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Ichthyoplankton Abundance, Diversity, and Spatial Pattern in the Georges Bank-Nantucket Shoals Area, Autumn and Winter Seasons 1971-1977

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Abstract

The distribution, abundance, and length-frequency data for all species of icthyoplankton have been examined for 30 ICNAF Larval Herring Surveys covering the period September 1971 to February 1977. Sampling on these cruises was conducted on a standard grid of bongo-net stations, at 3-4 week intervals throughout the autumn and bimonthly during the winter. Faunal zones were delimited for each cruise by the numerical classification technique of divisive information analysis (DIA) and compared with station temperature observations to delineate water mass types. Distinct and recurring faunal groups were found to be associated with broadscale intrusions of Slope Water onto the southern flank and around the perimeter of Georges Bank, lending support to the inferred clockwise mean residual flow. Ichthyoplankton distributional anomalies, such as geographical displacement following prolonged periods of wind stress, were clearly highlighted by this technique. Various species diversity indices also corroborated the faunal zones discriminated by the DIA technique. The general seasonal succession of ichthyoplankton and year-to-year fluctuations in species abundance are summarized.

Données répartition, abondance et fréquence de longueur pour tantes espèces d'ichthyoplancton ont été examiné pour 30 levées de hareng larvaire ICNAF pendant la période Septembre 1971 à Février 1977. L'echantillonage pendant ces campagnes fut conduit sur une grille standard de position de files bongo, à intervalle de 3-4 semaines par tout l'automne et bi-mensuel pendant l'hiver. Régions faunistique furent délimité pour chaque campagne par la technique de classification numérique d'analyse d'information qui entraîne la division (DIA) et comparé à observations de température de position pour décrire les types de masse d'eau. Des groupes faunaux distinct et récurrent furent trouvé d'être associé avec intrusion d'envergure étendu d'eau de pente sur le flanc méridional et autour le périmètre du Banc George, supportant l'écoulement résiduel moyen dans le sens des aiguilles d'une montre inféré. Des anomalies de répartition d'ichthyoplancton, ainsi que déplacement géographique suite de longues périodes de tension de vent, furent clairement mis en vedette par ce technique. Divers indices de diversité d'espèces aussé corroborent les zones faunaux discriminés par la technique DIA. La succession saisonaire général de l'ichthyoplancton et les fluctuations d'ans par ans d'abondance d'espèces sont résumés.

Introduction

From 1971 to 1979 the International Commission for the Northwest Atlantic (ICNAF) conducted surveys of larval Atlantic herring in the Georges Bank-Nantucket Shoals area (Figure 1) in order to gain a better understanding of the early life history of herring and its relationship to recruitment and spawning stock size. More than 50 of these surveys, sampling on a standard grid of stations, were conducted at three-four week intervals throughout the autumn and bimonthly during the winter. The distribution, abundance and length-frequency data for all species of ichthyoplankton have been summarized for 30 of these cruises covering the period September 1971 to February 1977 (Bolz and Lough, 1981). The present work is a more in-depth analysis of the ichthyoplankton species identified on these 30 cruises.

Many studies have reported on the distribution and abundance of ichthyoplankton in the Nantucket Shoals-Georges Bank region. These studies can be consolidated into two major categories: 1) those composed of species lists along with their abundances, length-frequency data, and distribution maps which attempt to monitor broadscale spatial and temporal fluctuations (Smith et al., 1980; Grimm, 1978; Joakimsson, 1978; Colton and Byron, 1977, 1976); and 2) those concentrating on some aspect of the growth, mortality, distribution, interactions with the physical and biological environment or abundance fluctuations of an individual species, especially ones of economic importance (Sherman et al., 1981; Lough et al., 1980; Lough and Bolz, 1979a, 1979b; Smith et al., 1979, 1978). Several studies also have been conducted relating zooplankton distribution with the hydrography of the Gulf of Maine, Georges Bank and Nantucket Shoals regions (Sherman and Shaner, 1968; Colton et al., 1962; Clarke et al., 1943; Redfield and Beale, 1940; Redfield, 1939; Bigelow, 1926). Where divisions of the study region being investigated have been made, they have been based on physical features, spawning grounds, or tradition, e.g., Nantucket Shoals, Georges Bank, Gulf of Maine, etc., without analyzing the total ichthyoplankton community to establish if valid biogeographical subdivisions do in fact exist. The present study is an attempt to address this problem. The Georges Bank-Nantucket Shoals region and its adjacent waters are analyzed to ascertain if discrete ichthyoplankton faunal zones can be delimited, and, if so, to see if they are correlated with station temperatures that may be characteristic of water mass types, and how these faunal groups and associated water masses are modified over time. It was found that distinct and recurring faunal groups could be discriminated by the numerical classification technique of divisive information analysis.

The intrusion of warmer Slope Water onto Nantucket Shoals and Georges Bank has been noted in past studies to be a commonly occurring feature of this area (Butman et al., 1981; Colton and Stoddard, 1972; Sherman and Shaner, 1968; Colton et al., 1962; Colton, 1961, 1959; Colton and Temple, 1961). One of the major aims of the present study is to identify the ichthyoplankton fauna associated with the Slope Water and to assess the impact of this warm water encroachment on the ichthyoplankton communities residing on the banks. Colton and Temple (1961) hypothesized that large numbers of larval fish are entrained at times into the Slope Water and transported from Georges Bank into warmer water, where they suffer high mortalities due to the lethal temperatures encountered, and as a consequence, they are lost to the fishery. A re-examination of this hypothesis viewed on the basis of the derived biogeographical subdivisions is another major objective of this paper.

The inferred circulation pattern on Georges Bank is characterized by a clockwise mean residual flow around the crest of the bank (60 m), which has been postulated by Butman et al. (1981), Boyar et al. (1973) and others as a mechanism for the retention of larval fish on Georges Bank (Figure 2). The clockwise gyre is circumscribed by a strong jetlike current flowing northeastward along the northern edge of Georges Bank, a southeasterly and southerly flow on the eastern edge of the bank, a southwesterly flow along the southern flank and a northerly flow along the eastern side of the Great South Channel. Although the gyre apparently is a persistent feature throughout the year, it is subject to periodic disruptions and variations in current strength. Analysis of the ichthyoplankton zones in this paper appear to support the inferred circulation patterns.

Sampling Methods and Processing

Vessels, cruise dates, and other pertinent information are listed in chronological order in Table 1 for the 30 surveys included in this study from 1971 to 1977. Cruise tracks and station positions for each of the surveys can be found in Lough and Bolz (1979a). A 3.5 knot double-oblique haul was made on station using a 61-cm bongo net sampler (0.505 and 0.333-mm mesh). A Braincon V-fin depressor (122 cm) was used to achieve the desired wire angle of 45° for the relatively high towing speed, and a Bendix or Benthos time-depth recorder was attached to the wire near the bongo for a permanent trace of the haul profile. General Oceanics flow meters were tied in the mouths of each bongo net to calibrate the amount of water strained. A figure of the gear configuration and other details can be found in Posgay and Marak (1980). The bongo gear was deployed at 50 m/min to a maximum depth of 100 m or to within 5 m of the bottom in shoaler areas, and the rate of retrieval was at 10 m/min. The standard bongo haul filtered between 100 and 1000 m^3 of water for each side of the net, depending on the maximum depth of the tow.

Total ichthyoplankton for the 0.333-mm mesh, 61-cm bongo samples was sorted and identified in Szczecin, Poland at the Morski Instytut Rybacki. All larvae were measured (standard length) to the nearest 0.1 mm. In those cases where large numbers of a species were found in a sample, a subsample of 100 individuals was measured to establish the size frequency distribution of the total number. Due to presorting and other discrepancies, it was necessary to substitute 0.505-mm mesh data for larval herring (Clupea harengus) on several of the cruises and for all ichthyoplankton on two of the cruises (Table 1). A complete discussion of the problems encountered can be found in Bolz (1980). The standard MARMAP sorting protocols used on the samples are given in Sherman et al. (1976) and Sherman and Colton (1976). Where specific identity of larvae could not be ascertained, separation was made to the generic, familial or ordinal level.

Basic station, haul, and standardized larval data from each cruise were processed through the MARMAP Biostatistical Unit, NEFC, Narragansett, R.I., and presented to us in the form of various standard computer summaries and plots (Station Activity Summary, Net Tow Data, Plankton Summary - station abundance of larvae by length categories). Examples of these computer outputs can be found in Lough (1976). Various internal audits have been incorporated into the computer routines to provide quality control of the data in addition to the initial quality control procedures prior to computer entry.

Presentation of Data

All ichthyoplankton were standardized to number per 10 m^2 by 1-mm length classes. The mean abundance for each of the 30 surveys studied was calculated using the delta (Δ)-distribution (Aitchison and Brown, 1957), which has been found by Pennington (1980) to be an efficient estimation of the mean density for egg and larval surveys containing a proportion of zero catches. The estimated arithmetic mean (c) of the delta-distribution given by Pennington (1980) is:

$$c = \left(\frac{m}{n}\right) e^{\bar{y}} \; x_m \; (\tfrac{1}{2}s^2)$$

where, m = number of non-zero catches
n = number of tows
$\bar{y}$ = sample mean of $\log_e$ (no. larvae/m^2) for non-zero catches
s^2 = sample variance of the log values
$x_m(t)$ = a function defined by an infinite series which can be found in the above references.

A thorough discussion of the variance of this mean and other details may be found in Pennington (1980). The mean (c) was then expanded by cruise duration and the area under consideration to yield total abundance estimates (Figures 3-4).

Biogeographical subdivisions of the study area were calculated using the numerical classification technique of divisive information analysis. The method as outlined by Kikkawa and Pearse (1969) employs the Shannon-Weiner information formula:

$$I = sn \ln n - \sum_{j=1}^{s} [a_j \ln a_j + (n - a_j) \ln(n - a_j)]$$

where, s = the total number of species observed
n = the number of stations surveyed
a_j = the number of occurrences of the j^{th} species.

"I" is first calculated for the whole population. The area is then divided into two subpopulations, one containing the j^{th} species and one in which the j^{th} species is absent, and I_{+j} and I_{-j} are calculated. A diversity drop for the j^{th} species is measured using the formula:

$$\Delta I = I - (I_{+j} + I_{-j}).$$

This procedure is continued until the diversity drop for all species is calculated. A biogeographical subdivision is made on the species with the largest diversity drop (I). The faunal zones thus produced may be further subdivided using the same technique.

All subdivisions were further checked by calculating their coefficients of agreement or community using the equation:

$$C = 2s_{xy}/(s_x + s_y)$$

where, s_x = the number of species in zone x
s_y = the number of species in zone y
s_{xy} = the number of species common to both zones.

A "C" value of 1.00 equals complete coincidence and indicates that the two zones should not have been separated and conversely, a "C" value of 0.00 equals complete dissimilarity, substantiating the separation. The diversity of each subdivision was also calculated using Simpson's Diversity Index (Poole, 1974).

When temperature data were available, the cruise was contoured into broad regions exhibiting the greatest mean temperature differences. All temperatures used in this paper were those recorded at a depth of 20 meters in order to diminish the effects of surface anomalies while remaining shallow enough to discriminate upper level water movements and encompass the depth of the seasonal thermocline. These temperature zones then were compared with the faunal zones using the coefficient of agreement formula outlined above.

Cruises and survey seasons then were compared with each other for spatial and temporal fluctuations in their biogeographical and temperature subdivisions, total ichthyoplankton abundances and spatial composition. Maps of each cruise showing the biogeographical subdivisions were constructed (Figures 5-10).

Results

I. Faunal Groups - Boundaries, Diversity, Abundance, Species Composition and Dominance

Divisive information analysis of the 30 cruises studied (Table 1) revealed that the study area could be subdivided into several distinct biogeographical groupings. In the majority of cases, three dynamic faunal zones were evident: 1) a zone centered about the 100-m isobath along the southern flank of Nantucket Shoals and Georges Bank; 2) a zone confined within the 100-m isobath; and 3) a zone located to the north of the Georges Bank-Gulf of Maine frontal edge. These subdivisions will be referred to as the southern faunal zone or group, the central faunal zone and the northern faunal zone.

A. Diversity and Abundance

The southern faunal group was in most cases a zone of high diversity and medium abundance. There was an average of 43 taxa per cruise in the southern zone with a mean abundance of $9928.7/10m^2$. A high mean Simpson's Diversity Index of 0.673 was calculated for the southern biogeographical subdivision. Abundance of ichthyoplankton in the southern zone tended to be very high in the early autumn and low throughout the late autumn and winter.

The central zone was an area of low diversity and high abundance. An average of 15 species per cruise with a mean abundance of $12396.4/10m^2$ was found in the central subdivision, giving a mean abundance per species of $826.4/10m^2$ which was 3.5 times higher than that found in the southern faunal zone ($230.9/10m^2$). A lower mean Simpson's Diversity Index of 0.314 was computed for the central group. Abundance was uniformly high throughout the season.

Only nine taxa per cruise with a mean $no/10m^2$ of 4745.5 were found in the northern faunal zone, giving a mean abundance of $527.3/10m^2$. The northern group was one of low diversity (0.329) and low abundance. The number of larvae in the northern zone was greatest in late autumn, particularly when the biogeographical subdivision extended south over the 100-m isobath onto Georges Bank. Very few individuals were recorded beyond the northern edge of Georges Bank in water deeper than 100 meters.

B. Species Composition and Dominance

A total of 209 taxa, comprising 75 families and 13 orders, were identified in the study area. Since 63 forms were identified to only the familial level, resulting in possible redundancies, the actual number of species is probably lower than the total reported.

The ichthyoplankton fauna in the southern biogeographical subdivision was composed primarily of mesopelagic and subtropical taxa, with the Myctophidae, Paralepididae, Gobiidae, Gonostomatidae and Ophidiidae being the most common families present. The southern species group was dominated by the horned lanternfish (*Ceratoscopelus maderensis*) and by the barracudina *Notolepis rissoi*. Most of the species recorded in the southern zone were represented by only one or two individuals per cruise.

The central zone was composed mainly of species endemic to Georges Bank and Nantucket Shoals. Silver hake (*Merluccius bilinearis*) and hake species (*Urophycis* spp.) were dominant in early autumn, Atlantic herring (*Clupea harengus*) in mid- to late-autumn, and pollock (*Pollachius virens*), cod (*Gadus morhua*) and sand lance species (*Ammodytes* spp.) in winter.

The northern zone was populated with species endemic to Georges Bank and Nantucket Shoals with silver hake, hake spp. and Atlantic herring being the most common. No single species was dominant in the northern subdivision.

II. Faunal Groups - Seasonal and annual fluctuations

In 1971 (Figure 5) the southern faunal zone occupied a broad region (33% of the study area) which encroached far up onto the southern flank of Georges Bank and Nantucket Shoals in late September and early October. As the season progressed, the southern zone rapidly diminished in extent so that by December it was restricted to a small area (12% of the total) off the southeastern edge of Georges Bank. The southern zone was absent from a small section of eastern Georges Bank during the latter half of October. A reduction in total ichthyoplankton abundance also occurred in late October throughout the study area. This break in the southern zone was of short duration, however, and high numbers were present again in November. The highest concentration of species in the study area occurred in the southern faunal zone throughout the season. Eighty-eight percent of the 83 taxa found during the survey period occurred at one time or another in this zone. The northern zone was very restricted in September and December of 1971 and absent in October. Only four taxa, occurring in September, were observed in the northern faunal group during the entire survey season.

As with the 1971 season, a wide southern faunal zone (32% of the study area) extended far up onto the southern flank of Nantucket Shoals and Georges Bank in early October of 1972 (Figure 6). Although the southern zone continued to occupy approximately 20% of the total area from late October through December, sections were absent from it during this period. A large portion of eastern and southeastern Georges Bank was occupied by the northern faunal zone in late October, and small segments of the central zone extended to the southern limits of the study area in the vicinity of Great South Channel in November and December. Abundance and diversity was low in 1972 from late October through December, ranking fifth in total abundance and sixth in number of taxa for the six years studied. The highest ichthyoplankton abundance occurred in the central zone due to the presence of large numbers of recently-hatched endemic species. The northern zone was more extensive and persistent than in 1971 and contained four to nine species throughout the season.

Of the six years studied, 1973 (Figure 7) exhibited the most extensive encroachment of the southern faunal zone onto Nantucket Shoals and Georges Bank, ranging from 53% of the total area in October to 31% in December. In October and November the southern faunal zone extended north through Great South Channel and eastward along the northern edge of Georges Bank. The southern zone became somewhat more restricted in December, but it still extended well north of the 100-m isobath onto Nantucket Shoals and Georges Bank. Compared to previous surveys, sampling was not as intensive in February, especially along the southern edge of Georges Bank, but the southern faunal zone appeared to have moved beyond the southern limits of the study area. The central zone was more fragmented in October and November than in the previous two years. In December and February it was well formed and occupied most of Nantucket Shoals and Georges Bank. A northern subdivision could not be distinguished in October and February but was well defined in November and December when it occupied most of the study area north of Georges Bank and Nantucket Shoals. Total abundance throughout the study area for the 1973 season was the highest in the time series.

As with the preceding season, the 1974 season (Figure 8) exhibited more northerly and uniform encroachment of the southern faunal zone onto Nantucket Shoals and Georges Bank throughout the autumn-winter, covering 35% of the study area in October, 31% in December and 17% in February. In September and October the southern faunal zone extended north through the Great South Channel, but it did not continue eastward along the northern edge of Georges Bank as in 1973. Another difference between the two seasons (1973 and 1974) was the continued presence of a southern faunal zone throughout the 1974-75 winter into February. In 1973 there was an eight-fold reduction in total ichthyoplankton abundance between December and February and in 1974, a two-fold reduction. The total number of taxa (135) observed during the 1974 season, which was the highest in the time series, reflected the broad and continued encroachment of the subtropical and mesopelagic species of the southern fauna onto the bank. The central zone was more cohesive in 1974 than in 1973. The northern fauna was more widespread than in 1973 and was similar in structure to that observed in 1972. In October, a section of the northern zone extended to the south and occupied a large area on eastern Georges Bank in which a high number of recently-hatched herring larvae resided.

The extent of the southern faunal zone in 1975 (Figure 9) was smaller than in 1973 and 1974, covering 33% of the study area in October, 16% in December and 15% in February. The 1975 season was similar in its faunal zones, abundance, and number of taxa to 1971. There were three notable features in the faunal subdivisions for the 1975 season: 1) the extension of a narrow band of the southern fauna north through the Great South Channel and eastward along the northern edge of Georges Bank; 2) the presence of only two zones in October and February; and 3) an east-west separation of the central and northern faunal zones, as opposed to the more common north-south division, in November. The faunal zones were not as well defined as in 1973 and 1974 and the lower number of species observed throughout the season (98) and the three- to five-fold reduction in abundance through December reflected this. No clearly defined central zone was apparent in October, November and February. The east-west division in November roughly separated the region north of the southern zone into a Nantucket Shoals fauna and a Georges Bank fauna with larval abundance being greater in the former.

In 1976 the southern faunal zone was well formed in October and December, poorly developed in November and absent in February. The most notable characteristic of the 1976 season was the poor development of the central zone in October and November and its absence in December. In February, the study area subdivided into a western Nantucket Shoals fauna and an eastern Georges Bank fauna. The Georges Bank subdivision was almost devoid of icthyoplankton, and abundance was 200-fold less than on Nantucket Shoals. During late October and November, abundance in the central zone was an order of magnitude lower than the preceding five years although the average number of species (20) remained approximately the same. The northern zone was more extensive than in other years of the time series and averaged a greater number (19) of species.

III. Temperature Zones

Temperature (20 m) zones were delimited by subdividing the study area into broad regions exhibiting the greatest mean temperature differences (Figure 5). The temperature and faunal zones were compared and exhibited a high coefficient of agreement; an average of 0.72 for the entire time series. The southern faunal zone had the greatest agreement with a mean coefficient of 0.75 and a range of 0.70-0.83 over the six years. The central and northern zones had values of 0.71 and 0.69. Mean temperatures and coefficients of agreement with the faunal zones for the three major subdivisions and for the total area are provided in Table 2. The most anomalous season was 1976, which on average was $2^{o}C$ or more cooler than the other five years.

Discussion

Divisive information analysis of the 30 cruises studied (Table 1) revealed that the study area (Figure 1) could readily be subdivided into several distinct biogeographical subdivisions. In the majority of cases, three dynamic faunal zones were evident: 1) a high diversity, medium abundance zone centered around the 100-m isobath along the southern flank of Nantucket Shoals and Georges Bank, which was composed primarily of mesopelagic and subtropical fish; 2) a low diversity, high abundance zone confined within the 100-m isobath and populated with species endemic to the Georges Bank and Nantucket Shoals areas; and 3) a low diversity, low abundance zone situated north of the Georges Bank-Gulf of Maine frontal edge, containing only a few species endemic to the central zone (2). These three subdivisions are referred to as the southern, central and northern faunal zones in the following discussion.

It was found that the southern faunal zone was a good indicator of Slope Water intrusions onto Nantucket Shoals and Georges Bank. Colton et al. (1962) and Sherman and Shaner (1968) found that oceanic species of copepods also were good indicators of Slope Water intrusions onto Georges Bank and Nantucket Shoals. The ichthyoplankton fauna in this subdivision was similar in composition to the "northern mesopelagic group" described by Backus et al. (1970) and was dominated by the myctophid Ceratoscopelus maderensis and the paralepidid Notolepis rissoi. Many other mesopelagic and subtropical families were represented in this zone (Argentinidae, Bathylagidae, Chauliodontidae, Gonostomatidae, Chlorophthalmidae, Myctophidae, Paralepididae, Synodontidae, Bregmacerotidae, Macrouridae, Ophidiidae, Exocoetidae, Fistulariidae, Scorpaenidae, Acanthuridae, Callionymidae, Gobiidae, Labridae, Scaridae, Bramidae, Carangidae, Kyphosidae, Lutjanidae, Trichiuridae, Nomeidae, Balistidae and Tetraodontidae). Most of these taxa are subtropical forms which have been expatriated northward by the Gulf Stream and are rare visitors to Nantucket Shoals and Georges Bank. Markle et al. (1980) discuss a similar phenomenon of expatriated species found on the Scotian Shelf.

As a broad generality, the southern faunal zone encroached well north of the 100-m isobath onto Nantucket Shoals and Georges Bank in the early autumn and regressed towards the south throughout the remainder of the survey season, becoming a thin band or disappearing completely by February. The high coefficient of agreement (0.75) between the highest temperature zone and the southern biogeographical subdivision lends support to the hypothesis that an actual encroachment of warmer Slope Water, rather than solely an isolated intrusion of ichthyoplankton, occurred onto the bank. Unfortunately, salinity data were not available to further substantiate these intrusions. An interesting feature noted on several cruises, particularly Belogorsk 73-01, Wieczno 73-40 and Belogorsk 75-02, was the northward extension of southern faunal species through the Great South Channel and continuing eastward along the northern edge of Georges Bank. This apparent transport of southern species is in agreement with the inferred long-term mean circulation patterns, i.e., the northward flow along the eastern side of the Great South Channel and the northeastward jetlike current along the northern edge of Georges Bank (Butman et al., 1981).

The general seasonal pattern noted above was not a fixed feature but varied from year to year, particularly in the width of the southern faunal zone and the extent of its intrusion onto Nantucket Shoals and Georges Bank. The six-year study may be divided into three groups of two survey seasons each: 1) 1971 and 1975, which had mediumly well-formed southern faunal zones and moderate total ichthyoplankton abundance; 2) 1973 and 1974, which had well-developed southern faunal zones and extremely high abundance; and 3) 1972 and 1976, which exhibited narrowly constricted southern faunal zones, or disruptions in the zone, and had very low seasonal abundance estimates. There appears to be an observable relationship between the degree of development and persistence of the southern faunal zone and the total abundance of ichthyoplankton on Georges Bank and Nantucket Shoals, although it is difficult to substantiate quantitatively because of the limited number of seasons studied thus far. In 1972 the southern faunal zone was absent from eastern Georges Bank in late October, and the abundance of species endemic to Georges Bank, which normally constitute 80% or more of the total ichthyoplankton abundance, was low for the remainder of the season. In late winter of the 1973 season, the southern faunal zone appeared to be absent and abundance declined eight-fold from its early winter level, whereas during the 1974 season, the zone persisted throughout the winter and abundance decreased only by two-fold. The southern faunal zone was poorly developed or absent and the northern and central faunal zones were indivisible during the 1976 season from early November through February. Ichthyoplankton abundance on Georges Bank during the 1976 season was the lowest observed in the time series. It appears that when the Shelf/Slope Water front is poorly developed, or beyond the southern limits of the study area, retention of larvae spawned on the bank is minimal. A well-developed southern faunal zone and an extremely high seasonal abundance, which were observed in the autumn and early winter of 1973 and 1974, would seem as evidence that a strong retention mechanism was operable on Georges Bank during this time period. This corroborates the supposition of Colton et al. (1962) that "overflows of oceanic water would tend to counteract the general offshore movement of surface water from Georges Bank."

Three possible hypotheses for the loss of larvae from Georges Bank are: 1) the larvae are entrained by the Slope Water and transported offshore (Bumpus, 1976); 2) a fragmented or less well-developed southern faunal zone permits larvae to be transported off the bank by the prevailing northwesterly winds and offshore surface drift (Colton and Temple, 1961); and 3) the encroachment of warmer Slope Water onto the bank, which subjects the larvae to temperatures beyond their tolerance limits. All three hypotheses are consistent with the earlier studies of Colton (1959) and Colton and Temple (1961). The low species diversity and ichthyoplankton abundance observed in the northern faunal zone throughout the study appears to rule out major losses of larvae off the northern edge of Georges Bank. Disruptions to the southern faunal zone were primarily on southeastern Georges Bank and in the vicinity of the Great South Channel, and strong northwesterly winds were observed in the survey season (1976-77) of lowest abundance. Both areas have variable currents with offshore components, giving support to the wind stress hypothesis. The loss of parcels of the southern faunal zone from one cruise to the next appears to argue in favor of the entrainment hypothesis. The lack of field condition factor data make it impossible to substantiate the loss of larvae as a result of lethal water temperatures. In all three cases, nevertheless, the larvae are presumably lost to the recruited populations.

Unusually strong and persistent northwesterly winds occurred during November, January and February of the 1976-77 season, which could conceivably move the southern Shelf/Slope Water front farther offshore and increase the transport of water and larvae off the southern edge of the banks (Ingham, 1979). This possibility was supported by the approximately 2^{o}C cooler water and the greater salinity values (the highest ever reported over Georges Bank) on Georges Bank and Nantucket Shoals at this time, indicating the movement of Gulf of Maine Water onto the bank (Wright, 1979). Computed monthly Ekman transport indices suggested a strong southerly transport throughout the 1976-77 autumn-winter (Lough et al., 1979b). Whether or not wind is the sole mechanism in the breakdown of the southern faunal zone and in the offshore transport of larvae has not as yet been fully assessed and bears further study.

Another prominent feature noted in November of 1975 and February of 1977 was the apparent shift of high ichthyoplankton abundance from the Georges Bank area to the Nantucket Shoals area. This shift was reflected in the biogeographical subdivisions of larval fish as well as in the zooplankton distribution (Cohen and Lough, 1981). It appeared that larvae spawned on Nantucket Shoals were retained in nearshore areas throughout the season, whereas larvae spawned on Georges Bank were transported offshore and lost (see above). Thus, in those years when the southern faunal zone breaks down and larvae on Georges Bank are lost to the Slope Water, the inshore area may provide a more favorable nursery ground for the retention and survival of larval fish.

Summary

1. Distinct and recurring biogeographical subdivisions of the Nantucket Shoals-Georges Bank region were delimited using the numerical classification technique of of divisive information analysis. Three faunal subdivisions were evident: 1) a high diversity, low abundance southern zone located about the 100-m isobath along the southern flank of Nantucket Shoals and Georges Bank; 2) a low diversity, high abundance central zone confined within the 100-m isobath; and 3) a low diversity, low abundance northern zone situated north of the Georges Bank-Gulf of Maine frontal edge.

2. The southern faunal zone was characterized by subtropical and mesopelagic taxa which apparently had been transported north by the Gulf Stream and onto Nantucket Shoals and Georges Bank by Slope Water intrusions.

3. The apparent transport of southern species north through the Great South Channel and east along the northern edge of Georges Bank corroborates the inferred long-term mean circulation patterns of Georges Bank.

4. The southern biogeographical subdivision or group was found to be associated with broadscale intrusions of Slope Water onto the southern flank of Nantucket Shoals and Georges Bank. This faunal zone fluctuated on-off the bank seasonally, generally receding farther offshore as the season progressed. Annually the southern faunal zone became more well developed in the high abundance years of 1973 and 1974, only moderately developed in the medium abundance years of 1971 and 1975, and poorly formed in the low abundance years of 1972 and 1976.

5. When the southern faunal zone was poorly developed or absent, total ichthyoplankton abundance was low. It is hypothesized that weakening of the southern faunal zone is indicative of a significant disruption on Georges Bank to the clockwise mean residual flow which acts as a retention mechanism for larvae spawned on the bank. This apparent breakdown in the clockwise gyre would

permit larvae to be transported south across the 100-m isobath to a greater extent than usual where they presumably incur a high mortality.

6. Based on the severe disruption of all the faunal zones during the winter of 1976-77 and on the unusually strong and persistent northwesterly winds that occurred in January and February, it is hypothesized that wind stress can be one of the major mechanisms in the breakdown of the southern faunal zone.

7. All of the faunal subdivisions had high coefficients of agreement or community with broadly contoured 20-m temperature zones, indicating that the three faunal groups are associated with distinct water mass types characteristic of the Georges Bank-Nantucket Shoals region.

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Table 1. Summary of cruise data, 1971-1977, used in abundance estimates of ichthyoplankton in the Georges Bank - Nantucket Shoals area (gear: 61-cm bongo; mesh size: 0.333 mm).

	Vessel	Cruise Number	Dates	Number of stations used in analysis
			1971	
1)	Delaware II*	71-04	21 Sep. - 04 Oct.	72
2)	Viandra	71-01	09 - 25 Oct.	64
3)	Walther Herwig	71-01	28 Oct. - 12 Nov.	71
4)	Albatross IV*	71-07	02 - 17 Dec.	71
			1972	
5)	Argus*	72-01	22 - 30 Sep.	45
6)	Wieczno	72-01	02 - 28 Oct.	80
7)	Argus	72-02	12 - 28 Oct.	75
8)	Anton Dohrn	72-01	31 Oct. - 12 Nov.	79
9)	Albatross IV**	72-09	02 - 20 Dec.	81
			1973	
10)	Cryos	73-01	16 - 28 Sep.	44
11)	Wieczno*	73-40	28 Sep. - 20 Oct.	79
12)	Belogorsk	73-01	15 Oct. - 01 Nov.	81
13)	Walther Herwig	73-43	28 Oct. - 08 Nov.	81
14)	Albatross IV	73-09	04 - 20 Dec.	82
15)	Albatross IV**	74-02	11 - 22 Feb.	57
			1974	
16)	Cryos	74-04	07 - 24 Sep.	65
17)	Prognoz	74-01	18 - 30 Oct.	79
18)	Anton Dohrn	74-01	16 - 23 Nov.	70
19)	Albatross IV	74-13	04 - 19 Dec.	83
20)	Albatross IV	75-02	12 - 28 Feb.	79
			1975	
21)	Belogorsk*	75-02	25 Sep. - 08 Oct.	80
22)	Belogorsk	75-03	17 - 30 Oct.	75
23)	Anton Dohrn	75-187	01 - 18 Nov.	85
24)	Albatross IV	75-14	05 - 17 Dec.	81
25)	Albatross IV	76-01	10 - 25 Feb.	82
			1976	
26)	Belogorsk	76-01	04 - 11 Oct.	50
27)	Wieczno	76-03	14 Oct. - 03 Nov.	82
28)	Anton Dohrn	76-02	15 - 29 Nov.	77
29)	Researcher	76-01	27 Nov. - 11 Dec.	74
30)	Mt. Mitchell	77-01	13 - 24 Feb.	82
				Total 2206

* 0.505-mm mesh data substituted for larval herring (*Clupea harengus*).
** 0.505-mm mesh data substituted for all ichthyoplankton.

Table 2. Mean temperatures (20 meters) and coefficients of agreement between the three major temperature and faunal zones in the Nantucket Shoals-Georges Bank region.

Cruise	Middate	Southern Faunal Zone		Central Faunal Zone		Northern Faunal Zone		Total Area	
		Mean Temp.	Coeff. Agree.	Mean Temp.	Coeff. Agree.	Mean Temp.	Coeff. Agree.	Mean Temp.	Coeff. Agree.
1971 Season									
Delaware II 71-04	27 Sep.	21.5	0.88	16.3	0.71	14.2	0.69	16.8	0.75
Viandra 71-01	17 Oct.	18.9	0.76	14.3	0.93	-	-	14.8	0.89
W. Herwig 71-01	05 Nov.	-	-	-	-	-	-	-	-
Albatross IV 71-01	09 Dec.	13.5	0.80	9.8	0.82	8.4	0.71	9.6	0.78
1972 Season									
Argus 72-01	26 Sep.	19.5	-	15.2	-	12.5	-	15.6	-
Wieczno 72-01	14 Oct.	18.5	0.79	14.3	0.65	12.0	0.47	14.7	0.64
Argus 72-02	20 Oct.	17.2	0.88	13.2	0.72	11.0	0.65	13.4	0.72
Anton Dohrn 72-01	05 Nov.	17.2	0.80	12.9	0.61	11.1	0.70	12.1	0.68
Albatross IV 72-09	10 Dec.	15.7	0.47	10.4	0.73	8.7	0.87	10.0	0.75
1973 Season									
Cryos 73-01	19 Sep.	-	-	-	-	-	-	-	-
Wieczno 73-40	09 Oct.	17.5	0.86	13.8	0.84	-	-	15.8	0.85
Belogorsk 73-01	23 Oct.	-	-	-	-	-	-	-	-
W. Herwig 73-43	02 Nov.	14.6	0.75	12.6	0.13	10.9	0.76	13.3	0.63
Albatross IV 73-09	13 Dec.	13.0	0.81	9.8	0.64	8.8	0.72	10.6	0.73
Albatross IV 74-02	14 Feb.	-	-	6.6	-	5.5	-	6.2	-
1974 Season									
Cryos 74-04	16 Sep.	19.9	0.67	14.1	0.55	10.1	0.29	16.3	0.56
Prognoz 74-01	24 Oct.	18.0	0.63	13.7	0.69	12.1	0.88	13.4	0.75
Anton Dohrn 74-01	19 Nov.	-	-	-	-	-	-	-	-
Albatross IV 74-13	13 Dec.	13.1	0.84	9.7	0.63	8.5	0.68	10.4	0.71
Albatross IV 75-02	14 Feb.	7.6	0.60	6.4	0.71	5.1	0.42	5.8	0.62
1975 Season									
Belogorsk 75-02	01 Oct.	17.4	0.59	13.6	0.59	11.1	0.43	15.1	0.58
Belogorsk 75-03	23 Oct.	16.2	0.76	13.0	0.87	-	-	14.1	0.84
Anton Dohrn 75-187	09 Nov.	18.5	0.77	13.0	0.47	11.3	0.52	13.0	0.55
Albatross IV 75-14	09 Dec.	15.1	0.70	9.8	0.70	8.5	0.58	9.8	0.66
Albatross IV 76-01	16 Feb.	7.9	0.77	5.1	0.86	-	-	5.6	0.90
1976 Season									
Belogorsk 76-03	08 Oct.	-	-	15.9	0.55	14.9	0.63	15.4	0.60
Wieczno 76-03	24 Oct.	-	-	-	-	-	-	-	-
Anton Dohrn 76-01	22 Nov.	13.2	0.68	11.1	0.54	9.3	0.88	10.5	0.74
Researcher 76-01	04 Dec.	11.8	0.85	8.7	0.92	-	-	9.8	0.90
Mt. Mitchell 77-01	18 Feb.	-	-	2.3	0.64	5.0	0.81	4.5	0.76

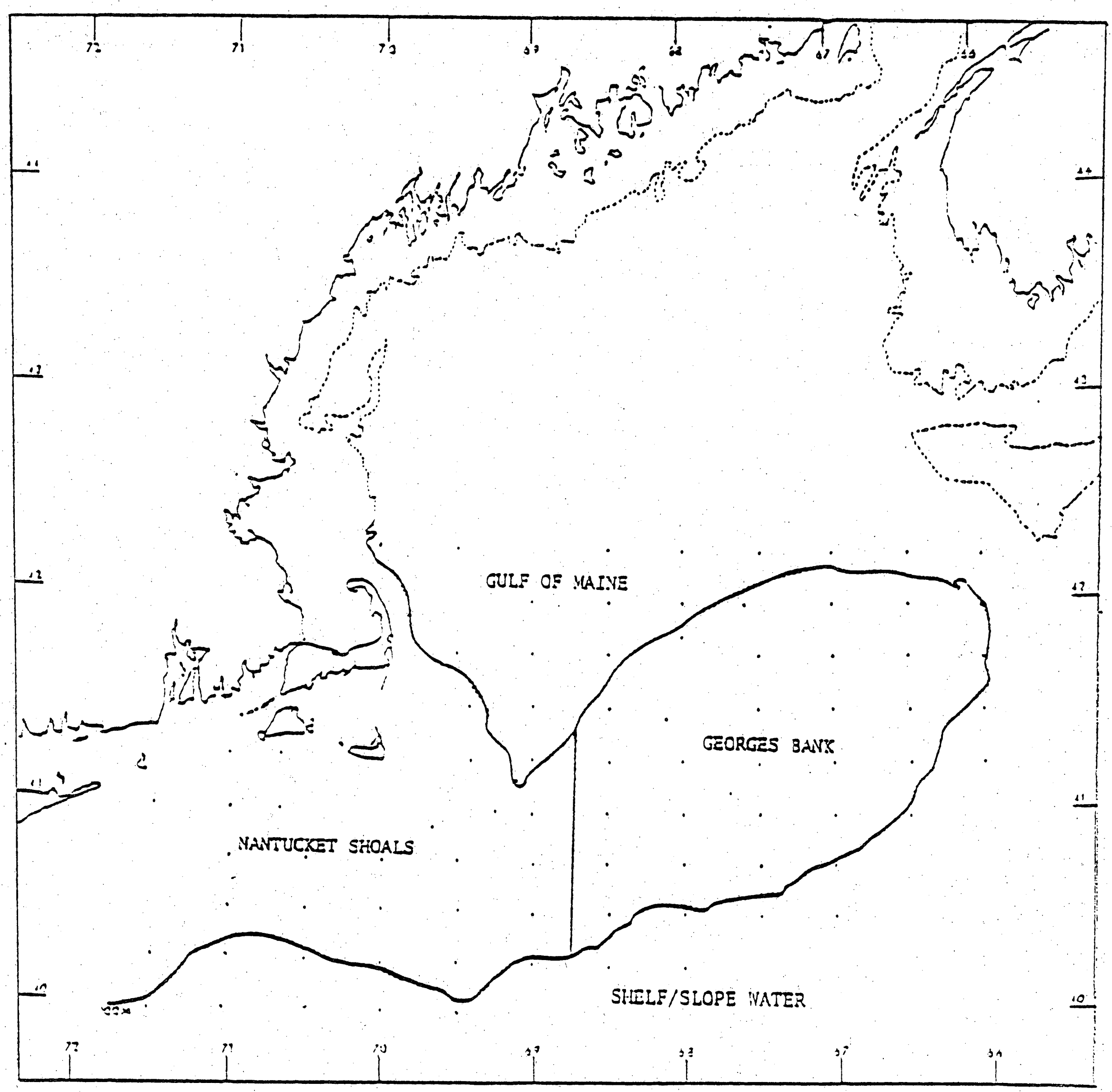


Figure 1. Station locations (dots) and geographical subdivisions of Georges Bank, Nantucket Shoals, Gulf of Maine, and Shelf/Slope Water used for abundance estimates of ichthyoplankton.

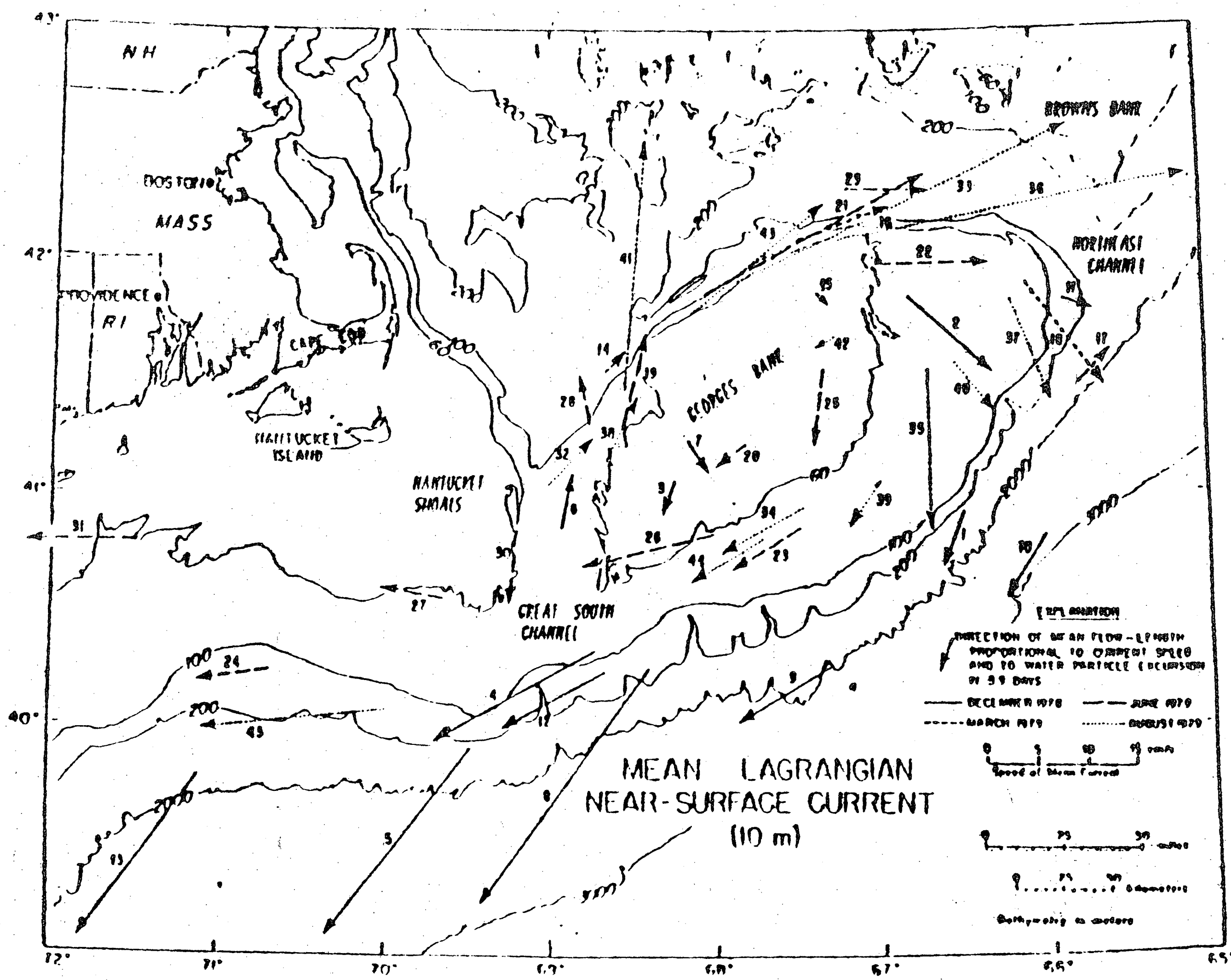


Figure 2. Mean circulation pattern of the Nantucket Shoals-Georges Bank area based on satellite-tracked drifters with 10-m window-shade drogues centered at 10 m depth. (From Butman. 1981)

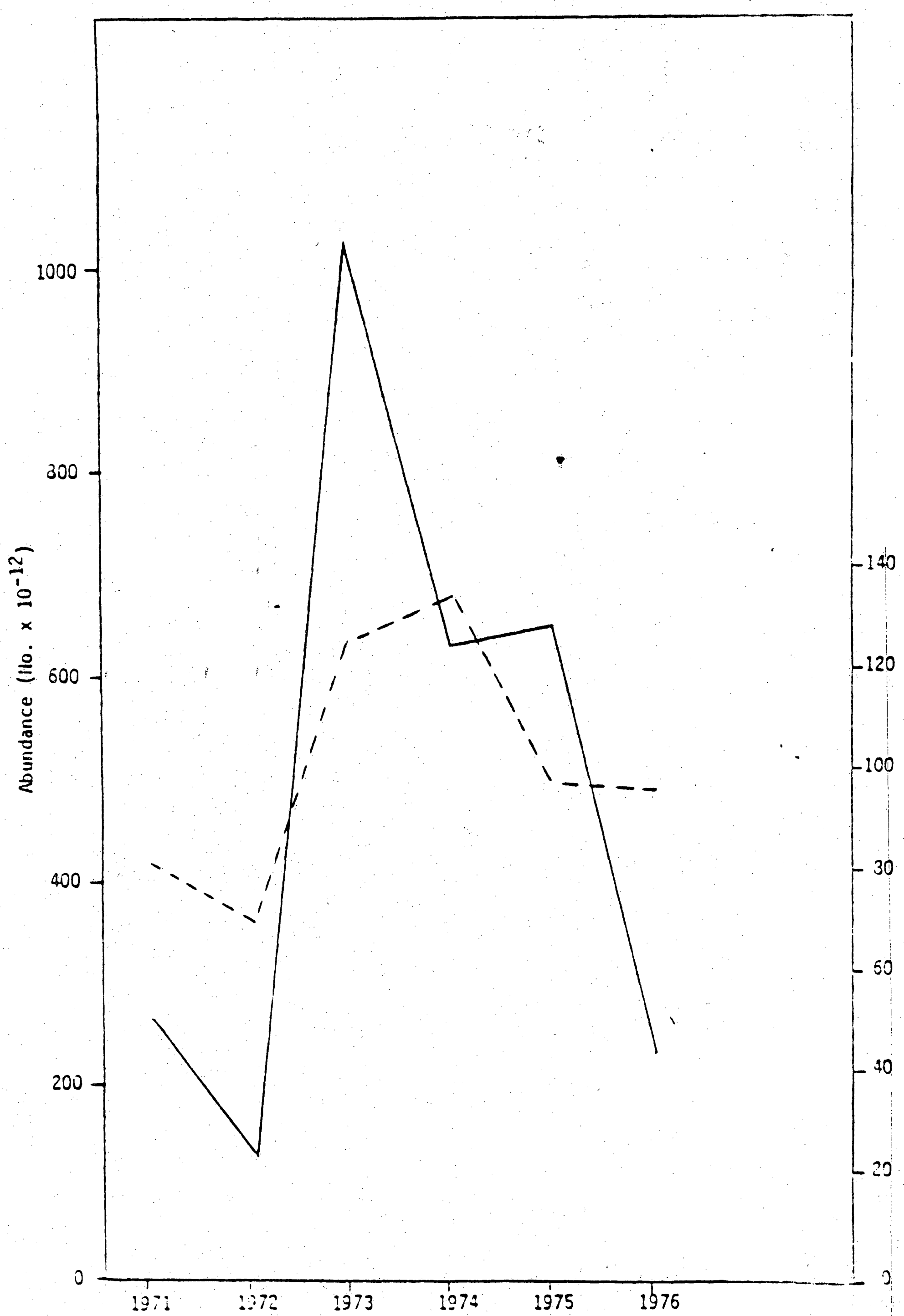


Figure 3. Yearly estimated abundance (solid line) of ichthyoplankton and total number of species (dashed line) for the Nantucket Shoals-Georges Bank area (1971-1972, through Dec.; 1973-1976, through Feb.).

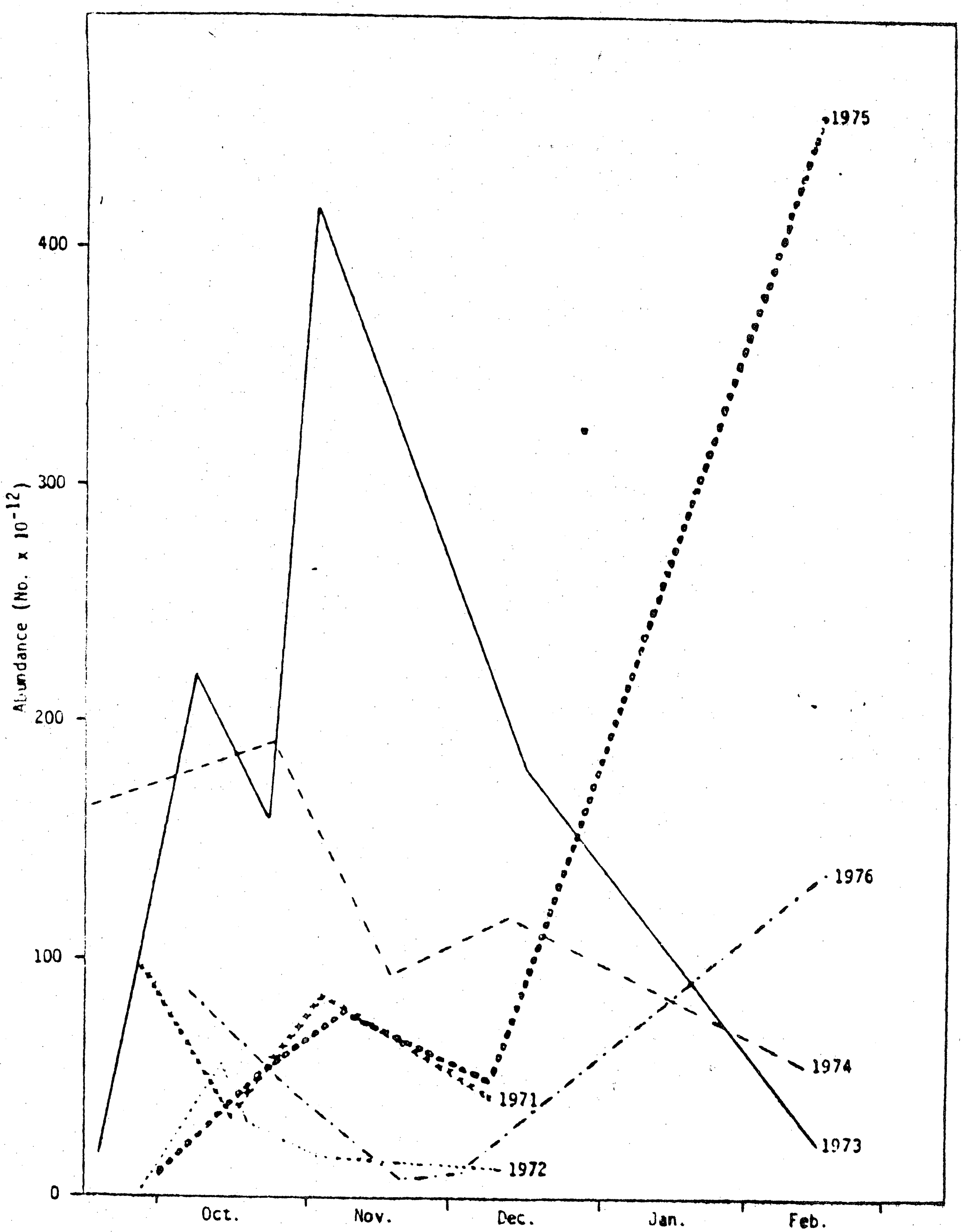
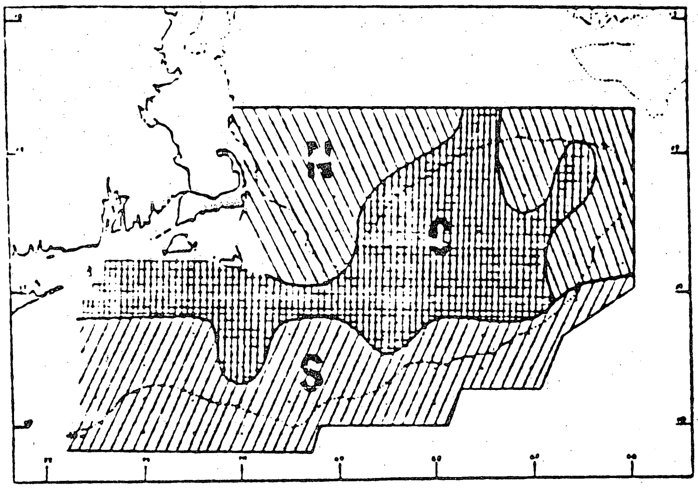
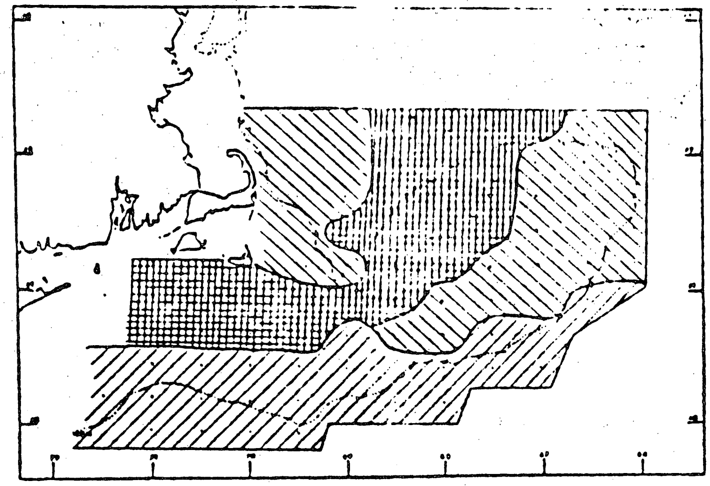


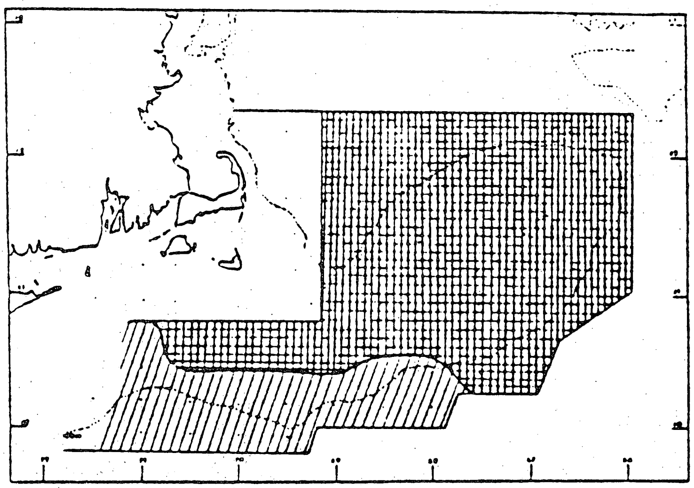
Figure 4. Estimated abundance of ichthyoplankton by cruise for the Nantucket Shoals-Georges Bank area for the 1971-1976 survey seasons.



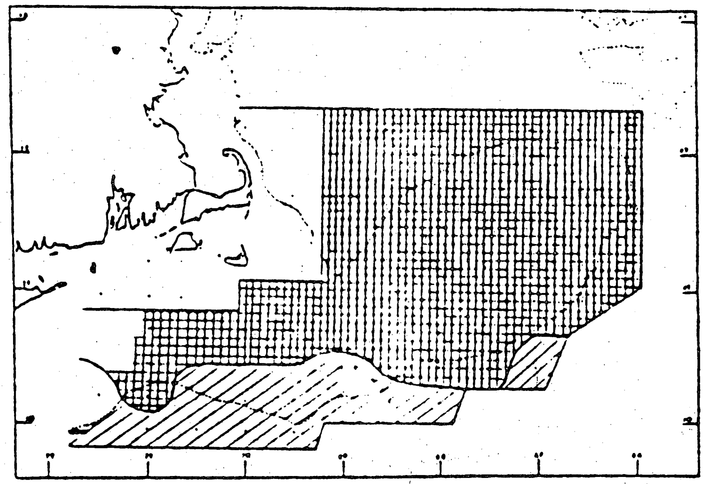
Delaware II 71-04 - faunal zones



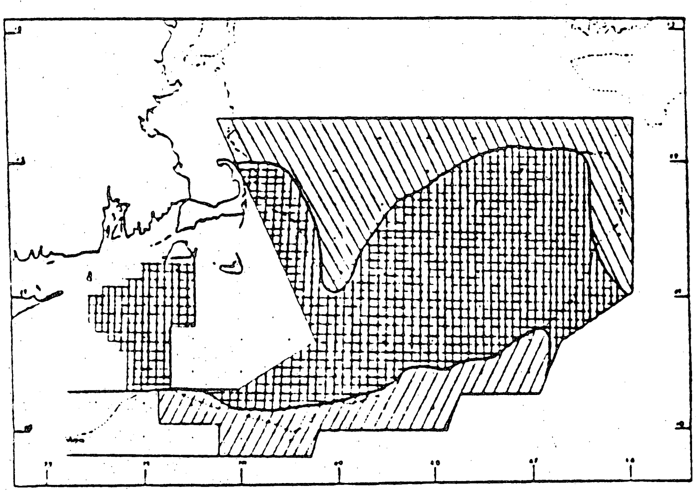
Delaware II 71-04 - temperature zones



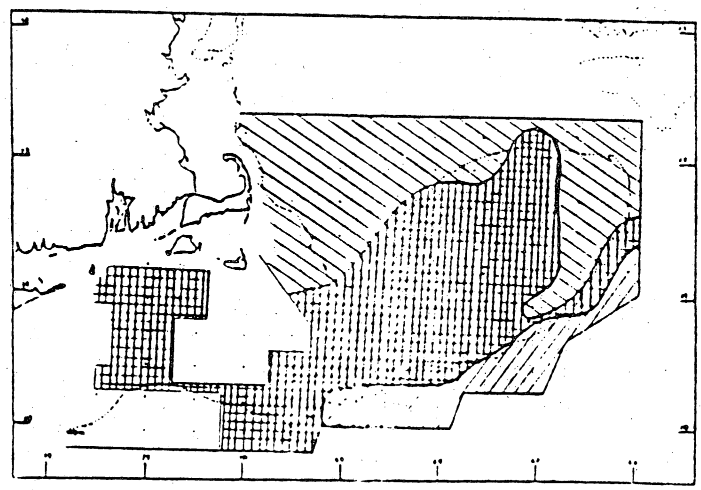
Viandra 71-01 - faunal zones



Viandra 71-01 - temperature zones



Albatross IV 71-07 - faunal zones



Albatross IV 71-07 - temperature zones

Figure 5. Faunal and temperature maps for the 1971 season showing the three major subdivisions - southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).

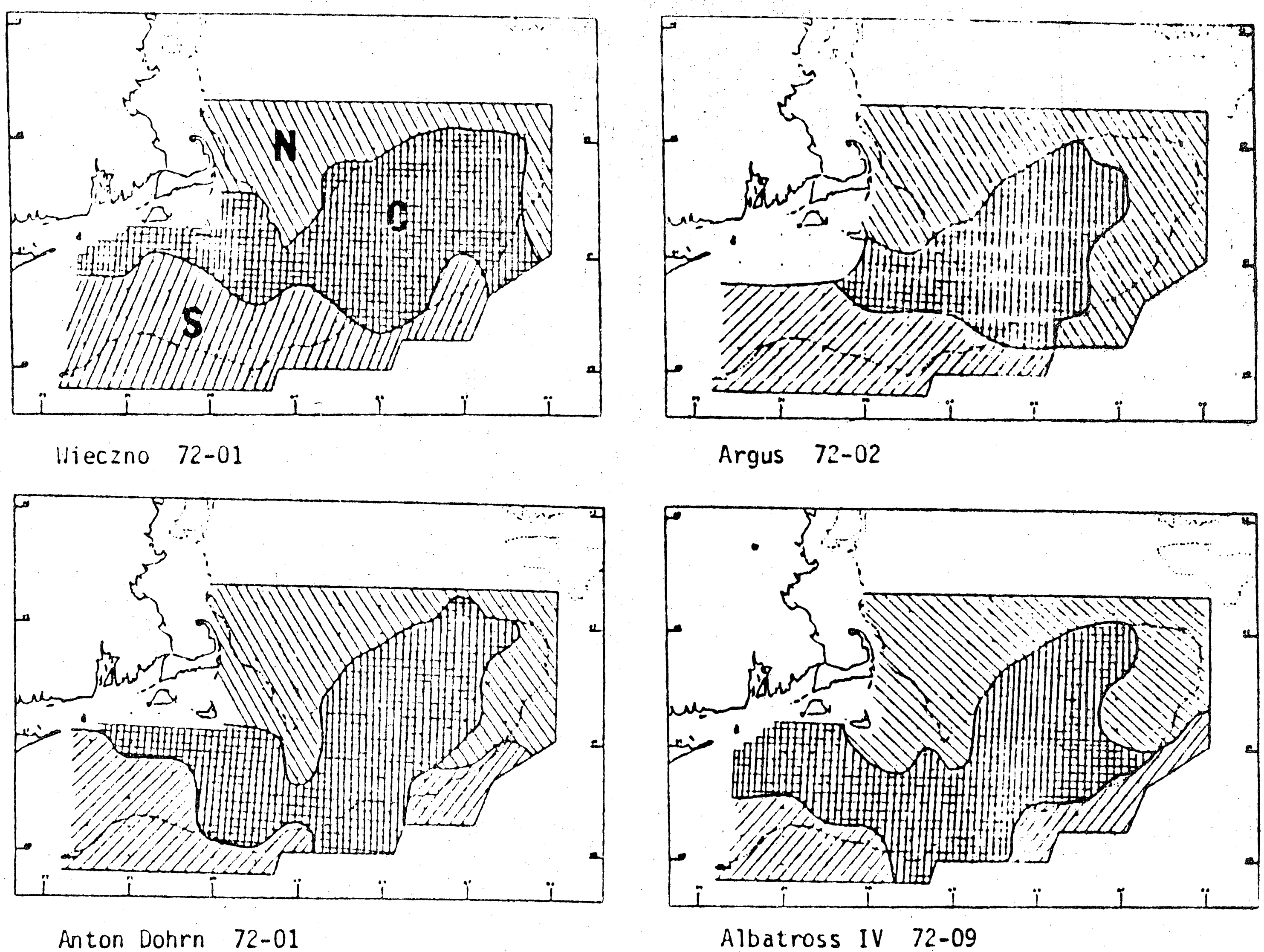


Figure 6. Faunal maps for the 1972 season showing the three major subdivisions- southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).

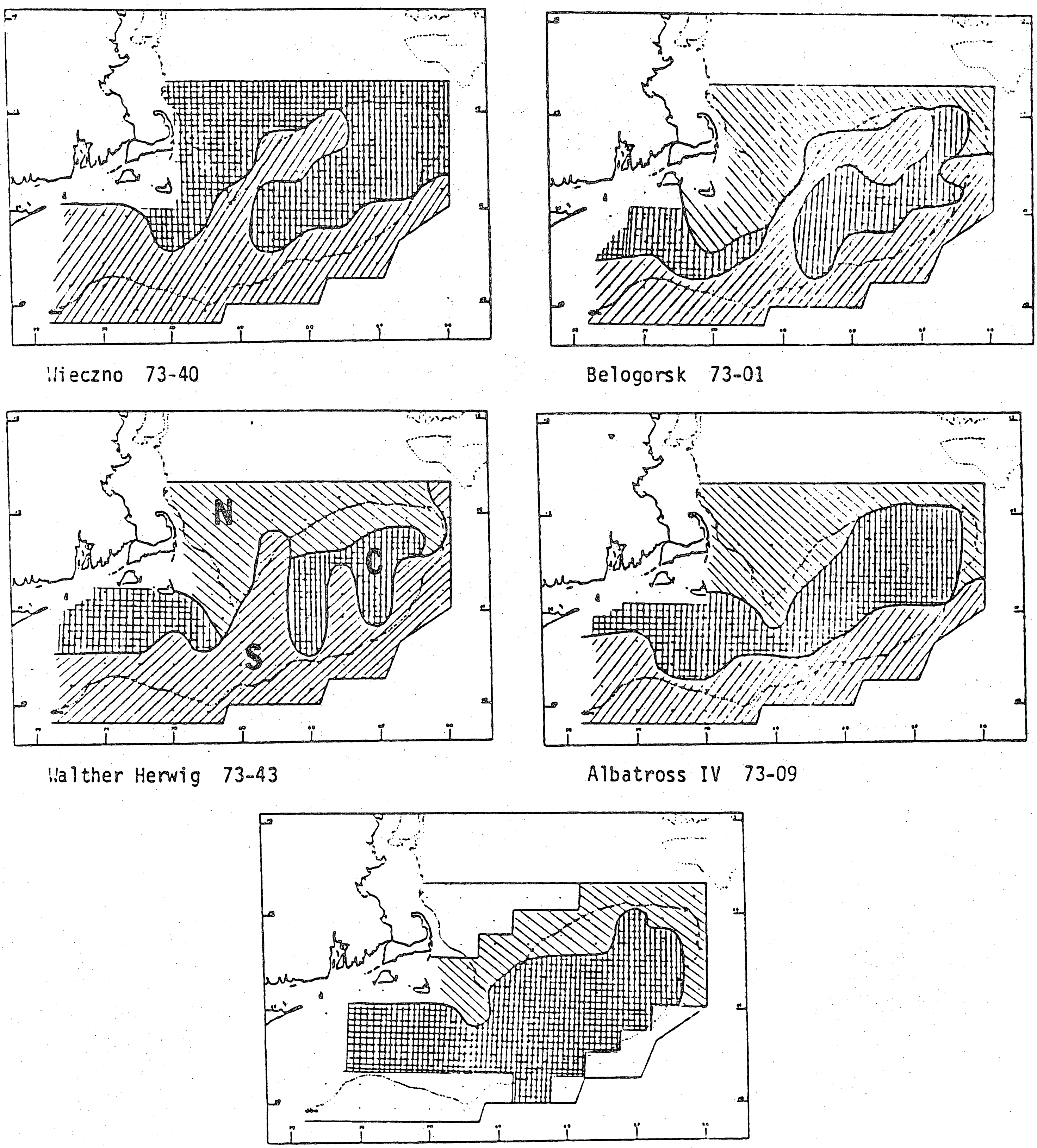


Figure 7. Faunal maps for the 1973 season showing the three major subdivisions- southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).

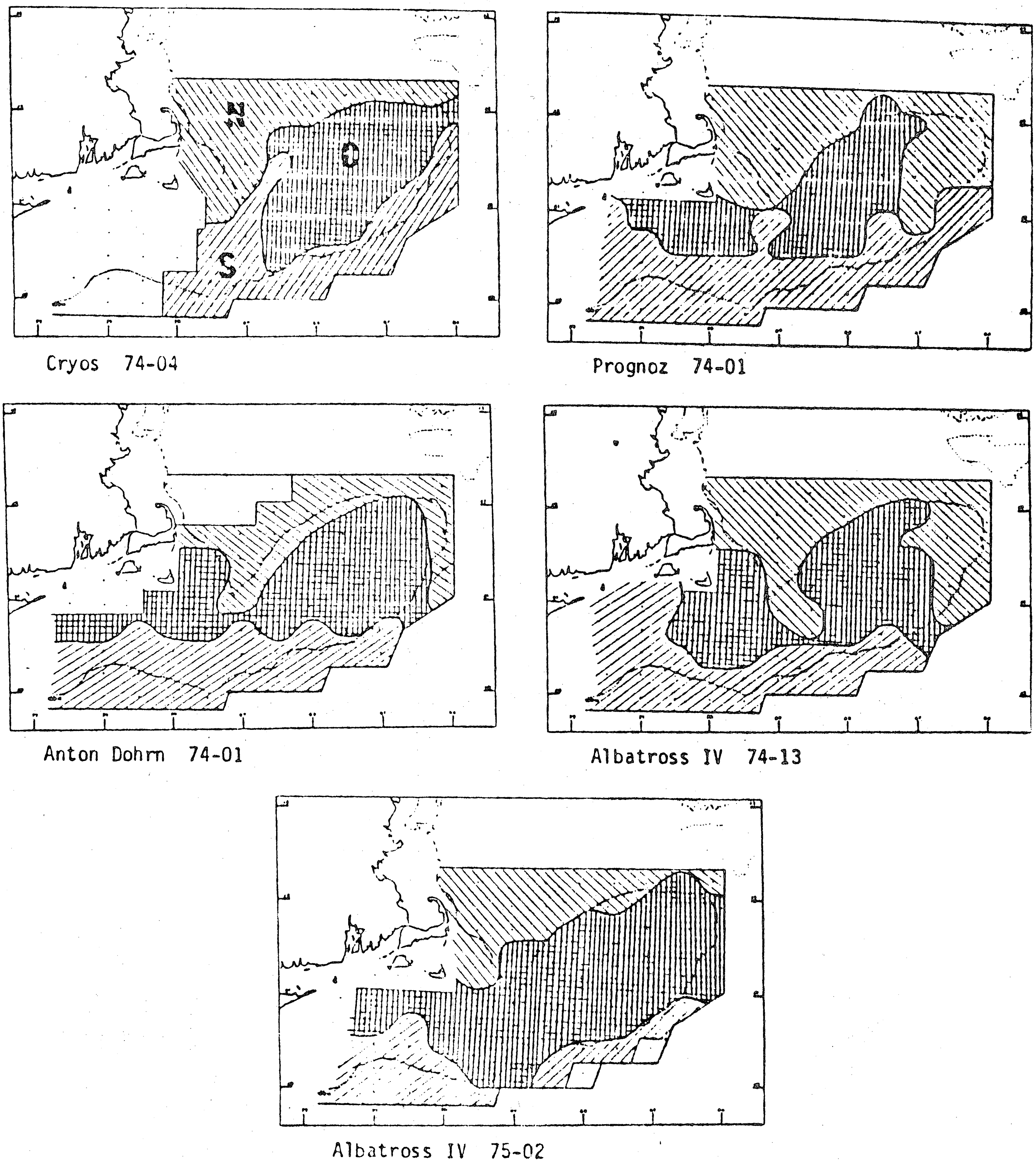


Figure 8. Faunal maps for the 1974 season showing the three major subdivisions-southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).

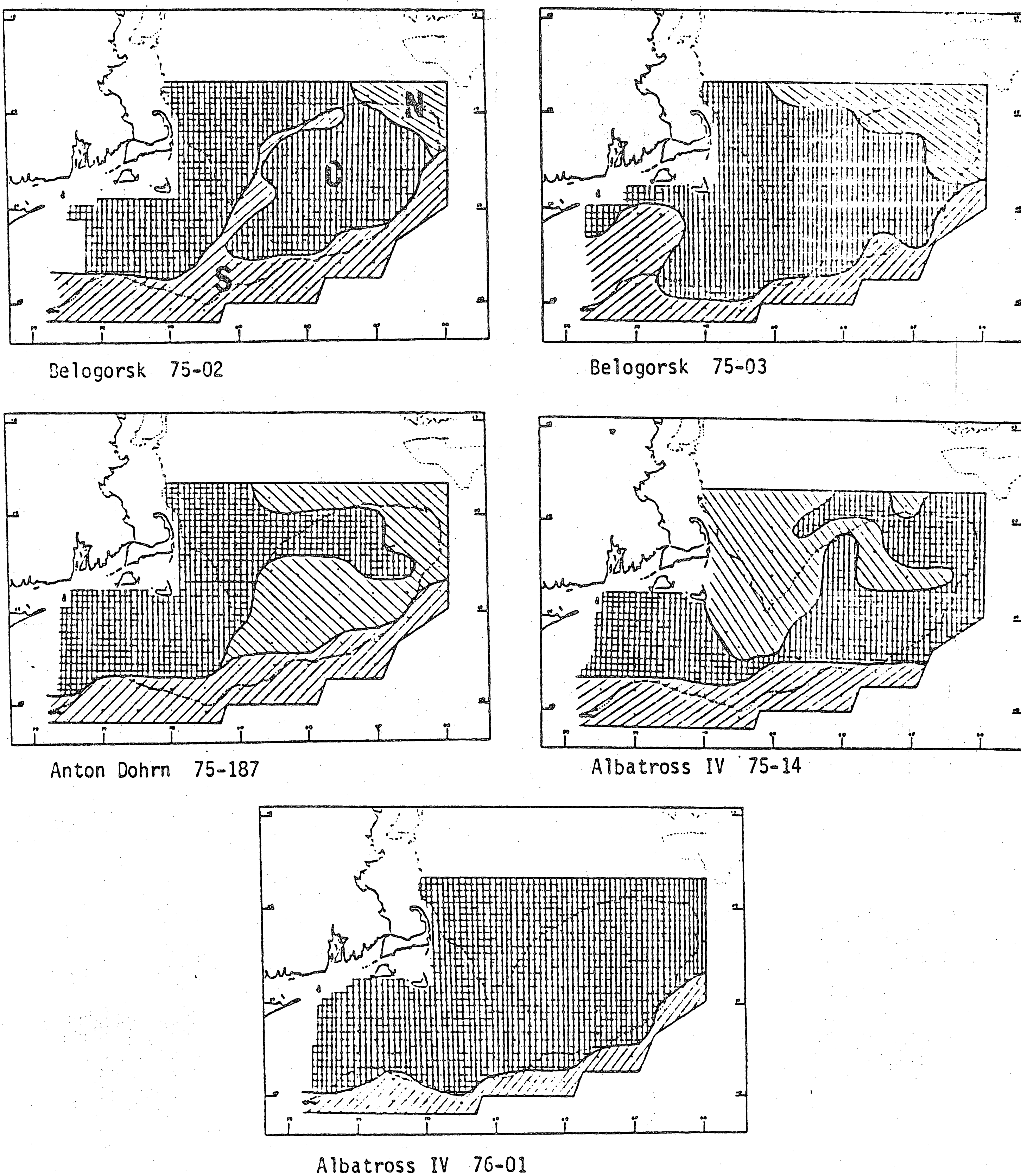


Figure 9. Faunal maps for the 1975 season showing the three major subdivisions- southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).

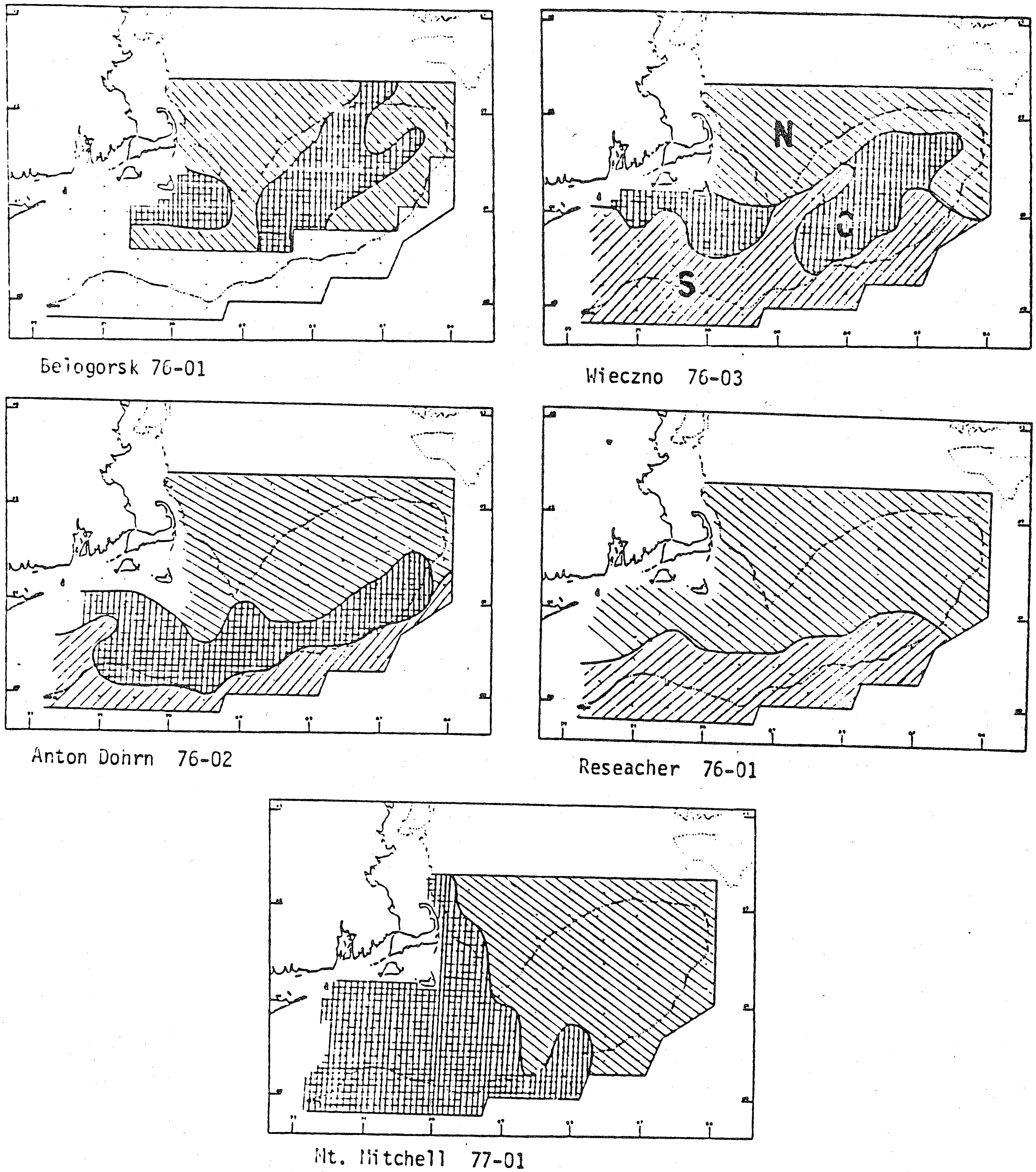


Figure 10. Faunal maps for the 1976 season showing the three major subdivisions- southern faunal zone (S), central faunal zone (C) and northern faunal zone (N).