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Changes in Time and Location of Herring, *Clupea harengus* L., Spawning Relative to Bottom Temperature in the Georges Bank and Nantucket Shoals Areas, 1971-77

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Abstract

The distributions of newly-hatched herring larvae were examined from data collected on 31 autumn surveys of the Georges Bank-Nantucket Shoals region in 1971-77. Sampling was conducted with bongo nets on the standard grid of stations at 3-4 week intervals from September to December. Plotted concentrations of small larvae (≤8 mm SL) were used to delineate spawning areas and bottom temperatures were judged to represent thermal conditions during spawning and hatching. Delay of spawning on Georges Bank after 1973 was found to be associated with a warming trend since 1971. Large volumes of warm water (>13°C) on Georges Bank may have affected herring spawning and/or the survival of eggs and larvae. The decline in abundance of herring on Georges Bank and the virtual absence of signs of spawning on the traditional spawning grounds since 1976 are discussed in conjunction with the continued spawning on Nantucket Shoals where mean bottom temperatures were considerably lower than those on Georges Bank.

Introduction

With the development of the offshore herring fishery in the Northwest Atlantic during the 1960's, Georges Bank became an area of major interest to distant-water fleets, primarily from European countries. The herring catch in the Georges Bank region (NAFO Division 5Z) increased rapidly to nearly 350,000 tons in 1968 and then declined virtually to zero in 1977 after the disappearance of the strong 1970 year-class (Anthony and Waring, MS 1980). Although intense fishing pressure was undoubtedly a principal factor in the decline, environmental factors may also have played a part. In particular, there was a general warming trend in the region during 1968-77, and water temperatures of 14° to 15°C were prevalent on Georges Bank during the herring spawning seasons of 1973, 1974, 1976 and 1977 (Davis, 1978), whereas temperatures around 9.5°C were prevalent on herring spawning beds in the western Gulf of Maine in 1974 (Cooper *et al.*, MS 1975). The onset of herring spawning on Georges Bank was delayed in 1973 and thereafter, and the duration of spawning was shortened after 1975. Herring spawning virtually ceased on northeastern Georges Bank after 1976 but continued on Nantucket Shoals where water temperatures did not reach the high values observed on Georges Bank.

These changes in timing and location of herring spawning in the Georges Bank-Nantucket Shoals region were revealed by intensive larval herring surveys during 1971-77 which were coordinated by the International Commission for the Northwest Atlantic Fisheries (ICNAF). Although the results of these surveys have been reported by Lough *et al.* (MS 1979), the relationship of water temperature to the observed changes in spawning activity has not been studied in detail. The purpose of this paper is to examine the location and timing of spawning and hatching success in relation to temperature on the spawning grounds by using the distribution of newly-hatched herring larvae as a spawning site indicator. This study covers the 1971-77 spawning seasons in the Georges Bank-Nantucket Shoals region and utilizes the data base described by Lough and Bolz (MS 1979).

Because individual "populations" of herring spawn on the seabed in well-defined areas at well-defined times of the year (Zijlstra, 1964), it is possible to use the distribution of early-stage larvae as spawning site and spawning time indicators. Isolation of herring stocks is easily recognizable at the time of reproduction (Iles and Sinclair, 1982). It has been clearly demonstrated that the Georges Bank stock is discrete from the Gulf of Maine and southwestern Nova Scotia stocks. Boyar *et al.* (1973) summarized the seasonal distribution of larval herring in the Georges Bank-Gulf of Maine region during 1962-70 and concluded that larvae originating from the three major spawning areas (Georges Bank, western Gulf of Maine, and southwestern Nova Scotia) remained discrete throughout the larval period due to restrictive circulation patterns. The larval herring surveys during 1971-77 confirmed that there was a low degree of mixing of larvae among the three stocks (Lough *et al.*, MS 1979), but larvae from Nantucket Shoals were considered to intermix with those from Georges Bank and the data for these two areas were combined in their studies. However, there are persistent differences between the two areas in period of herring spawning

and environmental conditions. These differences, together with evidence that spawning continued on Nantucket Shoals after the virtual disappearance of herring from Georges Bank in 1977, indicate that there is some discreteness between the groups of herring associated with these two spawning sites.

Materials and Methods

This study includes data from 31 larval herring surveys in 1971–77. Research vessels from Federal Republic of Germany (*Anton Dohrn* and *Walther Herwig*), France (*Cryos*), Poland (*Wieczno*), Union of Soviet Socialist Republics (*Argus*, *Belogorsk*, *Prognoz*, *Viandra*), and United States of America (*Albatross IV*, *Delaware II*, *Researcher*) participated in the surveys at various times during the autumn in these years (Table 1). Cruise tracks and station positions for these surveys have been illustrated by Lough and Bolz (MS 1979) and are not repeated here. The standard grid of sampling stations, 25–35 km apart, encompassed the main spawning grounds of the Georges Bank–Nantucket Shoals area (Fig. 1).

A double-oblique haul was made at each station with a 61-cm bongo sampler (Posgay and Marak, 1980) containing two plankton nets (mesh sizes of 0.505 and 0.333 mm). A V-fin depressor (122 cm) was used to achieve the desired wire angle (45°) at the relatively high towing speed (3.5 knots). A time-depth recorder, attached to the wire near the sampler, provided a permanent trace of the haul profile, and a flowmeter was located in the mouth of each bongo net to measure the volume of water strained. The bongo sampler was deployed at 5 m/min to a maximum depth of 100 m, or to within 5 m of bottom in shallower areas, and was retrieved at 10 m/min. Each net of the sampler filtered between 100 and 1,000 m^3 of water, depending on the depth of sampling.

Larval herring in the 0.505 and 0.333 bongo-net zooplankton samples were sorted at the Plankton Sorting Center, Szczecin, Poland, and measurements were recorded as standard length (SL) in millimeters. Computer summaries and plots of the data were prepared by the Biostatistical Unit, National Marine Fisheries Service, Narragansett, Rhode Island, USA. Estimates of the various sources of error in the data were made by Lough *et al.* (MS 1979). Some points relevant to the present paper are as follows:

1. Survey coverage of the Georges Bank–Nantucket Shoals area was not entirely adequate in all years: shallow areas (<25 m) on Nantucket Shoals were not sampled; the 1976 surveys appear to have missed some of the smaller larvae (<10 mm SL); and the towing profiles of the 1971 surveys lead to the belief that larval abundance in shallow areas was underestimated.

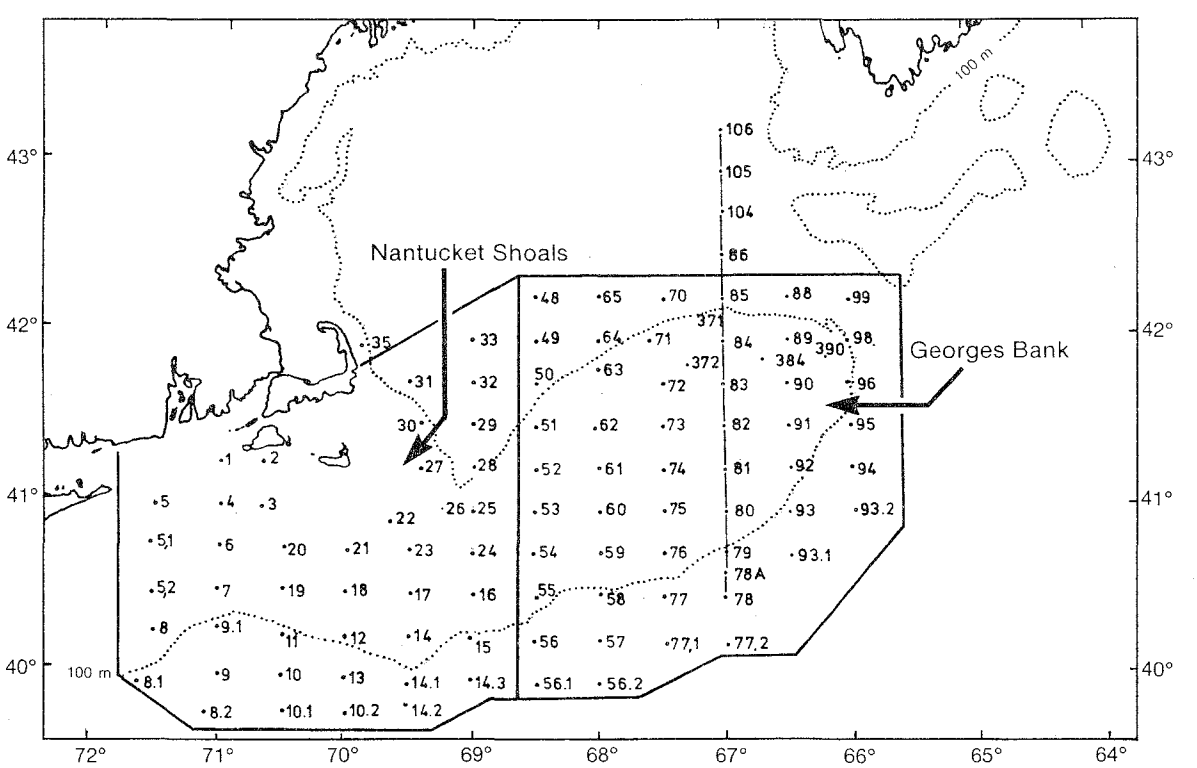


Fig. 1. Station positions for the 30 larval herring surveys during 1971–77. Stations 1–33 encompass the Nantucket Shoals area and Station 48–99 the Georges Bank area. The vertical line across Georges Bank represents the hydrographic section shown in Fig. 12.

TABLE 1. Mean bottom temperatures associated with stations where newly-hatched herring larvae (≤8 mm SL) were collected during 31 surveys of the Nantucket Shoals and Georges Bank grounds in 1971–77. Mean temperatures (T) and their standard deviations (SD) were calculated for (a) stations with high abundance (>10 per 10 m^2) of small larvae, and (b) positive stations where the ratio of small larvae to the total number of larvae was greater than 0.25. (Asterisks indicate that mean temperatures relate to traditional spawning areas; the symbol ... indicates no temperature data available.)

		Nantucket Shoals — mean bottom temperatures							Georges Bank — mean bottom temperatures						
			Stations with high abundance of small larvae			All positive stations with small larvae				Stations with high abundance of small larvae			All positive stations with small larvae		
Vessel	Survey dates	Survey middate	No.	T(°C)	SD	No.	T(°C)	SD	Survey middate	No.	T(°C)	SD	No.	T(°C)	SD
						1971									
Cryos	09-24 Sep	22 Sep	8*	6.9	1.9	0			14 Sep	4	15.0	1.5	8	13.9	2.3
Delaware II	21 Sep-04 Oct	02 Oct	6*	7.7	2.2	1	8.5	—	26 Sep	5	12.4	0.2	11	12.2	2.6
Viandra	09-25 Oct	23 Oct	3*	6.1	0.3	0			15 Oct	6	13.8	0.8	10	12.7	2.3
W. Herwig	29 Oct-12 Nov	11 Nov	6*	7.7	2.3	11	11.1	3.3	05 Nov	3	13.0	0.8	10	11.5	2.4
Albatross IV	02-17 Dec	14 Dec	6*	7.9	0.4	3	8.8	0.5	08 Dec	6*	9.1	0.6	0		
						1972									
Argus	22-30 Sep	—	—	—	—				25 Sep	2	13.0	1.2	3	13.5	1.2
Wieczno	02-28 Oct	04 Oct	2	13.3		9	12.6	2.8	16 Oct	3	11.7	1.6	7	11.4	1.9
Argus	12-28 Oct	14 Oct	5	7.9	3.0	8	8.7	3.3	21 Oct	6*	11.4	1.0	11	10.8	2.3
Anton Dohrn	31 Oct-12 Nov	02 Nov	3	9.7	1.8	10	9.5	3.0	07 Nov	2	11.3	0.8	9	10.9	1.0
Albatross IV	28 Nov-15 Dec	30 Nov	3	8.2	0.3	3	8.2	0.3	09 Dec	6*	9.0	0.6	3	9.0	0.2
						1973									
Cryos	16-28 Sep	17 Sep	4*	12.5	2.7	0			22 Sep	3	13.9	1.3	7	11.0	2.8
Wieczno	29 Sep-21 Oct	04 Oct	3	11.9	3.3	3	11.9	3.3	12 Oct	6	12.5	2.3	13	12.2	2.3
Belogorsk	15 Oct-01 Nov	17 Oct	6	...	...	11	...	...	26 Oct	6	...	...	14	...	...
W. Herwig	28 Oct-08 Nov	30 Oct	8	12.9	1.9	14	10.7	3.3	04 Nov	6	12.8	1.7	11	11.7	2.3
Albatross IV	04-20 Dec	05 Dec	3	12.7	1.3	14	10.9	2.5	14 Dec	2	11.8	0.1	7	10.9	0.7
						1974									
Cryos	07-24 Sep	16 Sep	5*	10.8	2.8	0			21 Sep	6*	15.3	2.1	0		
Wieczno	27 Sep-18 Oct	30 Sep	4	10.4	3.4	4	10.4	3.4	06 Oct	6	12.5	1.9	11	11.8	2.3
Prognoz	18-30 Oct	26 Oct	5	11.1	1.6	7	11.8	1.8	20 Oct	9	12.1	1.2	13	12.1	1.0
Anton Dorhn	16-23 Nov	17 Nov	5	...	...	13	...	...	20 Nov	4	...	...	17	...	...
Albatross IV	04-19 Dec	06 Dec	7	8.3	0.6	12	12.3	2.4	14 Dec	8*	9.4	0.3	3	11.1	2.1
						1975									
Belogorsk	25 Sep-09 Oct	28 Sep	1	9.6	—	1	9.6	—	04 Oct	2	8.1	0.3	5	9.0	0.9
Belogorsk	16-30 Oct	27 Oct	6	10.4	1.4	8	10.2	2.1	20 Oct	7	10.1	1.9	21	10.5	2.5
Anton Dohrn	01-18 Nov	13 Nov	9	10.3	2.1	11	7.4	1.7	06 Nov	6	11.3	0.7	23	11.8	1.7
Albatross IV	02-17 Dec	15 Dec	7	9.3	1.9	2	9.1	0.3	09 Dec	1	9.7	—	5	9.7	0.5
						1976									
Belogorsk	04-11 Oct	05 Oct	9*	10.1	2.8	5	...	...	08 Oct	6*	14.3	1.5	0		
Wieczno	14 Oct-03 Nov	18 Oct	9*	11.6	2.5	4	9.7	2.3	27 Oct	9*	13.1	0.7	8	15.0	2.3
Anton Dohrn	15-29 Nov	16 Nov	9*	8.7	1.3	0			23 Nov	7*	9.6	0.4	0		
Researcher	27 Nov-11 Dec	29 Nov	7*	8.5	0.5	1	8.3	—	05 Dec	7*	8.6	0.5	0		
						1977									
Wieczno	04-24 Oct	20 Oct	6*	9.2	2.2	3	9.1	1.6	13 Oct	6*	13.0	1.8	0		
Anton Dohrn	09-19 Nov	26 Nov	13*	9.1	2.3	1	10.8	—	11 Nov	12*	11.6	1.4	1	6.3	—
Delaware II	08-20 Dec	10 Dec	8*	7.8	0.3	0			16 Dec	9*	7.6	0.3	0		

2. Extrusion of small larvae through the meshes is a possible source of error in sampling larval herring. Comparison of measurements of the skull width with mesh diagonals indicates that the minimum retention lengths of larval herring could be 12.0 and 7.5 mm for meshes of 0.505 and 0.333 mm respectively (Colton *et al.*, 1980), but smaller larvae were in fact retained in nets of both mesh sizes, with 7 mm being the length of recently-hatched larvae at peak abundance. Data for the 0.505 and 0.333 mm nets were used interchangeably in this study, because station-by-station randomized paired-comparison tests revealed no significant differences in catchability of the nets.

3. Because newly-hatched larvae (<7 mm SL) have been observed close to the eggbeds during the first few days after hatching (Caddy and Iles, 1973;

Cooper *et al.*, MS 1975), their abundance, based on bongo-net sampling to about 5 m off the bottom, was likely to have been underestimated.

The study area was divided into two subareas (Nantucket Shoals and Georges Bank), according to Schlitz (MS 1975). Stations were chosen where small larvae (≤8 mm SL) occurred. Areas of larval concentration were defined by considering all stations where the ratio of the number of small larvae to the total number of larvae was greater than 0.25 and where the abundance of small larvae was greater than 10 per 10 m^2. Areas of lesser abundance of small larvae were identified as dispersal areas.

Plots of bottom temperatures were obtained from the Fishery Oceanography Unit, Northeast Fisheries Center, Woods Hole, Massachusetts, USA, with temperature values marked at all stations where small larvae occurred. Mean bottom temperatures and their standard deviations (Table 1) were calculated for both concentration and dispersal areas.

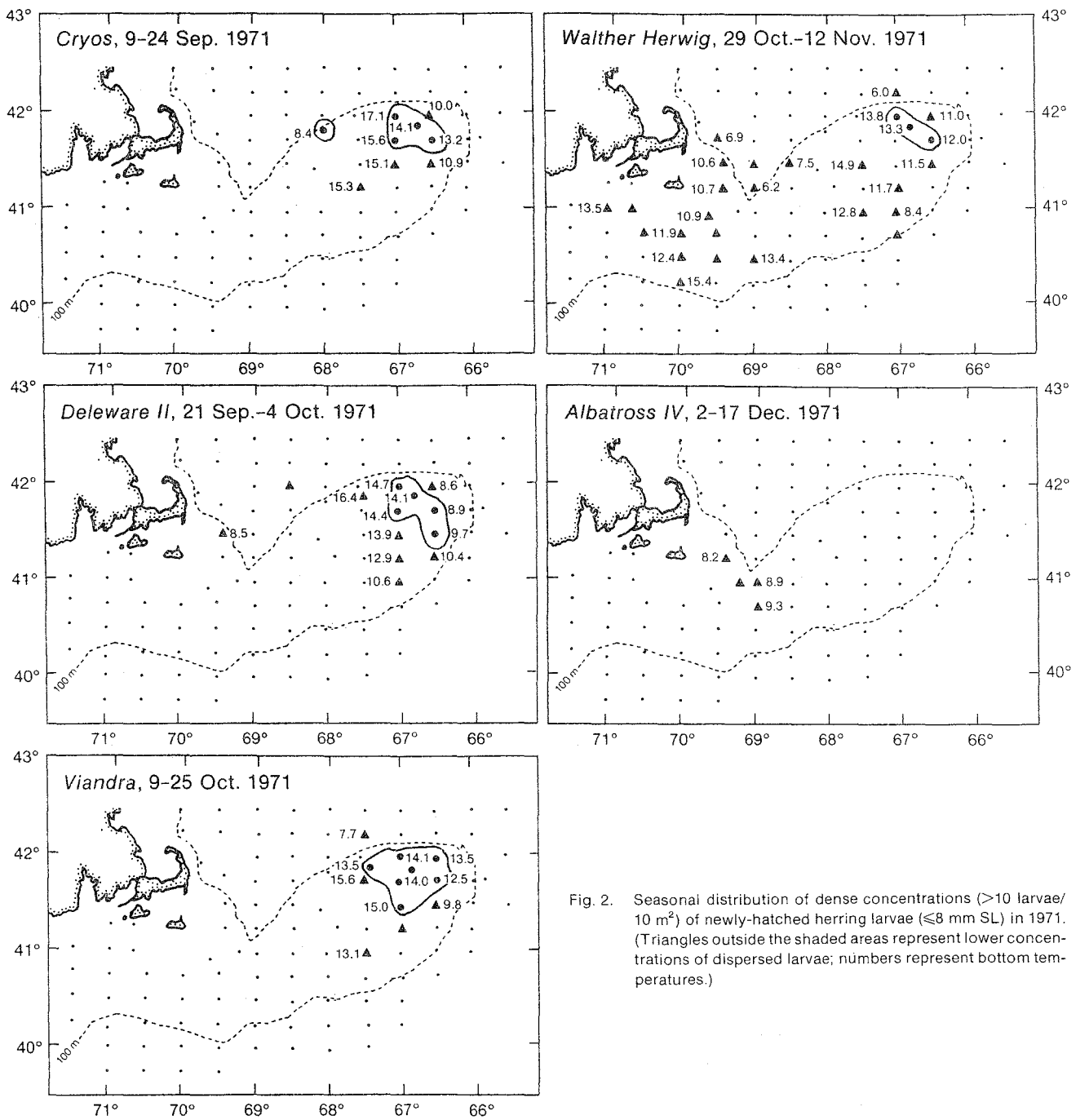


Fig. 2. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1971. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

Results

Location and time of spawning

The locations of herring spawing in the Nantucket Shoals-Georges Bank region, based on the occurrence of concentations of newly-hatched larvae are shown in Fig. 2-8. Spawning occurred progressively later in the season from east to west. The northeastern part of Georges Bank was the major spawning area. Newly-hatched larvae appeared there in September of the 1971-73 seasons and attained maximum abundance in mid- to late October, whereas, in 1974 and 1975, hatching began later in the season (early October), with peak abundance of newly-hatched larvae in November. In 1972 and 1973, hatching occurred later on Nantucket Shoals than on Georges Bank, with peak abundance on Nantucket Shoals in late October-early November. No concentrations of small larvae were found on Nantucket Shoals in September and October 1971, but some dispersed larvae were observed in November and December, possibly indicating a very low level of spawning in the area or that spawning occurred earlier in the year before the surveys began.

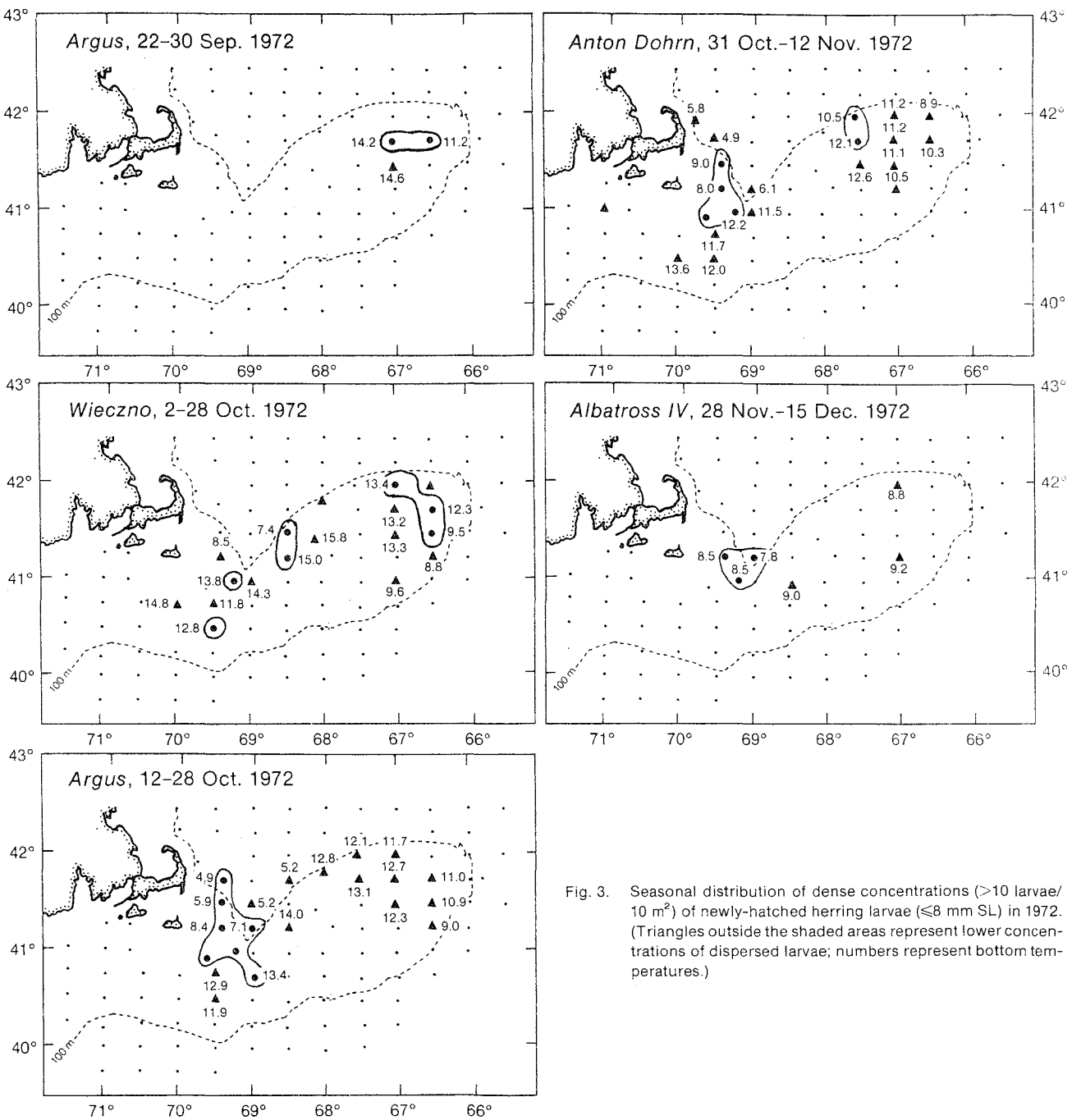


Fig. 3. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1972. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

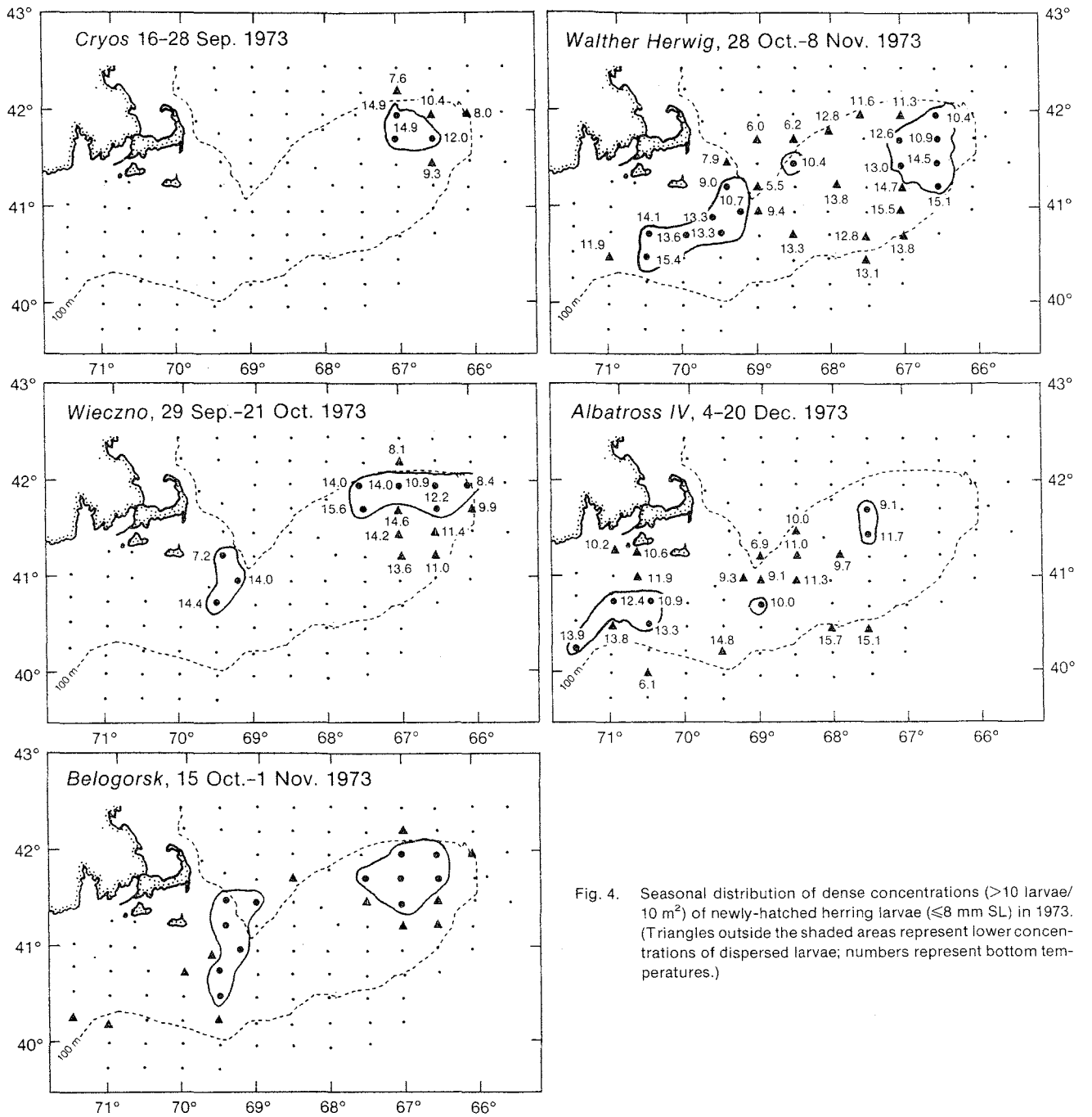


Fig. 4. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1973. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

Hatching of larvae on Georges Bank occurred over the longest period in 1973 (Fig. 9) and coincided with recruitment of the very strong 1970 year-class, the strongest in the last decade (Anthony and Waring, MS 1980). This year-class also contributed to intensive spawning in the 1974 and 1975 seasons (Table 2). On Nantucket Shoals, the period of hatching became progressively longer from 1972 to 1975, with the longest period in 1975 (Fig. 9). In 1976, spawning on Georges Bank was delayed until mid-October and terminated in early November, making this period the shortest in the time series. After 1976, newly-hatched larvae, indicative of herring spawning, were observed only in the Nantucket Shoals area (Table 2).

The location of herring spawning grounds on Georges Bank did not differ much during 1971-75 (Fig. 2-6). Concentrations of newly-hatched larvae appeared first on the northern edge of the bank in September, extended southwestward to Nantucket

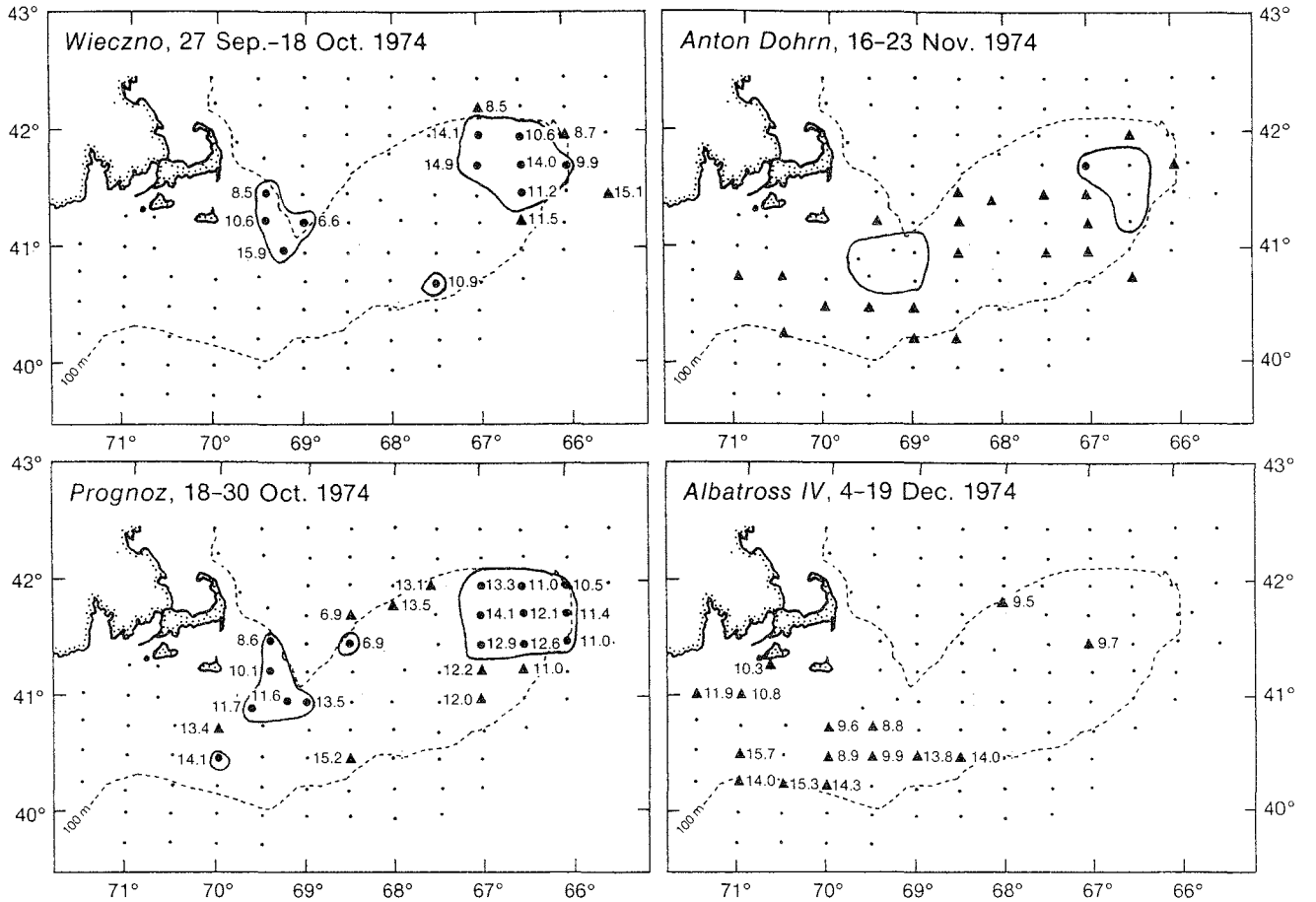


Fig. 5. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1974. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

Shoals in October, became contracted in November, and disappeared in December. In the period of peak hatching (October), the areas of high abundance of small larvae varied from about 4,500 km^2 in 1972 to about 10,000 km^2 in 1974. The highest abundance of small larvae on Georges Bank occurred in 1973 and 1974 (Table 2). The area around four sampling stations on Georges Bank (83, 84, 89 and 90 in Fig. 1) appears to have been the approximate center of the spawning ground on Georges Bank, because this is where the highest concentrations of newly-hatched larvae were observed during 1971-75 (Table 3). Bottom depths at these stations ranged from 58 to 82 m.

The dispersal patterns of small larvae on Georges Bank (Fig. 2-8) clearly show the spread of larvae from the spawning ground in a southeasterly direction at first and southwestward thereafter, generally coinciding with the anticyclonic circulation on Georges Bank. Bumpus (1976) and Lough *et al.* (MS 1979) summarized the dispersal of larval herring on Georges Bank by 5-mm length-groups and found a general correspondence of larval dispersal with mean current advection which is southwestward over the bank. Most of the larvae were found throughout the season over the bank within the 100-m contour. However, there is some indication from the time series (Fig. 2-6) that loss of larvae occurred, particularly in 1973, 1974 and 1975, when patches of newly-hatched larvae were widely distributed eastward and northward of the principal spawning area on Georges Bank.

On Nantucket Shoals during 1972-75 (Fig. 3-6), patches of newly-hatched larvae occurred most often at stations 26, 27 and 30 southeast of Cape Cod (Fig. 1, Table 4) from early October to mid-November, and even to mid-December in 1973 and 1975. Dense concentrations of small larvae usually occurred over a smaller area on Nantucket Shoals than on Georges Bank, except in 1973 when the distribution extended farther southwestward. It is possible that the lower estimates of larval abundance in the remaining years of the time series may have been due to inadequate coverage of the spawning grounds, because coastal spawning may have occurred outside the grid of stations that were sampled.

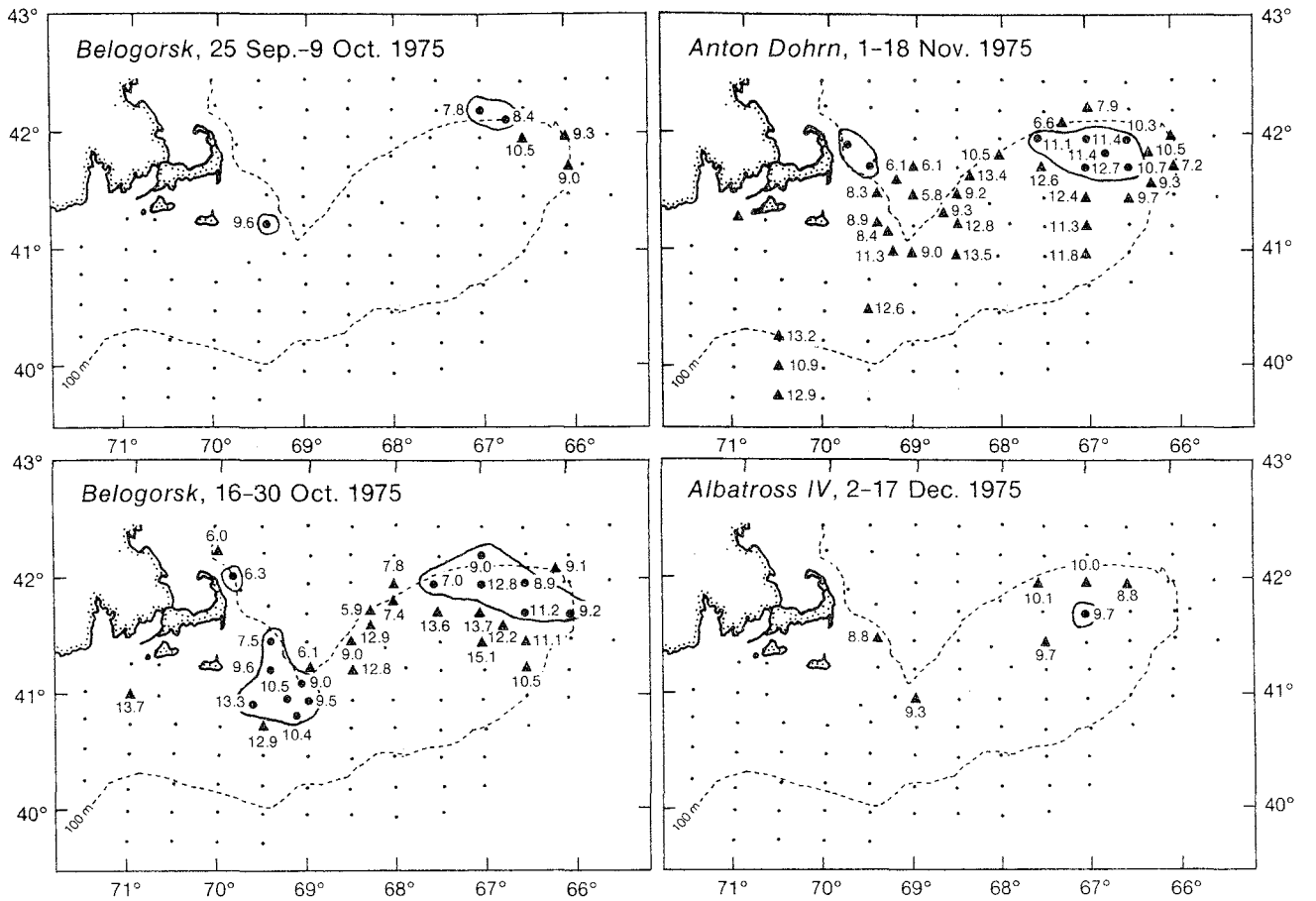


Fig. 6. Seasonal distributions of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1975. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

A much smaller spawning ground was evident on the western part of Georges Bank in the vicinity of station 51 (Fig. 1), where, except in 1971, larvae normally appeared later than on the principal Georges Bank spawning grounds, usually between mid-October and early November. No concentrations of newly-hatched larvae were observed on the southern part of Georges Bank, indicating that spawning did not occur in this area.

Lough *et al.* (MS 1980) noted that herring spawning occurred mainly on Georges Bank in 1971, 1973 and 1974 and in the Nantucket Shoals area in 1972 and 1975-77. In the following years to 1981, only a few herring larvae were found on Georges Bank (Smith *et al.*, MS 1980; Anon., MS 1980, MS 1981).

The length frequencies of larval herring sampled on Georges Bank during the various surveys in 1971-76 and on Nantucket Shoals in 1971-77 (Fig. 10 and 11) generally show typical unimodal distributions in the early part of the season, with dominance of small larvae, and polymodal distributions during later surveys. Newly-hatched larvae were dominant throughout the spawning season (September to November) in 1973-74 on Georges Bank and in 1972-74 on Nantucket Shoals, indicating very intensive and prolonged spawning activity.

Thermal conditions

The north-south hydrographic sections across Georges Bank (Fig. 1) during the peak of larval occurrence clearly show the existence of warm bank water (12° to 15° C) which is well-mixed to a depth of about 50 m and separated from stratified water of the Gulf of Maine to the north and slope water to the south (Fig. 12). Except in 1975, mean bottom temperatures associated with newly-hatched larvae (Table 1) and the minimum temperatures on the spawning grounds (Fig. 2-8) were much higher than the temperature (9.5° C) for herring spawning observed by Cooper *et al.* (MS 1975). The highest mean bottom temperature (15.3° C) was observed in September 1974 (range 11.9° to 19.1° C) and the lowest (8.1° C) in late September-early October 1975 (range 7.8° to 8.4° C). The herring

TABLE 2. Mean numbers of recently-hatched herring larvae (≤8 mm SL) per 10 m^2 taken during 31 autumn surveys of the Georges Bank-Nantucket Shoals region in 1971–77. (Percentages are based on the ratio of the number of recently-hatched larvae to the total number of larvae.)

	Nantucket Shoals				Georges Bank			
Vessel	Survey middate	Stations with small larvae (No.)	Mean No. of small larvae per 10 m^2	Percent small larvae	Survey middate	Stations with small larvae (No.)	Mean No. of small larvae per 10 m^2	Percent small larvae
				1971				
Cryos	22 Sep	0	0	0	14 Sep	9	159	70
Delaware II	02 Oct	1	2	100	26 Sep	14	231	72
Viandra	23 Oct[a]	—	—	—	15 Oct	12	159	37
W. Herwig	11 Nov	14	20	0.1	11 Nov	14	224	0.3
Albatross IV	14 Dec	4	6	0.1	08 Dec	0	0	0
				1972				
Argus	—	—	—	—	25 Sep	3	96	30
Wieczno	04 Oct	6	226	25	16 Oct	13	69	28
Argus	14 Oct	10	113	67	21 Oct	13	16	8
Anton Dohrn	02 Nov	12	86	31	07 Nov	9	20	22
Albatross IV	30 Nov	3	7	80	09 Dec	3	7	69
				1973				
Cryos	17 Sep	0	0	0	22 Sep	7	270	95
Wieczno	04 Oct	3	1,292	98	12 Oct	14	1,365	81
Belogorsk	17 Oct	11	2,750	75	26 Oct	14	1,667	71
Anton Dohrn	30 Oct	12	1,461	74	04 Nov	23	696	48
Albatross IV	05 Dec	14	53	25	14 Dec	8	200	33
				1974				
Cryos	16 Sep	0	0	0	21 Sep	0	0	0
Wieczno	30 Sep	4	233	93	06 Oct	11	1,107	100
Prognoz	26 Oct	7	258	83	20 Oct	17	2,410	74
Anton Dohrn	17 Nov	13	491	67	11 Nov	17	221	30
Albatross IV	06 Dec	11	11	7	14 Dec	3	4	3
				1975				
Belogorsk	28 Sep	1	171	100	04 Oct	6	64	100
Belogorsk	27 Oct	12	1,816	88	20 Oct	20	156	49
Anton Dohrn	13 Nov	15	77	22	06 Nov	23	149	35
Albatross IV	15 Dec	2	31	17	09 Dec	5	11	22
				1976				
Belogorsk	05 Oct	5	93	50	08 Oct	0	0	0
Wieczno	18 Oct	5	46	43	27 Oct	9	3	21
Anton Dohrn	16 Nov	0	0	0	23 Nov	0	0	0
Researcher	29 Nov	1	7	70	05 Dec	0	0	0
				1977				
Wieczno	20 Oct	4	49	50	13 Oct	0	0	0
Anton Dohrn	02 Nov	1	138	5	11 Nov	1	0	0
Delaware II	10 Dec	0	0	0	16 Dec	0	0	0

[a] Only southern part of Nantucket Shoals was surveyed.

spawning grounds on the northern edge of Georges Bank are not far from a sharp front which is not stationary but is advected back and forth by tides, so that some parts of the bank are subjected to twice daily temperature fluctuations of 6° to 7°C (Wright and Lough, MS 1979). However, from the temperature data collected during the larval herring surveys in 1971–77, there is no evidence of the presence of cold water over the spawning grounds as a result of such fluctuations.

Temperature conditions were much more variable on Nantucket Shoals than on Georges Bank, and concentrations of newly-hatched larvae occurred in areas where bottom temperatures differed between stations

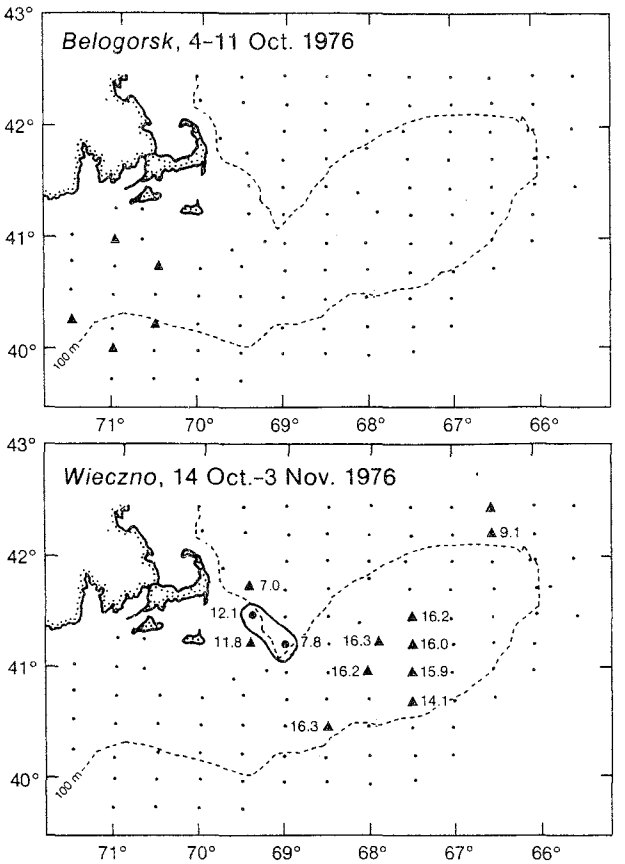


Fig. 7. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1976. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

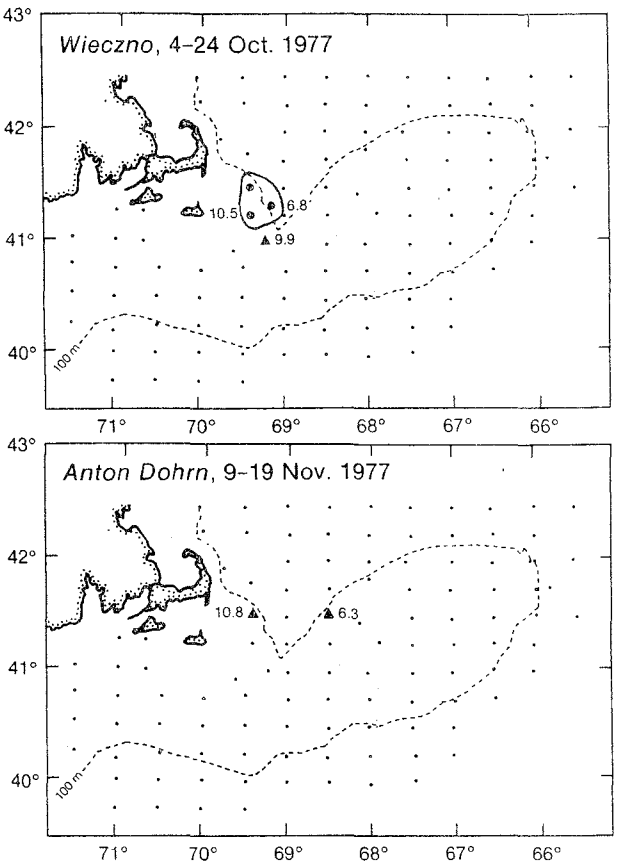


Fig. 8. Seasonal distribution of dense concentrations (>10 larvae/10 m^2) of newly-hatched herring larvae (≤8 mm SL) in 1977. (Triangles outside the shaded areas represent lower concentrations of dispersed larvae; numbers represent bottom temperatures.)

and surveys (Fig. 2-8). In 1971, 1976 and 1977, when dense concentrations of newly-hatched larvae were not found or were present in small numbers, mean bottom temperatures were calculated for the historical spawning areas (Table 1). In 1971, very low temperatures (means ranging from 6.1° to 7.9° C) were observed on these grounds, whereas the temperatures on the Georges Bank spawning grounds were, on the average, more than 6° C higher. In the 1972-77 spawning seasons, mean bottom temperatures on Nantucket Shoals were usually lower than on Georges Bank. This might be the result of a much smaller volume of well-mixed warm water over the spawning grounds on Nantucket Shoals and the frequent incursion of cold water from the Gulf of Maine.

Discussion

Herring spawn on Georges Bank on a very specific type of substrate (rounded gravel 2-10 mm diameter) in water characterized by strong mixing processes (Caddy and Iles, 1973; Drapeau, 1973) at a mean depth of 70 m (range 42-92 m). This is in contrast to Jeffreys Ledge (Cooper *et al.*, MS 1975) and the shallow grounds in the Gulf of St. Lawrence (Tibbo *et al.*, 1963), where red algae form the spawning substrate, and to those off southwestern Nova Scotia where sand and red algae are prevalent.

Hatching of larvae on Jeffreys Ledge has been observed by scuba-diving to occur 8-9 days after spawning at temperatures around 10° C (Cooper *et al.*, MS 1975). Pankratov and Sigajev (1973), from investigations of spawning beds on Georges Bank, found that eggs were laid in several layers, with maximum density (24.4 kg/m^2) in the center of the bed, and were developing at 11° to 14° C. Recently-hatched yolk-sac larvae may be retained for one to several days in clusters of algae if egg deposition is in an area of vegetation (Cooper *et al.*, MS 1975), or they may stay close to the seabed within 1 m of bottom (Caddy and Iles, 1973) for 1-3 days after hatching. Also, there are scuba-diver and submersible observations of dense aggregations

TABLE 3. Ranked comparison of the Georges Bank stations where high abundance of small larvae (≤8 mm SL) occurred with maximum frequency in 1971–75.

Station No.	Spawning seasons 1971	1972	1973	1974	1975	1971–75	Depth (m)
84	1	2	2	4	2	1	64
90	3–4	1	3	1	5	2	64
83	5	3	1	3	3–4	3	58
89	6	7	4	5	1	4	82
91	3–4	5	4	2	—	5	88
96	—	—	10	6	6	6	97
82	9	—	5	11–12	—	7	64
72	—	3	7	—	—	8	42
85	—	—	—	11–12	3–4	9	208
51	8	—	9	9	—	10	92

TABLE 4. Ranked comparison of Nantucket Shoals stations where high abundance of small larvae (≤8 mm SL) occurred with maximum frequency in 1971–77.

Station No.	Spawning seasons 1971	1972	1973	1974	1975	1976	1977	1971–77	Depth (m)
26	2	1	1	1	3	—	3	1	56
27	1	2	2	2	1	1–2	2	2	45
30	4	5	5	3	2	1–2	1	3	56
23	3	—	3	8	—	—	—	4	40
22	—	3	—	4	5	—	—	5	30
24	—	6	6	7	—	—	—	6	75

of yolk-sac larvae being carried by currents near the bottom adjacent to areas of egg deposition (Graham and Chenoweth, 1973).

Herring larvae (4–8 mm SL and about 1 week old) initially concentrate in the upper part of the water column over the spawning areas and subsequently are dispersed by surface and near-surface currents southwestward across Georges Bank at a speed of 2–12 km per day (Lough *et al.*, MS 1980). Larvae begin feeding before the yolk-sac is fully resorbed within 7 days of hatching (Lett and Kohler, 1976). Under laboratory conditions, resorption of the yolk-sac has been observed to occur in 4.5 days (Lough *et al.*, 1982). Therefore, the major spawning grounds can be delineated fairly precisely by using abundance and distribution patterns of ≤8 mm SL larvae from the plankton surveys to represent recently-hatched larvae.

Herring spawning grounds on Georges Bank extend in a wide band along the northern edge of the bank covering an area of about 10,000 km², within which Pankratov and Sigajev (1973) found egg beds ranging from 0.3 to 1.1 km² in size. Drapeau (1973) concluded that the grounds most favorable for herring spawning on northeastern Georges Bank lay within an area of 50 x 100 km between lat. 41°34'N and 42°08'N and long. 66°30'W and 67°45'W. This area is shown by the rectangle in Fig. 13, together with the spawning grounds delineated in the present study.

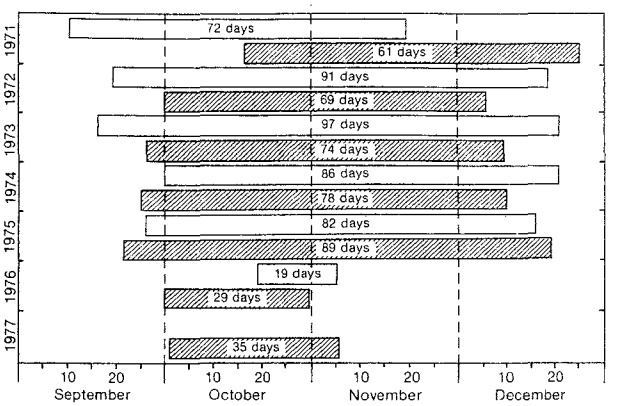


Fig. 9. Estimated duration of hatching of herring larvae on the Georges Bank and Nantucket Shoals spawning grounds in 1971–77, based on the occurrence of newly-hatched larvae (≤8 mm SL).

Quantitative surveys of herring spawning beds in the 1960's (Noskov and Zinkevich, MS 1967) indicated a progressive contraction in the spawning area and the number of eggs laid, from which a corresponding reduction in stock size was deduced. During the 1970's, as shown by the present study, herring spawning reached its greatest extent during the 1973–74 seasons, due to the recruitment of the strong 1970 year-class. Boyar *et al.* (1973) determined the location of spawning grounds on the basis of the distribution of ripe and running herring (maturity stage VI) and recorded, additionally to the spawning grounds on the northern edge of Georges Bank, several small spawning sites along the southern slope of the bank at depths of 50–200 m. Spawning along the southern slope was not confirmed in the present study, due possibly to the different methods used. However, reduction of spawning biomass with consequent contraction of spawning grounds may have been a contributing factor to the lack of spawning on southern Georges Bank in the 1970's.

Draganik and Długosz (1969, 1971) reported that the concentrations of adult herring, exploited by the Polish fishing fleet from June to September (1966–69), migrated along the southern slope of Georges Bank in a wide band at a depth of about 90 m, reaching the northern edge in September when spawning began. In October, the fishery was concentrated on the western part of the bank and on Nantucket Shoals. Information available from research vessel surveys in 1968–69 (H. Dornheim, Sea Fisheries Institute, Hamburg, Federal Republic of Germany, unpubl. data) indicated that maturity stage V herring were found on southern Georges Bank during September, whereas stage VI herring were present on the northern part of the bank and on Nantucket Shoals in September and October.

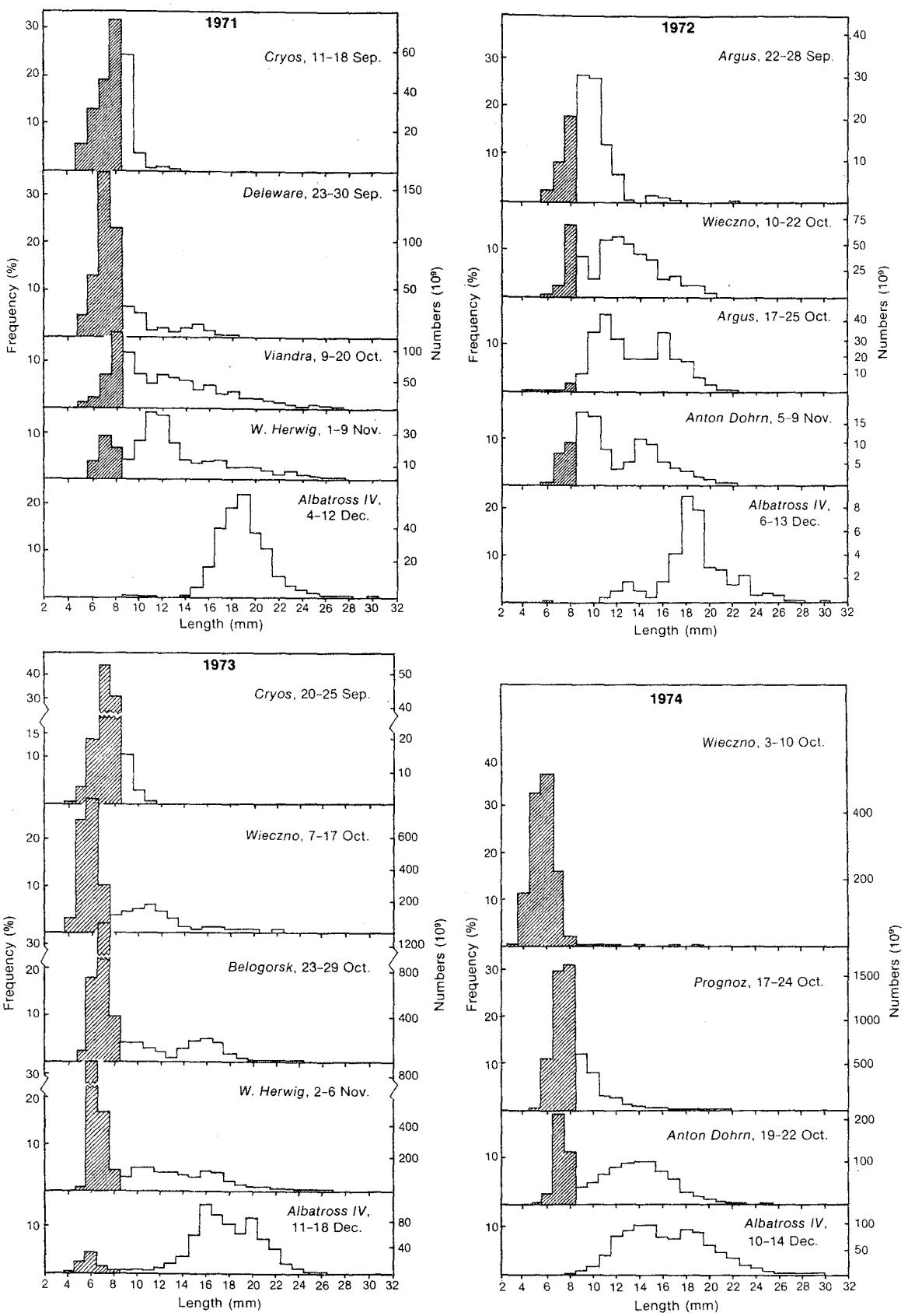


Fig. 10. (continued on next page.)

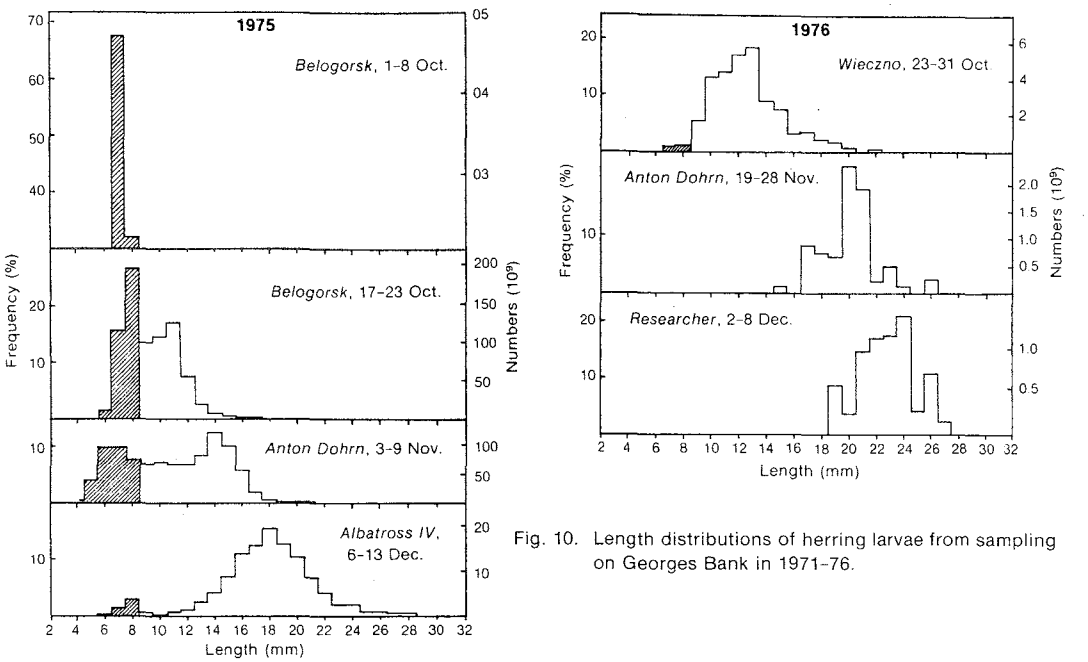


Fig. 10. Length distributions of herring larvae from sampling on Georges Bank in 1971-76.

Lough *et al.* (MS 1980) estimated hatching periods for the 1971-78 seasons on Georges Bank and Nantucket Shoals combined (Table 5). Spawning began during early September in 1971-73, near the end of September in 1974-75 and during the first half of October in 1976-78. Pankratov and Sigajev (1973) noted that spawning began on the eastern part of Georges Bank about 16-17 September 1970 and lasted for about 2 months. From the prevalence of maturity stages VI and VII in herring sampled during Polish research vessel surveys in 1972-74, Paciorkowski and Giedz (MS 1975) determined that peak spawning on Georges Bank occurred on 24-26 September in 1972 and 1973 and on 2 October in 1974.

The production of larval herring was extremely low on Georges Bank in 1976-78 (Tables 2 and 5), with significant spawning being limited to Nantucket Shoals, where, traditionally, it has occurred about 2 weeks later than on Georges Bank. Smith *et al.* (MS 1980) found only a few herring larvae on Georges Bank in 1978 and 1979, and similar results were obtained on surveys by the Polish research vessel *Wieczno* in 1980 and 1981 (Anon., MS 1980, MS 1981). It seems that the strong 1970 year-class was the last one to be recruited to the Georges Bank spawning stock in the 1970's and it spawned there until 1975. In contrast, herring spawning has continued uninterrupted on Nantucket Shoals throughout the period of study.

The question arises as to what extent abiotic conditions have contributed to poor recruitment after the successful 1970 year-class, to the delay in the onset of spawning, and to the westward shift in spawning activity. Davis (1978) indicated that there was a general warming trend (2° to 3° C increase in bottom temperatures) in autumn on Georges Bank during 1969-77, the highest mean temperatures being attained in 1971, 1973, 1974, 1976 and 1977 and the lowest values in 1969 and 1970 (10.4° and 10.5° C). The 8-year (1971-78) mean temperatures of 11.6° and 9.5° C for Georges Bank and Nantucket Shoals respectively were 0.6° and 0.7° C higher than the 1940-66 long-term means reported by Colton and Stoddard (1973) for these areas. In the area of larval concentration on Georges Bank in September-October, bottom temperature data for 1971-77 (Table 1) show no mean values lower than 11.4° C except in 1975 when means of 8.1° and 10.1° C were recorded for two surveys in October.

Because herring have continued to spawn on the northeastern part of Nantucket Shoals after the collapse of spawning on Georges Bank, it is possible that higher temperatures may have altered their migration patterns, resulting in a westward shift from the traditional spawning grounds on Georges Bank. The northeast part of Nantucket Shoals is an area affected by upwelling of cold Gulf of Maine water, and this area would be less affected by warm water incursions than the Georges Bank spawning grounds. In view of the large volume of very warm water (>13° C) observed on Georges Bank during October surveys since 1971, it is difficult to see how herring spawning would be unaffected if hatching success tends to decline at temperatures higher than 12° C (Blaxter, 1956). The proximity of a cold-water front to the northern edge of Georges Bank apparently did not affect the spawning beds there, as suggested by Wright and Lough (MS 1979). In contrast, the effect of upwelling on the Nantucket Shoals spawning beds is apparent from the lower mean

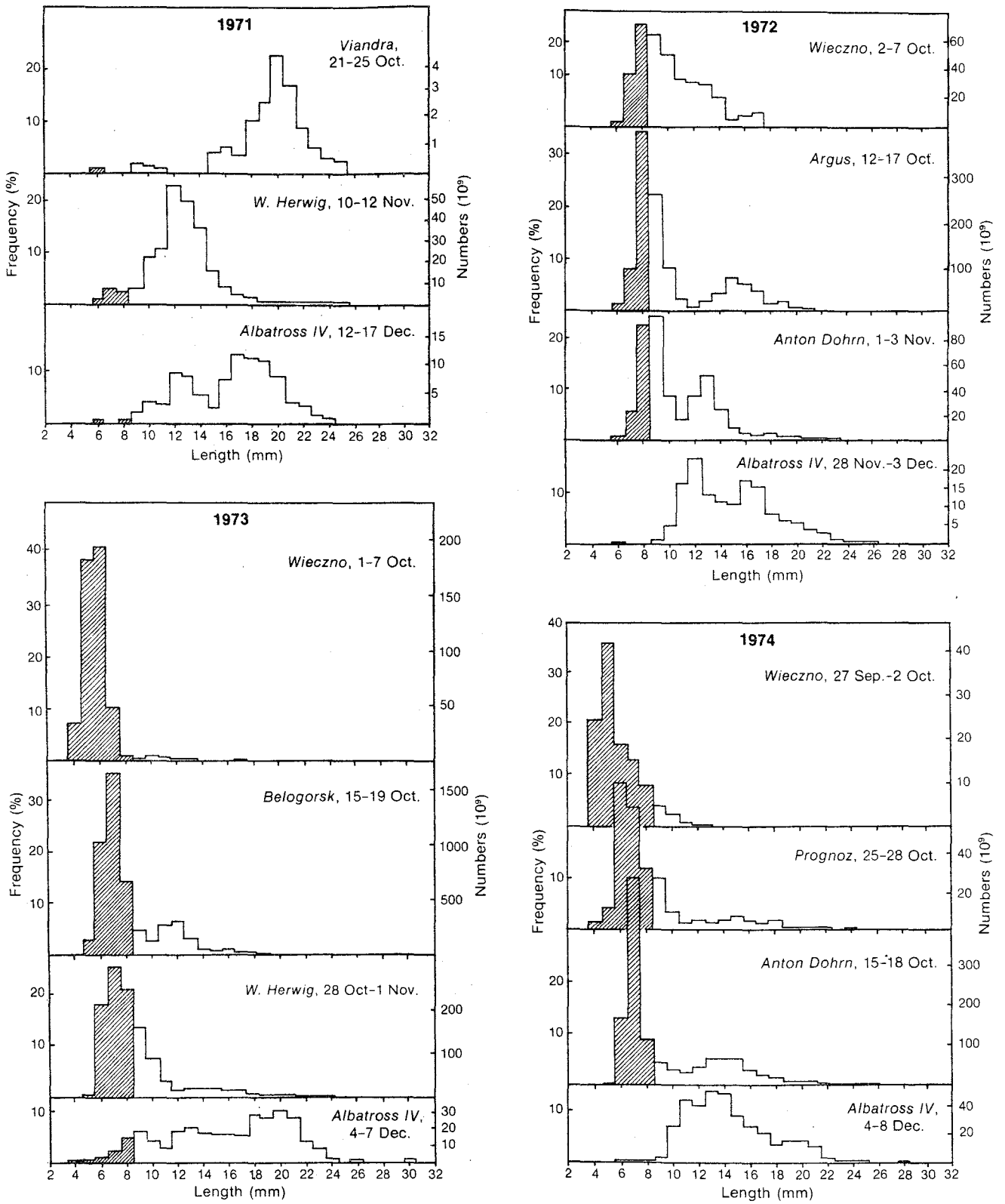
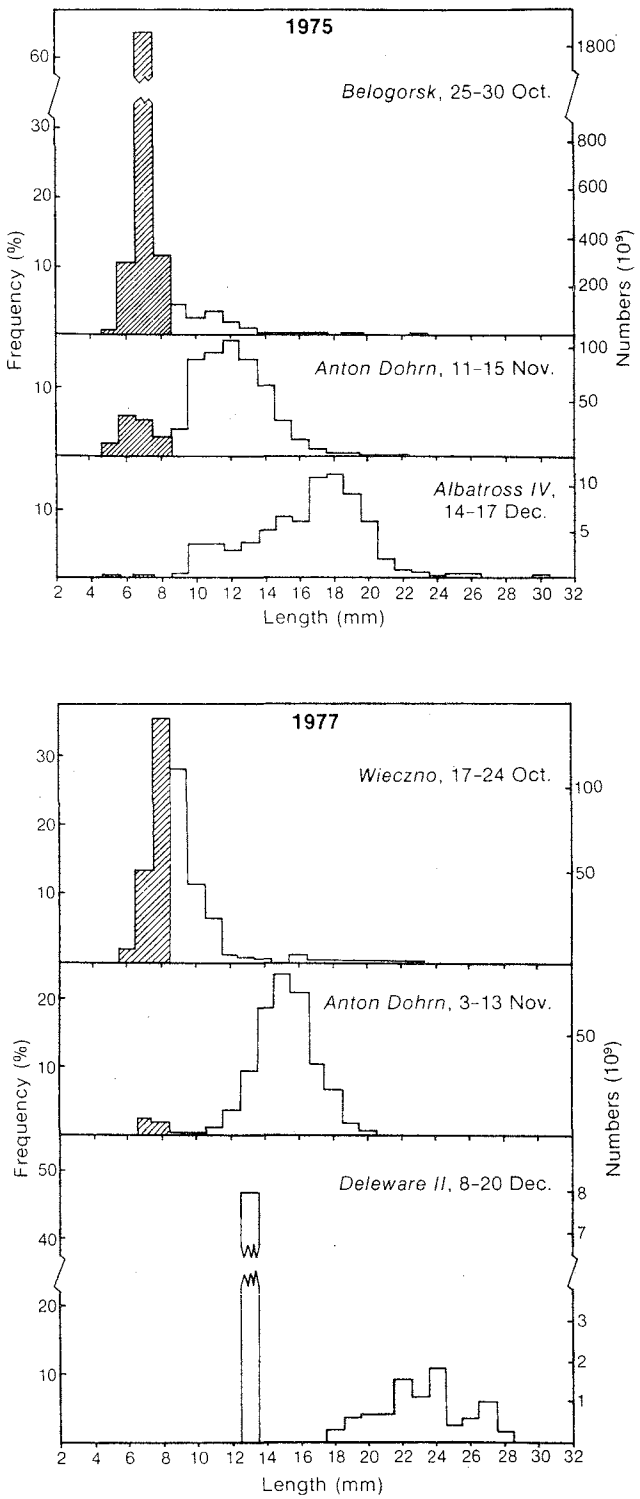


Fig. 11. (continued on next page.)



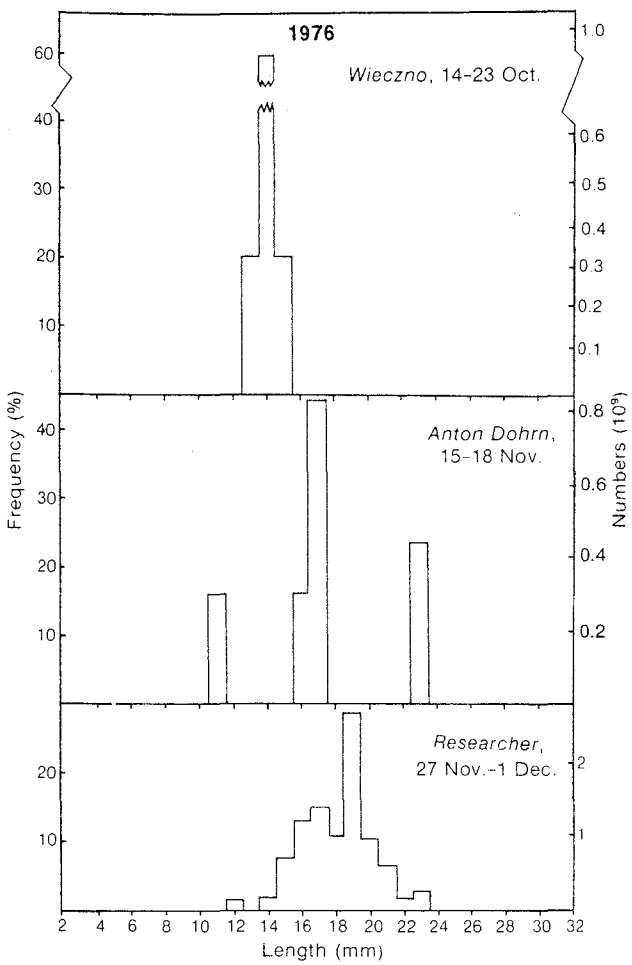
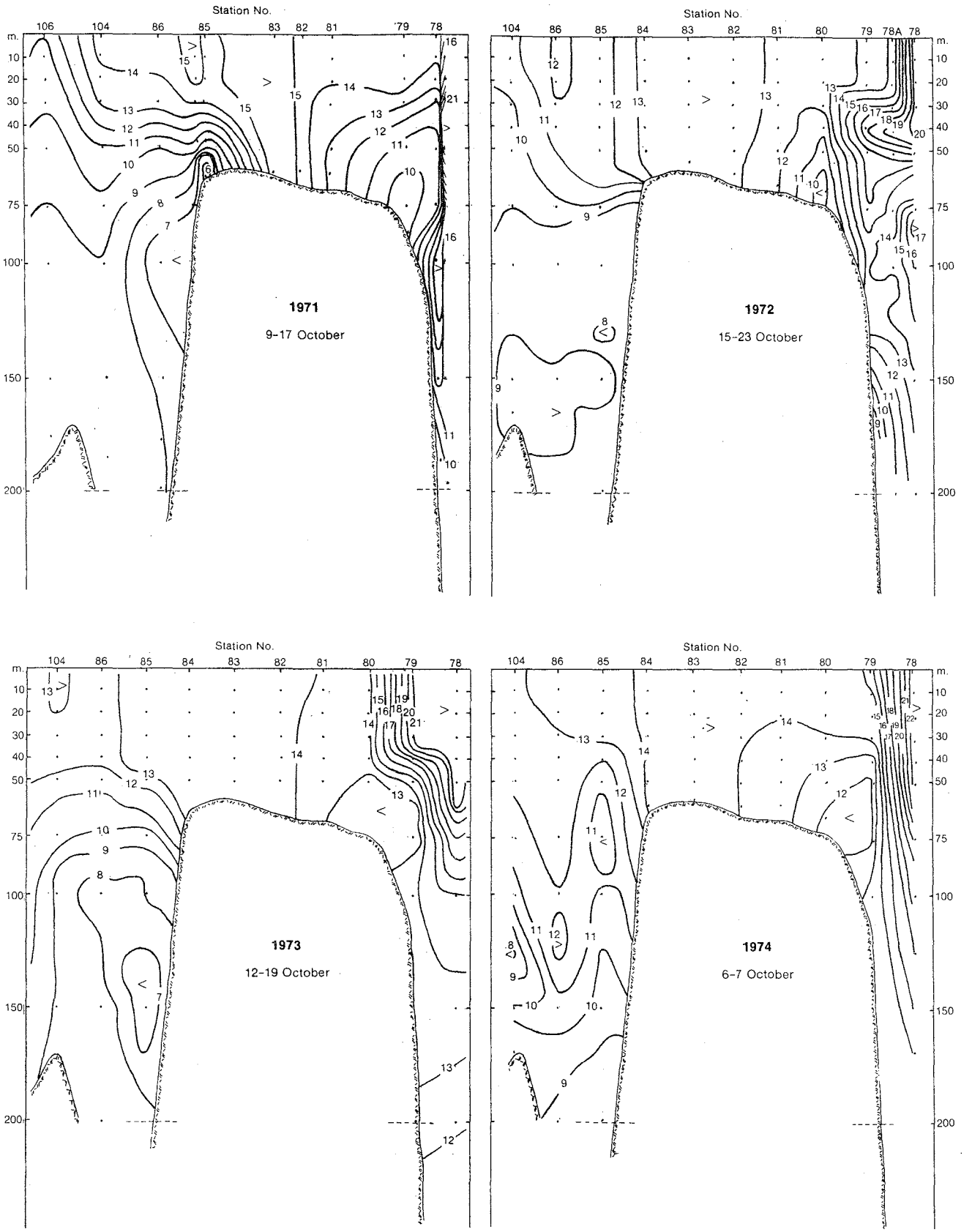


Fig. 11. Length distributions of herring larvae from sampling on Nantucket Shoals in 1971–77.

bottom temperatures observed in that area (see Table 1). Although herring spawning may occur over a wide range of temperature, Laevastu and Hela (1970), in their summary of many investigations, indicated that spring spawning occurred at a mean temperature of 7.4°C and autumn spawning at 10.7°C. This latter value is only slightly higher than 9.5°C observed by Cooper *et al.* (MS 1975) for egg beds on Jeffreys Ledge in 1974 and the range of 9.5° to 10°C noted by McCarthy *et al.* (MS 1979) for Jeffreys Ledge spawning over 6 years.

The egg and larval stages are undoubtedly the most critical periods in the life history of fish, due to the



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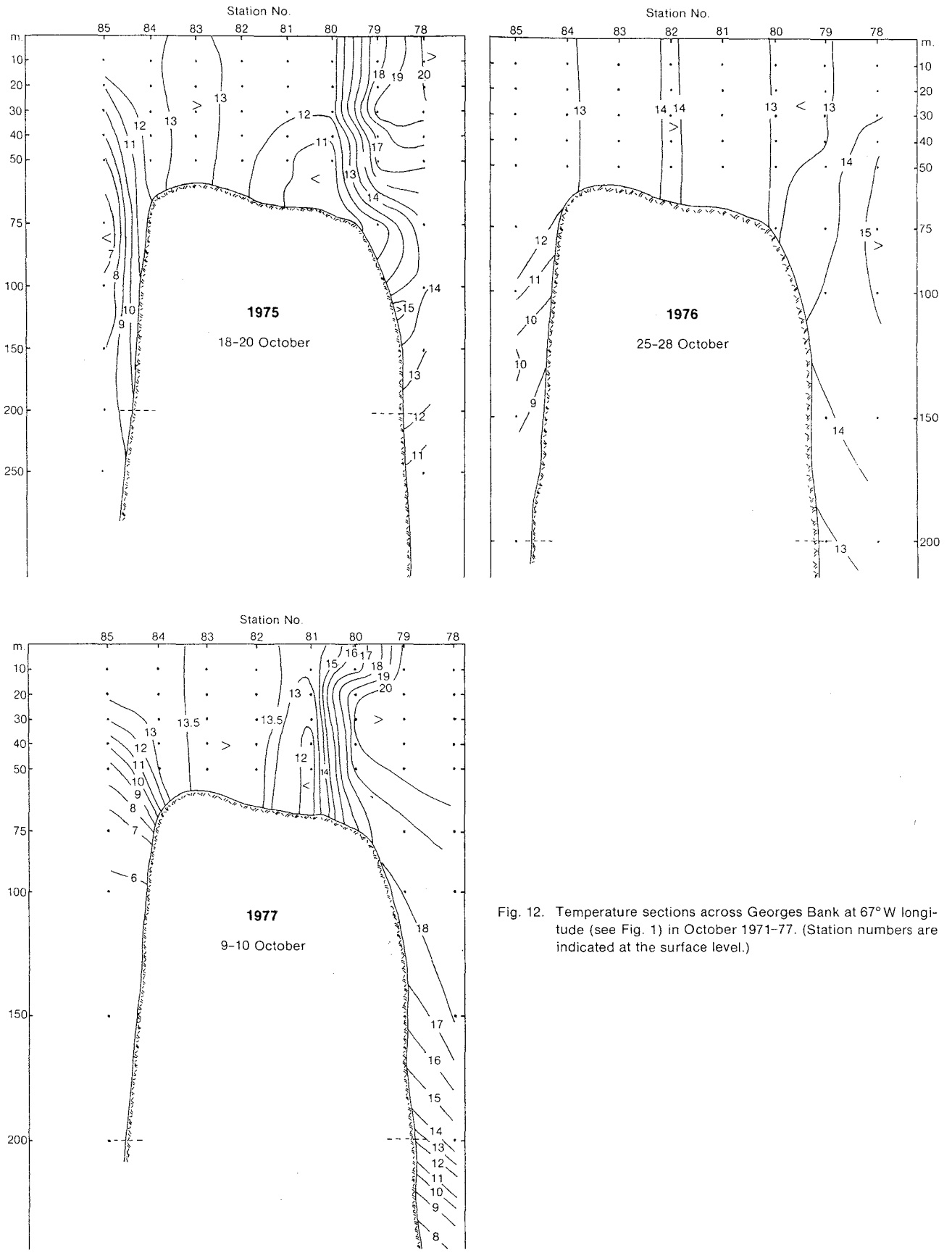

Fig. 12. Temperature sections across Georges Bank at 67° W longitude (see Fig. 1) in October 1971–77. (Station numbers are indicated at the surface level.)

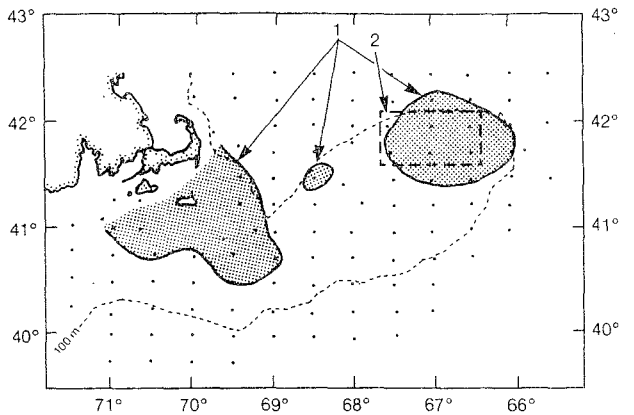

Fig. 13. Estimated boundaries of the spawning grounds on Georges Bank and Nantucket Shoals, derived from the occurrence of dense concentrations (>10 larvae/10 m^2) of newly-hatched larvae (≤8 mm SL) in 1971–77. (The rectangle represents the area most suitable for spawning on Georges Bank on the basis of geology and oceanography, according to Drapeau (1973).)

very great influence, both direct and indirect, of abiotic conditions. Alderdice and Velsen (1971), from experiments on the effect of temperature on survival rate of Pacific herring larvae, *Clupea pallasi*, found high mortality at 13.3°C and substantial numbers of deformed and dead larvae at 14° C within 4 days after hatching. In the present time series of data for Georges Bank, very high temperatures (>16° C) were recorded at the beginning of the spawning seasons in 1971–74, maximum values being 17.1° C in 1971 and 19.1° C in 1974. These high temperatures may have affected egg development and larval survival. It is interesting to note that the lowest larval mortality, reported by Lough *et al.* (MS 1980), occurred in 1975, the coldest season of the time series.

The experiments of Blaxter (1956) on hatching success at different incubation temperatures for autumn-spring herring tend to confirm the suggestion of Postuma (1971) that the relation between year-class strength and spawning temperature is a dome-shaped curve ranging from 5.5° to 14.5° C, with optimum conditions around 12° C. Postuma (1971) also found a significant relationship between year-class strength of autumn-spawning North Sea herring and temperature conditions on the spawning grounds which he believed may operate through differential egg mortality at different temperatures. According to Pankratov and Sigajev (1973), eggs spawned on the eastern grounds of Georges Bank were developing in homothermal environments at 13° to 14° C, whereas bottom temperatures on a spawning bed a few kilometers farther westward were 11° to 12° C.

From the pattern of catches on Georges Bank during the 1960's, Anthony and Waring (MS 1980) noted that the good year-classes of the early 1960's were derived from spawning on the northeast peak of the bank, whereas the 1970 year-class was derived from spawning on western parts of the bank, and they suggested that these areas traditionally may have had different spawning times. Their analysis indicated that Georges Bank herring exhibited faster growth, earlier maturity and higher fecundity in the 1970's than in the 1960's, and they attributed these changes to a delcine in stock size in the 1970's.

Another factor is the posible disruptive effects of a fishery on the spawning aggregations. The act of fishing on the spawning concentrations may directly reduce the effectiveness of spawning in a manner not reflected by the catch rates (Anthony and Waring, MS 1980). This would pertain especially to the period when bottom-trawling gear was widely used in the Georges Bank fishery, whereas the Nantucket Shoals spawning grounds were partially protected because of closer proximity to the coast and the much shallower distribution of some spawning beds.

The relationship between the Georges Bank and Gulf of Maine herring stocks is not entirely clear, because the United States fishery was directed primarily toward juveniles in coastal waters of the Gulf of

TABLE 5. Estimated hatching dates and season length for herring in the Georges Bank-Nantucket Shoals region, 1971–78 (Lough *et al.*, MS 1980), and percentages of small larvae originating in each area, based on abundance estimates of small larvae less than 10 mm SL.

Year	Estimated range of hatching time	Weighted middate	Season length (days)	Percent abundance larvae <10 mm SL	
				Georges Bank	Nantucket Shoals
1971	10 Sep–26 Dec	15 Oct	107	96	4
1972	16 Sep–28 Dec	22 Oct	103	14	86
1973	09 Sep–29 Dec	25 Oct	111	56	44
1974	28 Sep–22 Dec	02 Nov	85	86	14
1975	20 Sep–27 Dec	30 Oct	98	34	66
1976	10 Oct–08 Nov	24 Oct	29	3	97
1977	01 Oct–14 Nov	24 Oct	74	1	99
1978	16 Oct–19 Dec	08 Nov	64	1	99

Maine and the offshore stocks of adult herring were not exploited until the early 1960's. However, there was a great increase in the size of the Georges Bank stock during the early 1960's due to recruitment of two successful year-classes. Although recruitment declined by the mid-1960's, fishing effort continued to increase until 1972 and the stock declined to a very low level. Since then, the fishery was supported by the recruitment of a single successful year-class (1970) which had been fished out on Georges Bank by 1977.

The appearance of only three strong year-classes of herring during nearly two decades of the Georges Bank fishery indicates that conditions in most of these years were unfavorable for spawning, hatching or larval survival, or a combination of these events, because sufficient numbers of eggs and larvae seem to have been produced in the Georges Bank-Nantucket Shoals regions in most years of the 1971-77 period to have resulted in a strong year-class if conditions had been favorable (Lough *et al.*, MS 1980). It is evident that the size of herring year-classes on Georges Bank appears to be determined by environmental factors operating during the first month or two after hatching.

Summary

1. Distribution and abundance of newly-hatched herring larvae (≤8 mm SL) from 31 research vessel surveys of the Georges Bank-Nantucket Shoals region during the autumn spawning seasons of 1971-77 were used to delineate spawning areas, and bottom temperature data from these surveys were used to describe thermal conditions at spawning and hatching.
2. Spawning occurred on the northern part of Georges Bank from September to November or December in 1971-73, but it did not begin until October in 1974-76. On Nantucket Shoals, spawning usually occurred from October to December, except in 1971 when no concentrations of newly-hatched larvae were observed. After 1975, the onset of spawning was delayed and the spawning season was shorter in both areas. The period of hatching was longest on Georges Bank in 1973 and 1975 and on Nantucket Shoals in 1972-75.
3. The size of the spawning grounds, derived from the occurrence of dense concentrations of newly-hatched larvae in the various seasons, ranged from 4,500 km^2 in 1972 to about 10,000 km^2 in 1974 on Georges Bank and was about 3,500 km^2 on Nantucket Shoals. However, the lack of sampling in shallow areas (<25 m) on Nantucket Shoals may have resulted in underestimation of larval abundance and distribution in that area. The spawning grounds were located at depths of 58-82 m on Georges Bank and 30-75 m on Nantucket Shoals.
4. The dispersal of newly-hatched larvae, as shown by distribution of concentrations lower than 10 larvae per 10 m^2, was generally southwestward on Georges Bank, coinciding with a current pattern which favors the retention of larvae on the bank. However, there is some evidence from the 1971-77 data which indicate a loss of larvae, particularly toward the Gulf of Maine and the Northeast Channel. On Nantucket Shoals, the larvae tended to drift southwestward toward shallow coastal waters.
5. A general increase in water temperature of 2° to 3°C has been observed in the Georges Bank-Gulf of Maine region from the late 1960's to 1977. This was particularly evident on the herring spawning grounds of northeastern Georges Bank after 1970, with mean bottom temperatures of 12° to 15°C during the first month of spawning in 1971-74, 1976 and 1977. The large volume of warm water over the spawning beds on Georges Bank in these years may have affected spawning and/or hatching success.
6. On the Nantucket Shoals spawning grounds, mean bottom temperatures (6° to 13°C) were lower than those on Georges Bank, particularly in 1976 and 1977, when newly-hatched larvae were prevalent on Nantucket Shoals but not on Georges Bank. The lack of spawning on Nantucket Shoals in 1971 may be attributed to unusually low temperatures observed on the spawning grounds from September to December of that year.

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