

# Retention of Ichthyoplankton in the Georges Bank Region During the Autumn-Winter Seasons, 1971-77<sup>1</sup>

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## Abstract

The distribution, abundance and length-frequency data for all species of ichthyoplankton have been examined for 27 Coordinated Larval Herring Surveys covering the Georges Bank-Nantucket Shoals region during the period from September 1971 to February 1977. Two major faunal zones were delimited by the numerical classification technique of Divisive Information Analysis: a northern zone centered on Nantucket Shoals and Georges Bank and composed of taxa native to the shelf region, and a southern faunal zone dominated by subtropical and mesopelagic taxa which was 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. The persistence of this clockwise circulation pattern on the shoaler part of Georges Bank and the maintenance of a sharp frontal boundary along the southern flank of the bank by the Slope Water tend to retain fish larvae within the Georges Bank region. Ichthyoplankton distributional anomalies, such as geographical displacement following prolonged periods of wind stress or passage of warm-core eddies south of the shelf, were clearly highlighted by this technique.

## Introduction

During 1971-79, the International Commission for the Northwest Atlantic Fisheries (ICNAF) coordinated the undertaking of larval herring surveys in the Georges Bank-Nantucket Shoals region (Fig. 1), in order to gain a better understanding of the early life history of Atlantic herring, *Clupea harengus*, and its relationship to recruitment and spawning stock size. More than 50 of these surveys, sampling a standard grid of stations, were conducted at 3-4 week intervals throughout the autumn and bimonthly during the winter. The United States participation in the program was conducted concurrently as part of the MARMAP (Marine Resources Monitoring, Assessment and Prediction) program of the Northeast Fisheries Center,

which was designed to measure long-term changes in variability of fish stock abundance off the Northeast coast of the United States (Sherman, 1980). The distribution, abundance and length-frequency data for all species of ichthyoplankton have been summarized for 30 larval herring surveys covering the autumn and winter periods from September 1971 to February 1977 (Bolz and Lough, MS 1981). This paper is a more in-depth analysis of the ichthyoplankton species identified on 27 of these cruises.

Many reports exist on the distribution and abundance of ichthyoplankton in the Georges Bank-Nantucket Shoals region. These studies can be consolidated into two major categories: (a) those composed of species lists, together with their abundances, length-frequency data and distribution maps, which attempt to monitor broadscale spatial and temporal fluctuations (Colton and Byron, MS 1976, 1977; Berrien *et al.*, 1978; Joakimsson, MS 1978; Smith *et al.*, MS 1980); and (b) those concentrating on some aspect of growth, mortality, distribution, interactions with physical and biological environment, or fluctuations in abundance of individual species, especially those of economic importance (Boyar *et al.*, 1973; Lough, MS 1976; Lough and Bolz, MS 1979; Smith *et al.*, MS 1978, MS 1979; Lough *et al.*, MS 1979, MS 1980; Sherman *et al.*, 1981). Several studies have also related zooplankton distribution with hydrography of the Gulf of Maine, Georges Bank and Nantucket Shoals areas (Bigelow, 1926; Redfield, 1939; Redfield and Beale, 1940; Clarke *et al.*, 1943; Colton *et al.*, 1962; Sherman and Shaner, 1968). Where divisions of the study region have been

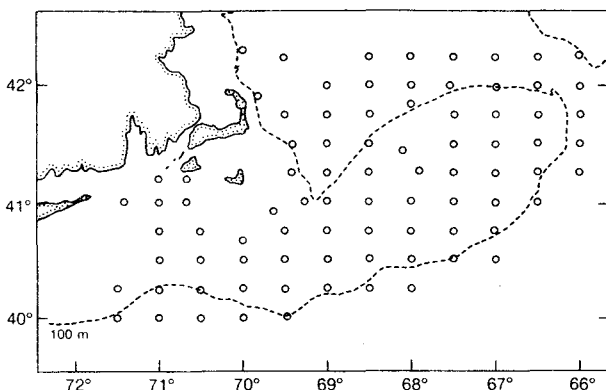


Fig. 1. Map of Georges Bank-Nantucket Shoals regions showing the locations of stations from which ichthyoplankton data were derived for analysis.

<sup>1</sup> MARMAP Contribution MED/NEFC 82-05

made, they have been based on physical features, spawning grounds or tradition (e.g. Nantucket Shoals, Georges Bank, Gulf of Maine, etc.), without quantitatively analyzing the total ichthyoplankton community to establish if valid biogeographical divisions do in fact exist. The present study attempts to address this question. Ichthyoplankton data for the Georges Bank-Nantucket Shoals region and adjacent waters are analyzed to ascertain if discrete faunal zones can be delimited, and, if so, to see if they are correlated with station temperatures which may be characteristic of water-mass types and how these faunal groups are associated with water-mass changes over time.

The intrusion of warm Slope Water onto Nantucket Shoals and Georges Bank has been noted in past studies to be a commonly-occurring feature of this region (Colton, 1959, 1961; Colton and Temple, 1961; Colton *et al.*, 1962; Sherman and Shaner, 1968; Colton and Stoddard, 1972; Butman *et al.*, 1982; Lough, 1982). A major aim of this study is to identify the ichthyoplankton fauna associated with the Slope Water and to measure the extent of this warm-water encroachment onto the bank. 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 mortality and are consequently lost to the fishery in subsequent years. A reexamination of this hypothesis on the basis of the derived biogeographical divisions is another 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 Boyar *et al.* (1973), Lough (MS 1981), Butman *et al.* (1982) and others as a mechanism for the retention of larval fish on Georges Bank (Fig. 2). The clockwise gyre is circumscribed by a strong jet-like

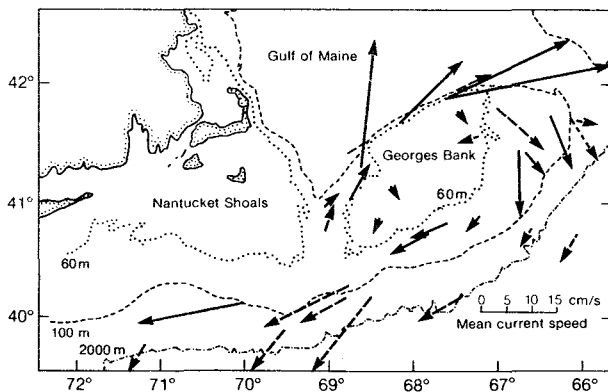


Fig. 2. Mean circulation pattern of the Georges Bank region, based on satellite-tracked drifters with 10-m window-shade drogues centered at 10-m depth. Measurements were made during December 1978 (long dash), March 1979 (short dash) and August 1979 (solid line). (Adapted from Butman *et al.*, 1982.)

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 Great South Channel. Although the gyre apparently is a persistent feature throughout the year, it is subject to periodic disruption and variation in current strength.

### Sampling and Processing Methods

Vessels, survey dates, and other pertinent information are listed chronologically in Table 1 for the 27 surveys during 1971-77, included in this study. Cruise tracks and station positions for each of the surveys have been reported by Lough and Bolz (MS 1979). A double-oblique haul at a speed of 3.5 knots (108 m/min) was made at each standard station (Fig. 1) with a paired 61-cm bongo sampler containing two nets (0.333 and 0.505 mm mesh). A V-fin depressor (122 cm) was used to achieve the desired wire angle of 45° for the relatively high towing speed, and a time-depth recorder was attached to the wire near the sampler to obtain a permanent trace of the haul profile. Flowmeters were located in the mouths of each sampler to monitor the amount of water strained. Gear configuration and other details have been described by 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 shallower areas, and retrieved at 10 m/min. (In 1971, gear was deployed to a maximum depth of 200 m, and retrieved at 20 m/min up to a depth of 40 m, followed by a step-oblique profile of 20 2-m steps of 1 min each.) A standard bongo haul filtered between 100 and 1,000 m<sup>3</sup> of water through each net, depending on the depth of the tow.

Ichthyoplankton contents of each sample from the 0.333-mm mesh net were sorted and identified at Morski Instytut Rybacki, Szczecin, Poland (Sherman and Ejsymont, MS 1976). All larvae were measured (standard length) to the nearest 0.1 mm. In cases where large numbers of a species were found in a sample, 100 individuals were subsampled and measured to establish a representative size distribution of the catch. Due to presorting and other discrepancies it was necessary to substitute 0.505-mm mesh data for larval herring from several surveys and for all ichthyoplankton from two surveys (Table 1). The standard MARMAP sorting protocols were described by Sherman *et al.* (MS 1976a, 1976b), and sampling biases were discussed by Lough *et al.* (MS 1980). 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 survey were processed at the MARMAP Biostatistical Unit, Northeast Fisheries Center, Narragansett, Rhode Island, and obtained in the form of

standard computer summaries and plots. The computer routines include various internal audits to provide quality control of the data in addition to the initial control procedures prior to computer entry.

Biogeographical divisions of the study area were determined by using the numerical classification technique of Divisive Information Analysis (I). The method, as outlined by Kikkawa and Pearse (1969), uses the Shannon-Weiner information formula:

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

where  $s$  = total number of species observed,

$n$  = number of stations surveyed,

$a_j$  = number of occurrences of the  $j$ th species,

and  $\ln$  = natural logarithm.

"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 values of  $I_{+j}$  and  $I_{-j}$  are calculated. A diversity drop for the  $j$ th species is measured by 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 division is made on the species with the largest diversity drop ( $\Delta I_{\max}$ ). The faunal zones thus produced may be further subdivided by the same technique. All divisions were further checked by calculating their Coefficients of Agreement or Community (C) from the following equation:

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

where  $s_x$  = number of species in zone  $x$ ,

$s_y$  = number of species in zone  $y$ ,

and  $s_{xy}$  = number of species common to both zones.

A C-value of 1.00 implies complete coincidence and indicates that the two zones should not have been separated; conversely a "C" value of 0.00 implies complete dissimilarity, substantiating the separation. The diversity of each division also was measured by calculating the number of species per  $\text{km}^2$ .

Although temperature profiles were available from each survey to characterize the study area, salinity observations were either not made or only partially completed during most of the surveys. Both temperature and salinity observations are needed to ade-

quately characterize a water-mass type, but data from only one survey (*Prognoz 74-01*) were complete enough for thorough examination of T-S characteristics in relation to faunal zones. Nevertheless, temperature observations during autumn and winter were still useful to detect gross differences between the cool Georges Bank water and the much warmer Slope Water south of the bank under the influence of the Gulf Stream (Hopkins and Garfield, 1981). For this purpose, the mean temperature of each survey's faunal zone, based on the 20-m depth observation, was determined, and these were compared to infer the existence of different water-mass types in the faunal zones. The Shelf Water generally is well-mixed during the autumn-winter period with no thermocline (Hopkins and Garfield, 1981), so that temperature-salinity observations at 20-m depth would in all likelihood represent the water column on the shelf at this time. Also, the limited information available on vertical distribution of fish larvae spawned on Georges Bank shows them to be broadly distributed throughout the water column to 80-m depth, with maximum concentration typically between 20 m and 40 m regardless of season (Miller *et al.*, 1963; Lough and Cohen, MS 1982; Potter and Lough, MS 1982).

Data were compared by surveys and seasons for spatial and temporal fluctuations in biogeographical and temperature divisions, total ichthyoplankton abundance, and spatial composition. Maps of each cruise were constructed, showing the biogeographical divisions.

## Results

Divisive Information Analysis of the data from 27 surveys revealed that the study area could be divided into distinct biogeographical zones. In the majority of cases, two dynamic faunal zones were evident, one located about the 100-m isobath along the southern flank of Nantucket Shoals and Georges Bank, and the other on Nantucket Shoals and Georges Bank and extending northward into the Gulf of Maine. These divisions will be referred to as the southern faunal zone and the northern faunal zone.

### Diversity and abundance

Abundance of total ichthyoplankton during September-December fluctuated by a factor of 6.5 over the 6 years, ranging from a high of  $744 \times 10^{12}$  individuals in 1973 to a low of  $114 \times 10^{12}$  in 1976 (Table 1). With the exception of the 1975 and 1976 seasons, when large numbers of *Ammodytes* sp. inflated the late winter estimates, abundance peaked in early autumn and declined throughout the remainder of the survey season. A total of 209 taxa, comprising 75 families and 13 orders, were identified in the study area. Because 63

TABLE 1. Survey data and estimates of total ichthyoplankton abundance, number of species, area and density for the northern and southern faunal zones in the Georges Bank-Nantucket Shoals region, 1971-76 survey seasons.

Year	Vessel	Cruise number	Cruise dates	No. of stations used	Abundance (No. x 10 <sup>12</sup> )		Number of species		Area (% of total)		Density (species/km <sup>2</sup> )	
					North	South	North	South	North	South	North	South
1971	1. <i>Delaware II</i> <sup>a</sup>	71-04	Sep 21-Oct 4	72	30.7	72.4	24	71	68.0	32.0	0.4	2.7
	2. <i>Viandra</i>	71-01	Oct 9-25	64	34.8	5.3	23	33	79.7	20.3	0.4	2.2
	3. <i>Albatross IV</i> <sup>a</sup>	71-07	Dec 2-17	71	37.3	0.4	7	8	83.1	16.9	0.1	0.6
	Total			207	102.7	78.1	37	78	76.8	23.2	0.3	1.8
1972	4. <i>Wieczno</i>	72-01	Oct 2-28	80	28.3	56.9	17	34	68.8	31.2	0.3	1.2
	5. <i>Argus</i>	72-02	Oct 12-28	75	23.2	1.8	15	11	75.7	24.3	0.2	0.5
	6. <i>Anton Dohrn</i>	72-01	Oct 31-Nov 12	79	14.9	3.0	14	35	79.7	20.3	0.2	1.9
	7. <i>Albatross IV</i> <sup>b</sup>	72-09	Dec 2-20	81	14.7	1.2	13	13	82.7	17.2	0.2	0.8
	Total			315	81.2	62.9	37	51	76.7	23.3	0.2	1.1
1973	8. <i>Wieczno</i> <sup>a</sup>	73-40	Sep 28-Oct 20	79	78.7	220.5	13	63	47.5	52.5	0.3	1.3
	9. <i>Belogorsk</i>	73-01	Oct 15-Nov 1	81	64.9	50.3	19	63	58.7	41.3	0.3	1.6
	10. <i>Walther Herwig</i>	73-43	Oct 28-Nov 8	81	131.7	120.2	17	54	53.1	46.9	0.3	1.2
	11. <i>Albatross IV</i>	73-09	Dec 4-20	82	133.5	14.2	27	42	69.1	30.9	0.4	1.4
	12. <i>Albatross IV</i> <sup>b</sup>	74-02	Feb 11-22	57	18.3	—	13	—	100.0	—	0.2	—
	Total			380	427.1	405.2	48	111	63.6	36.4	0.3	1.4
1974	13. <i>Cryos</i>	74-04	Sep 7-24	65	12.1	70.1	17	54	66.2	33.8	0.3	2.1
	14. <i>Prognoz</i>	74-01	Oct 18-30	79	219.7	28.5	20	52	64.2	35.8	0.3	1.5
	15. <i>Anton Dohrn</i>	74-01	Nov 16-23	70	42.1	13.4	16	67	68.1	31.9	0.3	2.6
	16. <i>Albatross IV</i>	74-13	Dec 4-19	83	55.1	13.7	25	55	67.5	32.5	0.4	1.8
	17. <i>Albatross IV</i>	75-02	Feb 12-28	79	42.1	5.0	20	20	81.1	18.9	0.3	1.2
Total			376	371.5	130.7	53	114	69.4	30.6	0.3	1.8	
1975	18. <i>Belogorsk</i> <sup>a</sup>	75-02	Sep 25-Oct 8	80	8.6	10.8	21	29	67.5	32.5	0.3	1.0
	19. <i>Belogorsk</i>	75-03	Oct 17-30	75	56.3	1.4	22	25	75.6	24.4	0.3	1.1
	20. <i>Anton Dohrn</i>	75-18	Nov 1-18	85	50.5	1.6	15	39	76.9	23.1	0.2	1.8
	21. <i>Albatross IV</i>	75-14	Dec 5-17	81	41.6	4.0	44	40	79.4	20.6	0.6	2.2
	22. <i>Albatross IV</i>	76-01	Feb 10-25	82	304.3	11.9	17	22	84.1	15.9	0.2	1.5
	Total			403	461.3	29.8	47	77	76.7	23.3	0.3	1.5
1976	23. <i>Belogorsk</i>	76-01	Oct 4-11	50	14.3	16.0	15	28	27.9	72.1	0.9	0.7
	24. <i>Wieczno</i>	76-03	Oct 14-Nov 3	82	5.9	67.2	30	47	59.7	40.3	0.5	1.2
	25. <i>Anton Dohrn</i>	76-02	Nov 15-29	77	2.8	3.2	19	52	82.9	17.1	0.3	3.4
	26. <i>Researcher</i>	76-01	Nov 27-Dec 11	74	2.2	7.7	12	38	64.0	36.0	0.2	1.2
	27. <i>Mt. Mitchell</i>	77-01	Feb 13-24	82	57.9	—	18	—	100.0	—	0.2	—
	Total			365	83.0	94.1	46	82	69.9	30.1	0.4	1.6
Grand Total				2,046	1526.9	800.8	87	171	71.7	28.3	0.3	1.5

<sup>a</sup> Data from 0.505 mm mesh sample substituted for larval herring.

<sup>b</sup> Data from 0.505 mm mesh sample substituted for all ichthyoplankton.

forms were identified only to the familial level, resulting in possible redundancies, the actual number of species is probably lower than the total reported.

**Southern faunal zone.** The ichthyoplankton fauna was composed primarily of mesopelagic and subtropical taxa, with Myctophidae, Paralepididae, Gobiidae and Ophidiidae being the most common families present (Table 2). The most dominant species were horned lanternfish (*Ceratospelus maderensis*) and Gulf Stream flounder (*Citharichthys arctifrons*). Although the southern zone averaged only 28.2% of the total study area, 81.8% (171) of the 209 taxa recorded were

found in it. Most of the species were represented by only one or two individuals per survey. In most cases, this zone had a high diversity (1.5 species per km<sup>2</sup>) and medium abundance with an average of 40 taxa per survey and a mean total abundance of 29.2 x 10<sup>12</sup> individuals. Abundance tended to be very high in early autumn and low throughout late autumn and winter.

**Northern faunal zone.** This was an area of low diversity (0.3 species per km<sup>2</sup>) and high abundance with an average of 19 species per survey and mean total abundance of 56 x 10<sup>12</sup> individuals (Table 1). Although this zone occupied an average of 71.8% of the study

TABLE 2. Major taxa collected in the northern and southern faunal zones of the Georges Bank-Nantucket Shoals region, with percentage occurrence by cruise in 1971-76. (Surveys 1-27 are those listed after year in Table 1.)

Taxa	Occurrence (% of total)		Abundance (% of total)		Occurrence by survey								
	North	South	North	South	1971	1972	1973	1974	1975	1976			
<b>Common southern zone taxa</b>													
<i>Syacium</i> sp.	—	100.0	—	100.0	1,2,-	4,-,6,7	8,9,10,-	-,-	13,14,15,-	-,-	18,-,20,-,-	-,-	-24,25,-,-
Scaridae	2.3	97.7	1.4	98.6	1,2,-	4,-,6,-	8,9,10,11,-	-	13,14,15,16,-	-	-,19,20,21,-	-	23,24,25,26,-
<i>Ceratoscopelus maderensis</i>	5.3	94.7	1.5	98.5	1,2,-	4,5,6,-	8,9,10,11,-	-	13,14,15,16,-	-	18,19,20,21,22	-	23,24,25,26,-
Labridae	5.9	94.1	3.8	96.2	1,2,3	4,5,6,7	8,9,10,11,-	-	13,14,15,16,-	-	18,19,20,21,-	-	23,24,25,26,-
<i>Bothus ocellatus</i>	8.7	91.3	3.2	96.8	1,2,-	4,5,6,7	8,9,10,11,-	-	13,14,15,16,-	-	18,19,20,21,-	-	23,24,25,26,-
Gobiidae	11.2	88.8	7.9	92.1	1,2,3	4,5,6,7	8,9,10,11,-	-	13,14,15,16,-	-	18,19,20,21,-	-	23,24,25,26,-
<i>Notolepis rissoi</i>	14.9	85.1	9.6	90.4	1,-,3	4,-,6,-	8,9,10,11,-	-	13,14,15,16,17	-	18,19,20,21,22	-	23,24,25,26,27
Engraulidae	15.1	84.9	11.6	88.4	1,2,3	-,5,6,-	8,9,10,11,-	-	13,14,15,16,-	-	18,19,20,21,-	-	23,24,25,26,-
Ophidiidae	16.7	83.3	4.6	95.4	1,2,-	4,5,6,-	8,9,10,11,-	-	13,14,15,16,-	-	18,19,-,-,-	-	23,24,25,26,-
<i>Citharichthys arcifrons</i>	27.6	72.4	9.1	91.9	1,2,-	4,-,6,-	8,9,10,11,-	-	13,14,15,-,-	-	18,-,20,21,-	-	23,24,25,26,-
<b>Common northern zone taxa</b>													
<i>Pollachius virens</i>	90.6	9.4	95.7	4.3	-,-,3	-,-,-,7	-,-,-,11,12	-	-,14,15,16,17	-	-,19,20,21,22	-	-,-,-,26,27
<i>Ammodytes</i> sp.	90.0	10.0	96.9	3.1	-,-,-	-,-,-,-	-,-,-,11,12	-	-,-,-,16,17	-	-,-,-,21,22	-	-,-,-,26,27
<i>Melanogrammus aeglefinus</i>	88.1	11.9	90.0	10.0	-,-,-	-,-,-,-	-,-,-,12	-	-,-,-,17	-	-,19,-,-,22	-	-,-,-,27
<i>Gadus morhua</i>	88.1	11.9	97.0	3.0	-,-,3	-,-,6,7	-,9,-,11,12	13,-	-,15,16,17	-	-,19,20,21,22	-	-,-,25,26,27
<i>Clupea harengus</i>	79.2	20.8	76.6	23.4	1,2,3	4,5,6,7	8,9,10,11,12	-	13,14,15,16,17	-	18,19,20,21,22	-	23,24,25,26,27
<i>Scophthalmus aquosus</i>	68.8	31.2	68.3	31.7	1,2,-	4,5,6,7	8,9,10,11,12	-	13,14,15,16,17	-	18,19,20,-,22	-	23,24,25,26,27

area and accounted for 65.5% of the total abundance, only 41.6% of the 209 taxa were found there. Abundance was uniformly high throughout the sampling season. The fauna was composed mainly of species endemic to Georges Bank and Nantucket Shoals (Table 2), with Atlantic herring, *Clupea harengus*, dominating in autumn and pollock *Pollachius virens*; Atlantic cod, *Gadus morhua*; and sand lance, *Ammodytes* sp., in winter. Very few species found in this zone were recorded north of Georges Bank in water deeper than 100 m.

**Seasonal and annual fluctuations**

**Season 1971.** The southern faunal zone occupied 27% of the study area and encroached far onto the southern flank of Georges Bank and Nantucket Shoals in late September and early October (Fig. 3). As the season progressed, the southern zone rapidly diminished in extent and by December was restricted to a small area (14% of study area) off the southeastern edge of Georges Bank. The southern zone was not evident in a small area of eastern Georges Bank during late October. Total ichthyoplankton abundance declined rapidly from a high of 103.1 x 10<sup>12</sup> individuals in September to 40.1 x 10<sup>12</sup> in late October. The highest concentration of species in the study area occurred in the southern faunal zone throughout the season. Of 83 taxa found during the survey period, 78 occurred at one time or another in the southern zone and only 37 species were found in the northern zone. Species density averaged 1.8 species per km<sup>2</sup> in the southern zone but only 0.3 species per km<sup>2</sup> in the northern zone.

**Season 1972.** As in the 1971 season, a wide southern faunal zone (29% of study area) extended far onto the

southern flank of Nantucket Shoals and Georges Bank in early October (Fig. 4). Although this zone continued to occupy approximately 20% of the total area from late October to December, sections of the zone were not evident during part of the period. The southern faunal zone was missing from a large portion of eastern and southeastern Georges Bank in late October, and small segments of the northern zone extended to the southern limit of the study area in the vicinity of Great South Channel in November and December. Abundance and diversity were low from late October to December, ranking fifth in total abundance and sixth in number of taxa for the 6 years studied. Except in early October, the highest abundance occurred in the northern zone due to the presence of large numbers of recently-hatched larvae of endemic species. Total abundance declined rapidly from 85.2 x 10<sup>12</sup> in early autumn to 16.0 x 10<sup>12</sup> in December. Species density was slightly lower than in 1971, averaging 1.1 species per km<sup>2</sup> in the southern zone and 0.2 per km<sup>2</sup> in the northern zone.

**Season 1973.** Of the 6 years studied, this season exhibited the most extensive encroachment of the southern faunal zone onto Nantucket Shoals and Georges Bank, ranging from 49% of the study area in October to 29% in December (Fig. 5). In October and November, the southern faunal zone extended northward through Great South Channel and eastward along the northern edge of Georges Bank. This zone became somewhat more restricted in December, but it still extended well north of the 100-m isobath onto Nantucket Shoals and Georges Bank. Sampling in February was not as intensive as in previous surveys, especially along the southern edge of Georges Bank, but the southern faunal zone appeared to have moved southward beyond the limit of the study area. The

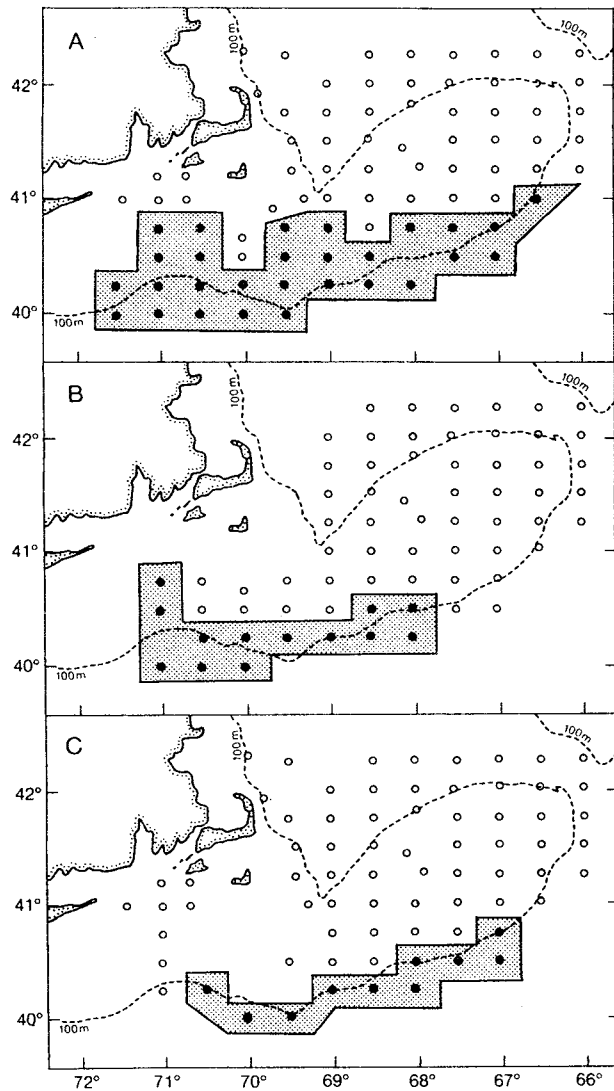


Fig. 3. Faunal maps for the 1971 survey season, showing the northern (open circles) and southern (shaded) faunal zones: A, 21 September-4 October; B, 9-25 October; C, 2-17 December.

northern zone was more fragmented in October and November than in the previous 2 years, but, in December and February, it was well formed and occupied most of Nantucket Shoals and Georges Bank. Total abundance throughout the study area during the 1973 season was the highest of the time series, ranging from  $229.2 \times 10^{12}$  individuals in early October to  $147.6 \times 10^{12}$  in December. Of the 122 species collected, 91% were found in the southern zone and 39% in the northern zone, with average densities per  $\text{km}^2$  of 1.4 and 0.3 species respectively.

**Season 1974.** As in the preceding season, this season exhibited more northerly and uniform encroachment of the southern faunal zone onto Nantucket Shoals and Georges Bank throughout autumn and winter, covering 34% of the study area in October and

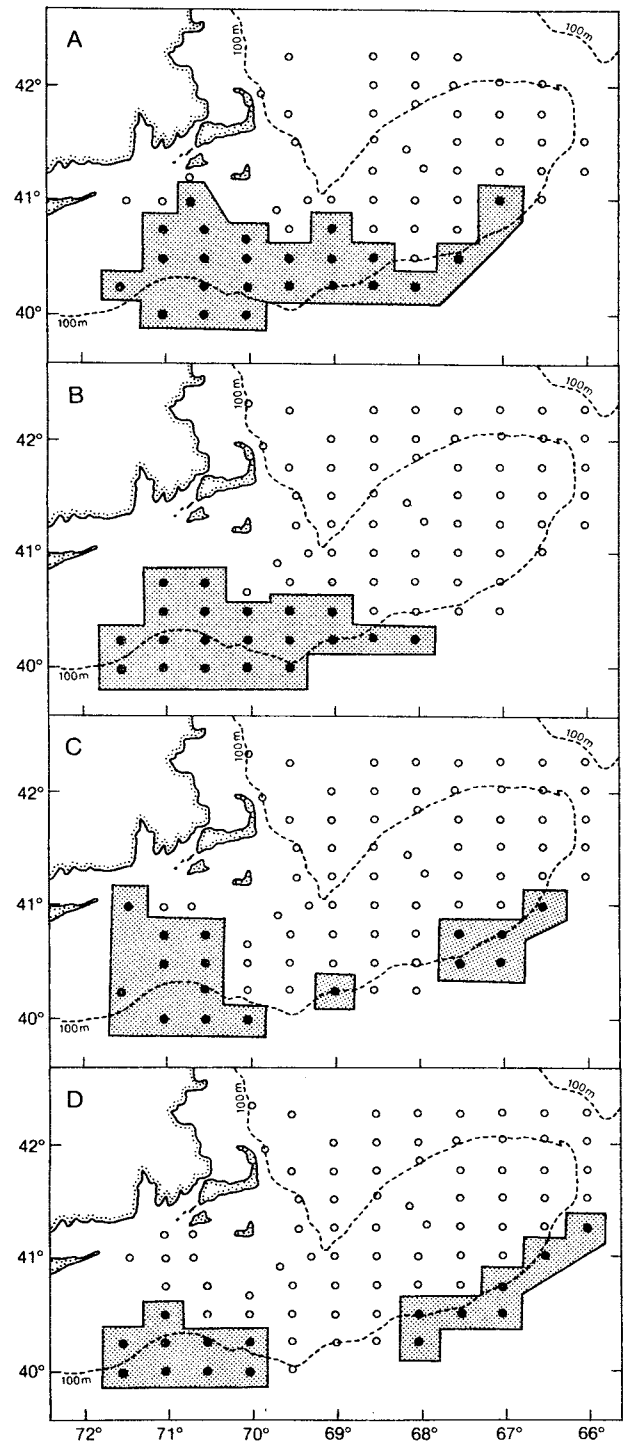


Fig. 4. Faunal maps for the 1972 survey season showing the northern (open circles) and southern (shaded) faunal zones: A, 2-28 October; B, 12-28 October; C, 31 October-12 November; D, 2-20 December.

16% in February (Fig. 6). In September and October, the southern zone extended northward through Great South Channel, but it did not continue eastward along the northern edge of Georges Bank as in 1973. In 1974, there was a 1.5-fold reduction in total ichthyoplankton

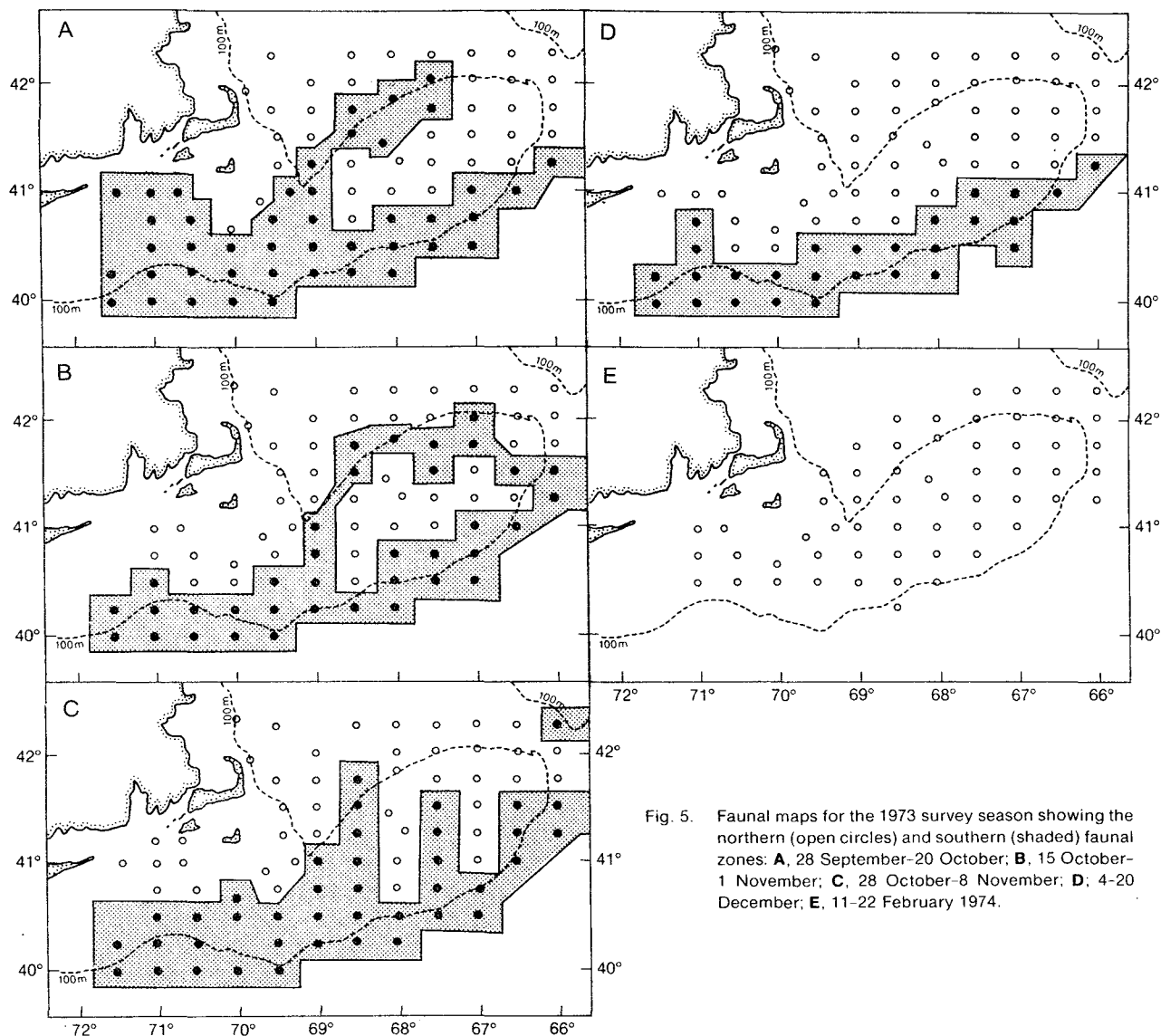


Fig. 5. Faunal maps for the 1973 survey season showing the northern (open circles) and southern (shaded) faunal zones: **A**, 28 September–20 October; **B**, 15 October–1 November; **C**, 28 October–8 November; **D**, 4–20 December; **E**, 11–22 February 1974.

abundance from December to February, whereas the reduction was 8-fold in 1973. The total number of taxa (133) observed in 1974 (highest for the time series) reflected the broad and continued encroachment of subtropical and mesopelagic species of the southern fauna onto the bank. Species densities were 1.8 species per km<sup>2</sup> in the southern zone and 0.3 per km<sup>2</sup> in the northern zone.

**Season 1975.** The extent of the southern zone was smaller than in 1973 and 1974, covering 30% of the study area in October, 19% in December and 15% in February (Fig. 7). The season was similar in faunal composition and abundance to those of 1971 and 1972. The most notable feature in the faunal divisions was the extension of a narrow band of southern fauna species northward through Great South Channel and eastward along the northern edge of Georges Bank. The

faunal zones were not as well developed as in 1973 and 1974, and this is reflected by the lower number of species (99) observed throughout the season and the 3-fold to 5-fold reduction in abundance from late September to December. In the northern zone, 94% of total abundance occurred in 1975, compared to 51% in 1973 and 74% in 1974.

**Season 1976.** Although coverage in early autumn was not as extensive as in previous years, the southern faunal zone appeared to have been well-formed (72% of study area) in early October and extended over most of Georges Bank (Fig. 8). From late October to December, abundance in the northern zone was an order of magnitude lower than in the preceding 5 years, although the average number of species remained approximately the same. In February, the southern faunal zone was not present, and the northern faunal zone

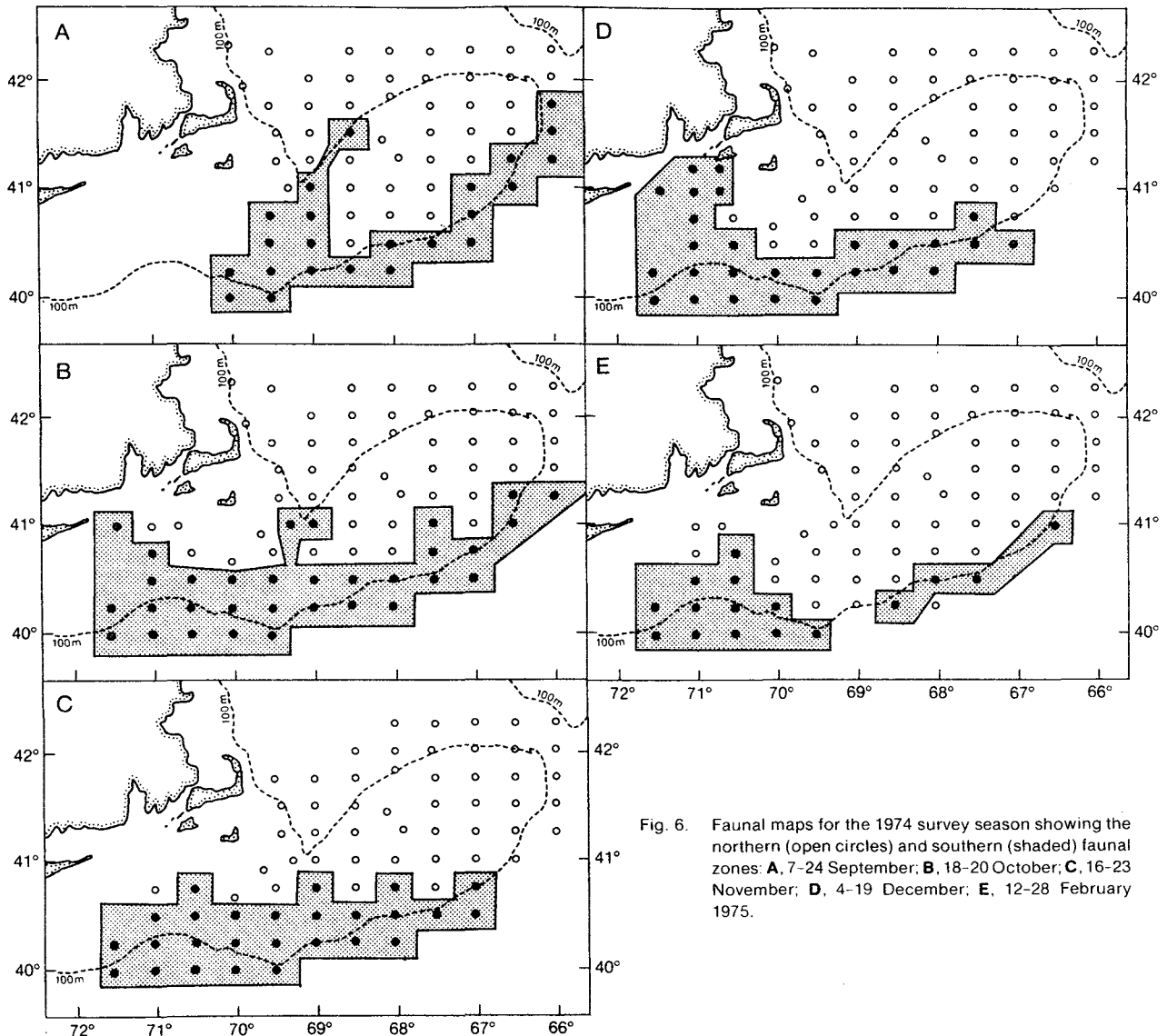


Fig. 6. Faunal maps for the 1974 survey season showing the northern (open circles) and southern (shaded) faunal zones: A, 7-24 September; B, 18-20 October; C, 16-23 November; D, 4-19 December; E, 12-28 February 1975.

was divisible, based on abundance, into a western Nantucket Shoals zone and an eastern Georges Bank zone. The Georges Bank zone was almost devoid of ichthyoplankton, and abundance was 200-fold less than on Nantucket Shoals.

#### Faunal zone and water-mass association

Temperature and salinity data (20 m) from the *Prognoz* survey in 1974, which had the best coverage of these parameters for the entire time series, were examined in relation to the defined faunal zone types. A temperature-salinity plot (Fig. 9) segregated the two faunal zones into fairly discrete regimes with evidence of some intermixing. The mean temperature and salinity in the northern faunal zone (12.8°C and 32.7‰) fell within the annual minimum and maximum values of temperature (3.5° to 14.6°C) and salinity (32.1–32.9‰) reported for Georges Bank water by Hopkins and Gar-

field (1981). The higher mean temperature (15.9°C) and salinity (34.2‰) values in the southern faunal zone are typical of the upper Slope Water which bounds the southern flank of Georges Bank and is itself bounded to the south by the Gulf Stream (Hopkins and Garfield, 1981).

On the basis of mean temperature alone, the northern and southern faunal zones could be associated with their respective water masses over the 6-year time series studied. Mean temperatures of the northern and southern faunal zones differed significantly ( $P < 0.05$ ) when the data from all 27 surveys were analyzed separately, and, when combined, the mean temperature in the southern zone was 3.4°C higher than in the northern zone. On an annual basis (Fig. 10), the mean temperature ranged from a high of 13.8°C (1971) to a low of 11.4°C (1976) in the southern faunal zone and from a high of 10.4°C (1973) to a low of 9.3°C



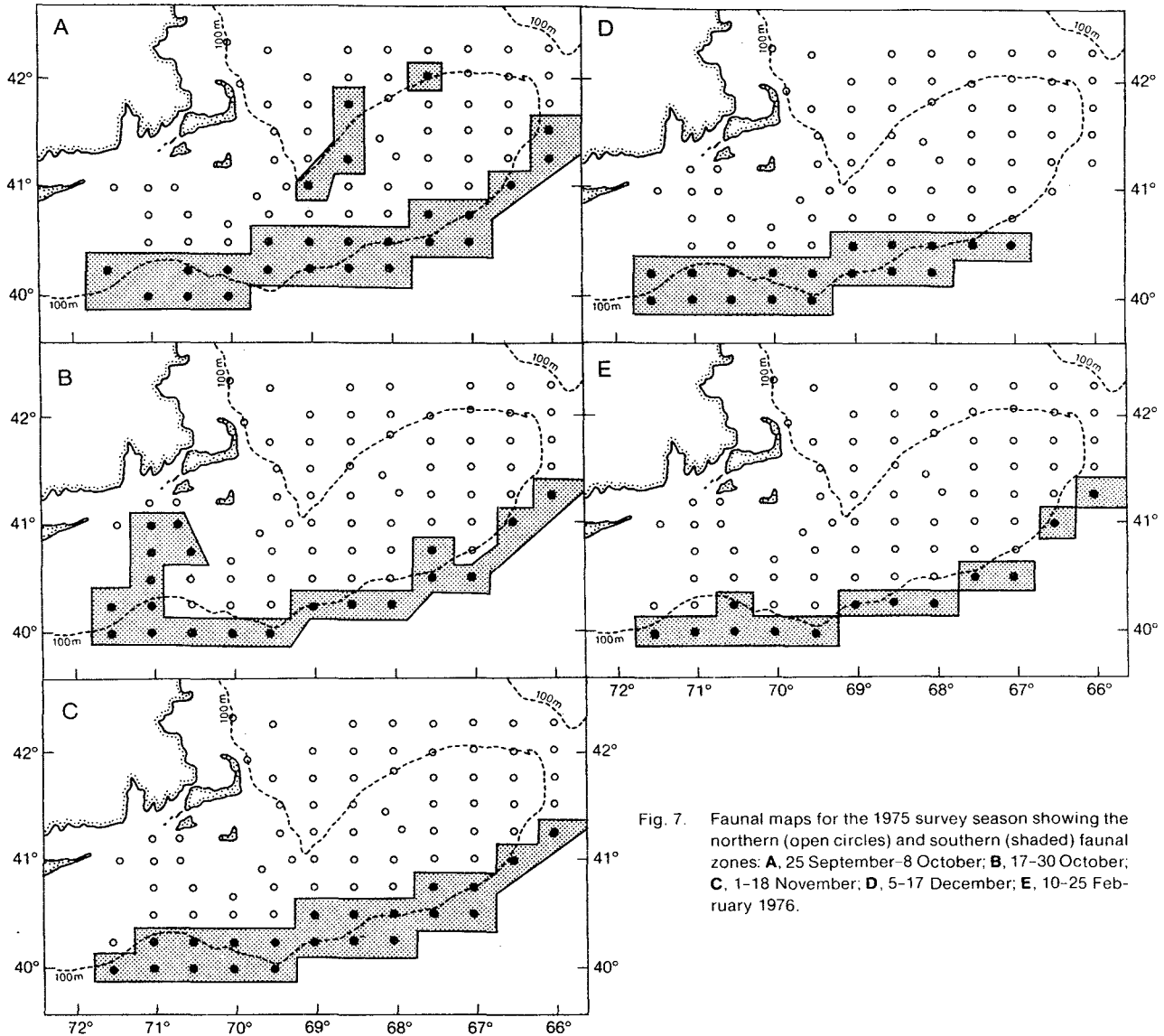


Fig. 7. Faunal maps for the 1975 survey season showing the northern (open circles) and southern (shaded) faunal zones: **A**, 25 September–8 October; **B**, 17–30 October; **C**, 1–18 November; **D**, 5–17 December; **E**, 10–25 February 1976.

(1976) in the northern faunal zone. Within the survey season (September–February), the mean temperatures in the southern zone declined from 18°C in early autumn to 12.7°C in early winter and to 7.3°C by late winter, whereas those in the northern zone declined from 14.3° to 9.2°C and to 5.3°C respectively.

### Discussion

Based on analysis of faunal zone and water-mass association, the southern faunal zone appears to be a good indicator of Slope Water intrusions on Nantucket Shoals and Georges Bank. The ichthyoplankton fauna in this zone was similar in composition to the "northern mesopelagic group" described by Backus *et al.* (1970). Dominant species were the myctophid *Ceratoscopelus maderensis* and the bothid *Citharichthys arctifrons*, but many other mesopelagic and subtropical families

were represented (Argentinidae, Bathylagidae, Chauiodontidae, 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 were expatriated northward by the Gulf Stream and are rare visitors to the Nantucket Shoals-Georges Bank region. Markle *et al.* (1980) discuss a similar phenomenon of expatriated species of ichthyoplankton on the Scotian Shelf. Grice and Hart (1962) found that many species of zooplankton are often indicative of specific water masses, and Colton *et al.* (1962) and Sherman and Shaner (1968) state that oceanic species of copepods are particularly good indicators of Slope Water intrusions onto Georges Bank and Nantucket Shoals.

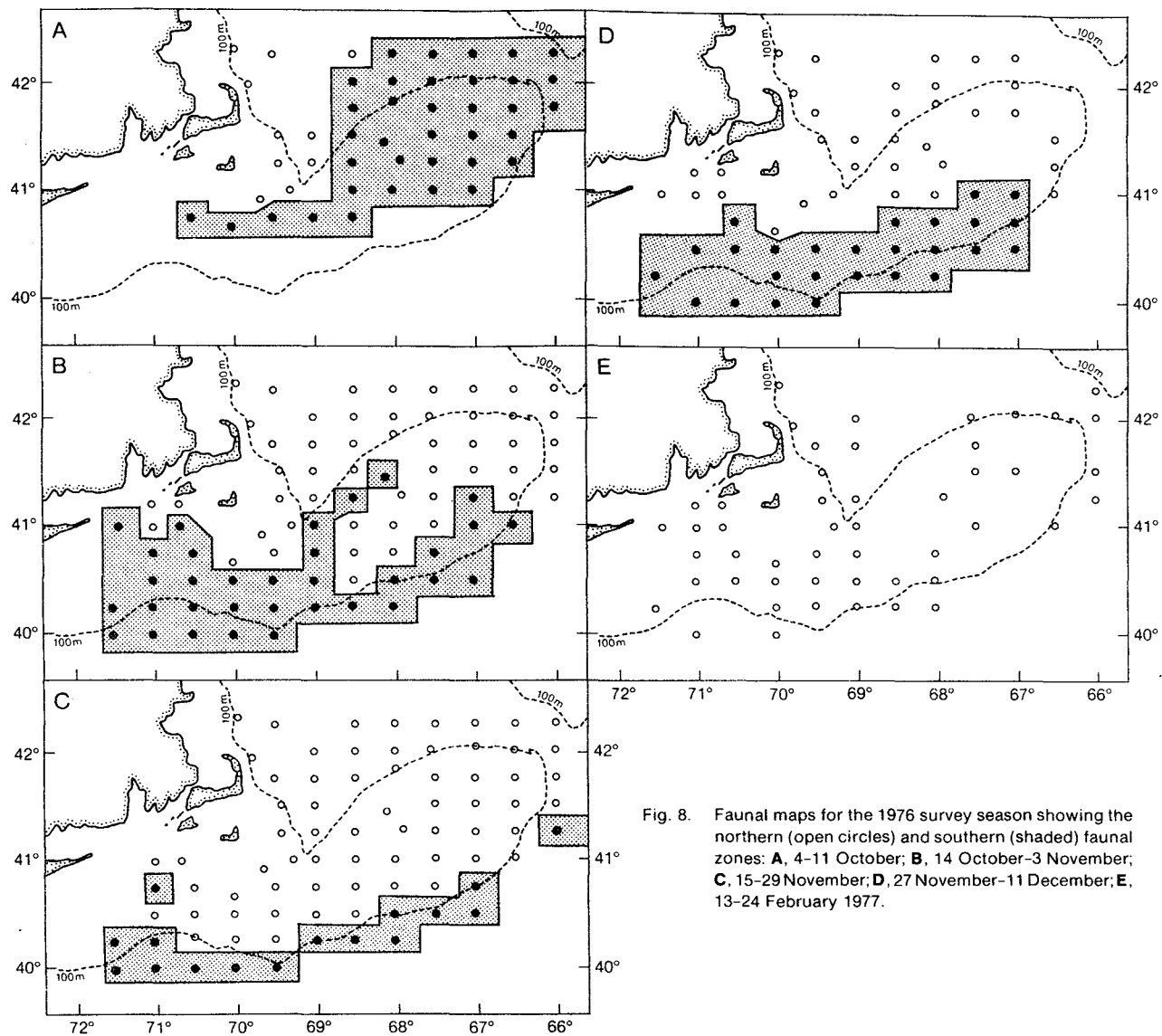


Fig. 8. Faunal maps for the 1976 survey season showing the northern (open circles) and southern (shaded) faunal zones: A, 4-11 October; B, 14 October-3 November; C, 15-29 November; D, 27 November-11 December; E, 13-24 February 1977.

In general, the southern faunal zone encroached well north of the 100-m isobath, especially on Nantucket Shoals, in early autumn and regressed southward during the remainder of the survey season, eventually being absent or reduced to a narrow band by February. The temperature-salinity analysis of data from the *Prognoz* cruise in October 1974 indicated that the distributional pattern of the faunal zone was associated with water characteristics of Slope Water intrusions onto the bank. This association was reinforced by the high temperatures recorded in this zone throughout the study period. An interesting feature observed on several cruises, notably *Belogorsk* 73-01, *Wieczno* 73-40 and *Belogorsk* 75-02, was the northward extension of water containing southern faunal species through the Great South Channel and its continuation eastward along the northern edge of Georges Bank. This apparent transport of southern species agreed with inferred long-term mean circulation pat-

terns, i.e. a northward flow along the eastern side of Great South Channel and a northeastward jet-like current along the northern edge of Georges Bank (Butman *et al.*, 1982).

The general seasonal pattern noted above was not a fixed feature but varied from year to year, especially in the extent of intrusion of the southern faunal zone onto Nantucket Shoals and Georges Bank. 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 total ichthyoplankton, 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 8-fold from the early winter level, whereas, during the 1974 season, this zone persisted throughout the winter and abundance decreased only by 2-fold. An intrusion of the southern

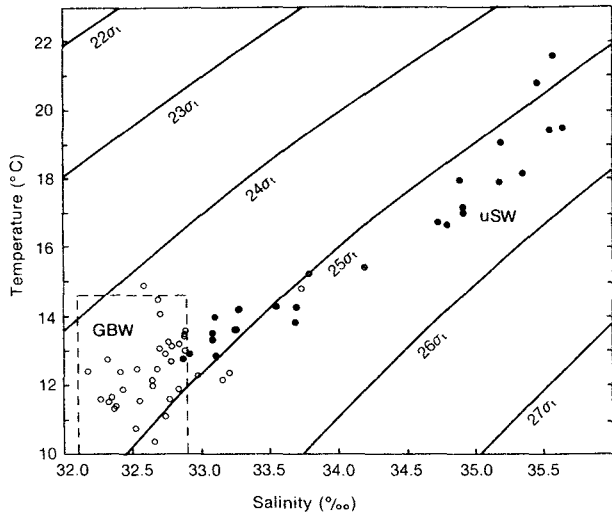


Fig. 9. Temperature-salinity plot (20 m) for stations sampled during *Prognosis* survey of 18-30 October 1974. (o = northern faunal zone; ● = southern faunal zone; GBW = Georges Bank Water; uSW = upper Slope Water.)

faunal zone covered most of Georges Bank early in the 1976 season, but this zone was disrupted or absent from early November to February, and ichthyoplankton abundance during this season was the lowest observed in the time series. From the abundance estimates of ichthyoplankton and the extent and seasonal variation of the southern faunal zone, the six survey seasons may be categorized into three broad groups: (a) 1971, 1972 and 1975, when the zone was mediumly well-formed with occasional disruptions and moderate total ichthyoplankton abundance; (b) 1973 and 1974, when the zone was well-developed and persistent with extremely high abundance; and (c) 1976, when there was extreme fluctuation and disruption in the zone with very low seasonal abundance of ichthyoplankton.

When the intrusion of Slope Water onto Georges Bank was absent or of limited extent, retention of larvae derived from spawning on the bank was apparently minimal throughout the season. When an extensive and prolonged northward intrusion of Slope Water occurred, as observed in autumn and winter of 1973 and 1974, abundance of larvae was high, implying that conditions were favorable for their retention on the bank. Colton *et al.* (1962) observed that "overflows of oceanic water would tend to counteract the general offshore movement of surface water from Georges Bank". Parrish *et al.* (1981) hypothesized that deviations from normal transport conditions, to which reproductive strategies are adapted, may be a cause of the very large recruitment variations observed in the important coastal fisheries of the California Current.

The southern faunal zone was sometimes absent or disrupted on the southeastern edge of Georges Bank and also in the vicinity of Great South Channel.

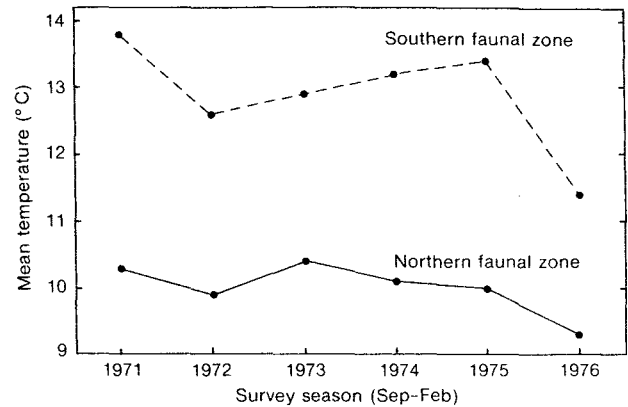


Fig. 10. Mean temperatures (at 20 m) for the southern and northern faunal zones during the autumn-winter survey seasons, 1971-76.

Because both of these areas are characterized by having variable currents with strong offshore components, transport of larvae off the bank at these locations is more probable than in areas where currents are less variable. Strong and persistent northerly winds, as occurred during November, January and February of the 1976/77 season, with resultant offshore surface drift, would contribute to the movement of the Shelf-Slope Water front farther to the south (Ingham, 1979). The low temperatures (4° to 6°C) and high salinities (33.5-34.0‰), characteristic of Gulf of Maine water, found over Georges Bank during autumn-winter of 1976/77 (Wright, 1979) and the computed Ekman transport indices (Lough *et al.*, MS 1979) indicate strong southerly transport.

In addition to northerly wind stress, the presence of warm-core Gulf Stream eddies (or rings) in the Slope Water south of Georges Bank can draw considerable volumes of Shelf Water offshore during their normal passage from east to west (Crist and Chamberlin, 1977). Three eddies, one of which was quite large and infringed on Nantucket Shoals and southwestern Georges Bank in August-September 1976, were in the vicinity of Georges Bank during the following autumn and winter and could have contributed to the low abundance of ichthyoplankton in that survey season by the offshore transport of Shelf Water. In contrast, no eddies were reported in the region during autumn and early winter of 1974 (Mizenko and Chamberlin, 1979), when larval abundance was high.

The retention of larvae in the shallow water of Georges Bank and Nantucket Shoals is a complex function of variable circulation patterns. Wind-driven currents on the shelf and passage of warm-core eddies south of the shelf appear to be important mechanisms responsible for the transport of larvae off the southern edge of the banks, but the significance of this loss on the recruitment process of the fish stocks in this region needs further study.

### Summary

1. Distinct and recurring biogeographical divisions of the Georges Bank-Nantucket Shoals region were delimited with the use of a numerical classification technique. Two faunal zones were evident: a southern zone of high diversity and medium abundance of ichthyoplankton, located along the southern flank of Nantucket Shoals and Georges Bank, and a northern zone of low diversity and high abundance, located in the shallow water of Nantucket Shoals and Georges Bank and extending into the Gulf of Maine.
2. The two faunal divisions had significantly different temperature regimes (at 20-m depth), indicating that the faunal groups are associated with distinct water-mass types characteristic of the Georges Bank-Nantucket Shoals region. A temperature-salinity analysis of data from one survey supported this conclusion.
3. The southern faunal zone was characterized by subtropical and mesopelagic taxa which apparently had been transported northward by the Gulf Stream and onto the shelf by Slope Water intrusions. The apparent transport of these southern species northward through Great South Channel and eastward along the northern edge of Georges Bank corroborates the inferred long-term circulation patterns of the region.
4. The extent of intrusion of the southern faunal zone onto the shelf fluctuated seasonally, usually being more pronounced in early autumn and generally receding farther offshore as the season progressed. Ichthyoplankton abundance was high in 1973 and 1974 when the southern faunal zone was well-developed and persistent, medium in 1971, 1972, and 1975 when the zone was only moderately developed, and low in 1976 when the zone exhibited extreme fluctuation.
5. It is hypothesized that a poorly-developed or absent southern faunal zone, with its accompanying low abundance of ichthyoplankton, is indicative of significant disruption on Georges Bank of the clockwise flow, which acts as a retention mechanism for larvae spawned on the bank. The occasional breakdown of the clockwise gyre, resulting possibly from passage of warm-core eddies south of the shelf and from wind-driven currents, permits the transport of larvae southward across the 100-m isobath to a greater extent than usual with consequent effects on recruitment to the fish stocks of the region.

### Acknowledgement

The ICNAF larval herring surveys represent a decade of intense, cooperative activity by five principal

fisheries institutes: Institut für Meerskunde, Kiel, Federal Republic of Germany; Institute Scientifique et Technique des Pêches Maritimes, St. Pierre et Miquelon, France; Sea Fisheries Institute, Gdynia, Poland; Atlantic Research Institute of Marine Fisheries and Oceanography, Kaliningrad, USSR; and Northeast Fisheries Center, Woods Hole, Massachusetts, USA. We thank the many scientists who participated in the surveys, as well as those who were instrumental in the planning and coordination of cruises and data analyses. Larvae from the 0.505-mm mesh bongo-net samples were processed at the participating institutes, and those from the 0.333-mm mesh samples by the Ichthyoplankton Sorting Center, Szczecin, Poland. Preliminary data-processing, involving quality control and the production of standardized data summaries and station plots, was accomplished by the Biostatistical Group, Northeast Fisheries Center, Narragansett Laboratory, National Marine Fisheries Service, Narragansett, Rhode Island.

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