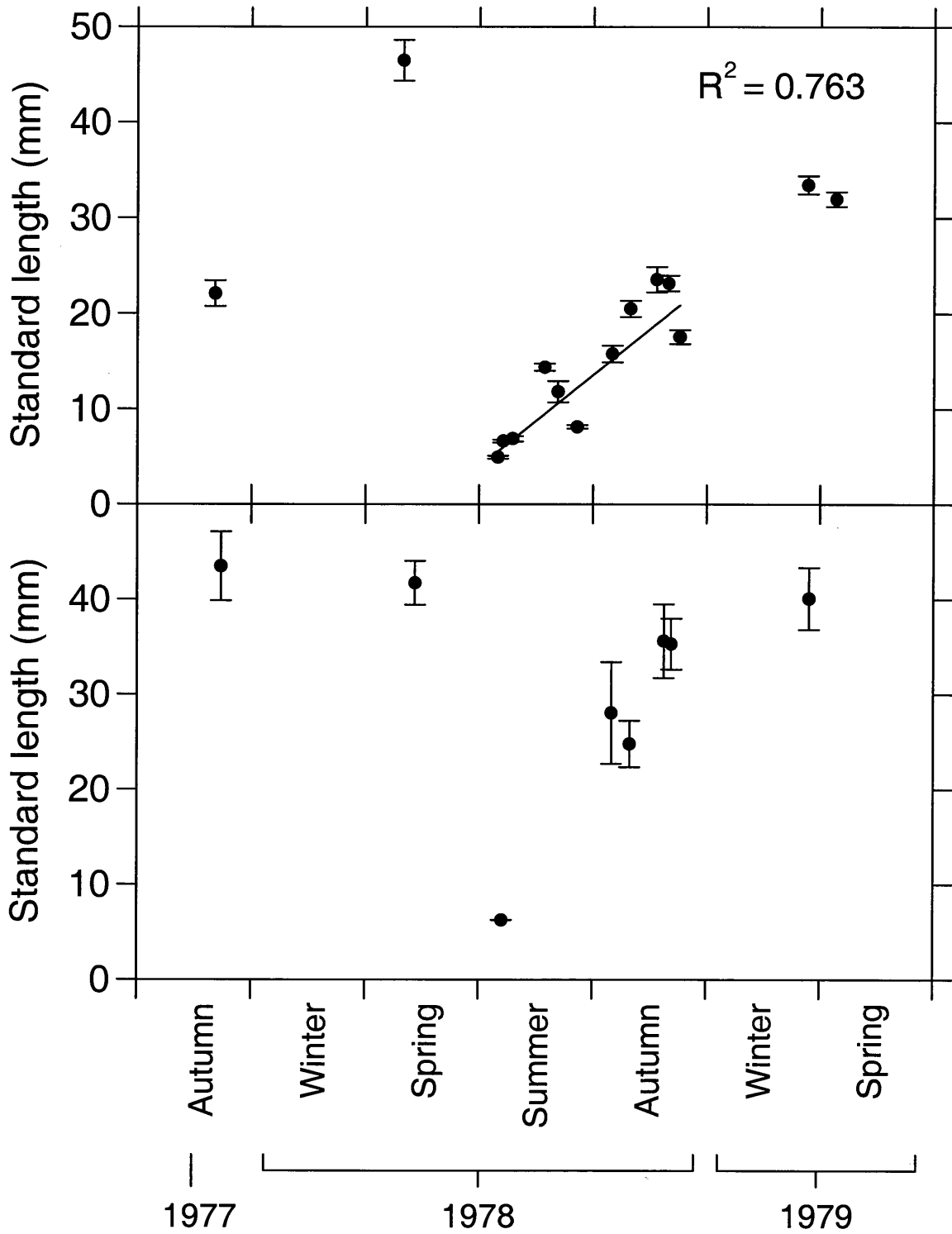


Figure 4. -- Seasonal variation in mean standard length (\pm SE) of *Mallotus villosus* larvae collected in bongo (top panel) and neuston (bottom panel) tows in bays and over the continental shelf and slope near Kodiak Island, October 1977 - March 1979, and regression of larval length with sampling date for summer through autumn of 1978.

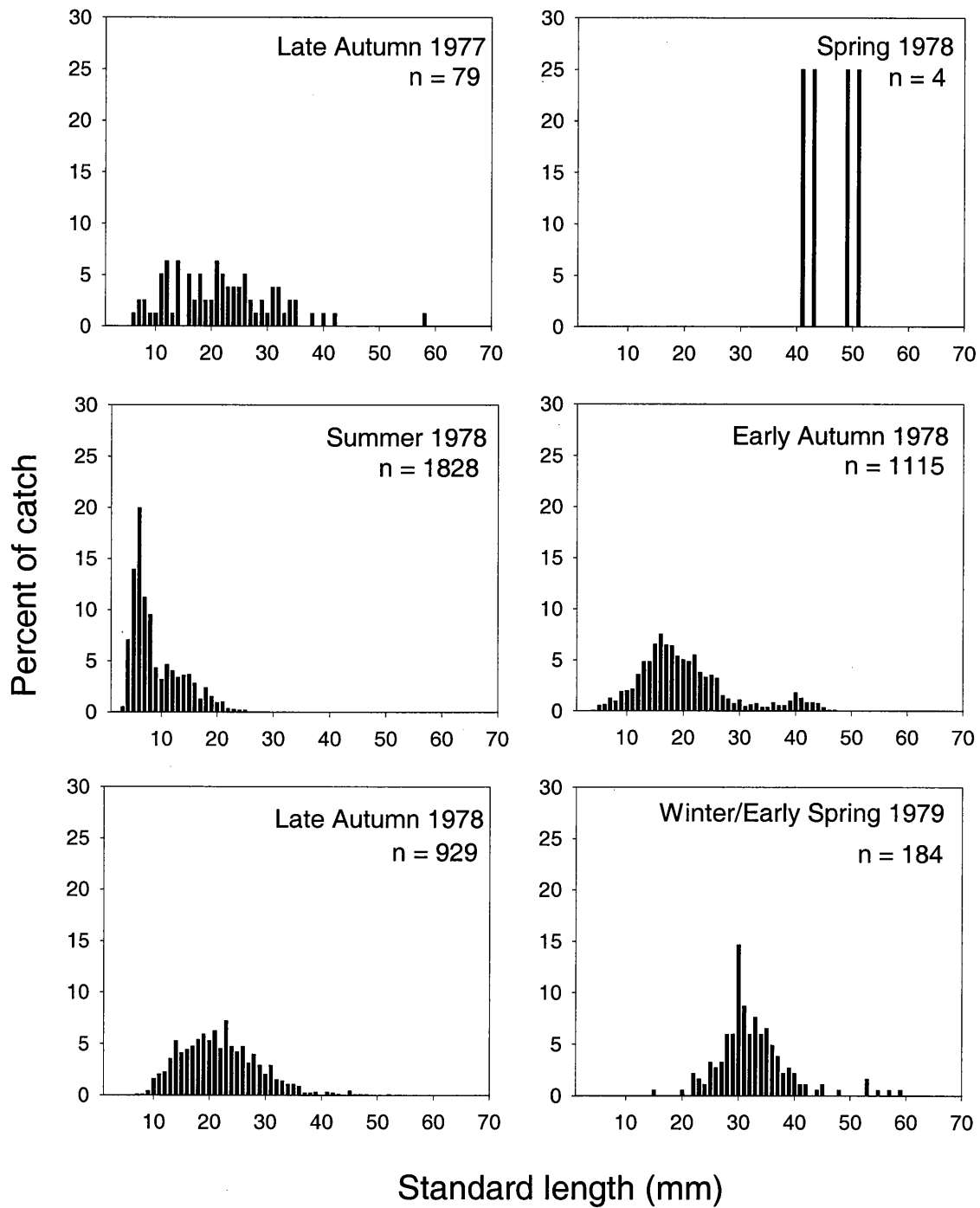
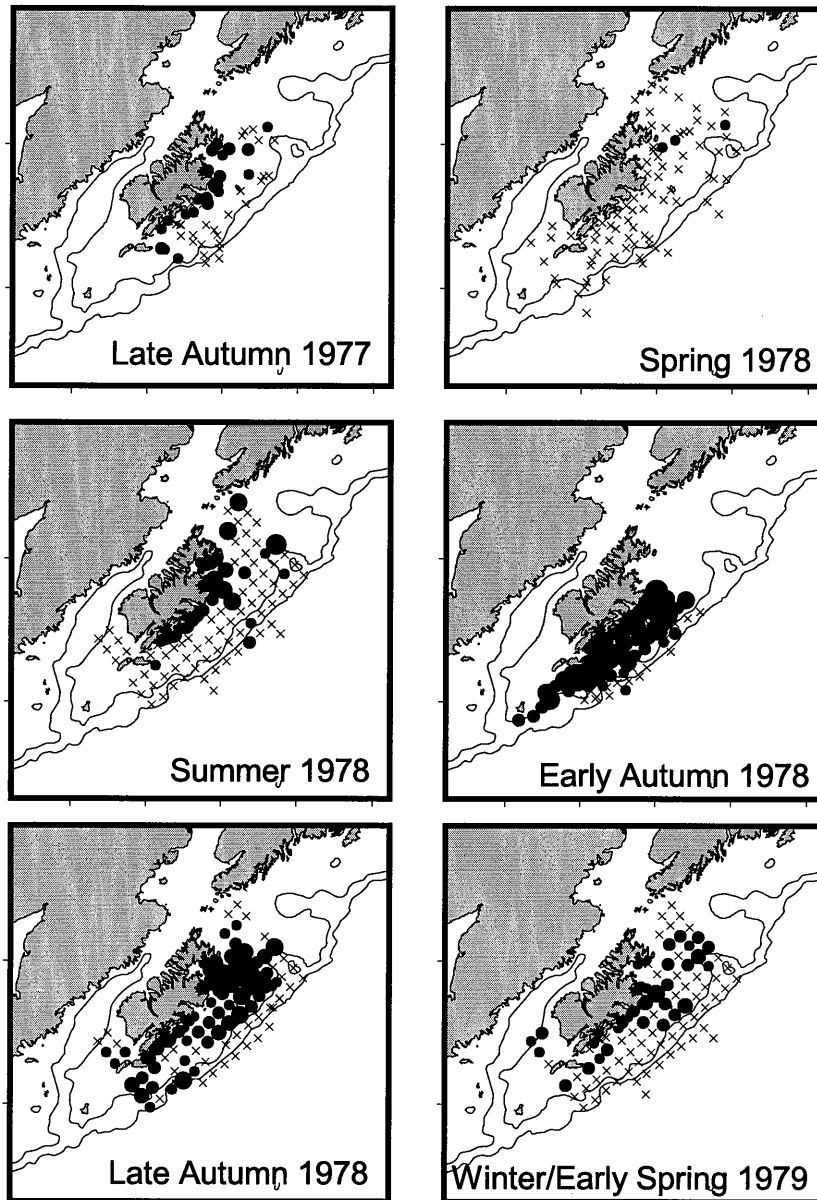


Figure 5. -- Seasonal variation in length frequency of *Mallotus villosus* larvae collected in bongo tows in bays and over the continental shelf and slope near Kodiak Island, 1977-79. n = number of fish larvae measured



Larval abundance (number per 10 m²)

- × 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

Figure 6. -- Seasonal variation in distribution and abundance (number per 10 m²) of *Mallotus villosus* larvae collected in bongo tows in bays and over the continental shelf and slope near Kodiak Island, 1977-79.

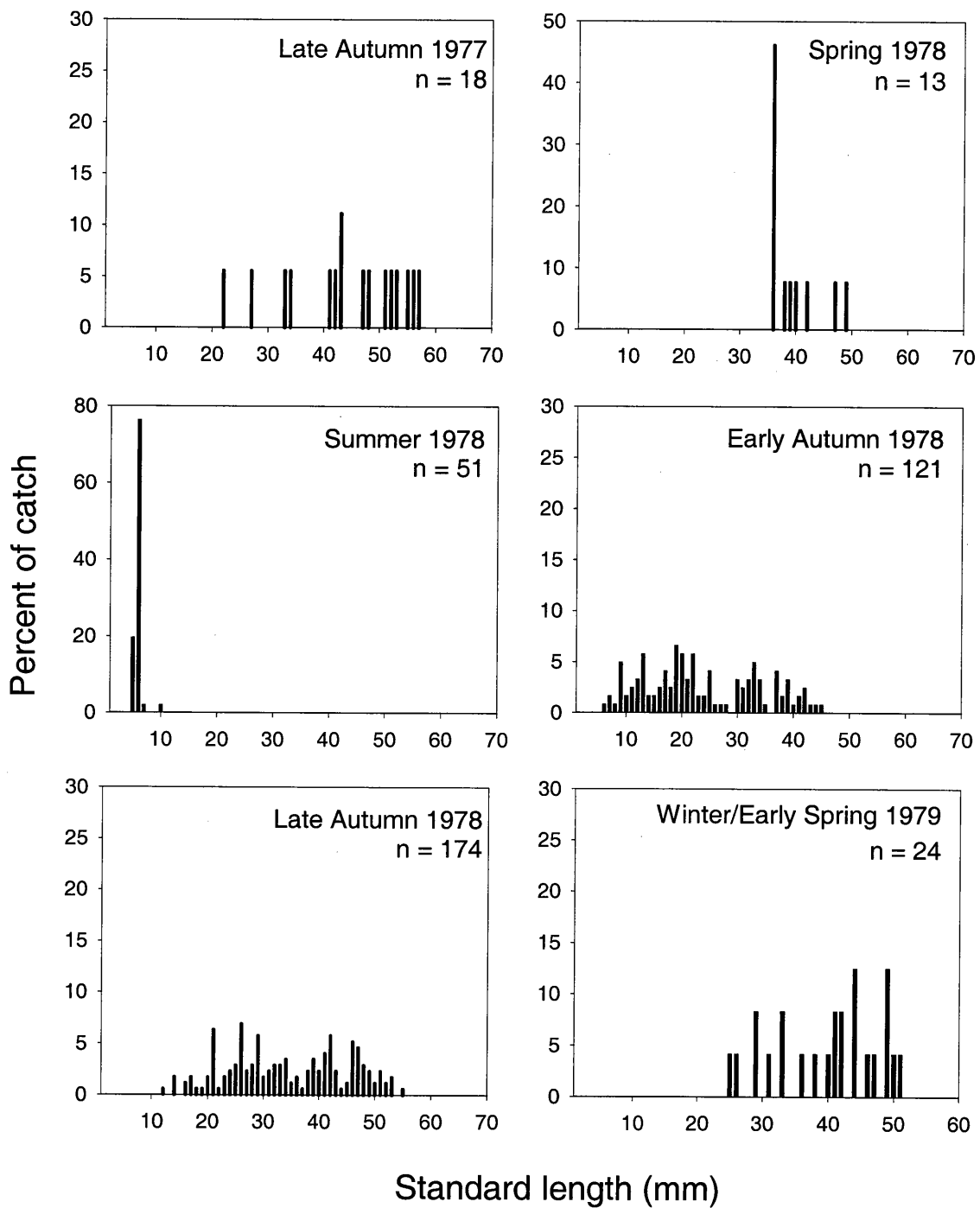
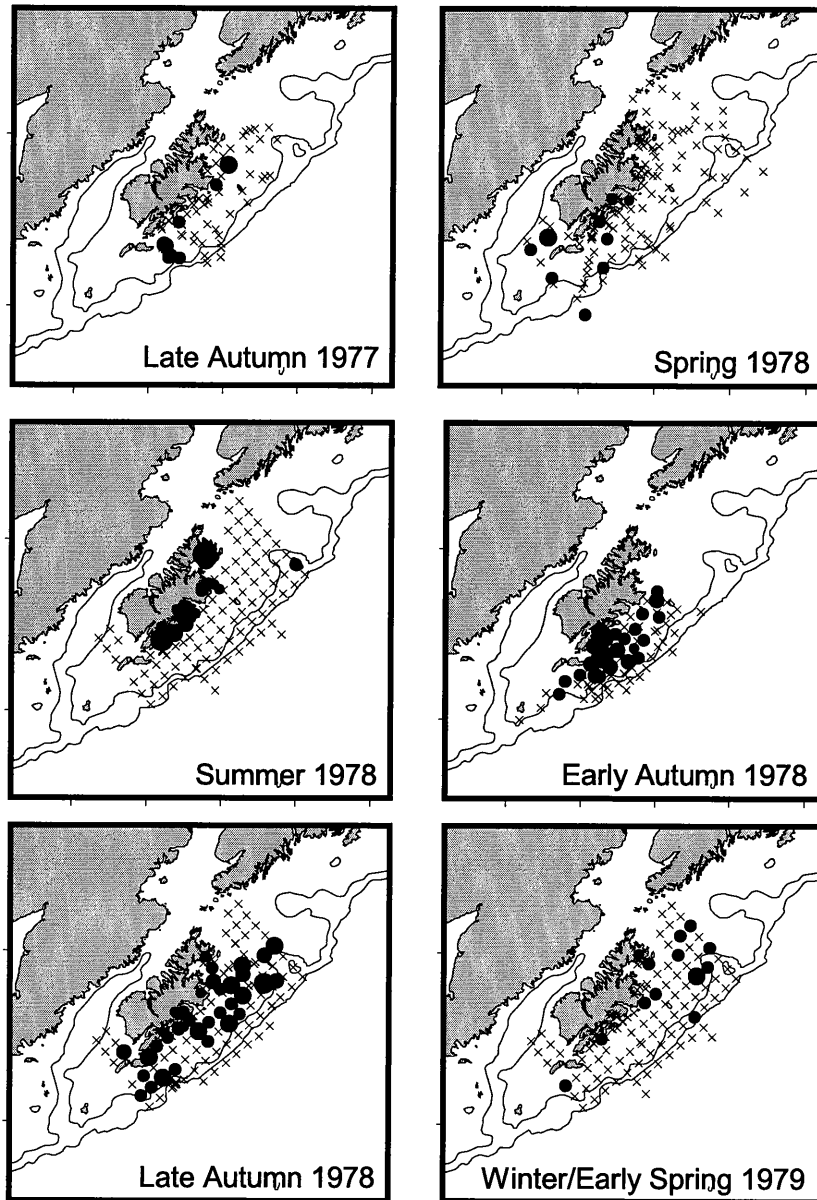


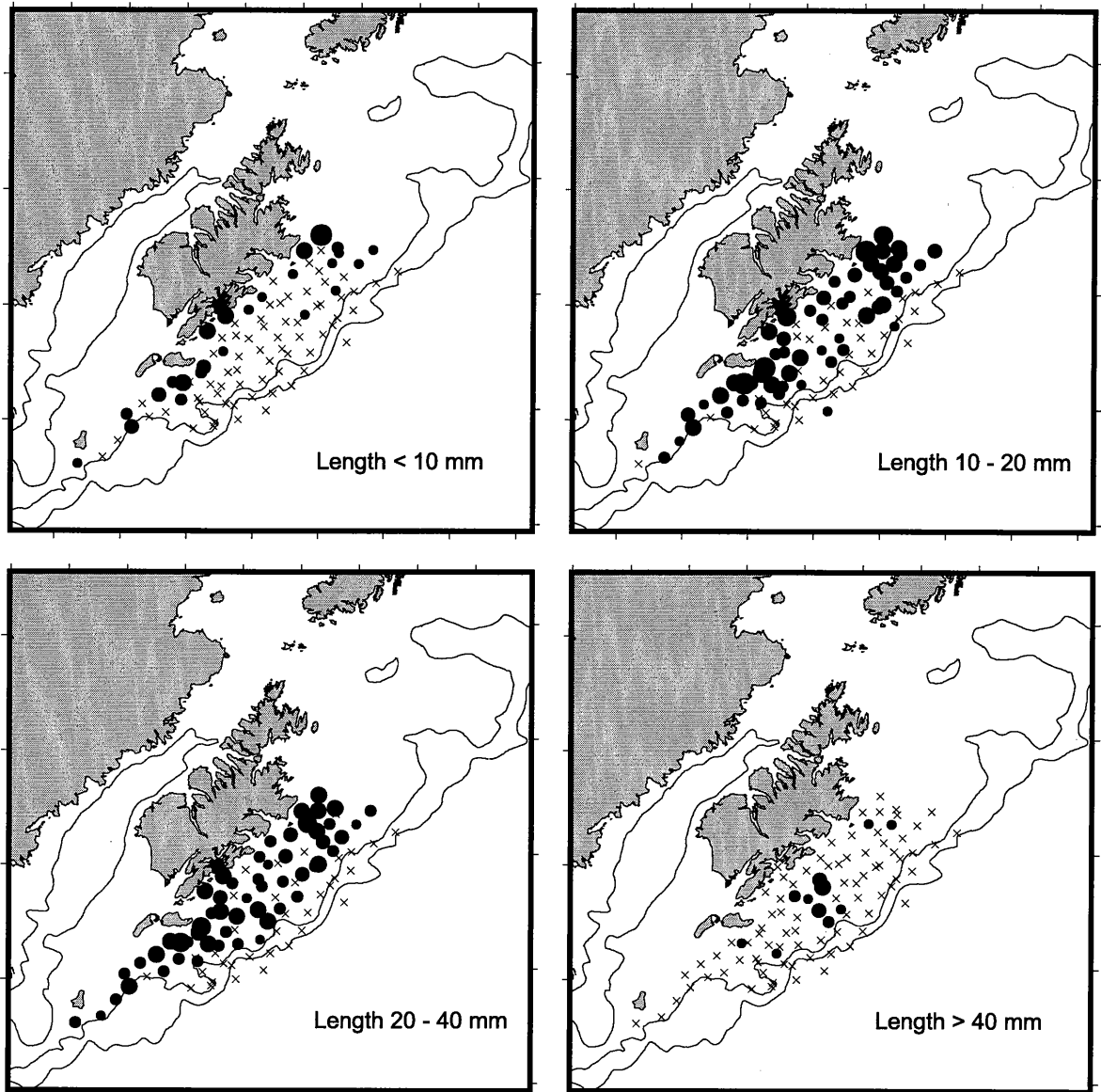
Figure 7. -- Seasonal variation in length frequency of *Mallotus villosus* larvae collected in neuston tows in bays and over the continental shelf and slope near Kodiak Island, 1977-79. n = number of fish larvae measured



Larval abundance (number per 1000 m³)

- × 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

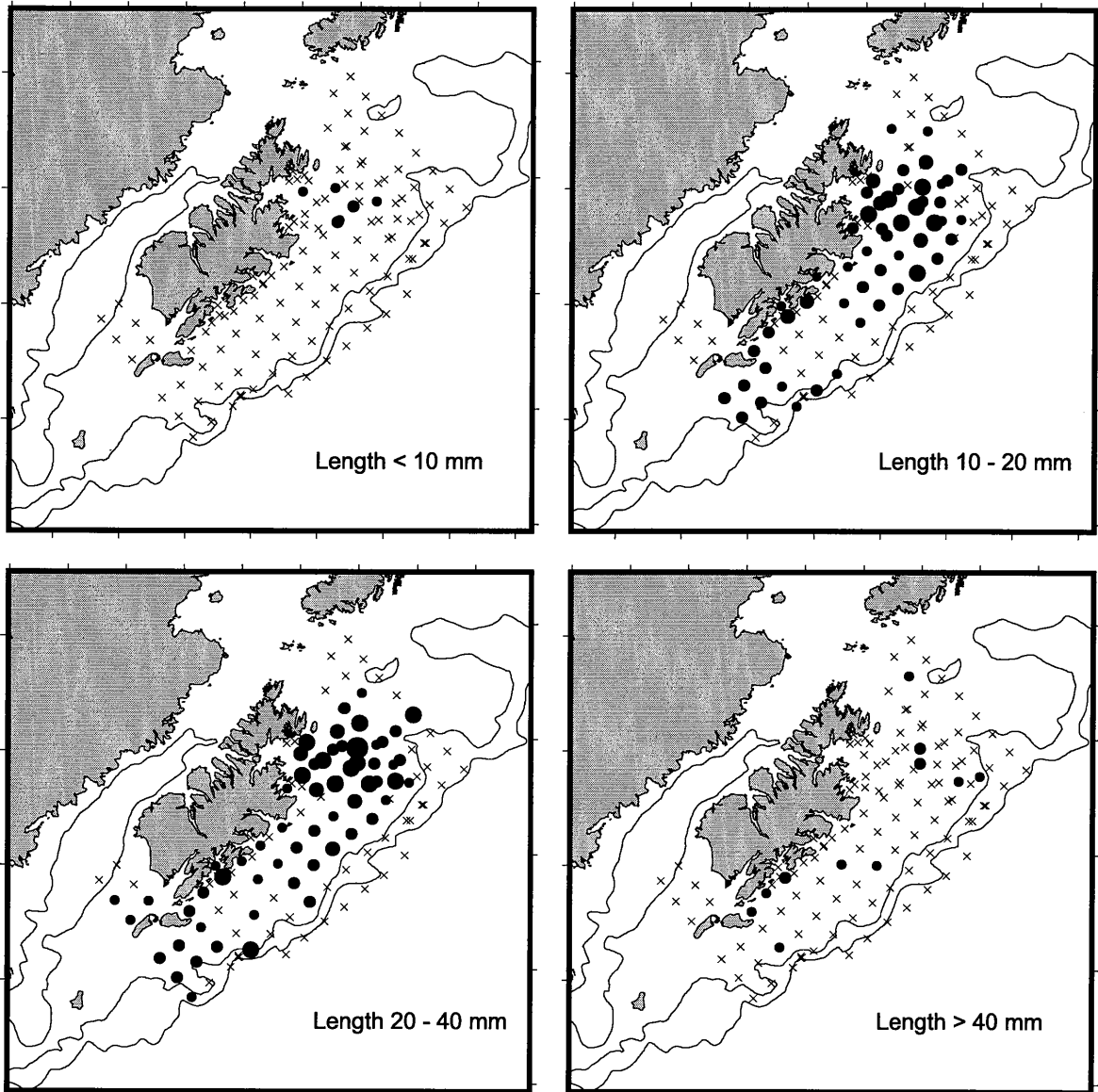
Figure 8. -- Seasonal variation in distribution and abundance (number per 1000 m³) of *Mallotus villosus* larvae collected in neuston tows in bays and over the continental shelf and slope near Kodiak Island, 1977-79.



Larval abundance (number per 10 m²)

- x 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

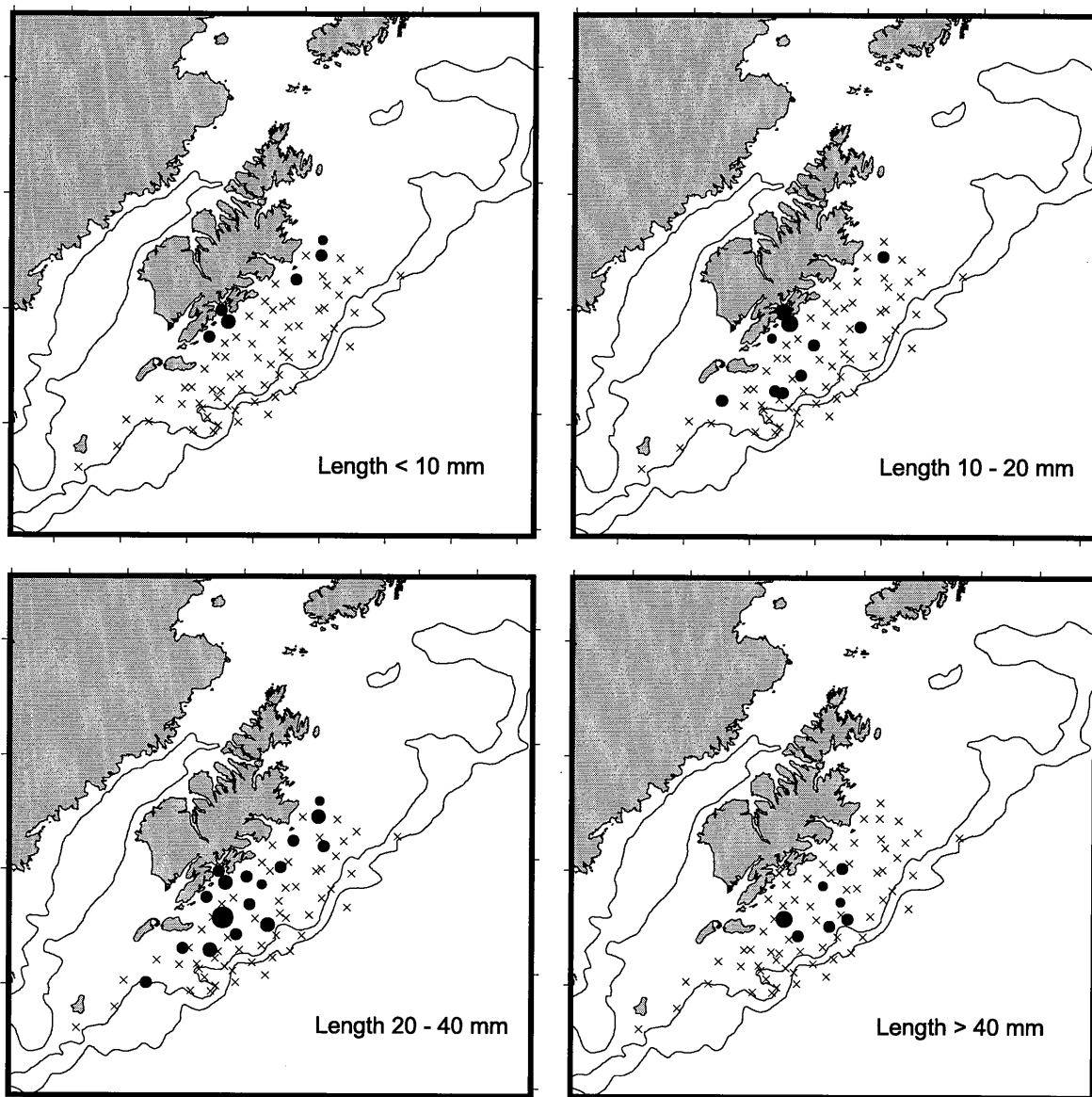
Figure 9. -- Distribution of four size-categories of *Mallotus villosus* larvae in bongo samples collected during early autumn 1978.



Larval abundance (number per 10 m²)

- × 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

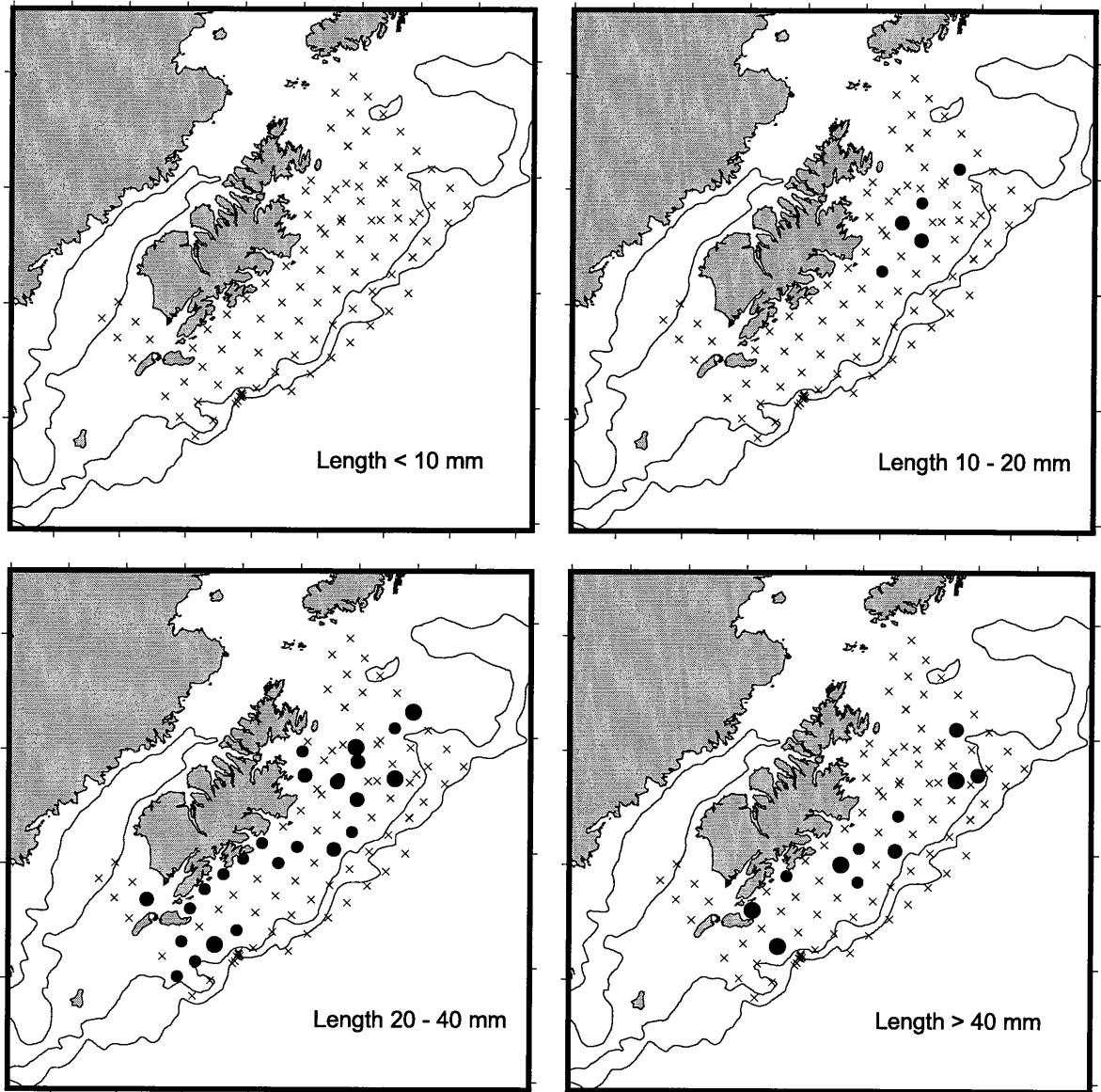
Figure 10. -- Distribution of four size-categories of *Mallotus villosus* larvae in bongo samples collected during late autumn 1978.



Larval abundance (number per 1000 m³)

- × 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

Figure 11. -- Distribution of four size-categories of *Mallotus villosus* larvae in neuston samples collected during early autumn 1978.



Larval abundance (number per 1000 m³)

- × 0
- 0 - 10
- 10 - 50
- 50 - 100
- 100 - 500
- 500 - 1000
- > 1000

Figure 12. -- Distribution of four size-categories of *Mallotus villosus* larvae in neuston samples collected during late autumn 1978.

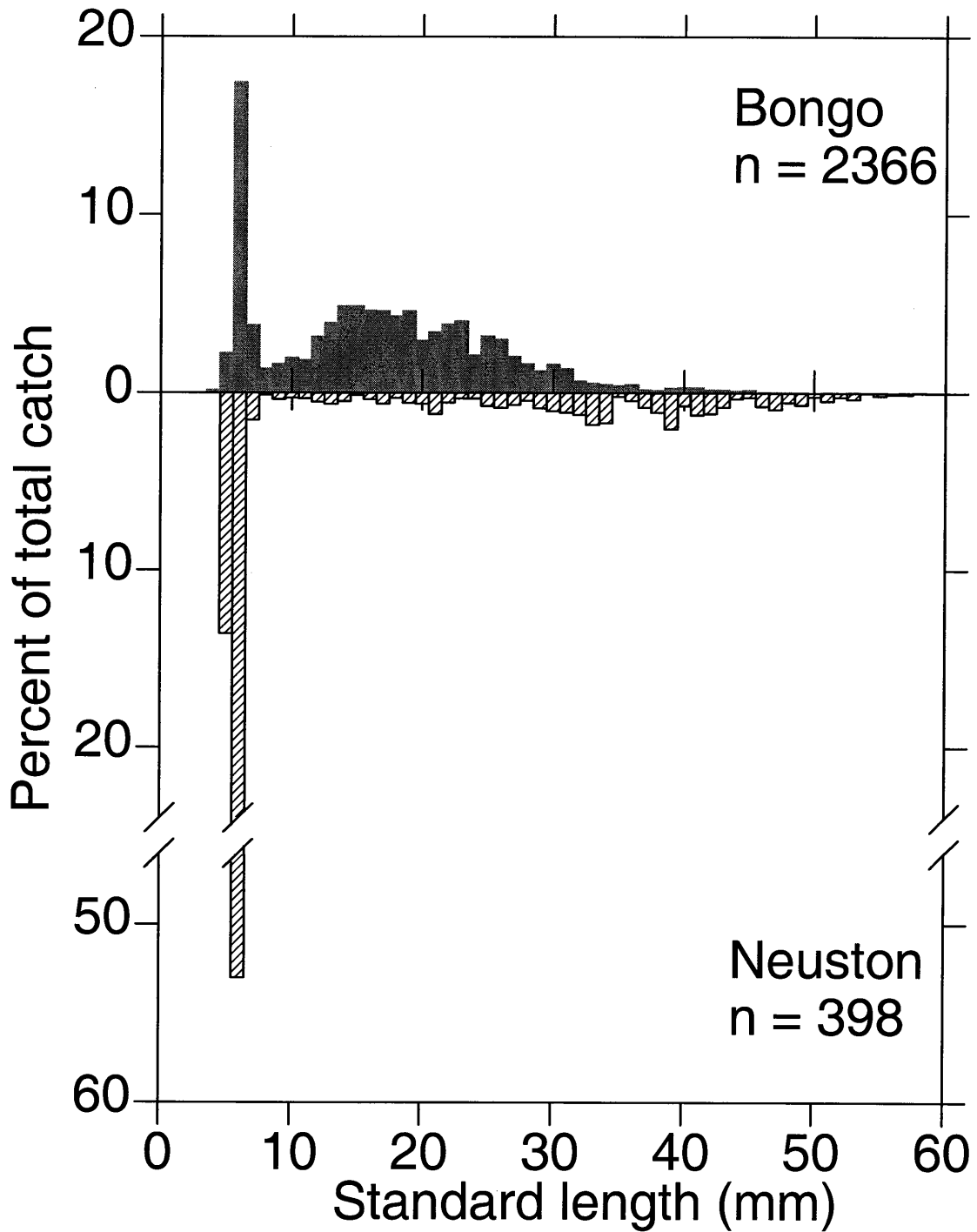


Figure 13. -- Comparison of length frequencies for *Mallotus villosus* larvae collected in bongo (top panel) and neuston tows (bottom panel) - data from all cruises combined. n = number of fish larvae measured.

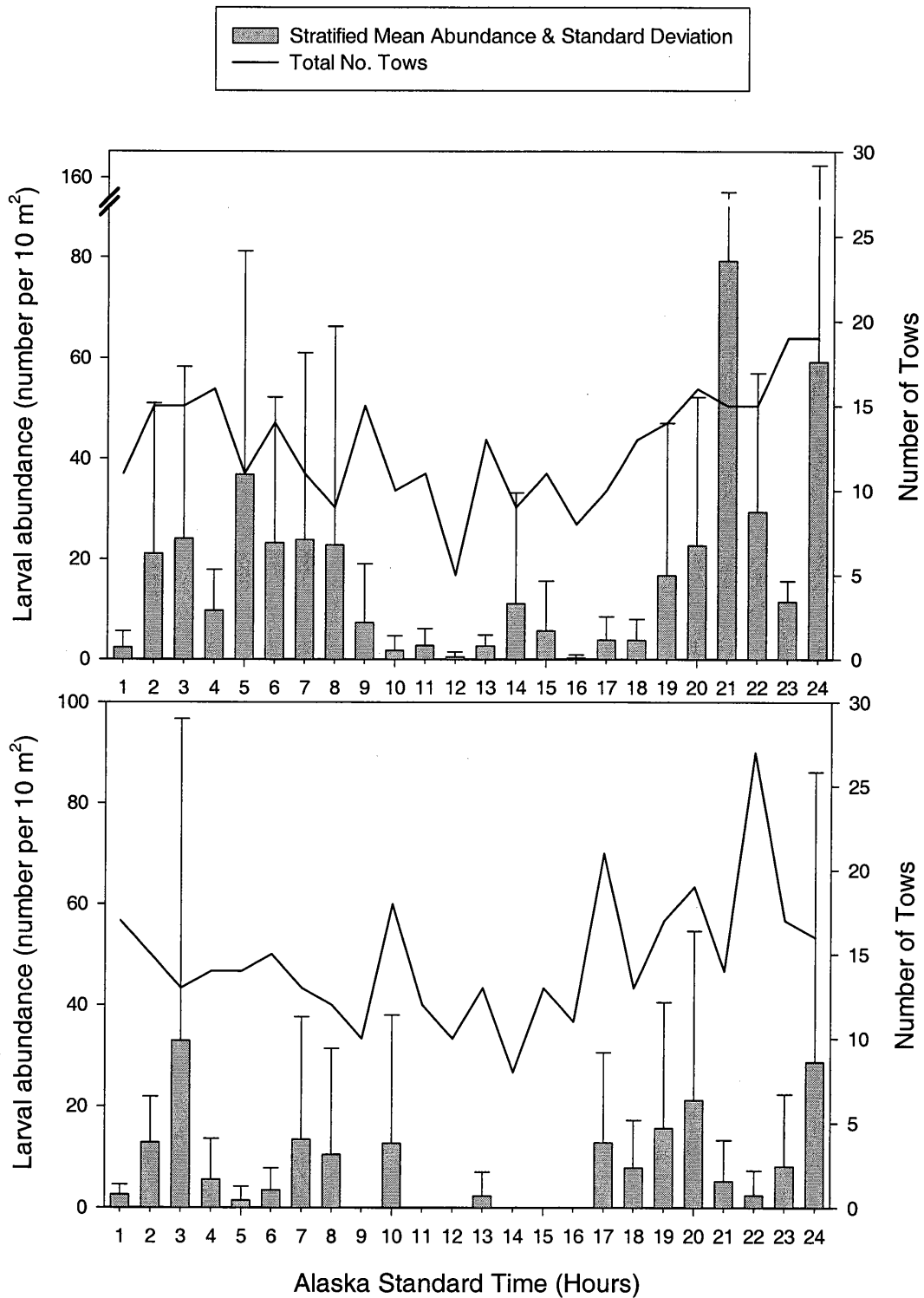


Figure 14. -- Diel variation (hourly intervals) in mean stratified abundance (+SD) of *Mallotus villosus* larvae in bongo samples (top panel - data combined from cruises 4MF77, 2MF78, 1WE78 and 1MF79), and neuston samples (bottom panel - data combined from cruises 4MF77, 4DI78, 1WE78 and 1MF79).

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