

Comparison of Georges Bank zooplankton community in relation to growth and mortality of herring larvae during two winter periods.

by

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Abstract

The composition, abundance, and distribution of the larger zooplankton on Georges Bank during February 1975 and 1976 were compared. Zooplankton volumes were higher and more uniformly dispersed in 1976 than in 1975, and the mean density of zooplankters was also higher in 1976. Species diversity indices (Simpson and Shannon-Weaver Indices) were basically similar between the two years, and stations with greatest diversity occurred near the center of Georges Bank suggesting that this area was favorable to a large number of species. All the dominant species (Centropages typicus, Sagitta elegans, Calanus finmarchicus, Metridia lucens, Pseudocalanus minutus, Limacina retroversa, Centropages hamatus) increased in abundance in 1976, with the exception of C. finmarchicus and C. hamatus, and their distributions were more uniform corresponding to the greater mixing of waters on Georges Bank based on more homogeneous temperature and salinity patterns and higher wind stress values in 1976. Wind stress values used as an index of mixing were three times greater in February 1976 compared to 1975. Also, resultant Ekman transport values were anomalously high and in a southeasterly direction for February 1976 compared to the usual southwesterly transport for February 1975. Population centers of most of the dominant species which had sharp distributional borders along southern Georges in 1975, appeared to shift their centers more to the southeastern part in 1976, extending off the southern edge of the Bank. The most abundant larval fish both years was Ammodytes spp. and its distribution on Georges Bank was similar to that of larval herring. The greater growth and consequently lower mortality of larval herring reported for winter 1976 compared to 1975 corresponded to the increased abundance of its principal food organism, Pseudocalanus minutus, in 1976. An examination of the community trophic structure and species occurrence in relation to the hydrography of Georges Bank is included.

Introduction

An intensive field program has been underway since 1971 to investigate the physical and biological mechanisms controlling the recruitment process of sea herring in the Georges Bank-Gulf of Maine area (Figure 1). Year-class success of sea herring is believed to be largely determined during its first six months of life: the larval period. In order to monitor yearly changes in larval production, growth, mortality, and dispersal during the fall spawning season, at least four plankton-hydrography surveys have been conducted from October through December, and another survey in February, starting in 1974, to cover the overwintering period. Most of the sampling effort has focused on the Georges Bank-Nantucket Shoals area.

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One of the hypotheses being investigated is that the number of recruits available in the spring is dependent upon larval survival through the winter when planktonic food organisms may be sparse. Further, the linking mechanism is believed to be an inverse relationship between larval growth and mortality, which may be a density-dependent process regulated by the available food supply. A 3-year series of December-February larval herring growth and mortality rates estimated by Lough (1976) for the Georges Bank-Nantucket Shoals areas provided support for the inverse relationship of growth and mortality and the critical overwintering period hypothesis. A marked difference occurred during the 1974-75 and 1975-76 winters when larval growth rates were 0.15 mm/day and 0.2 mm/day, respectively, with corresponding instantaneous mortality rates of 4.40%/day and 1.52%/day.

Research is in progress at the Northeast Fisheries Center (NEFC) to examine possible relations between changes in critical population parameters and larval condition factors, prey selection through gut analysis, and potential prey availability. This paper presents our first look at the zooplankton community during the two winters, 1975 and 1976, of contrasting larval herring growth and mortality. The major plankton taxa and particularly the known or potential prey of herring larvae are compared and contrasted in relation to hydrographic conditions during the two winters with the objective of gaining some insight into the mechanisms that govern survival through the winter period.

Methods

A grid of standard stations spaced 30' Lat. by 15' Long., each representing a rectangular area approximately 1.16×10^9 m², are covered during a survey. Standard plankton tows and hydrographic casts are made at each station. A double-oblique plankton haul is made at 3.5 knots using a 61-cm diameter bongo (.333 and .505 mm mesh) and 20-cm bongo (.253 and .165 mm mesh) tandem arrangement. The sampling gear is set at 50 m/min to 100 m maximum depth or to within 5 m of the bottom and retrieved at 10 m/min. Temperature and salinity depth profiles are obtained at the end of each tow.

The two periods of interest were surveyed the first winter by Albatross IV during 4-19 December 1974 (Cruise 74-13), 12-28 February 1975 (Cruise 75-02), and the second winter during 5-17 December 1975 (Cruise 75-14), 9-25 February 1976 (Cruise 76-01). All herring larvae were sorted and measured (standard length) from the .505 mm mesh samples for all stations on the four cruises listed above and the various estimates of overwinter growth and mortality have been derived previously by Lough (1976). For the present study of the Georges Bank winter zooplankton community, only every other station was selected for the two February surveys as shown in Figure 2. The .505 mm mesh sample from each of the selected stations was subsampled using a Folsom splitter to reduce the number of organisms identified to a range of 250-500. Organisms were identified to species or major taxonomic groups, and standardized to number per 1000 m³ and per 10 m². Relative abundance measures of all species for each February, made according to the methods of Fager (1957), consisted of mean rank, dominance, range, mean (\bar{X}), variance (S^2), standard deviation (S), coefficient of variation (S/\bar{X}), coefficient of dispersion (S^2/\bar{X}), and frequency of occurrence. Species diversity and equitability measures were made using Simpson Diversity (D) and Shannon-Weaver Diversity (H') indices

and equitability coefficient (J) as detailed by Poole (1974). Night/day variability also was examined using the diversity measures above. A Mann-Whitney U-test (Tate and Clelland, 1959) was used to interpret differences in the abundance of dominant or important species between the two Februaries.

Total plankton volume (cc/10 m²) and selected species (no./10 m²) are plotted by station and contoured to illustrate geographical distributions. The abundance estimates (no./10 m²) are plotted rather than the density estimates (no./1000 m³) in order to take into account the wide range of sampling depths in the Georges Bank study area. A comparison of both abundance and density plots for selected species did not show any significant differences in geographic distribution between the two methods. Simpson's Diversity values also were plotted.

Temperature and salinity data at various depth levels for both surveys were plotted and contoured by the Fishery Oceanography Investigation, NEFC. These data as well as a fuller treatment of the methods and results presented in this paper can be found in Dubé, Lough, and Cohen (1977) and Lough (1976).

Georges Bank Hydrography, Februaries 1975 and 1976

Temperature and salinity distributions were basically the same during Februaries 1975 and 1976. Vertically and horizontally well-mixed waters of 4-6°C, and 32.5-33.5 ‰ predominated over Georges Bank. Higher temperatures and salinities were observed along the shelf-slope water front and lower temperatures and salinities were observed along the northern and eastern border of Georges Bank. The temperature was somewhat warmer and salinity about 0.5 ‰ less saline on central Georges Bank in February 1976 compared to 1975. Also, both temperature and salinity were more uniform with depth and more homogeneous across Georges Bank indicating that stronger vertical mixing occurred during February 1976. These data are supported by monthly resultant wind stress values (supplied by the Atlantic Environmental Group (AEG), NEFC, for 42° Lat., 66° Long.) which can be used as an index of the amount of water column mixing energy generated by the wind. The wind stress index (10⁻³ dynes/cm²) for February 1976 (670) was nearly three times that for February 1975 (235). Another important difference between the two Februaries, especially in regard to the dispersal of planktonic organisms on Georges Bank, is shown by the resultant Ekman transport values provided below for the same location.

Period	Ekman transport index (10 ³ metric tons/sec/km)	Direction from North
February 1975	24.4	215°
February 1976	69.1	165.5°

An anomalously high southeasterly transport occurred during February 1976. An eastward component of the Ekman transport occurred during February only once before (1971) in 31 years of recording, and then at only half the 1976 magnitude. The transport index for February 1975 was normal and to the southwest based on a 10-yr mean.

Total Zooplankton Volume

The mean displacement plankton volume for the 20 stations in the study area was higher during February 1976 (\bar{X} = 71.8 cc/10 m²) than February 1975 (\bar{X} = 60.5 cc/10 m²) and statistically different at the 10% level by the Mann-Whitney U-test.

Coefficients of variation (S/\bar{X}) differed considerably, 0.86 and 1.24 for February 1976 and 1975, respectively, indicating that the February 1976 plankton volumes were more uniformly distributed over Georges Bank compared to a patchy distribution during 1975. Plots of total plankton volume for February 1975 and 1976 (Figure 3) illustrate these differences. The February 1975 plot shows low plankton volumes ($<50 \text{ cc}/10 \text{ m}^2$) over most of the study area with higher volumes on the northeast peak and along a narrow strip from central Georges to the southwestern end. By contrast; the February 1976 plot shows a broad, centrally located, high plankton volume area of the Bank. Station 54 in the southwestern corner had high plankton volumes during both years.

Total Zooplankton Numerical Abundance

The mean total number of zooplankters per 1000 m^3 for each station is given in Tables 3 and 4, and the mean number of each species is given in Tables 1 and 2. A higher total mean number of zooplankters was found during February 1976 ($50,963/1000 \text{ m}^3$) than February 1975 ($41,397/1000 \text{ m}^3$), a 23% increase corresponding to a 19% increase in mean zooplankton volumes. Coefficients of variation (C.V.) for the mean number of zooplankton per station showed greater variation between stations for February 1975 (C.V. = 0.94) compared to February 1976 (C.V. = 0.69); corresponding to the higher variability of displacement volumes for February 1975. Zooplankton abundance and volumes, therefore, corresponded closely. Copepods and chaetognaths were the two most important groups in this study based on either abundance or volume.

Species Diversity and Diurnal Variation

The number of species, total number of individuals, and the various diversity indices for each station in day and night blocks are listed in Table 3 for February 1975 and Table 4 for February 1976. The mean number of species per station was similar for the two years (16.9 in 1975 and 15.1 in 1976) as were the diversity indices. Simpson's diversity index was 0.68 for February 1975 and 0.69 for February 1976, suggesting similar contributions by the dominant species each February. Mean H' indices were equal (1.60) both years indicating that the components of overall species equitability contributed by the species of intermediate abundance did not differ.

Somewhat higher mean numbers of individuals per 1000 m^3 were collected at night compared to day stations both years; however, the mean number of species for day and night stations was the same in 1975 (16.9) and similar in 1976 ($D = 14.6$, $N = 15.5$ species). Four taxonomic groups contributed to the February 1975 night increase in mean abundance over day stations: copepods (46% night increase), mysids (18%), euphausiids (18%), and chaetognaths (9%). In February 1976; mysids and euphausiids contributed 71% of the night/day difference, chaetognaths, 27%, and copepods; less than 5%. Both years were characterized by greater between-station variability of zooplankton densities in the day samples (note C.V. values Tables 3 and 4) which may reflect the more variable daylight conditions.

Plots of the geographical distribution of Simpson's diversity values (Figure 4) show that stations of highest diversity were usually located on the central part of Georges Bank both years, but they covered a broader central area during February 1976.

Zooplankton Components

A total of 62 species were collected during both Februaries, 45 species during 1975 and 46 species during 1976. Only 34 species were common to both years. Species or taxa found in each February survey appear in Tables 1 and 2 by order of mean rank. Fifteen predominant species, based on the criteria for species present in concentrations $>1/m^3$ mean density and/or in $>50\%$ of the samples, occurred in February 1975 (Calanus finmarchicus, Centropages typicus, Sagitta elegans, Limacina retroversa, Metridia lucens, Pseudocalanus minutus, Centropages hamatus, Crustacean larvae, Vertebrate (fish) eggs, Centropages spp., Spisula solidissima larvae, Pollachius virens larvae, Meganyctiphanes norvegica, Gadus morhua larvae, Clupea harengus larvae) and in February 1976 (Centropages typicus, Sagitta elegans, Calanus finmarchicus, Metridia lucens, Pseudocalanus minutus, Limacina retroversa, Centropages hamatus, Hyperiidea, Gammaridea, Crustacean larvae, Candacia armata, Unidentified calanoid copepod, Ammodytes dubius? larvae, Neomysis americana, Clupea harengus larvae).

Copepoda

Copepods made the greatest contribution of any group to zooplankton abundance both years. The mean density of copepods per station in February 1975 (25,718/1000 m^3) comprised 62% of the total mean zooplankton density per station; mean copepod density in February 1976 (32,688/1000 m^3) comprised 64%. Fifteen copepod species were observed in February 1975 and 16 species in 1976. The abundance of calanoid copepods far exceeded the abundances of the cyclopid and harpacticoid orders. Twelve of the 21 species identified were common to both years and comprised virtually all of the copepod abundances for 1975 and 1976. The unidentified species of calanoid, cyclopid, and harpacticoid copepods comprised approximately 1% of the group for either year. Five copepod species were dominant at one or more stations in both years (Calanus finmarchicus, Centropages typicus, Centropages hamatus, Metridia lucens, Pseudocalanus minutus) and are discussed individually below.

The distribution pattern of Calanus finmarchicus during both Februaries was similar and relatively uniform across most of Georges Bank with an intermediate abundance of 1,001-10,000/10 m^2 (Figure 5). In both years high densities occurred on the northeast and northwest edge of the Bank. However, a low density front was observed along the southern edge of the Bank in 1975, but not in 1976. The 1975 mean density (11,135/1000 m^3) was 33% higher than the 1976 mean density (7,441/1000 m^3), which was found to be significantly different at the 20% level by Mann-Whitney U-test (Tables 1 and 2). Correspondingly, C. finmarchicus dropped from the highest ranked zooplankton in February 1975 (dominance frequency 13/20) to the third highest ranked species in February 1976 (dominance frequency 5/20).

There appears to have been a marked change in the abundance and distributional pattern of Centropages typicus between the two Februaries (Figure 6). Abundance of C. typicus across Georges Bank was generally in the range of 1,001-10,000/10 m^2 both years. In 1975, a sharp decrease in abundance occurred along the southern edge, but in 1976 their distribution extended off the southern edge of the Bank in a more irregular pattern. The mean density in 1976 (11,265/1000 m^3) was significantly higher (5% level, Mann-Whitney U-test) than the mean density in 1975 (6,058/1000 m^3) (Tables 1 and 2). C. typicus ranked higher than all other

zooplankters in February 1976 with a dominance frequency of 10/20 and somewhat lower in 1975 when it was ranked second with a dominance frequency of 5/20. The distributional patterns as indicated from the coefficients of variation (C.V.) also were quite different between the years. In 1975 the C.V. = 1.41 for the 20 stations in the study area indicated a patchy distribution, whereas in 1976 the C.V. = 0.87 indicated a greater uniformity of their distribution.

Centropages hamatus appeared to be more restricted to the western half of Georges Bank and delimited by the 100 m depth contour to the north and south of the Bank during both Februaries (Figure 7). In 1975, the higher area of abundance (1,000-10,000/10 m²) appeared to be localized in the southwestern part, whereas in 1976 the higher station abundances were localized in the central part of Georges Bank. Mean densities both years were similar (2,421 and 2,178/1000 m³, 1975 and 1976, resp.). C. hamatus ranked 11th in 1975 and 7th in 1976 of all zooplankters and had the same dominance frequency (1/20) both years.

The mean density of Metridia lucens was higher in 1976 (7,564/1000 m³) than in 1975, by almost a factor of 3, although they were not found to be significantly different (>20% level) by Mann-Whitney U-test. M. lucens was ranked 5th in abundance in 1975 (dominance frequency 4/20) and 4th in 1976 (dominance frequency 8/20). Distributional patterns were similar both years, decreasing in high abundance around the perimeter of the Bank to a zero abundance region in the central part (Figure 8).

Pseudocalanus minutus was ranked 6th and 5th in abundance during February 1975 and 1976, respectively, and was dominant in 1/20 samples both years. Mean density was somewhat higher in 1976 (3,210/1000 m³) than 1975 (2,372/1000 m³), but not significantly different (>20% level) by Mann-Whitney U-test. The P. minutus distributional pattern appeared to be quite different between the two years (Figure 9). In February 1975, its distribution was marked by a large relatively sparse region in the northwestern part of Georges Bank, a narrow zone of intermediate density along the southern part extending north along the eastern and western ends, and a decrease in density along the southern 100 m contour. In February 1976, its distribution formed a broad central area of the Bank of intermediate abundance with some hint of extension across the southern 100 m depth contour. The greater patchiness evident during 1975 compared to 1976 was supported by their coefficients of variation; the 1975 value (C.V. = 2.16) was nearly twice that of 1976 (C.V. = 1.28).

Chaetognaths

Chaetognaths, >99% by numbers of the species Sagitta elegans, had the 3rd highest rank in abundance during 1975 and 2nd highest rank in 1976 with dominance frequencies of 5/20 and 7/20 for the two years, respectively. Mean density in February 1976 (9,222/1000 m³) was nearly twice that observed in 1975 (4,654/1000 m³) and was significantly different (1% level) by the Mann-Whitney U-test. The distribution of S. elegans in February 1975 occurred in the central part of the Bank and appeared to be delimited by the 100 m contour (Figure 10). In February 1976, its distribution was broader, extending off the Bank, particularly along the southern edge. An area of high abundance occurred in the southwestern part both years, but another high density area occurred in the central part of the Bank in 1976.

Mollusca

The molluscs were represented primarily by two species, the pteropod mollusc, Limacina (=Spiratella) retroversa, and the pelagic bivalve larvae of the surf clam, Spisula solidissima.

L. retroversa comprised an important part of the zooplankton community ranking 4th in abundance in 1975 and 6th in 1976. It occurred in almost every sample and mean densities were similar both years (1000-2000/1000 m³). The distributional pattern of L. retroversa (Figure 11) indicated that the highest abundance usually occurred in the deeper water around the Bank during both years. Although its distribution on the western half of the Bank was similar both years, there is some indication that higher abundances occurred on the eastern half in 1976.

S. solidissima larvae occurred at high densities ($\bar{X} = 4,484$, Table 1) during 1975, but only at five stations in the central part of Georges Bank. No larvae of this species were observed in 1976.

Ichthyoplankton

A total of eight larval fish species were collected both years: Ammodytes dubius? (Northern sand lance), Clupea harengus harengus (Atlantic herring); Pollachius virens (pollock); Gadus morhua (Atlantic cod); Melanogrammus aeglefinus (haddock); Anguilla rostrata (eel), Cyclopteridae, and Congridae. The mean ichthyoplankton density in February 1976 (581/1000 m³) was more than twice the mean in 1975 (223/1000 m³), due primarily to the greater abundance of Ammodytes spp. larvae in 1976. The two most important species considered here are Ammodytes spp. and C. harengus. All samples from the Georges Bank and Nantucket Shoals areas were sorted previously for Ammodytes spp. from February 1975 and C. harengus from February 1975 and 1976.

Ammodytes spp. was the most abundant fish larva both years. Its 1976 mean density (555/1000 m³) was more than five times the mean for the previous year (94/1000 m³). Comparing the Georges Bank distribution only for the periods in Figure 12, Ammodytes spp. was largely confined to the 100 m contour with highest abundances in the central part of the Bank both years. There is some suggestion that the high area of larval abundance in 1976 was located more northeasterly along the southern edge of Georges, whereas in 1975 it was in a more southwesterly part of the Bank.

The abundance of C. harengus larvae was quite similar during both years ($\bar{X} = 20/1000$ m³ Feb. 1975, $\bar{X} = 21/1000$ m³ Feb. 1976) with a distributional pattern (Figure 13) similar to that of Ammodytes spp. Both Februaries were characterized by a high abundance of C. harengus larvae in the central part of Georges Bank extending across the Great South Channel. In February 1976, there appeared to be a second major area of high larval abundance in the northeast part of the Bank.

Other Groups

Mysids (Neomysis americana) were collected both years on several stations across southern Georges Bank but in higher densities during February 1976.

Euphausiids were represented by Meganyctiphanes norvegica and Thysanoessa spp. both years. In 1975, euphausiids represented 4% of the zooplankton community, in 1976, only 0.3%. Mean density of M. norvegica was an order of magnitude higher in 1976 than 1975, while mean density of Thysanoessa spp. was the same both years.

Most polychaetes that occurred in the samples were believed to be Dysponetus pygmaeus(?). The mean density of polychaetes was about an order of magnitude greater in February 1976 than in 1975.

The majority of crustacean larvae collected were decapod zoeal stages with smaller numbers of mysids and euphausiids. Highest densities of larvae occurred in the central and western regions of the study area.

Vertebrate eggs consisted mostly of large, well-developed fish eggs with pigmented embryos. No positive identification was made. Similarly low densities occurred both years. Highest numbers of eggs were observed in the eastern and central parts of Georges Bank.

Although hydrozoans were not quantified in this study, their presence or absence was dramatically different between the two years. Hydrozoans were collected at two stations in 1975 and 11 stations in 1976. Four species were identified: Sertularella sp., Thuiaria sp., one species belonging to the Campanularidae family, and fragments believed to be Nanomia cara, a cold water siphonophore found in the Gulf of Maine. The presence of N. cara only in February 1976 was consistent with the high abundance observed throughout the Fall 1975 larval herring surveys by Rogers (1976). She found high numbers of this species along the northern edge of Georges Bank and moderate numbers in the central region in 1975.

Other taxa collected in the samples both years can be referred to in Tables 1 and 2.

Species Occurrence in Relation to Hydrography

A review of the physical oceanography of Georges Bank was recently provided by Bumpus (1976) using successive periods of larval herring distribution as evidence of dispersion and advection. During the winter months, a southerly flow of surface waters is suggested on Georges Bank with a westerly component across Great South Channel. Dispersal of young herring larvae through the fall is generally southwesterly at the rate of 1-8 miles per day. Older larvae are still collected on Georges Bank through the winter and spring. Surface water circulation during the winter may respond more to the high, short-term wind effects than during the spring and summer seasons when a clockwise eddy appears to develop. It is generally believed that winds exert their greatest influence on the shallow Georges Bank waters through vertical mixing of the water column. Wind stress values used as an index of mixing for Georges Bank were nearly three times greater during February 1976 compared to 1975 and may explain the more homogeneous temperature and salinity pattern in 1976. Also, the distribution of the more abundant zooplankters consistently showed greater uniformity in 1976. The resultant Ekman transport values, used as an index of water transport, were anomalously high and in a southeasterly direction for February 1976 compared to the usual southwesterly transport for February 1975. Correspondingly, in February 1976, population centers of most of the dominant species appeared to shift more to the southeastern part of Georges,

extending off the southern edge of the Bank. In 1975, several species had sharp distributional limits along southern Georges in the vicinity of the shelf-slope boundary. The wind data also support the southerly occurrence in February 1976 of Nanomia cara, a cold water siphonophore species native to the Gulf of Maine and rarely seen below Cape Cod.

Copepods, because of their abundance, also can be used as indicator species of water masses and currents in the Gulf of Maine. The presence of Acartia spp. (A. longiremis, A. clausi, A. tonsa) Tortanus discaudatus, and Temora longicornis on Georges Bank supports evidence of a southerly surface drift as they are all species common to nearshore coastal waters of the Gulf of Maine (Wilson, 1932). A number of warm water species serve as indicators of the Gulf Stream influence flowing northeasterly along the southern border of Georges Bank. Six tropical species occurred at nine stations in 1975 with the following frequencies: Nannocalanus minor (8/20), Pleuromamma robusta (4/20), Paracalanus parvus (1/20), Gaetanus minor (1/20), Neocalanus gracilis (1/20), and Rhincalanus nasutus (2/20). Five warm water species occurred with the following frequencies at four southwestern stations of the study area in 1976: N. minor (3/20), Eucalanus attenuatus (3/20), R. nasutus (1/20), R. cornutus (1/20), and Undinula vulgaris (1/20). The mean number of tropical copepods was slightly higher in 1976 (146/1,000 m³) than in 1975 (115/1,000 m³) but the dispersion of warm water species was considerably wider in 1975 than in 1976. The nine stations at which the southern species were collected in 1975 were widely dispersed across Georges Bank. In contrast, warm water species in 1976 were limited to four stations along the southwestern edge of the Bank. All the warm water species noted are copepods of the Florida current with the exception of P. parvus (Owre and Foyo, 1967). Although the stations at which tropical species were found in either year were usually not characterized by water of correspondingly high temperatures, the presence of southern species on Georges Bank is indicative of the influence the Gulf Stream may have on the fauna of the area.

Colton and Temple (1961) remarked from their plankton studies in the fifties that it was puzzling how so many species are able to maintain themselves on Georges Bank when hydrographic conditions seemed too unfavorable for the retention of their pelagic larvae during most of the year. They believed that most fish eggs and larvae were transported off Georges Bank into the slope waters and lost to the recruited populations. Only in exceptional years would large numbers of eggs and larvae be retained on Georges Bank. However, there is opposing evidence to suggest that many planktonic organisms endemic to Georges Bank are retained to a great degree during most years. In the Gulf of Maine, breeding stocks of calanoids (e.g., Calanus finmarchicus, Metridia lucens?) are believed to be concentrated by a large counterclockwise eddy, and in the Georges Bank region, endemic calanoids (e.g., Centropages spp., Pseudocalanus minutus) and the chaetognath, Sagitta elegans, are believed to be concentrated by a clockwise eddy during the spring and summer months (Bigelow, 1926; Redfield, 1939; Redfield and Beale, 1940; Clarke, Pierce, and Bumpus, 1943). The drift of an invading Limacina population in the Gulf of Maine eddy was shown in Redfield's (1939) classical study. During the fall and winter months the eddies appear to break down (Bumpus and Lauzier, 1965). The southern side of the Gulf of Maine eddy breaks down into a drift across Georges Bank. Redfield estimated that at least one-half of the Gulf's plankton population escapes over Georges Bank and the Northeast Channel each winter. The Georges Bank eddy also breaks down into a southerly flow with a westerly component across the

Great South Channel. Nevertheless, evidence from the larval herring surveys suggests that larvae are somehow retained within the shelf waters (Bumpus, 1976). The distributions of other planktonic species observed during the two winters in this study also suggest a common retention mechanism on Georges Bank; depending in part upon wind induced advection of surface waters. Strong semi-diurnal rotary tidal currents with speeds greater than 2 knots and ellipses 4 to 8 miles in length are a distinctive feature of Georges Bank (Bumpus, 1976) and may be an important influence as a retention mechanism for many planktonic species. As yet, we don't fully understand the physical and biological mechanisms involved to account for this apparent retention.

Trophic Structure in Relation to Larval Herring

Prey selection of herring larvae in relation to changes in the zooplankton populations on Georges Bank during a number of winter periods (December-February); as well as through the fall spawning season, is now in progress at the Northeast Fisheries Center. No quantitative data on larval gut contents are available at this time. Sherman (1976) and Sherman and Honey (1971) have described the seasonal variation in food of larval herring in coastal waters of Maine. As larvae increase in size, their range of prey item also increases. The selection of prey is believed to initially be based on size and secondarily on taste and texture (Blaxter, 1963). The naupliar and copepodite stages of Pseudocalanus minutus and Oithona spp. were the predominant prey of small larvae in the fall and the adults of these two species through the winter along the Maine coast. Pseudocalanus adults were by far the most important prey species occurring in greater than 50% of the larger larvae. Preliminary analysis of larval herring gut contents collected from the 1975 and 1976 February surveys on Georges Bank also indicate Pseudocalanus minutus and Oithona spp. to be their principal prey; as well as high numbers of Centropages spp. copepodites on some stations. Pseudocalanus minutus and most other potential food organisms were more abundant and widespread during February 1976 compared to February 1975, paralleling the greater growth of larval herring in 1976. Although many of the small adult copepods and juvenile stages of species such as Oithona sp. and Paracalanus parvus and to some degree Pseudocalanus minutus are not retained quantitatively by the .505 mm mesh analyzed for this study, the relative population size of the most important prey species, P. minutus, was estimated for these two February surveys. Finer mesh samples (.333 and .165 mm) from the same hauls are presently being sorted and analyzed to include population estimates of the smaller prey selected by herring larvae.

Sherman and Honey (1971) and Chenoweth (1970) observed that feeding incidence and condition of larval herring were low during the winter when plankton volumes were low. Recent theoretical models (Cushing, 1973, 1974, 1975; Jones and Hall, 1974; Ware, 1975; Laurence, 1976) indicate that larval growth and mortality are density-dependent processes regulated by food availability. During the 1976 winter, a significant decrease in the mortality rate was associated with the increase in growth for the Georges Bank larval herring population (Lough, 1976) coincident with what appears to be an increase in their food organisms. The absolute level of their food organisms may not be as important as their spatial distribution or patchiness (Lasker, 1976). Neither do we know what effect changes in predation or possible competition may have had on larval survival. One area presently under investigation is the feeding overlap between Ammodytes spp. and herring larvae whose distributions both coincide in the Georges Bank area through the winter and spring. A very

encouraging study relating feeding conditions, abundance of larvae and subsequent year-classes was made by Lisivnenko (1961) for Baltic herring in the Gulf of Riga. The links between densities of suitable food organisms and recruitment success still need to be clearly established for herring in the Georges Bank-Gulf of Maine area.

An overview of the plankton communities of the Gulf of Maine was recently made by Cohen (1976) summarizing information on the seasonal and geographic changes in species composition of phytoplankton and zooplankton, biomass, and productivity data. While it is not the purpose of this paper to provide quantitative estimates of energy transfer to higher trophic levels, we can examine the limited data presented in a qualitative sense for possible differences between the various species of dominant zooplankton observed in February 1975 and 1976.

Copepods were the most numerically abundant component of the zooplankton both Februaries. Small copepods are generally herbivorous, large ones carnivorous, but omnivorous species range widely in size (Jeffries and Johnson, 1973). Both Centropages typicus and C. hamatus are omnivorous but prefer animal food (Anraku and Omori, 1963). The other dominant copepods collected (Calanus finmarchicus, Pseudocalanus minutus, Metridia lucens) are all herbivorous:

The chaetognaths, dominated by Sagitta elegans, are carnivores feeding primarily on copepods such as Pseudocalanus, Oithona, Acartia, and Tortanus spp. (Pearre, 1973). The most abundant euphausiid in the study area, Meganyctiphanes norvegica, can either filter feed, capture large zooplankton such as Sagitta and copepods, or feed in bottom detritus (Mauchline, 1959). Species of Thysanoessa collected also are omnivorous. The pteropod mollusc, Limacina retroversa, is known to feed on unicellular algae, often diatoms.

A summary of the major components of the trophic structure of the zooplankton community based on mean values for the two years follows. In February 1975, the zooplankton was composed of 62% copepods (mostly herbivores), 16% molluscs (herbivores), 11% chaetognaths (carnivores), 5% mysids and euphausiids (omnivores), and 1% amphipods (mostly carnivores). In February 1976, the zooplankton community was composed of 64% copepods, 18% chaetognaths, 14% molluscs, 2% mysids and euphausiids, and 2% amphipods. There was a somewhat larger carnivore/herbivore ratio in 1976 due to the larger percentage of chaetognaths and smaller percentage of molluscs that year. It is noteworthy that in 1976, the omnivorous Centropages spp. outranked the next most numerous copepod Calanus which is herbivorous, while the reverse occurred in 1975. Also, the carnivorous copepod, Candacia armata, occurred in substantial numbers in 1976 but was not observed in 1975.

The basic pattern that seems to emerge is that the greater mixing observed on Georges Bank during February 1976, based on temperature, salinity, and wind stress data, provided more favorable conditions for growth and reproduction of a number of zooplankton species endemic to Georges Bank. Pseudocalanus and Centropages increased in population abundance so that one would also expect an increase in the carnivorous species such as Sagitta. A recent study by Dagg (1977) on some effects of patchy food environments on copepods may provide insight into different survival strategies for a number of species on Georges Bank. Centropages typicus requires

a constant high concentration of food in its environment and are therefore sensitive to small-scale patchiness, whereas Pseudocalanus minutus and Calanus finmarchicus can sustain longer periods without food and can therefore survive small-scale variability in their food. Centropages would be expected to thrive in a well-mixed and productive area such as Georges Bank and indeed it was the most abundant organism in February 1976.

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Table 1 Relative abundance of zooplankton on Georges Bank during February 1975 (ALBATROSS IV, 75-02, 61-cm bongos, 0.505 mm mesh).

Species	Mean ¹ Rank	Dominance ²	Abundance ³			Dispersion		Frequency of Occurrence	
			Range	Mean/1,000 ³	Variance	Standard Deviation	C.V. (s/ \bar{x})		s ² / \bar{x}
<i>Calanus finmarchicus</i>	15.70	13/20	314-51,630	11,135	1.5x10 ⁸	12,147	1.09	13,252.06	20/20
<i>Centropages typicus</i>	13.40	5/20	12-35,158	6,058	7.7x10 ⁷	8,758	1.45	12,660.18	20/20
<i>Sagitta elegans</i>	12.50	4/20	38-32,454	4,654	6.7x10 ⁶	8,195	1.76	14,432.11	20/20
<i>Limacina retroversa</i>	12.20	1/20	0- 4,985	1,434	2.0x10 ⁷	1,414	0.99	1,395.16	19/20
<i>Metridia lucens</i>	11.02	4/20	0-13,601	2,691	1.4x10 ⁷	3,785	1.41	5,323.15	17/20
<i>Pseudocalanus minutus</i>	10.40	1/20	0-23,761	2,372	2.6x10 ⁷	5,116	2.16	11,034.12	18/20
<i>Centropages hamatus</i>	8.05	1/20	0-24,339	2,421	3.2x10 ⁷	5,700	2.35	13,423.29	15/20
Crustacean larvae	6.85	0/20	0- 4,920	1,293	2.3x10 ⁶	1,533	1.19	1,817.09	14/20
Vertebrate eggs (fish eggs)	5.58	0/20	0- 4,107	531	1.1x10 ⁵	1,030	1.94	1,996.72	12/20
<i>Centropages</i> spp.	5.02	0/20	0- 2,611	396	5.4x10 ⁵	735	1.86	1,365.74	12/20
<i>Spisula solidissima</i>	3.58	2/20	0-69,648	4,484	2.5x10 ⁸	15,935	3.55	56,627.79	5/20
Unidentified Calanoida	3.55	0/20	0- 2,675	181	3.5x10 ⁵	596	3.30	1,965.87	7/20
<i>Euchaeta norvegica</i>	3.02	0/20	0- 712	65	2.5x10 ⁴	158	2.42	382.47	9/20
Thaliacea (salps)	2.92	0/20	0- 1,188	175	1.3x10 ⁵	356	2.03	724.13	6/20
Sipunculida	2.78	0/20	0- 2,861	173	4.1x10 ⁵	637	3.63	2,344.35	7/20
Unidentified Harpacticoida	2.75	0/20	0- 1,396	108	9.9x10 ⁴	315	2.91	917.04	8/20
Polychaeta	2.45	0/20	0- 1,047	75	5.4x10 ⁴	233	3.11	725.33	6/20
<i>Nannocalanus minor</i>	2.38	0/20	0- 849	71	3.6x10 ⁴	190	2.67	507.42	8/20
<i>Thysanoessa</i> spp.	2.10	0/20	0- 222	30	3.8x10 ³	61	2.08	128.18	6/20
<i>Pollachius virens</i>	2.00	0/20	0- 403	59	1.3x10 ⁴	112	1.83	210.48	12/20
<i>Pleuromarma robusta</i>	1.90	0/20	0- 528	33	1.4x10 ⁴	118	3.63	428.23	4/20
<i>Meganyctiphanes norvegica</i>	1.75	1/20	0-34,562	1,753	6.0x10 ⁷	7,723	4.40	34,015.33	3/20
<i>Temora longicornis</i>	1.75	0/20	0- 1,958	125	1.9x10 ⁵	435	3.49	1,520.15	6/20
<i>Gadus morhua</i>	1.58	0/20	0- 289	28	4.3x10 ³	65	2.35	153.85	10/20
Unidentified Bivalvia larvae	1.33	0/20	0- 9,852	510	4.8x10 ⁶	2,200	4.31	9,485.19	3/20
<i>Clupea harengus</i>	1.18	0/20	0- 281	34	5.6x10 ¹	75	2.20	164.27	10/20
<i>Melanogrammus aeglefinus</i>	0.80	0/20	0- 31	3	6.4x10 ¹	8	2.31	18.47	7/20
Cumacea	0.72	0/20	0- 873	63	4.4x10 ²	209	3.32	695.52	2/20
<i>Crangon septemspinosa</i>	0.70	0/20	0- 127	7	8.0x10 ²	28	4.23	120.03	2/20
Larvacea	0.68	0/20	0- 349	22	6.3x10 ³	79	3.66	290.46	2/20
<i>Neonysis americana</i>	0.65	0/20	0- 5,760	330	1.7x10 ⁶	1,286	3.90	5,016.39	3/20
<i>Paracalanus parvus</i>	0.65	0/20	0- 75	4	2.8x10 ²	17	4.47	75.00	1/20
Unidentified fish larvae	0.52	0/20	0- 231	12	2.7x10 ³	52	4.32	222.72	2/20
Polychaeta (larvae)	0.52	0/20	0- 131	7	8.6x10 ²	29	4.47	131.00	1/20
Hyperidea	0.50	0/20	0- 87	9	7.0x10 ²	26	3.03	81.49	2/20
Paralapedidae	0.50	0/20	0- 23	2	3.3x10 ¹	6	2.95	17.03	3/20
<i>Metridia longa</i>	0.45	0/20	0- 72	4	2.6x10 ²	16	4.47	72.00	1/20
Unidentified Cyclopoida	0.40	0/20	0- 859	43	3.7x10 ⁴	192	4.47	859.00	1/20
<i>Gaetanus minor</i>	0.38	0/20	0- 38	2	7.2x10 ¹	9	4.47	38.00	1/20
Invertebrate eggs	0.32	0/20	0- 53	3	2.0x10 ¹	14	4.47	63.00	1/20
<i>Neocalanus gracilis</i>	0.25	0/20	0- 21	1	2.2x10 ¹	5	4.47	21.00	1/20
<i>Phincalanus nasutus</i>	0.25	0/20	0- 11	1	7.5x10 ⁰	3	3.22	8.83	2/20
<i>Tortanus discaudatus</i>	0.20	0/20	0- 178	9	1.6x10 ³	40	4.47	178.00	1/20
<i>Pteropoda</i> sp.	0.12	0/20	0- 11	1	6.1x10 ⁰	2	4.47	11.00	1/20
Cyclopteridae	0.05	0/20	0- 1	<1	5.0x10 ⁻²	0.22	4.47	1.00	1/20
Congridae	0.05	0/20	0- 1	<1	5.0x10 ⁻²	0.22	4.47	1.00	1/20
Isopoda	0.05	0/20	0- 2	<1	2.0x10 ⁻¹	0.45	4.47	2.00	1/20

¹Species or taxonomic groups were ranked within each sample on the basis of numbers of individuals. Ranks for each species or taxonomic group were averaged over the 20 station samples. Highest density sample was assigned highest rank.

²Proportion of samples in which the species was among those making up 50 percent of the individuals.

³Range and mean of numbers of individuals per 1,000 M³ of water in samples in which the species was found.

Table 2 Relative abundance of zooplankton on Georges Bank during February 1976 (ALBATROSS IV 76-01, 61-cm bongos, 0.505-mm mesh).

	Mean ¹ Rank	Dominance ²	Abundance ³			Dispersion			Frequency of Occurrence
			Range	Mean/1,000M ³	Variance	Standard Deviation	c.v. (s/ \bar{x})	s ² / \bar{x}	
<u>Centropages typicus</u>	12.70	10/20	22-35,311	11,265	9.5x10 ⁷	9,760	0.87	8,456.00	20/20
<u>Sagitta elegans</u>	11.65	7/20	0-46,048	9,222	1.7x10 ⁸	13,114	1.42	18,648.00	19/20
<u>Calanus finmarchicus</u>	11.28	5/20	22-31,390	7,441	6.8x10 ⁷	8,245	1.11	9,136.60	20/20
<u>Metridia lucens</u>	9.55	8/20	0-32,690	7,564	1.6x10 ⁷	12,542	1.66	20,793.64	18/20
<u>Pseudocalanus minutus</u>	9.50	1/20	0-13,261	3,210	1.7x10 ⁷	4,105	1.28	5,249.70	18/20
<u>Limacina retroversa</u>	8.60	1/20	80- 6,443	1,938	4.2x10 ⁶	2,041	1.05	2,148.28	20/20
<u>Centropages hamatus</u>	5.58	1/20	0-14,029	2,178	2.5x10 ⁵	4,978	2.29	11,377.60	11/20
<u>Hyperidea</u>	4.88	0/20	0- 3,188	672	9.3x10 ⁵	965	1.44	1,385.95	15/20
<u>Gammaridea</u>	4.68	0/20	0- 3,428	388	5.3x10 ⁵	760	1.96	1,490.99	13/20
<u>Crustacean larvae</u>	4.48	0/20	0- 1,845	316	2.8x10 ⁵	533	1.68	897.20	11/20
<u>Candacia armata</u>	4.40	0/20	0- 1,968	337	2.5x10 ⁵	504	1.50	753.69	13/20
<u>Unidentified calanoida</u>	4.15	0/20	0- 1,841	373	2.3x10 ⁵	484	1.30	626.60	15/20
<u>Ammodytes dubius</u>	3.90	0/20	0- 3,665	555	1.2x10 ⁷	1,097	1.98	2,168.06	12/20
<u>Neomysis americana</u>	3.58	3/20	0-31,817	3,450	7.4x10 ⁶	8,607	2.49	21,471.65	5/20
<u>Vertebrate eggs (fish eggs)</u>	2.72	0/20	0- 5,142	483	1.4x10 ⁶	1,194	2.47	2,953.44	8/20
<u>Polychaeta</u>	2.50	0/20	0-10,517	684	5.5x10 ⁵	2,340	3.42	7,996.80	8/20
<u>Cumacea</u>	1.72	0/20	0- 2,744	177	3.7x10 ⁵	610	3.44	2,100.13	5/20
<u>Unidentified Bivalvia larvae</u>	1.68	0/20	0- 1,074	117	8.4x10 ⁴	290	2.48	721.14	4/20
<u>Meganyctiphanes norvegica</u>	1.40	0/20	0- 824	61	3.5x10 ⁴	187	3.05	569.16	4/20
<u>Thysanoessa spp.</u>	1.32	0/20	0- 477	49	1.7x10 ⁴	131	2.70	352.30	4/20
<u>Hannocalanus minor</u>	1.10	0/20	0- 1,161	71	6.8x10 ³	260	3.67	955.01	3/20
<u>Euchaeta norvegica</u>	0.88	0/20	0- 253	27	4.9x10 ⁴	71	2.64	185.75	3/20
<u>Centropages spp.</u>	0.78	0/20	0- 637	45	2.1x10 ⁴	146	3.23	472.40	3/20
<u>Unidentified Harpacticoida</u>	0.75	0/20	0- 457	47	1.2x10 ³	109	2.31	252.30	5/20
<u>Thaliacea (salps)</u>	0.72	0/20	0- 338	17	5.7x10 ⁴	76	4.47	338.00	1/20
<u>Eucalanus attenuatus</u>	0.70	0/20	0- 536	36	1.5x10 ⁴	123	3.40	419.97	3/20
<u>Porifera</u>	0.70	0/20	0- 108	41	1.9x10 ³	139	3.41	472.51	3/20
<u>Acartia spp.</u>	0.65	0/20	0- 184	19	2.5x10 ²	50	2.59	130.28	3/20
<u>Clupea harengus</u>	0.60	0/20	0- 128	17	9.9x10 ²	31	1.88	59.30	12/20
<u>Rhincalanus nasutus</u>	0.55	0/20	0- 536	27	1.4x10 ²	120	4.47	536.00	1/20
<u>Unidentified Cyclopoida</u>	0.48	0/20	0- 123	12	1.1x10 ²	33	2.77	91.90	3/20
<u>Pteropoda sp.</u>	0.48	0/20	0- 119	9	8.3x10 ³	29	3.29	94.83	2/20
<u>Rhincalanus cornutus</u>	0.42	0/20	0- 357	18	6.4x10 ²	80	4.47	357.00	1/20
<u>Undinula vulgaris</u>	0.30	0/20	0- 56	3	1.6x10 ²	13	4.47	56.00	1/20
<u>Tortanus discaudatus</u>	0.25	0/20	0- 119	15	1.4x10 ³	37	2.47	90.93	3/20
<u>Temora longicornis</u>	0.20	0/20	0- 89	4	4.0x10 ²	20	4.47	89.00	1/20
<u>Echinoderm larvae</u>	0.20	0/20	0- 89	4	4.0x10 ²	20	4.47	89.00	1/20
<u>Rhynchocoela</u>	0.20	0/20	0- 89	4	4.0x10 ³	20	4.47	89.00	1/20
<u>Unidentified fish larvae</u>	0.18	0/20	0- 184	9	1.7x10 ¹	41	4.47	184.00	1/20
<u>Sipunculid</u>	0.15	0/20	0- 22	1	2.4x10 ¹	5	4.47	22.00	1/20
<u>Crangon septemspinosa</u>	0.12	0/20	0- 28	1	3.9x10 ¹	6	4.47	0.11	1/20
<u>Caprelliidea</u>	0.10	0/20	0- 40	2	8.0x10 ⁻¹	9	4.47	40.00	1/20
<u>Anguilla rostrata</u>	0.05	0/20	0- 1	<1	5.0x10 ⁻²	0.22	4.47	1.00	1/20

¹Species or taxonomic groups were ranked within each sample on the basis of numbers of individuals. Ranks for each species or taxonomic group were averaged over the 20 station samples. Highest density sample was assigned highest rank.

²Proportion of samples in which the species was among those making up 50 percent of the individuals.

³Range and mean of numbers of individuals per 1,000 M³ of water in samples in which the species was found.

Table of Diversity Indices

Table 3

ALBATROSS IV 75-02, 61-cm bongos, 0.505-mm mesh

Station	Time of Day ¹ (D or N)	No. of Species	No. Individ. per 1,000 M ³	Indices		
				D ² Simpson's Index	H' ³ Information Index	J ⁴ Equitability
52	D	15	47,551	0.76	1.76	0.649
54	D	16	115,506	0.77	1.76	0.634
56	D	17	19,411	0.59	1.33	0.469
63	D	12	27,080	0.75	1.71	0.687
77	D	18	19,734	0.49	1.05	0.362
79	D	17	3,732	0.81	1.96	0.691
81	D	19	25,360	0.85	2.14	0.728
90	D	20	20,178	0.79	1.94	0.648
92	D	17	2,529	0.77	1.78	0.627
98	D	18	18,924	0.77	1.75	0.605
D	\bar{x}	16.90	30,000	0.74	1.72	0.610
A	s	2.23	32,542	0.11	0.31	0.111
Y	c.v.	0.13	1.08	0.15	0.18	0.183
50	N	14	35,493	0.52	1.17	0.443
59	N	16	28,626	0.52	1.25	0.453
61	N	22	161,974	0.75	1.83	0.591
71	N	14	18,562	0.69	1.60	0.608
73	N	23	55,067	0.77	1.81	0.577
75	N	17	68,955	0.79	1.83	0.645
83	N	20	26,415	0.81	2.04	0.681
85	N	13	75,369	0.50	1.14	0.443
88	N	17	34,250	0.37	0.91	0.323
95	N	13	23,233	0.57	1.15	0.447
N	\bar{x}	16.90	52,794	0.63	1.47	0.521
I	s	3.67	43,031	0.15	0.39	0.115
G	c.v.	0.22	0.82	0.24	0.27	0.220
H						
T						
D	\bar{x}	16.90	41,397	0.68	1.60	0.566
A	s	2.95	38,929	0.14	0.37	0.119
&	c.v.	0.17	0.94	0.21	0.23	0.210
N						
I						
G						
H						
T						

¹Day begins at sunrise plus ½ hour; night begins at sunset plus ½ hour.

$${}^2D = 1 - \lambda; \lambda = \sum_{i=1}^s \frac{n_i(n_i-1)}{N(N-1)} \text{ where}$$

n_i is the number of individuals of the i^{th} species, N is the number of individuals in all species, and s is the number of species.

$${}^3H' = -\sum_{i=1}^s P_i \ln P_i \text{ where}$$

s is the number of species and P_i is the proportion of the total number of individuals consisting of the i^{th} species.

$${}^4J = H'/H'_{\max} \text{ where } H'_{\max} = \ln s.$$

ALBATROSS IV 76-01, 61-cm bongo, 0.505-mm mesh

Station	Time of Day ¹ (D or N)	No. of Species	No. Individ. per 1,000 M ³	Indices		
				D ² Simpson's Index	H' ³ Information Index	J ⁴ Equitability
56	D	20	25,635	0.71	1.88	0.629
59	D	13	15,913	0.68	1.49	0.581
61	D	22	66,664	0.86	2.24	0.724
71	D	11	31,631	0.46	1.11	0.463
73	D	15	121,647	0.82	2.01	0.743
79	D	12	63,172	0.72	1.58	0.637
88	D	9	24,693	0.46	1.02	0.464
90	D	17	52,902	0.82	1.97	0.697
95	D	12	12,318	0.58	1.17	0.470
D	\bar{x}	14.56	46,064	0.68	1.61	0.601
A	s	4.33	34,653	0.15	0.44	0.113
Y	c.v.	0.30	0.75	0.22	0.28	0.188
50	N	11	85,806	0.69	1.41	0.587
52	N	19	29,501	0.73	1.70	0.576
54	N	22	67,395	0.51	1.23	0.399
63	N	16	70,688	0.77	1.75	0.630
75	N	15	109,919	0.81	1.89	0.698
77	N	9	36,552	0.60	1.22	0.554
81	N	19	46,581	0.82	2.08	0.707
83	N	17	108,353	0.82	2.02	0.714
85	N	16	9,326	0.71	1.64	0.591
92	N	18	12,584	0.79	1.84	0.638
98	N	8	27,981	0.38	0.79	0.380
N	\bar{x}	15.45	54,971	0.69	1.60	0.589
I	s	4.41	35,900	0.14	0.39	0.113
G	c.v.	0.29	0.65	0.21	0.25	0.191
H						
T						
D						
A						
Y	\bar{x}	15.05	50,963	0.69	1.60	0.594
&	s	4.29	34,708	0.14	0.41	0.110
N	c.v.	0.28	0.68	0.21	0.25	0.185
I						
G						
H						
T						

¹Day begins at sunrise plus ½ hour; night begins at sunset plus ½ hour.

$${}^2D = 1 - \lambda; \lambda = \sum_{i=1}^s \frac{n_i(n_i-1)}{N(N-1)} \text{ where}$$

n_i is the number of individuals of the i^{th} species, N is the number of individuals in all species, and s is the number of species.

$${}^3H' = -\sum_{i=1}^s P_i \ln P_i \text{ where}$$

s is the number of species and P_i is the proportion of the total number of individuals consisting of the i^{th} species.

$${}^4J = H'/H'_{\max} \text{ where } H'_{\max} = \ln s.$$

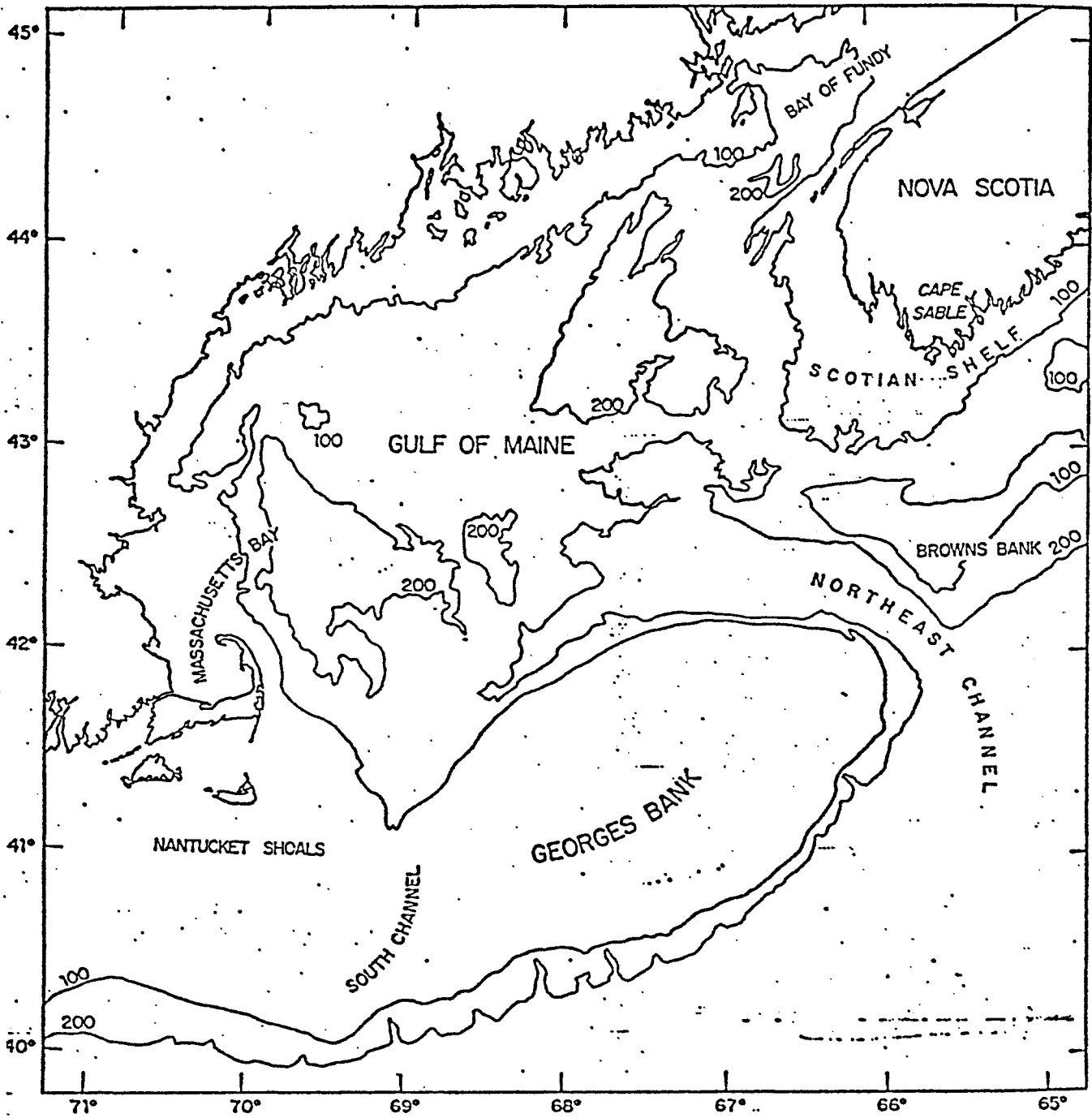


Fig. 1. The Gulf of Maine. (Depths are in meters).

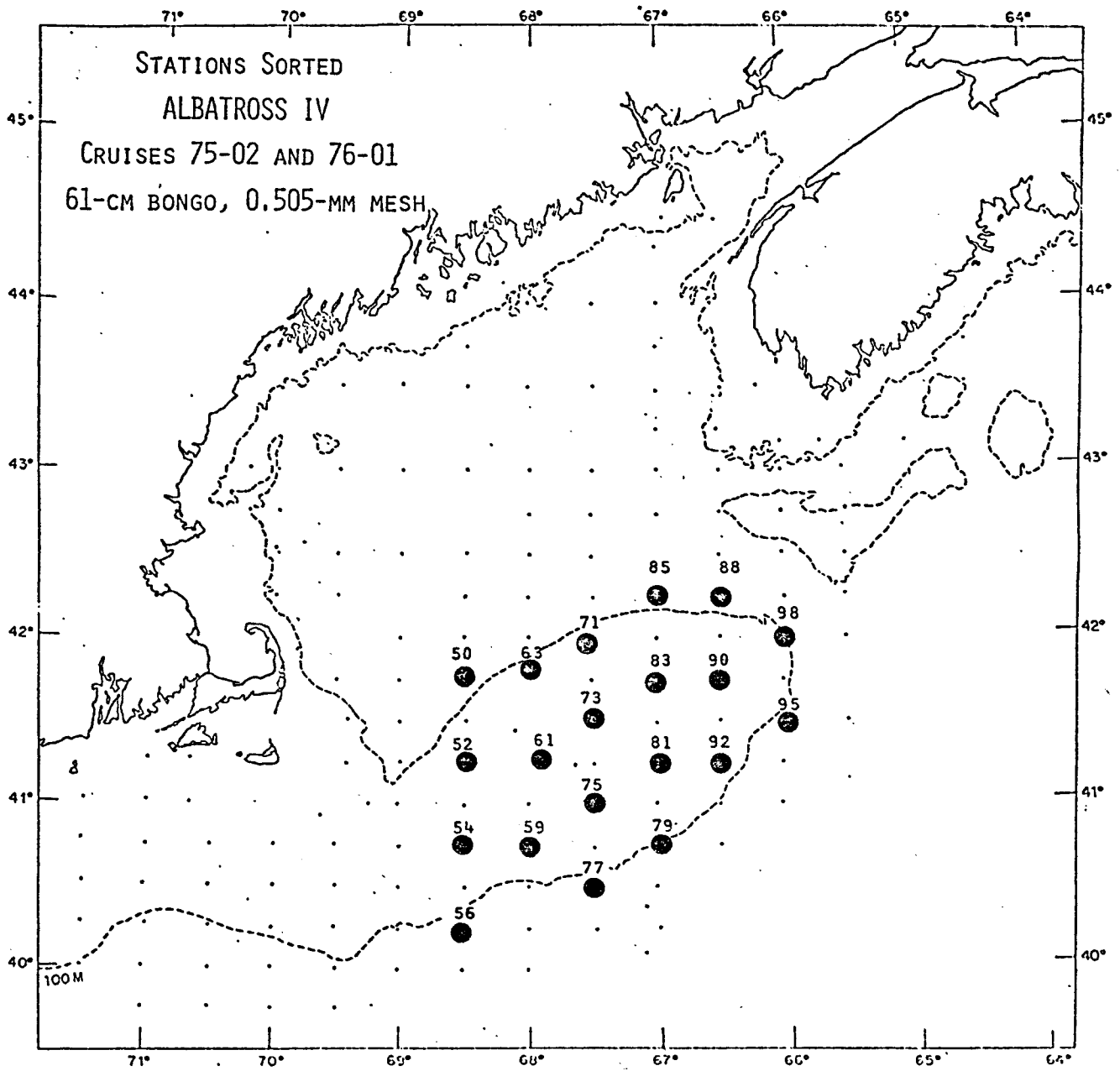


Figure 2.

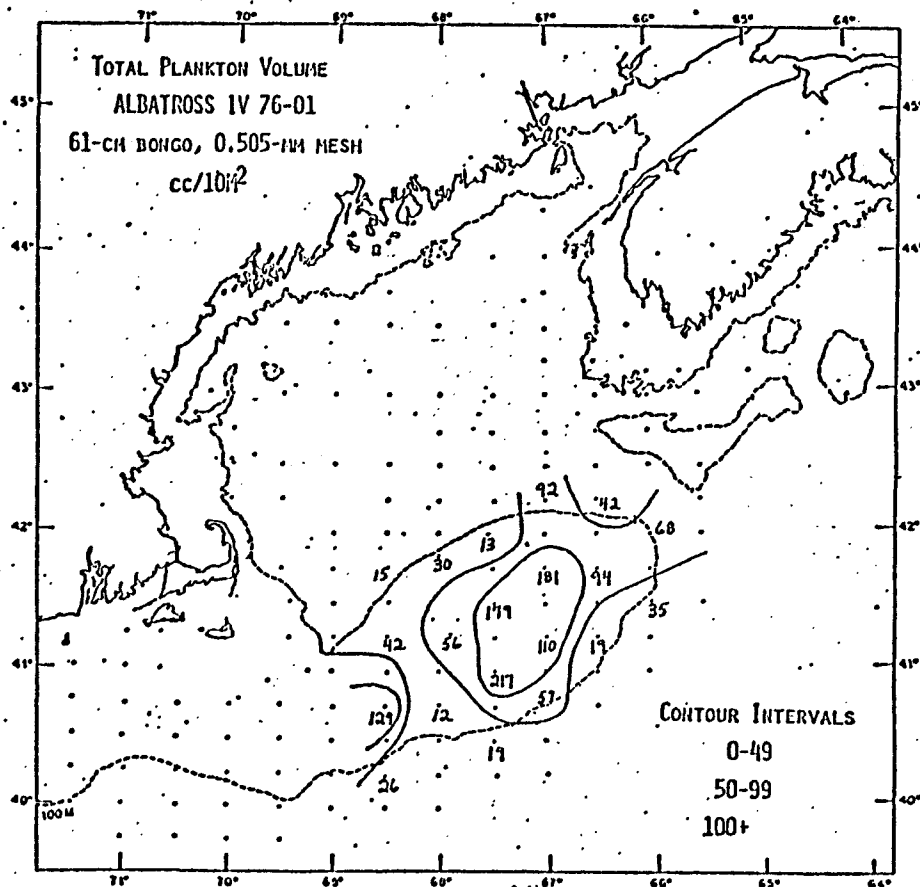
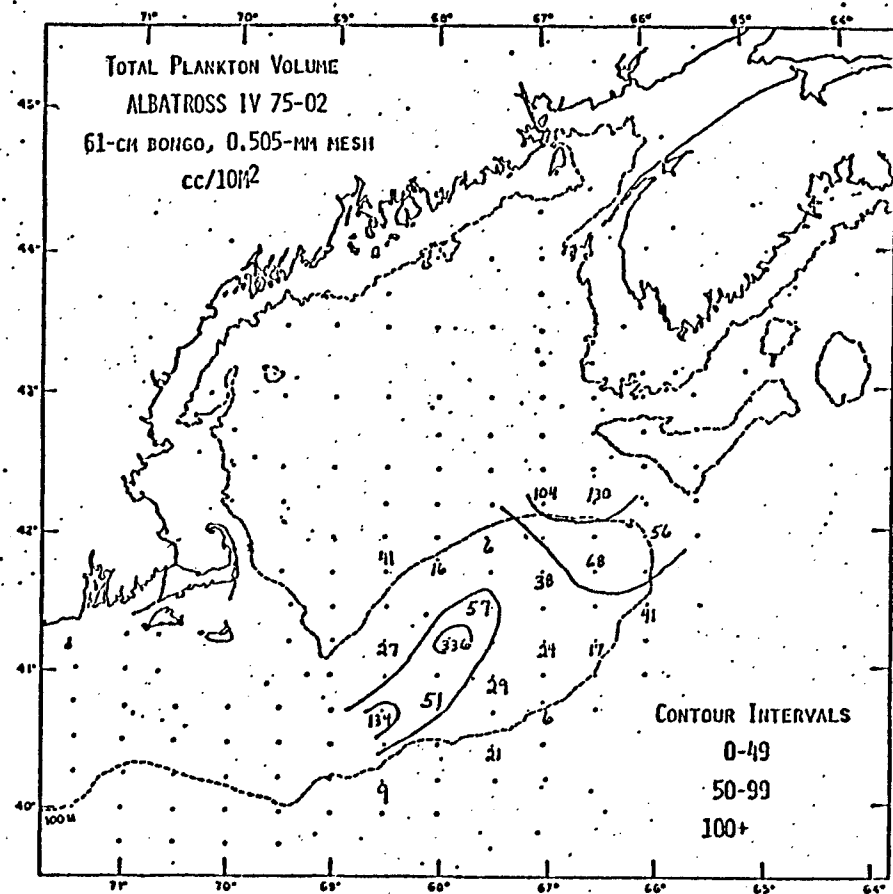


Figure 3.

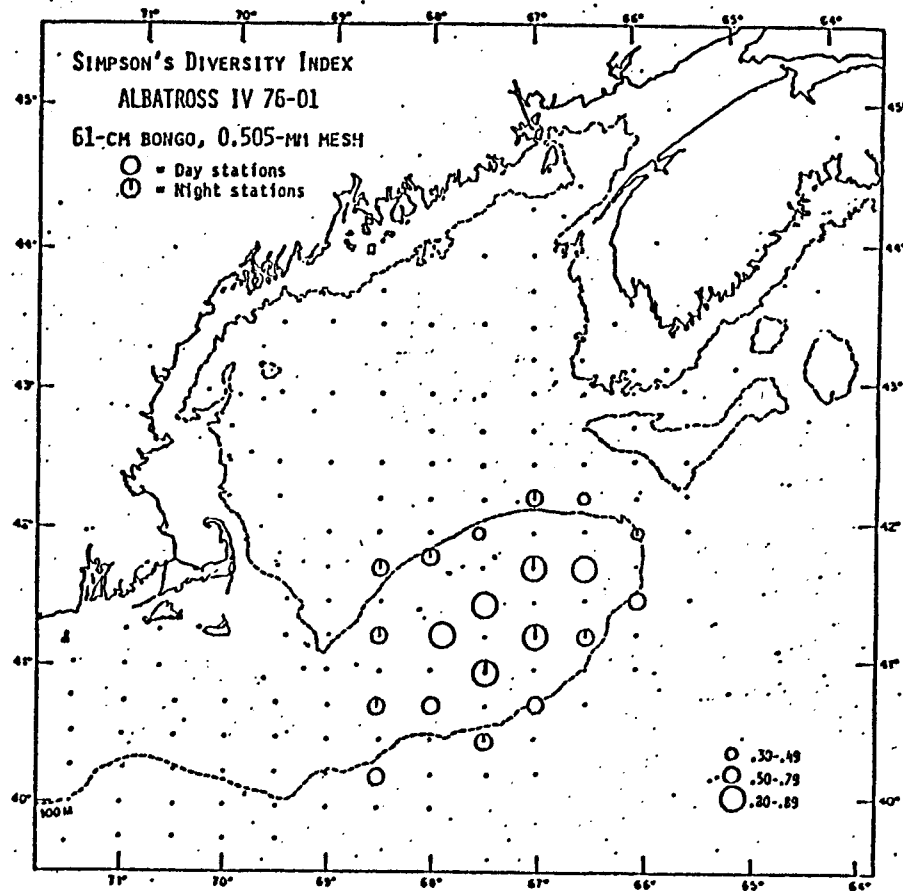
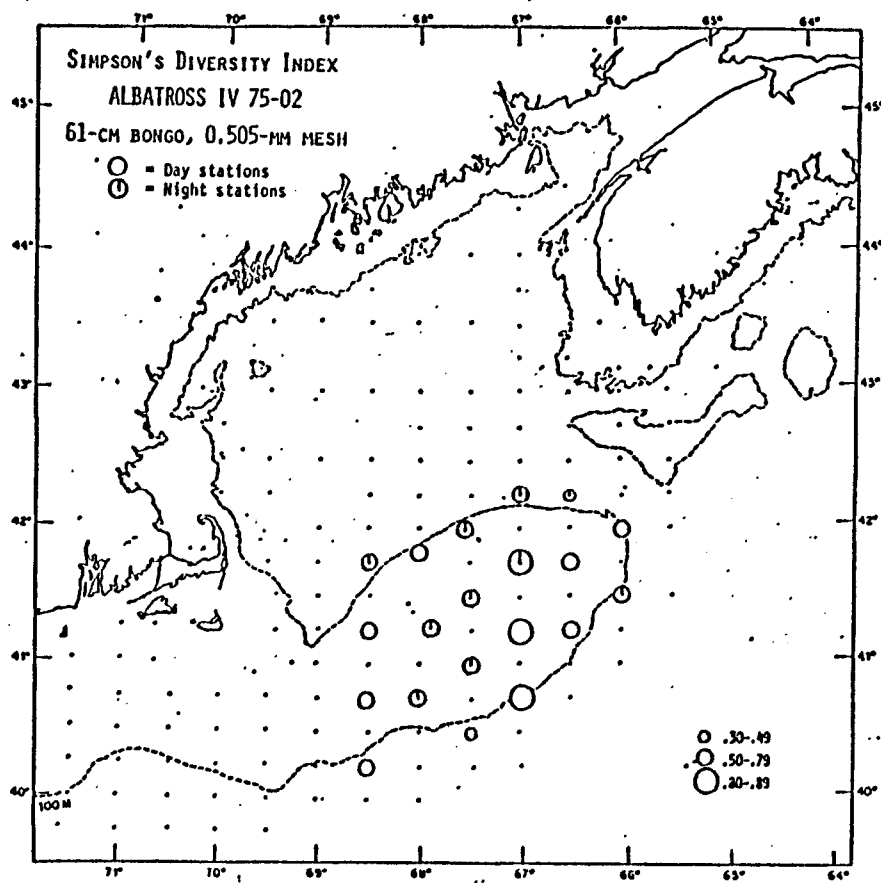


Figure 4.

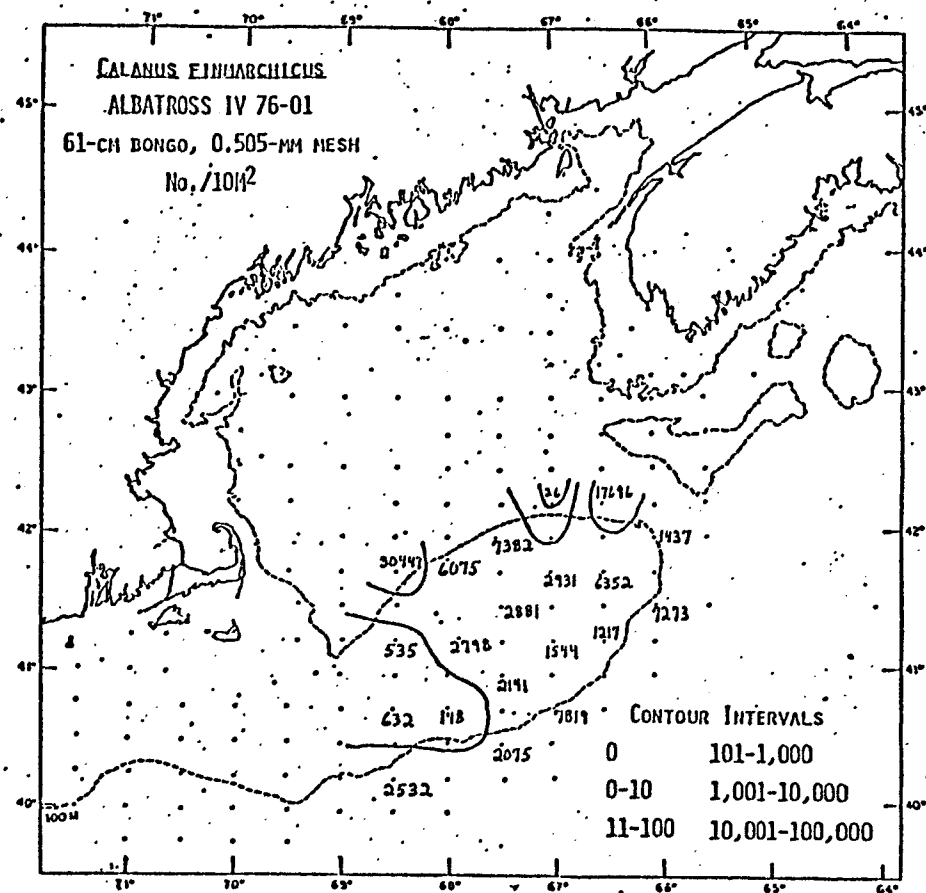
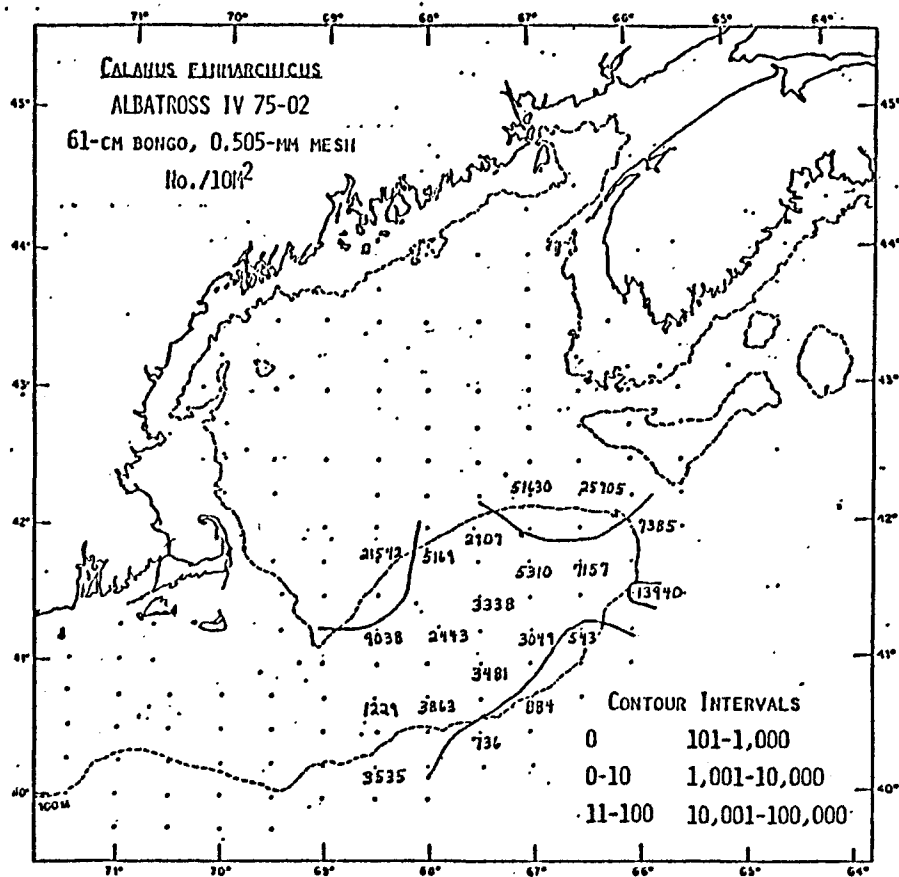


Figure 5.

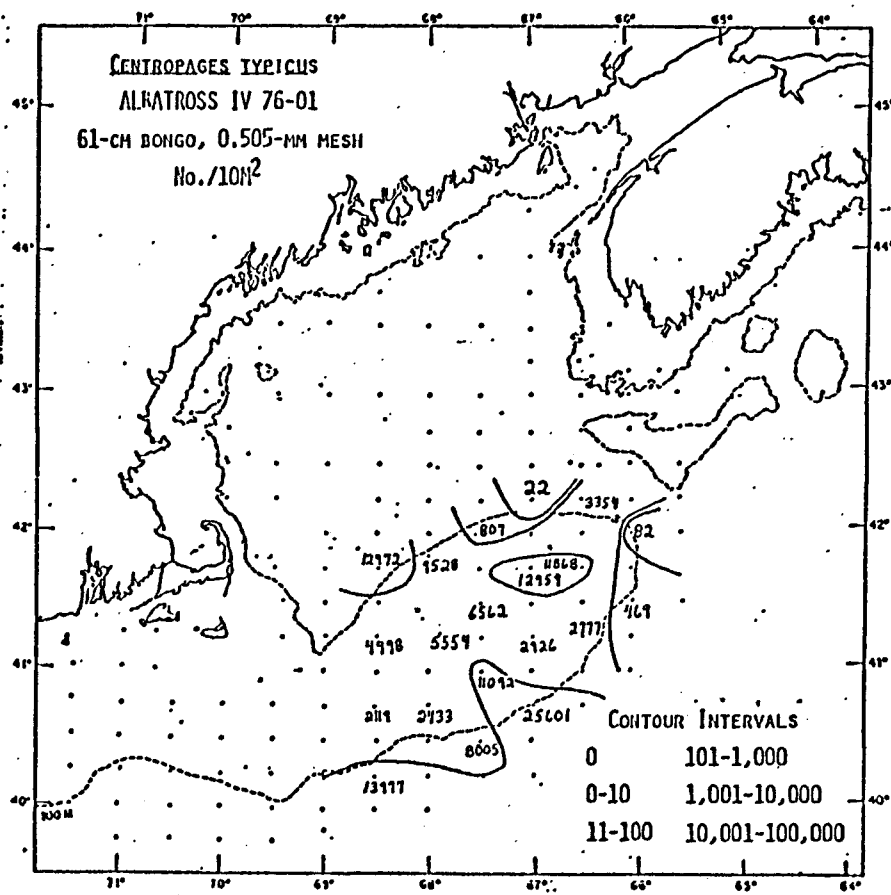
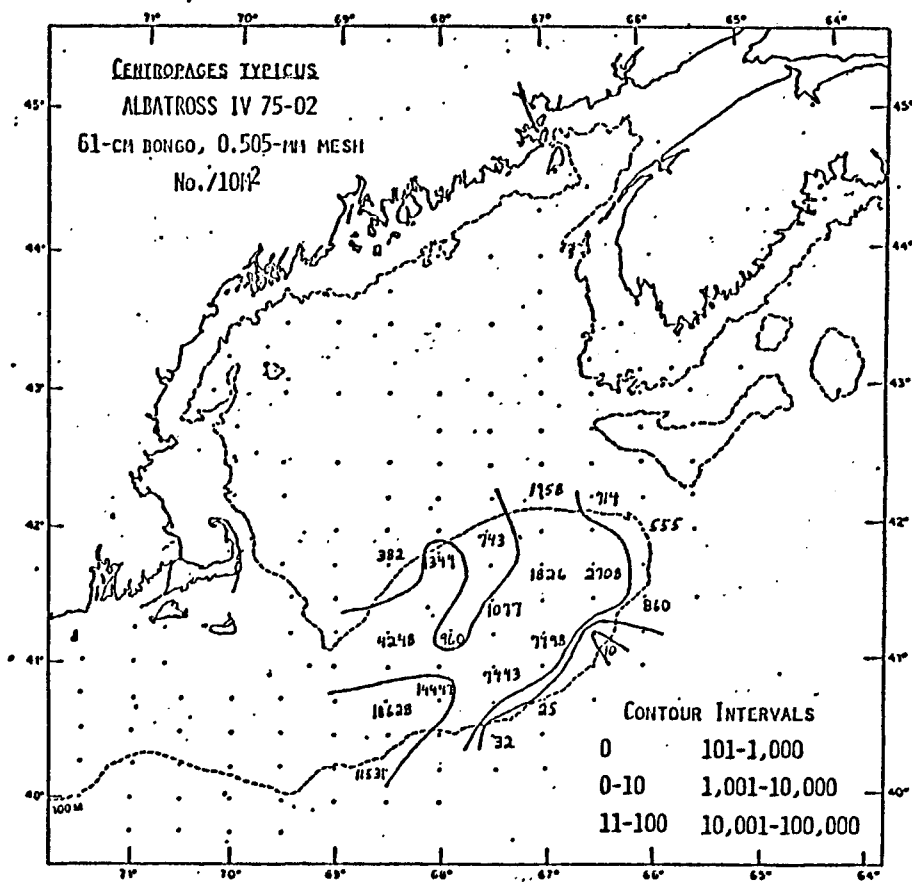


Figure 6.

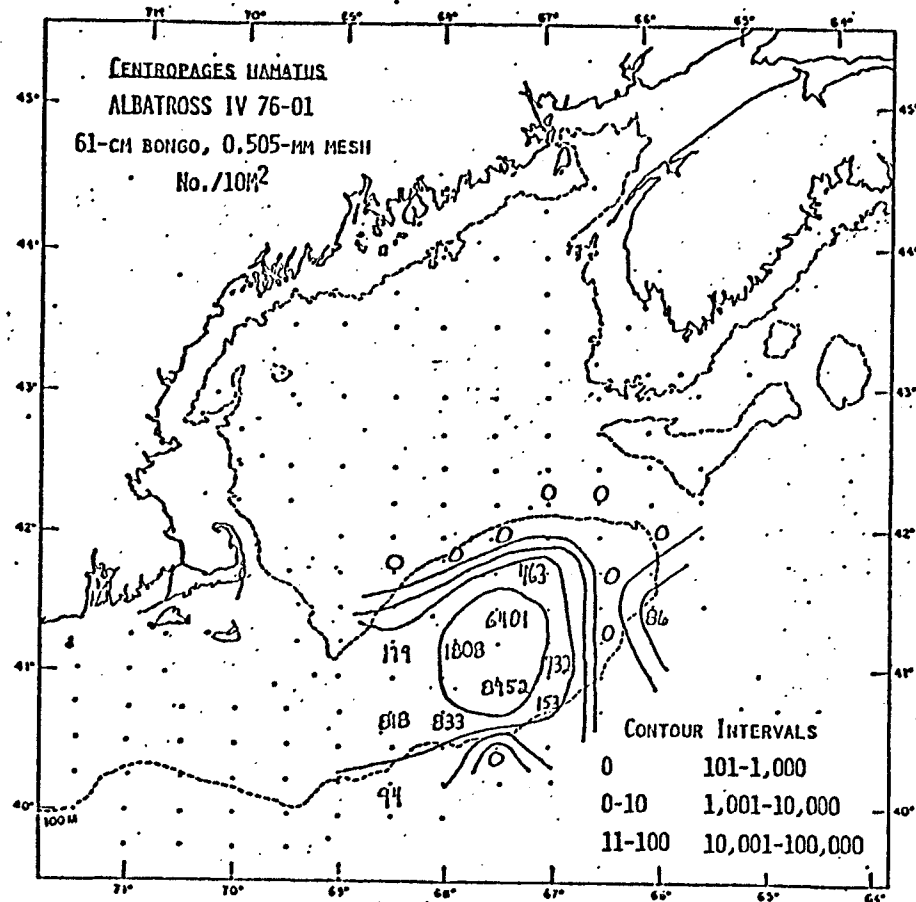
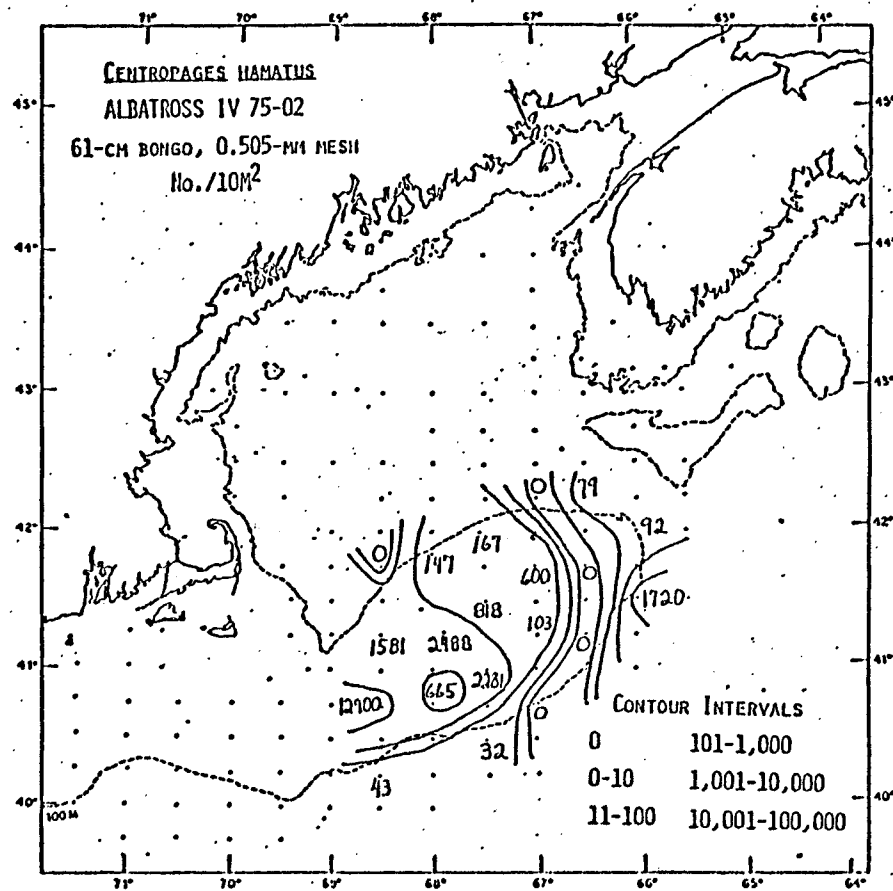


Figure 7.

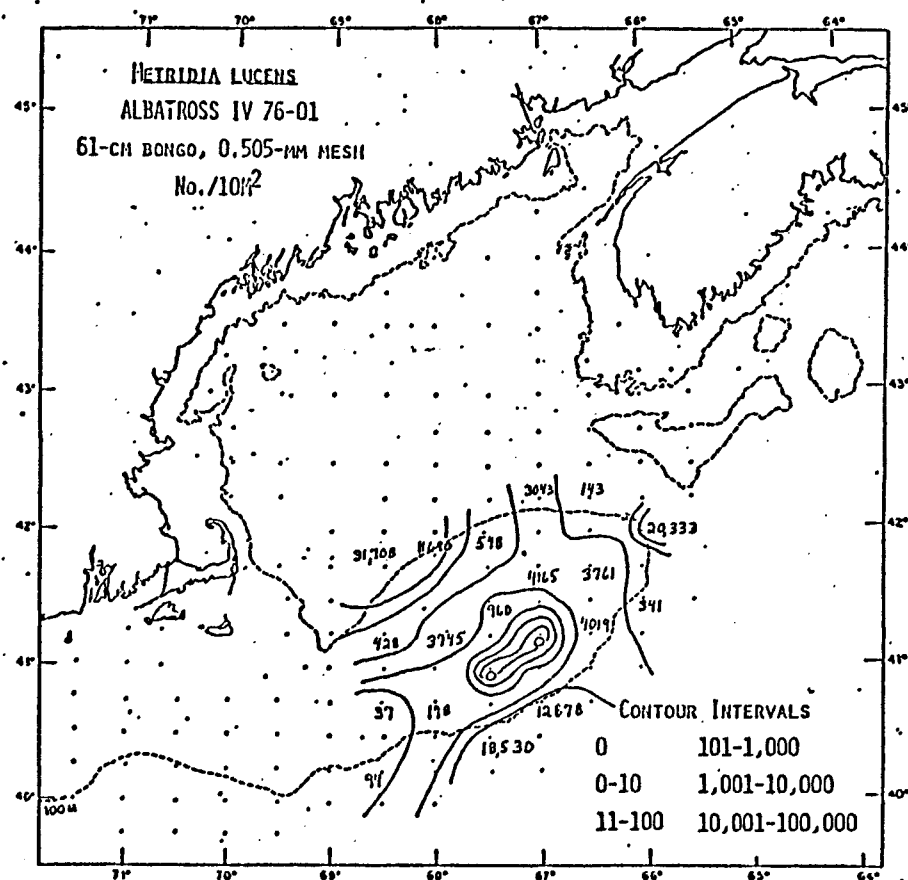
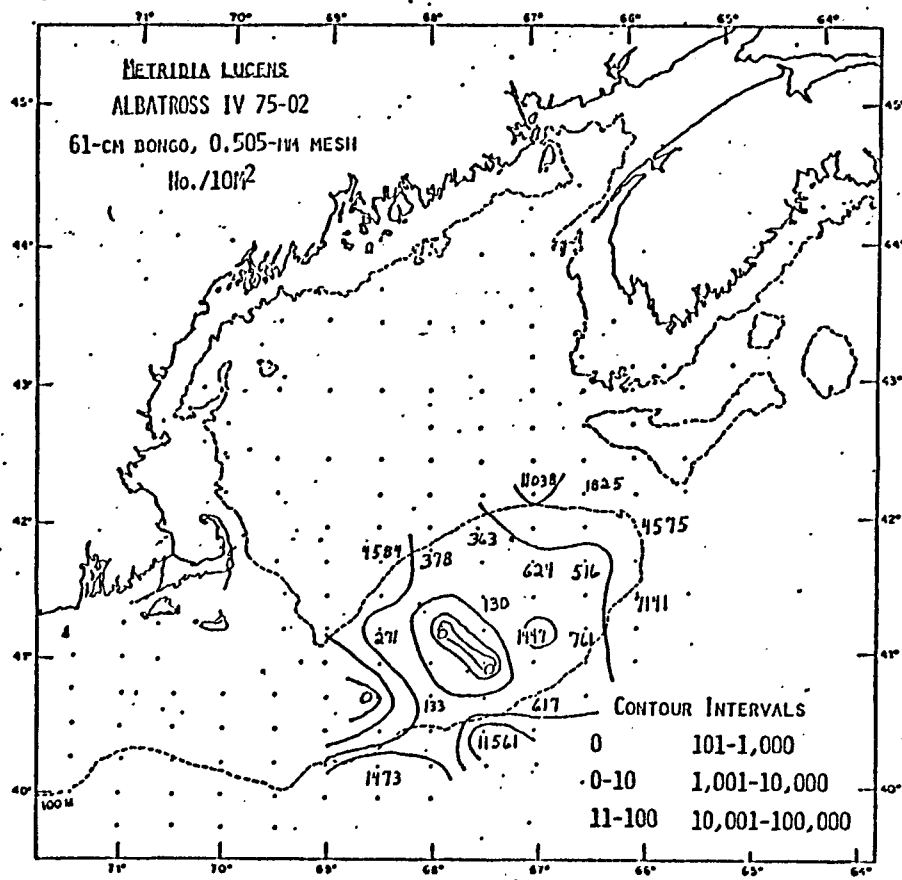


Figure 8.

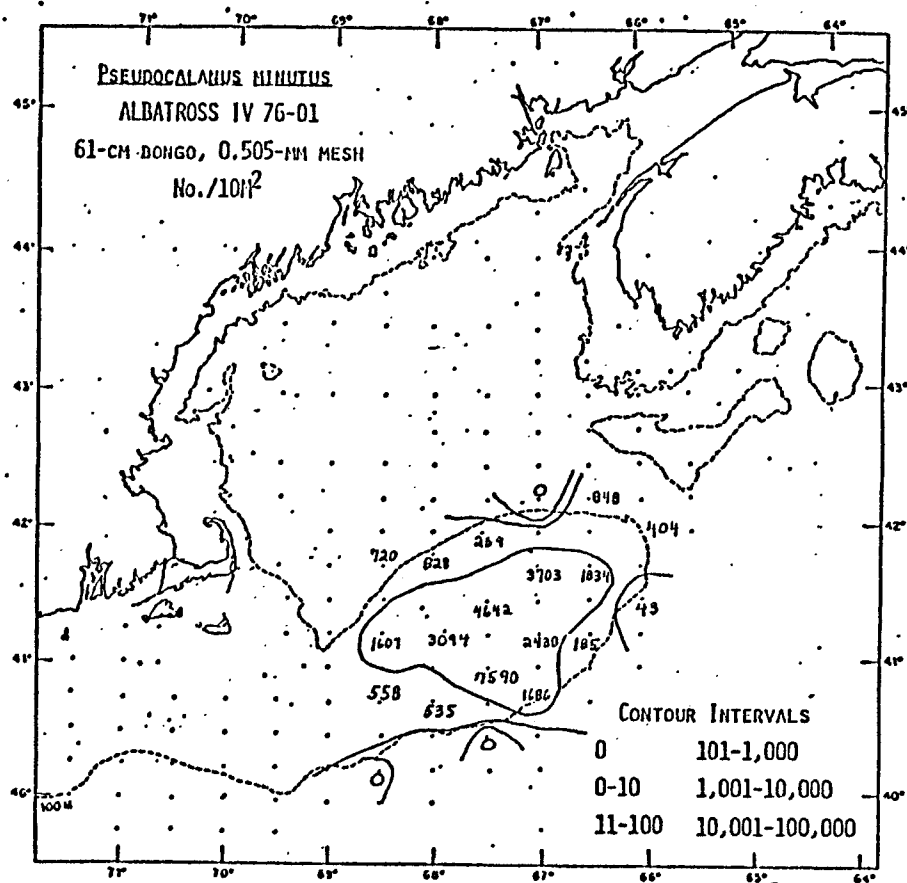
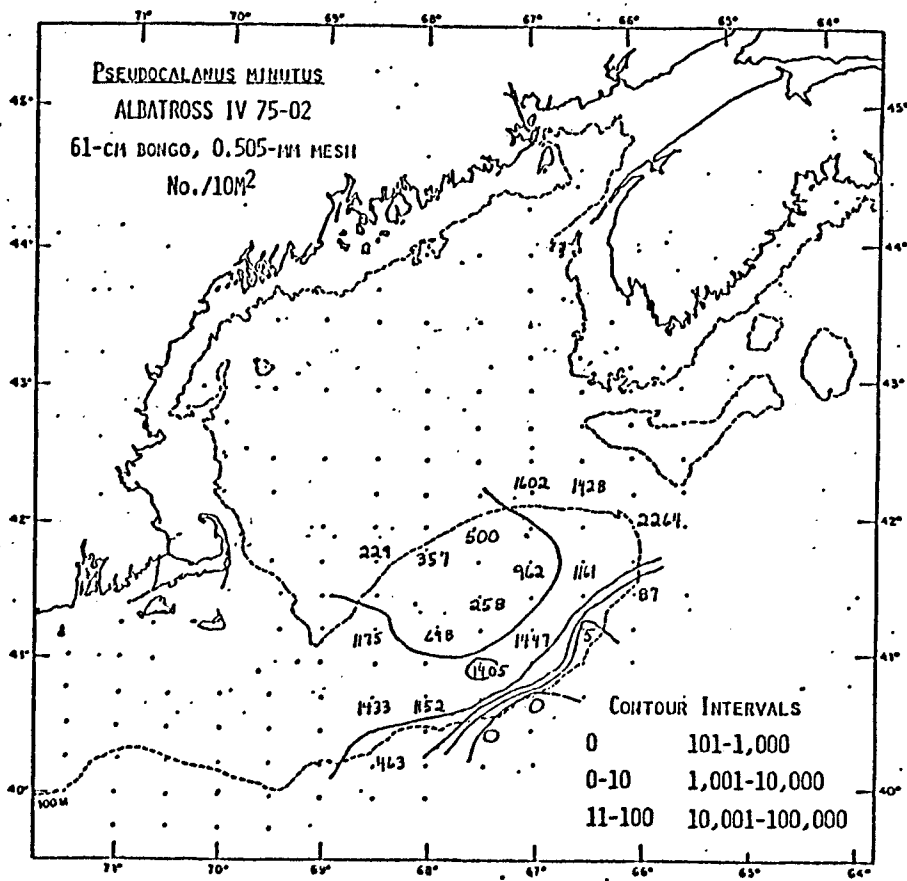


Figure 9.

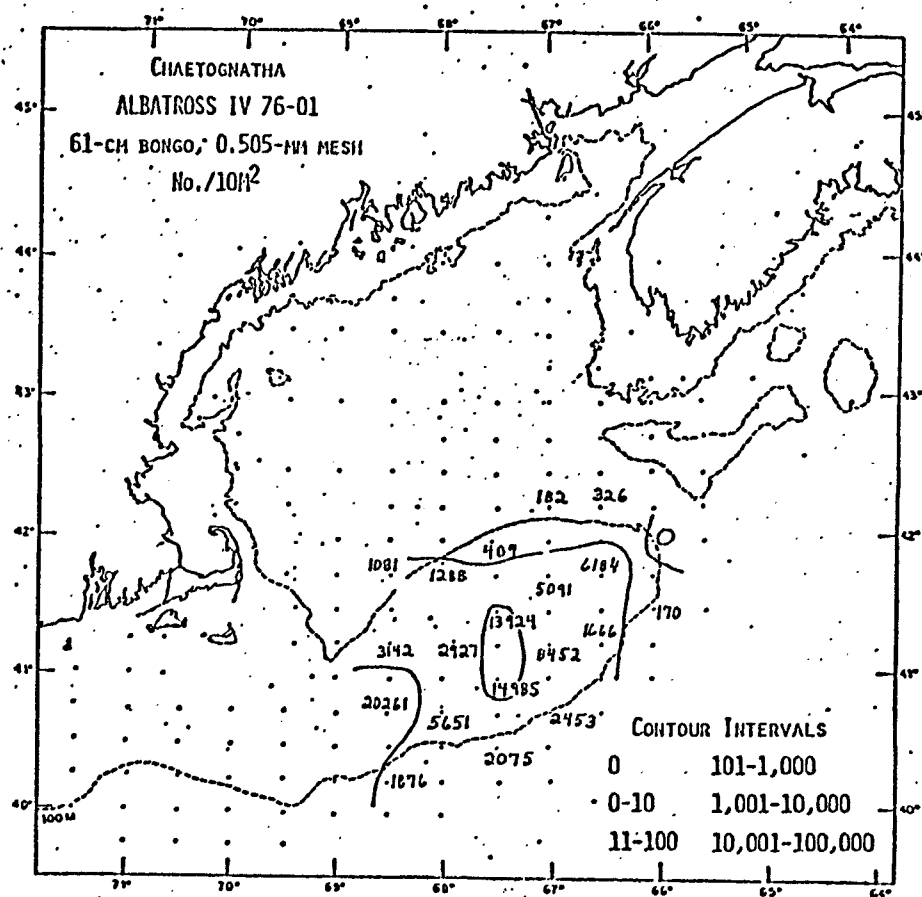
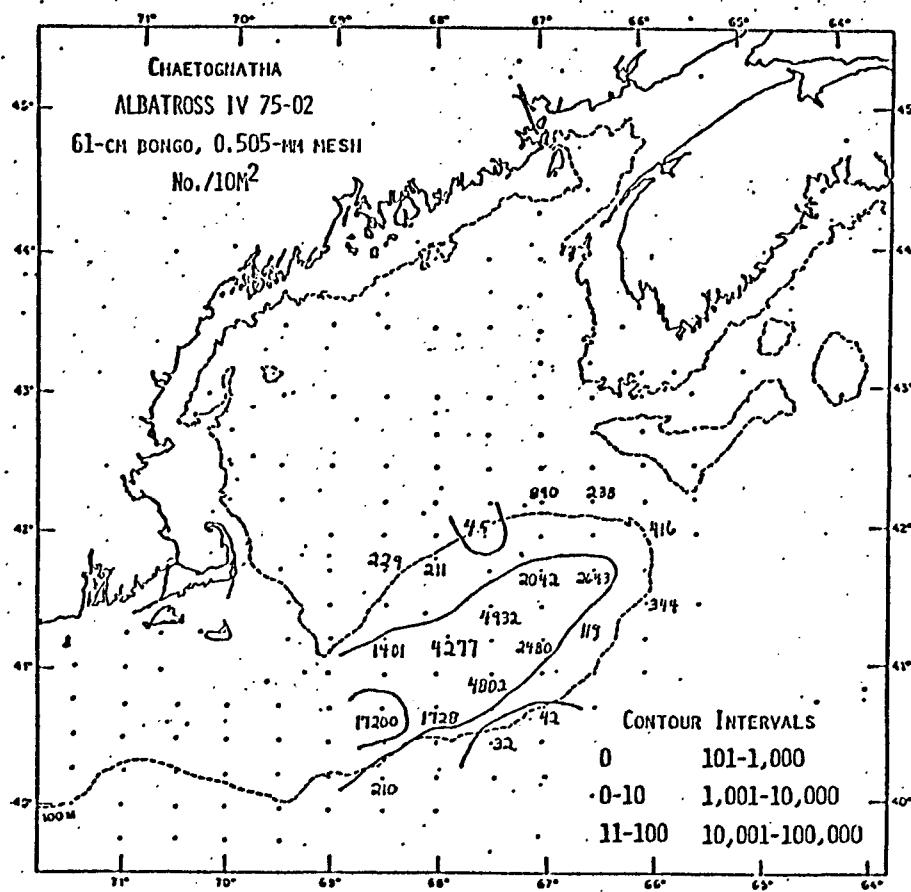


Figure 10.

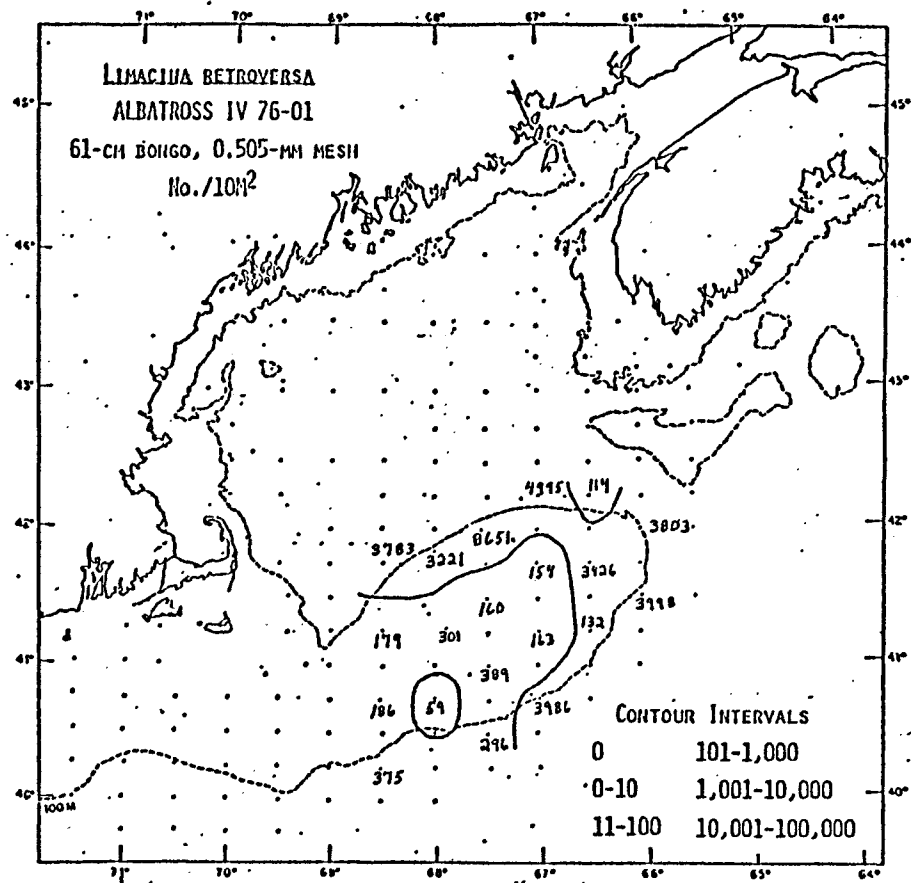
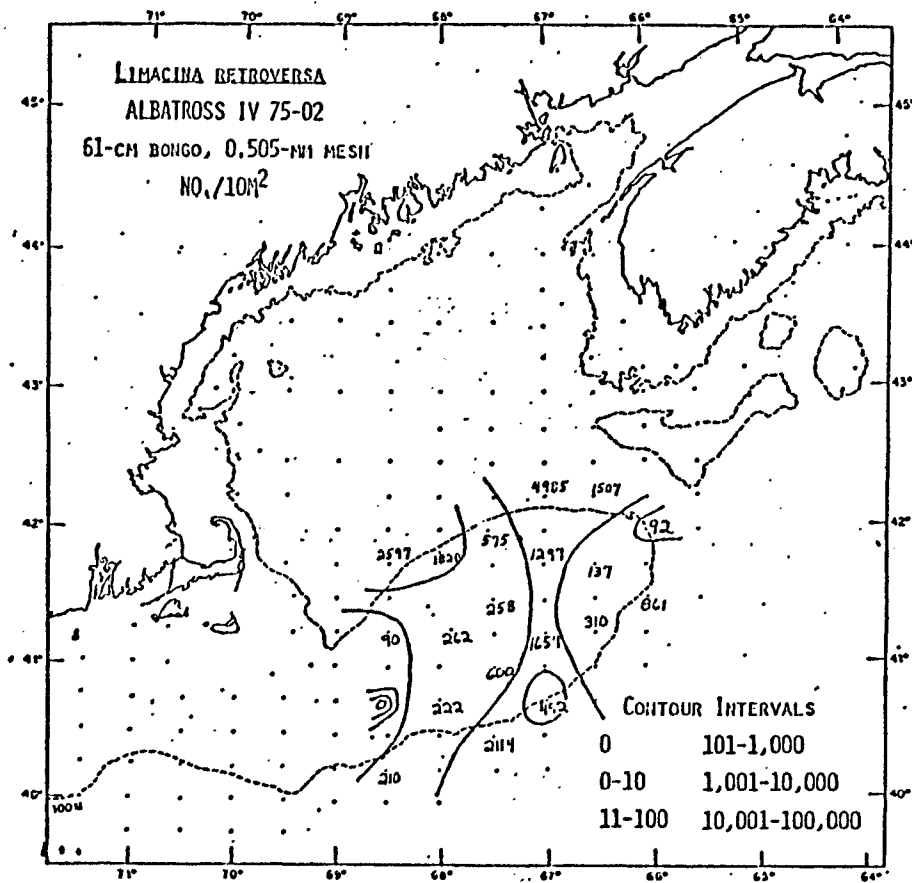


Figure 11.

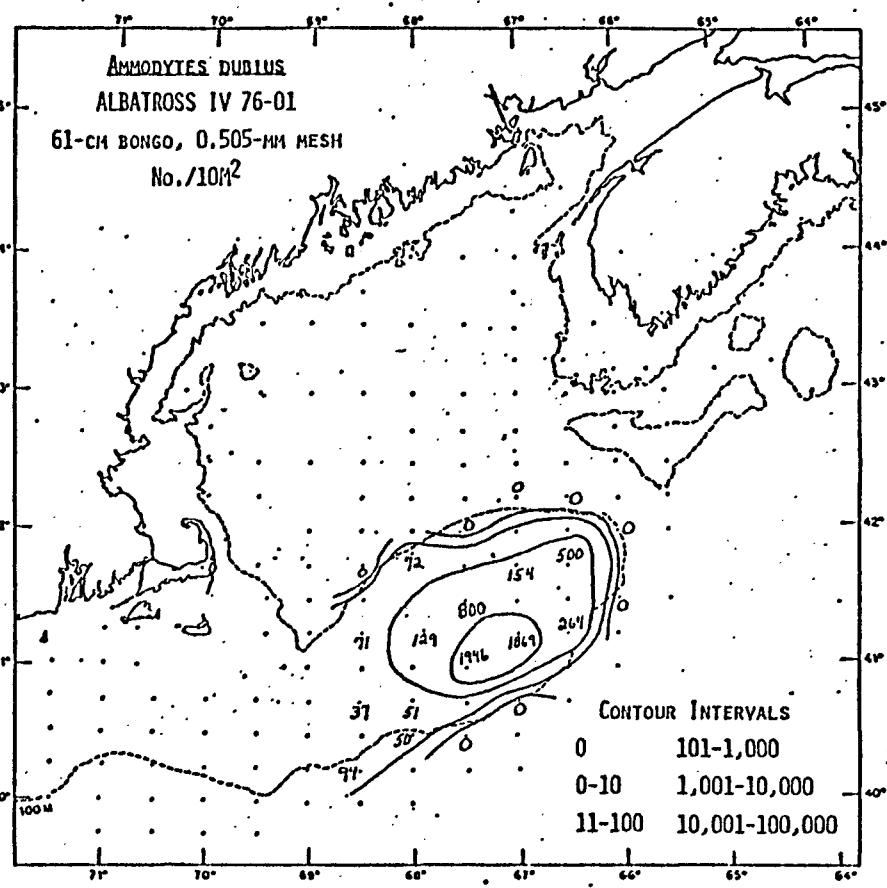
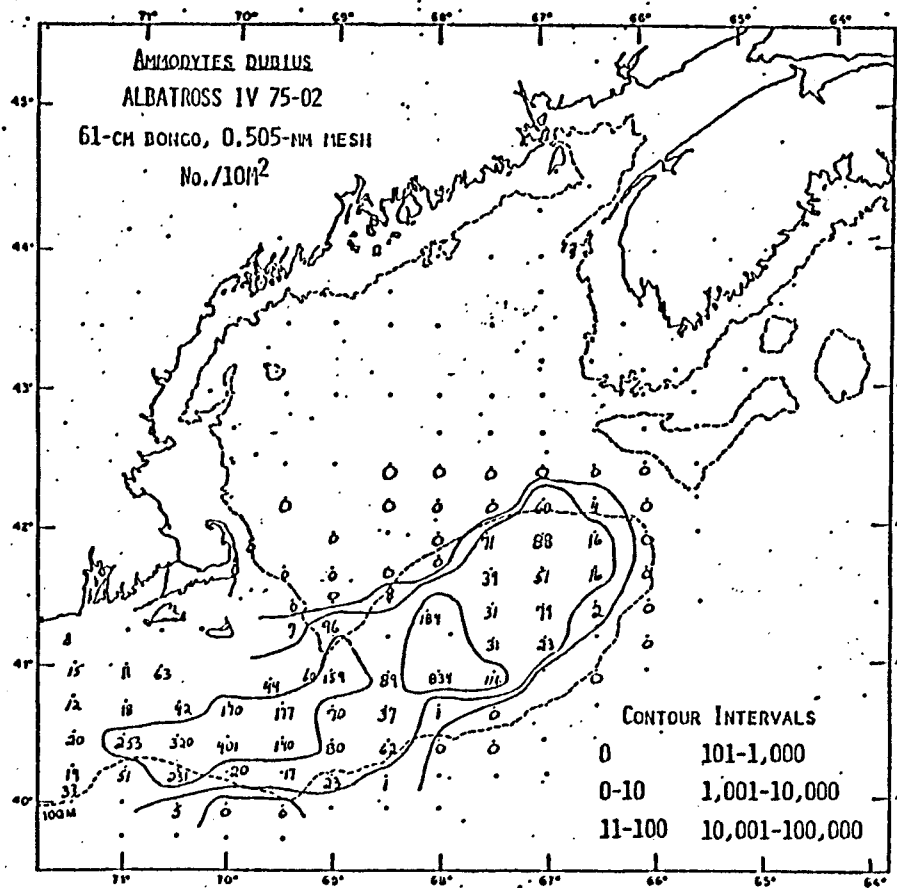


Figure 12.

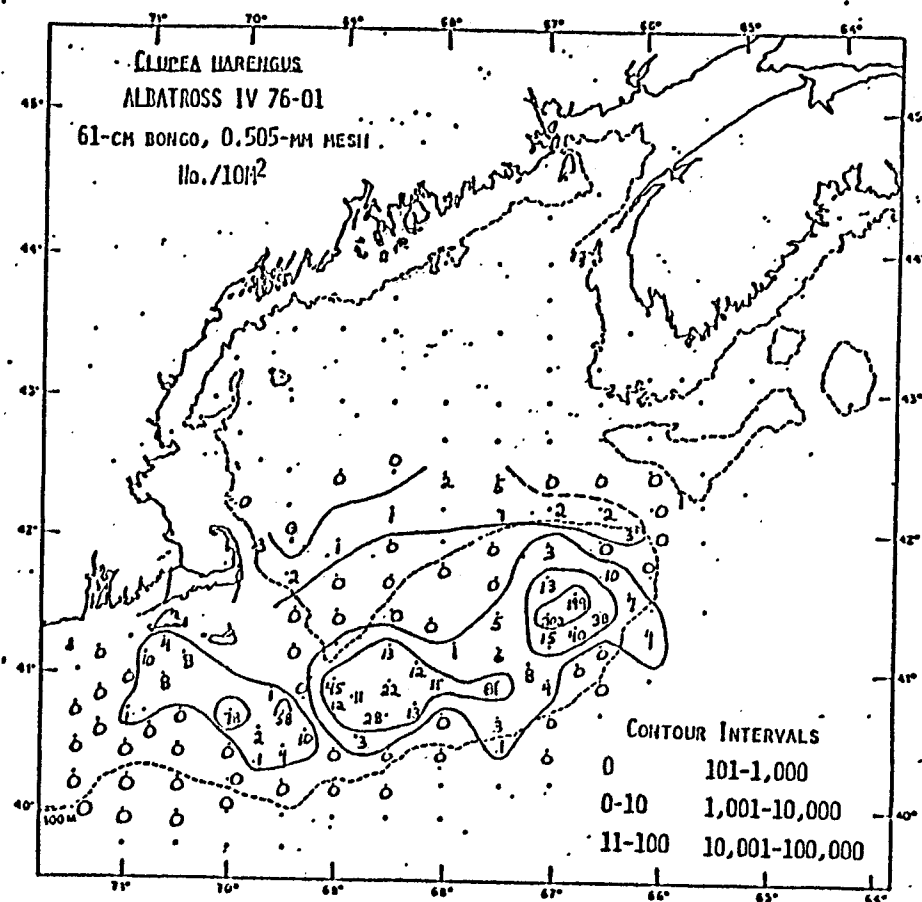
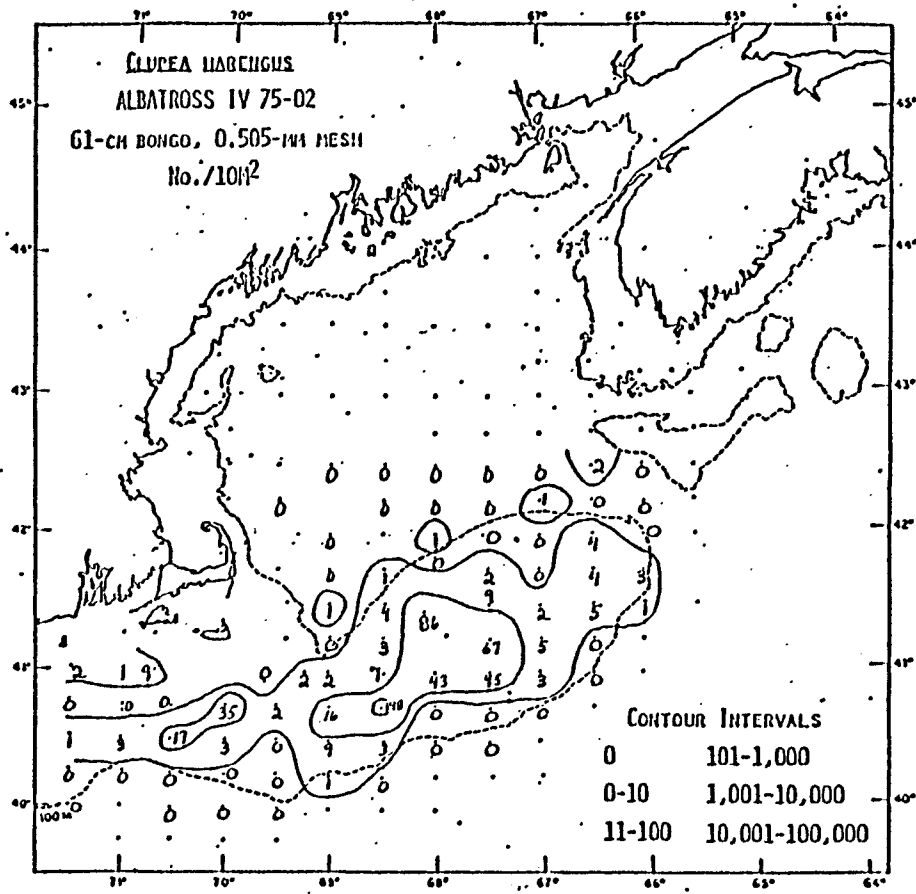


Figure 13.