Atlantic mackerel, *Scomber scombrus*, total annual egg production and spawner biomass estimates for the Gulf of St. Lawrence and northeastern United States waters, 1987.

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ABSTRACT

Total egg production estimates for Atlantic mackerel, Scomber scombrus, were calculated from a series of ichthyoplankton surveys off the northeastern United States and in Gulf of St. Lawrence waters in 1987 and used to derive spawner biomass estimates for the two areas. Six surveys were conducted in U.S. waters between April and July and two in the Gulf of St. Lawrence during June and July. In U.S. waters spawning began in mid-April, peaked in mid-May and had virtually ceased by mid-July. In Canadian waters spawning occurred later and peaked in mid-June. Total egg production in U.S. waters was 55.5 $x10^{12}$ and in the Gulf of St. Lawrence was 484.2 $x10^{12}$. Converting these numbers to spawner biomass produced estimates of 110,573 and 940,957 metric tons for U.S. and Canadian waters respectively.

INTRODUCTION

A cooperative project was undertaken in 1987 by the Northeast Fisheries Center (NMFS, United States), Fisheries and Oceans (Canada) and Morski Instytut Rybacki (Poland), to estimate the absolute abundance of Atlantic mackerel in the western North Atlantic Ocean between Cape Hatteras and the Gulf of St. Lawrence. This was part of a broader based initiative designed to gather information on several aspects of mackerel biology and the fishery.

While the annual population size of Atlantic mackerel has been estimated over the past two decades by virtual population analysis (Cons. and Util. Div., 1987), the relative magnitude of spawning contingents in U.S. vs. Canadian waters has not been determined. There has been some question as to what proportion of the whole population actually spawns in the two general areas. The only previous information directly bearing on this issue is that of Sette (1943, 1950), who concluded that during the early part of this century approximately 10 times as many Atlantic mackerel eggs were spawned south of Cape Cod as in the Gulf of St. Lawrence. However, Sette's (1943) conclusions were based on disparate sampling between the two areas; i.e., he assessed mackerel egg densities in U.S. waters between Cape Cod and Cape Hatteras during 1932 and compared his results with densities, reported by Dannevig (1919), which were observed during 1915 in the Gulf of St. Lawrence. There have been no studies since to confirm or refute Sette's conclusions. Furthermore, no one has heretofore sampled and analysed planktonic mackerel eggs for both areas simultaneously.

This paper addresses the objectives of determining total egg production and spawner biomass of Atlantic mackerel in the western North Atlantic. The results are based on sampling conducted in the spring and summer of 1987 in both the Gulf of St. Lawrence and off northeastern United States.

METHODS

Six surveys were conducted in shelf waters off the U.S. East Coast, from Oregon Inlet, NC north to the Gulf of Maine and Georges Bank, and two in Canadian waters in the southern Gulf of St. Lawrence. Surveys in the two general areas (U.S. and Canada) did not repeat identical area coverage on successive cruises. Those in U.S. waters, based on a decadal series of ichthyoplankton surveys (Morse et al. 1987), shifted with the known northeastward progression of spawning (Figures 1 and 2). Those in the Gulf of St. Lawrence, while centered on the same area, differed in that the second survey covered less area than the first (Figure 3). The areal coverage on individual surveys ranged from 99,555 to 144,309 km^2 in U.S. waters, and 46,278 to 85,081 km^2 in Canadian waters (Table 1). The surveys included varying numbers of stations, depending on areal coverage, and ranged from 86 to 106 in U.S., and from 38 to 93 in Canadian waters.

Plankton sampling procedures followed those described by Sibunka and Silverman (1984) except that 20-cm bongos were substituted for 61-cm bongos routinely used on broadscale ichthyoplankton surveys conducted by the Northeast Fisheries Center. The change was implemented to reduce plankton volumes and expedite sample processing time. The 20-cm bongos were fitted with 0.505 and 0.333-mm mesh nets (Posgay and Marak 1980) and weighted with a 45-kg lead ball. The 0.505-mm side was used for Atlantic mackerel egg collections. A flowmeter suspended in the net mouth monitored water volume filtered. In U.S. waters a bathykymograph recorded tow profile and maximum depth sampled. Plankton tows in U.S. waters were smooth, double-oblique tows, made by adjusting vessel speed to maintain a 45° wire angle throughout the haul. Sampling was to within 5 m of the bottom or to a maximum depth of 200 m. Vessel speed was usually around 2.8 km/hr (1.5 kt). See Sibunka and Silverman (1984) for a detailed description of plankton sampling procedures.

In Canadian waters the tow procedures differed in that the ship speed was 2.5 kt, the sampler was weighted with a 100-kg depressor, maximum tow depth was 50 m and tow duration was 10 min or greater. This requirement on tow duration usually necessitated making multiple double-oblique tows.

Plankton samples were hardened and preserved in a 5% formalin solution in seawater. All fish eggs were removed from the 0.505-mm mesh samples and the eggs of Atlantic mackerel were identified and further separated into developmental stages. Two stages were used: from just spawned to just before blastopore closure, and from blastopore closure to just before hatching. All catches were adjusted to become the number of eggs sampled per $10m^2$ of sea surface area using the standardization procedure of Smith and Richardson (1977).

Incubation rates of Atlantic mackerel eggs were calculated from Worley's (1933) data. Stage endpoints, in hours from spawning, stated in his text or derived from his Figure 5, were regressed on temperature (X) in °C, and their relationships described by the following:

$$\text{age at hatching} = 17079.0938X^{-1.9063} \qquad (1)$$

$$\text{age at blastopore closure} = 6375.7270X^{-1.9450} \qquad (2)$$

with correlation coefficients of 0.999 and 0.993 respectively. The incubation temperature associated with planktonic eggs at each station in U.S. waters was determined as the mean of water temperatures, from the surface to 15 m, weighted by appropriate depth intervals. For Canadian samples, mean incubation temperatures were based on observations within the surface to 10-m layer.

Mean egg densities and their standard error terms were used to estimate total egg production for each survey. Frequency distributions of spawned egg densities were highly skewed, but ln-transformation of non-zero densities produced relatively normal distributions as compared with distributions of non-transformed densities (Figure 4). The degree of normality so obtained was assessed with the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). Four of the five surveys tested were found to represent normal distributions while only the fifth (survey #7) was rejected by this test as normal, P(Dmax < .01). A data set with a proportion of zero values and which has a ln-normal distribution of non-zero values conforms to the Δ-distribution (Aitchison 1955). Estimates for the mean of a Δ-distribution were calculated by following procedures of Pennington (1983).

Given the survey mean densities (no. eggs per $10m^2$) for each of the two stages and the corresponding developmental stage endpoints from equations 1 and 2, mortality rates were calculated where possible. The following mortality rate function (from Ricker 1975) was used:

$$X_t = X_s e^{-Zt} \tag{3}$$

where X_t = number of eggs at age t (days),
X_s = number of eggs at age 0, just spawned, and
Z = instantaneous daily mortality rate.

Given the function described by equation 3 and the relationships illustrated by the survival curve in Figure 5, equations 4 to 7 were derived.

Given that: $$A_{ij} = \int_{t_i}^{t_j} X e^{-Zt} dt = -(X_s \div Z) e^{-Zt} \Big|_{t_i}^{t_j} = (X_s \div Z)(e^{-Zt_i} - e^{-Zt_j}) \tag{4}$$

then $$A_1 = (X_s \div Z)(e^{-Zt_0} - e^{-Zt_1}) \tag{5}$$

and $$A_2 = (X_s \div Z)(e^{-Zt_2} - e^{-Zt_3}) \tag{6}$$

it follows that $$A_2 \div A_1 = (e^{-Zt_2} - e^{-Zt_3}) \div (e^{-Zt_0} - e^{-Zt_1}) \tag{7}$$

Equation 7 cannot be solved analytically for Z; it was solved numerically (iteratively).

If calculation of a reasonable Z value was not possible because of sparse egg occurrence and low egg densities with a resulting lack of one of the two stages or the presence of proportionately too many late-stage eggs, substitute values of Z were derived from the next closest survey in time. From equation 3 and estimates of Z, total incubation time (H) and egg density on station (X_c), the density of eggs spawned daily (X_s) at each station is obtained by:

$$X_s = (X_c Z) \div (1 - e^{-ZH}) \tag{8}$$

Similarly, daily hatching density (X_H) was calculated for each station:

$$X_H = (X_c Z) \div (e^{-ZH} - 1) \tag{9}$$

Individual station values of spawning (X_S) and hatching (X_H) densities were calculated using equations 8 and 9 respectively and summarized by survey. Mean spawning and hatching densities and variance (mean) values were calculated for each survey using procedures applicable to the Δ-distribution (Pennington 1983).

The median age of eggs caught (m) was calculated for each station using the following equation which was derived from equation 3 and Figure 5, where $A_1 = A_2$:

$$m = \left[\ln 2 - \ln\left(e^{-ZH} + 1\right)\right] \div Z \qquad (10)$$

The median age (m), when weighted by each station's estimate of egg spawning density, was used to adjust each survey's observed midpoint of egg occurrence (JD_C) to become the point in time associated with the estimated spawning density. Likewise the weighted value of H-m, the time from the median age until hatching, was used to adjust each survey's observed midpoint of egg occurrence (JD_C) to become the point in time associated with the estimated hatching density. Thus for each survey:

$$JD_S = JD_C - \text{weighted } m \qquad (11)$$

$$JD_H = JD_C + \text{weighted}\left(H - m\right) \qquad (12)$$

where JD_S = Julian date of spawning,
JD_H = Julian date of hatching,
JD_C = Julian date midpoint of catches,
m = median age, and
H = total incubation time, until hatching.

The number of days represented by a given survey was calculated as the time interval between halfway points preceeding and following the Julian date midpoint (JD_S or JD_H) of the survey in question.

Mean densities of eggs spawned per $10m^2$ per day (K_S) for each survey were expanded by the area surveyed to yield the daily rate of egg production applicable to each survey. These daily rates were then multiplied by the number of days represented by each survey and the products summed over all surveys to derive the annual egg production estimates (N_S) for U.S. and Gulf of St. Lawrence waters separately. The same procedure was followed in expansion of hatching densities (K_H) to derive annual estimates of eggs hatching (N_H) for the two areas, U.S. and Canada. It was necessary to determine starting and ending dates of spawning and put definite endpoints on egg production thereby enclosing the area under the production curves estimated. For Canadian waters the beginning of spawning was set at June 8 and the end at Aug 15 (Ware and Lambert 1985). For U.S. waters the respective dates were set at Apr 11 (Sette 1950) and Aug 6 (Berrien et al. 1981).

Standard error terms associated with the expanded means (K_S and K_H) were proportionately expanded, weighted by appropriate factors of area and days represented, then summed to derive annual estimates of standard error:

$$se(N) = \sqrt{\Sigma\left[\omega_{ij}^{2}\, var(K_{ij})\right]} \qquad (13)$$

where; se(N) = std error associated with estimates of total eggs spawned or hatched,

W_{ij} = weighting factor, (days represented x area), for the ith survey in area j,

var(K_{ij}) = variance of mean associated with ith survey in area j.

To convert eggs spawned to spawner biomass the following procedures were followed. The fecundity for a mean-length female was calculated through the fecundity-at-length functions provided by Silverman and Griswold (1988 ms). The female and male mean weights were summed and related to the fecundity at mean length noted above to derive a mean egg production per unit weight of spawners (with a 1:1 sex ratio). Total egg production, derived from the plankton surveys, was divided by the number of eggs per unit weight of spawners to obtain estimates of spawner biomass for U.S. and Canadian waters.

Adult mackerel, sampled in spring off the U.S. East Coast from the recreational fishery and by Polish ships R/V Admiral Arciszewski and R/V Kublin and in summer from the Nova Scotia trap net and gill net fisheries by Fisheries and Oceans (Canada), provided measures of mean fish length and mean weight in the total population as well as samples for fecundity determination in the two areas.

Estimates of potential annual fecundity by size (Silverman and Griswold 1988 ms.) used in this study were, for U.S. waters:

$$\ln F = 8.915669 + 0.011845\ FL \qquad (14)$$

where $n = 169$, $r = 0.86$

and for Canada;

$$\ln F = 9.583724 + 0.010064\ FL \qquad (15)$$

where $n = 125$, $r = 0.66$

and, for both areas, F = total annual fecundity and FL = fork length (mm).

RESULTS

Atlantic mackerel eggs were collected in U.S. waters on all six surveys and occurred between April 16 and July 9. Eggs were first observed in the inshore half of shelf waters off Delaware Bay and off southern New Jersey (Figure 1, Survey 1). Thereafter, spawning spread northward and eastward, increasing to maximum intensity in mid-May (Survey 2) with the largest catches taken in the area from off eastern Long Island to Martha's Vineyard. During the third and fourth surveys in late May and into June (Figures 1 and 2), spawning diminished in intensity, was dispersed over a greater area and shifted northward to shelf waters between the New York Bight and western Gulf of Maine. The highest egg densities at that time occurred from Block Island, RI, to Nantucket Island and off Cape Ann, MA. During late June and into July (Figure 2, Survey 5) spawning diminished further and, by the time of the last survey, had virtually ceased within the area surveyed.

The Gulf of St. Lawrence was surveyed twice (Figure 3). During both surveys Atlantic mackerel eggs were found at virtually all stations, with the highest densities found on the first of the two surveys. At the observed peak of spawning, average egg densities were 27 times greater in Canadian waters than in U.S. waters (Table 1).

Instantaneous daily mortality rates (Z) of Atlantic mackerel eggs are presented in Table 1. On three surveys (#1, 4 and 8) the values given are those derived for adjacent surveys in time; these substitute values are differentiated from others by parentheses. During survey #1 there were no later-stage eggs sampled, therefore Z could not be calculated. During surveys #4 and #8 there were proportionately too many later-stage eggs for the calculation of a reasonable Z value. Since both these surveys occurred after the observed peak in spawning, a general decline in the rate of spawning coupled with an undetermined variation of spawning intensity between days could have led to proportionately too many later-stage eggs. Estimated mortality rates ranged from 0.2469 to 1.0155, which represent daily mortality rates of 21.9% to 63.8%.

Egg production curves for U.S. and Canada (Figure 6) and integrated totals (Tables 1 and 2) show the difference in both spawning times and total production in the two areas. Egg production for U.S. waters was 55.5104 $x10^{12}$ and for the Gulf of St. Lawrence was 484.1883 $x10^{12}$, an almost 9-fold difference between the two areas. Eggs reaching hatching, 1.4084 $x10^{12}$ and 100.1924 $x10^{12}$ in U.S. and Canadian waters respectively, represented 2.5% and 20.7% of the eggs spawned in the two areas. These figures represent a 71-fold difference in numbers of eggs reaching hatching in Canadian waters as compared to U.S. waters.

Population estimates for spawner biomass were calculated as described above. Based on means of 348 mm and 344 mm FL and 461.6 gm and 453.7 gm total weight for females and males respectively in U.S. waters, combined with a 1:1 sex ratio and the fecundity function at length, a value of 502,023,705 eggs per MT of spawners was calculated. Dividing this number into total eggs spawned in U.S. waters yielded an estimate of 110,573 MT of spawners in U.S. waters. Similarly, mean sizes of fish from Canadian waters, 348 mm and 342 mm FL and 478.8 gm and 458.3 gm total weight for females and males respectively, in conjunction with a 1:1 sex ratio and the fecundity function at length,provided a value of 514,569,794 eggs per MT of spawners. This was divided into the total number of eggs spawned to yield an estimate of 940,957 MT of spawners in Canadian waters, which is approximately 8.5 times the biomass estimated as spawning in U.S. waters.

DISCUSSION

For a series of ichthyoplankton surveys to provide a good estimate of a species' annual egg production according to the method outlined above, the entire spawning season should be sampled and the entire spawning area should be sampled frequently enough to determine the egg production rate over time. For U.S. waters it can be seen that we met the criteria with the possible exception of a lack of coverage on survey 4 in the Gulf of Maine where an additional 20,600 km^2 might have been included in the survey area to assure full coverage of spawning near Cape Ann. This added area would expand the survey-4 estimate of egg production by 14%, add an additional 2.25% to the season total, and result in an egg production estimate of 56.766 $x10^{12}$. Additionally, an unknown amount of spawning may have occurred in some inshore bays and sounds.

For Canadian waters, the criteria were less clearly satisfied. Only two surveys were made, both after the onset of spawning, and neither of which included the entire spawning area, as evidenced by a lack of zero-egg catches. Surveys were lacking near the beginning and end of spawning, thus making determination of the area beneath the production curve dependant on, and sensitive to, the placement of the starting and ending dates of spawning, both of which were determined from the literature. Despite these apparent shortcomings, the resulting estimate (484.2 $x10^{12}$ eggs spawned) is in the same order of magnitude as estimates from recent years. For the period 1983 to 1986, annual egg production estimates for the Gulf of St. Lawrence of 152.3 $x10^{12}$ to 1,078.1 $x10^{12}$ have been reported (Table 8 in Ouellet,1987). Had the estimated spawning rate for the second Canadian survey been applied to the entire Canadian survey area of 85,081 km^2, rather than to 46,278 km^2 actually sampled, the total season's estimate would be increased by 30.7% to 632.8 $x10^{12}$ eggs.

It is apparent that spawner biomass and egg production have fluctuated over the years. In 1932, Sette (1943) reported that 64 $x10^{12}$ eggs were produced in U.S. waters by a spawning population of 320 $x10^6$ fish. Berrien et.al. (1981) estimated that 303.2 $x10^{12}$ eggs were produced by 1,224.7 $x10^6$ spawners in 1977. Thus the 55.2 $x10^{12}$ mackerel eggs spawned in U.S. waters in 1987 was approximately equal to the spawning intensity of 1932 and only about 20% of that in 1977.

The 1987 effort is noteworthy in that it is the first time that Atlantic mackerel eggs in both U.S. and Canadian waters were surveyed and analysed in the same year. This level of effort allowed for the direct comparisons noted above (i.e., 9 times as many eggs spawned by 8.5 times the spawner biomass in the Gulf of St. Lawrence as in U.S. waters for that year). These ratios are contrary to the situation reported by Sette (1943) concerning the Atlantic mackerel population earlier in this century. He concluded that the southern contingent (U.S.) had approximately 10 times as many spawners as the northern contingent (Canada).

Atlantic mackerel in U.S. waters apparently behaved somewhat differently in 1987 than in the other years noted above (1932 and 1977). Based on the distribution of eggs on our April survey the spring spawning migration onto shelf waters began off Delaware Bay, or somewhat farther north of the area off Virginia previously reported as typical (Sette 1950). Also, the New York Bight area did not figure as prominently in spawning as it has in other years (Berrien 1978, Berrien et al. 1981) and southern New England waters were relatively more important.

These results and the earlier work by Sette (1943) support the hypothesis that the southern and northern contingents are separate and independent spawning entities. The relative intensity of spawning between U.S. and Canadian waters has not remained stable over different years and over different population levels. In fact, the ratio of spawner abundance between the two areas (U.S.:Canada) has apparently reversed, from approximately 10:1 earlier this century to 1:8 in 1987. It would be edifying to calculate such ratios for other years.

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Table 1. Summary of Atlantic mackerel egg production in United States and Canadian waters, 1987.

Surv. No.	N	N_f	Area (km^2)	Mortality Rate (=Z)	Mean Egg Density (no./10m^2/day)	s.e. (mean)	Mean Spawning Date (=JD_S)	Days Represented	Eggs Spawned in area/day ($x10^9$)	Eggs Spawned in area/survey ($x10^{12}$)
United States waters										
1	91	3	99,555.	(0.5324)	0.3545	0.2049	104.6375	15.9028	3.529	0.0561
2	100	28	126,012.	0.5324	133.8824	53.0094	131.8055	22.1175	1,687.072	37.3138
3	73	29	111,555.	0.3888	60.9003	18.1974	148.8724	12.1739	679.375	8.2706
4	106	20	144,309.	(0.3888)	49.8545	22.4989	156.1533	12.2267	719.443	8.7964
5	98	10	141,412.	0.2469	2.9873	1.1409	173.3258	16.0649	42.243	0.6786
6	86	2	133,068.	1.0155	1.3509	0.9541	188.2830	21.9621	17.976	0.3948
										U.S. Total = 55.5104
										s.e.(Total) = 15.5011
Gulf of St. Lawrence										
7	93	92	85,081.	0.2540	3618.2425	920.4001	169.2238	9.9708	30,784.470	306.9458
8	38	38	46,278.	(0.2540)	1325.7764	345.7085	178.9415	28.8881	6,135.485	177.2425
										Gulf of St. Lawrence Total = 484.1883
										s.e.(Total) = 90.7336

Table 2. Summary of Atlantic mackerel eggs hatched in United States and Canadian waters, 1987.

Survey No.	N	N_f	Area Surveyed (km^2)	Mean Egg Density (no./10m^2/day)	s.e.(mean)	Mean Hatching Date (=JD_H)	Days Represented	Eggs Hatched in area/day ($x10^9$)	Eggs Hatched in area/survey ($x10^{12}$)
United States waters									
1	91	3	99,555.	0.0005	0.0004	116.8320	15.1761	0.005	0.0001
2	100	28	126,012.	0.7803	0.3618	141.3521	19.2952	9.833	0.1897
3	73	29	111,555.	3.5624	1.1780	155.4223	10.3868	39.740	0.4128
4	106	20	144,309.	3.6801	1.6403	162.1256	11.4095	53.107	0.6059
5	98	10	141,412.	0.8962	0.3485	178.2413	15.6005	12.673	0.1977
6	86	2	133,068.	0.0077	0.0058	193.3266	21.5044	0.102	0.0021
									U.S. Total = 1.4084
									s.e.(Total) = 0.3244
Gulf of St.Lawrence									
7	93	92	85,081.	832.7525	246.7427	175.5478	6.7578	7,085.164	47.8801
8	38	38	46,278.	413.5789	138.9693	184.5525	27.3317	1,913.978	52.3123
									Gulf of St. Lawrence Total = 100.1924
									s.e.(Total) = 22.5886

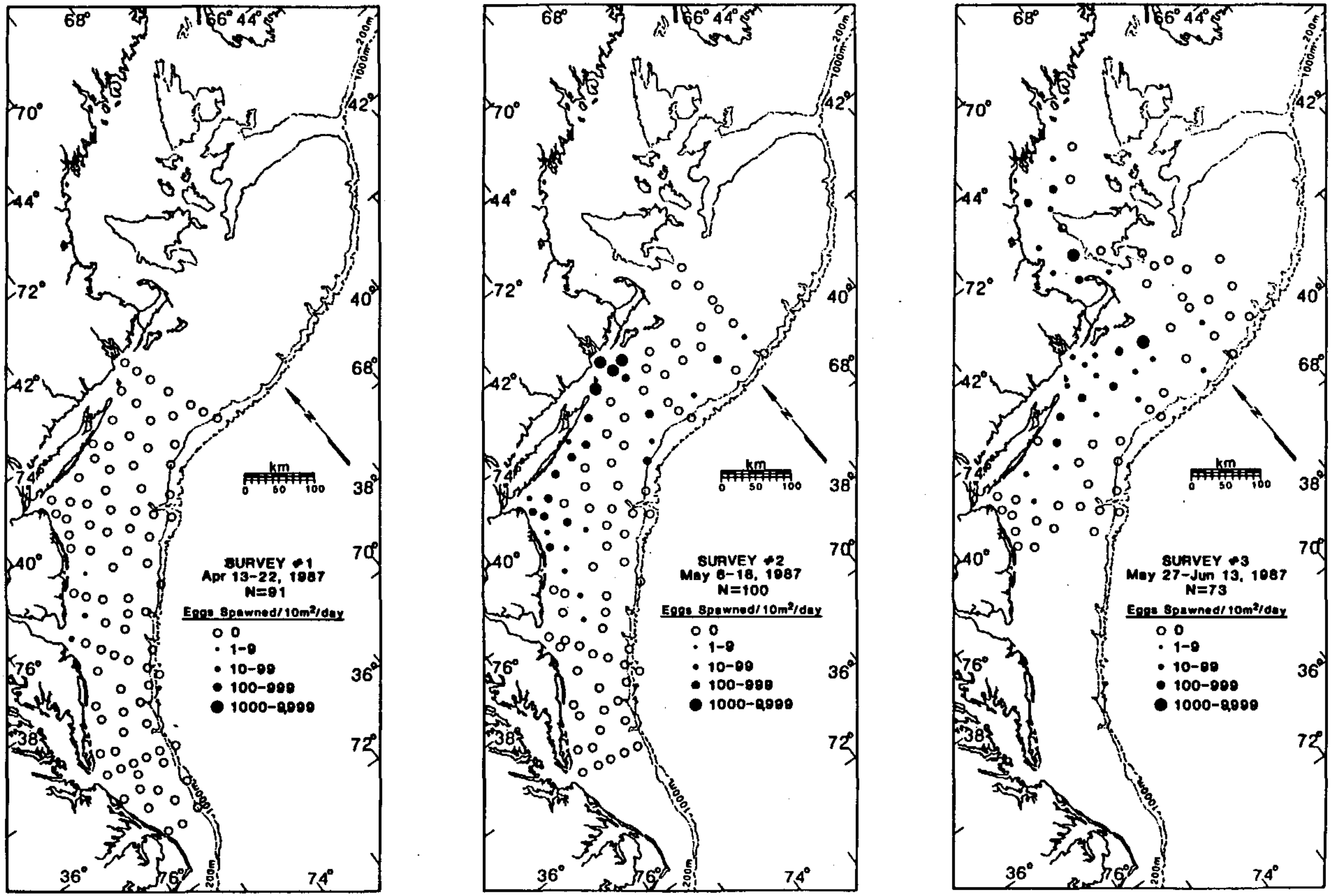


Figure 1. Spawning density of Atlantic mackerel in U.S. waters during surveys 1, 2 and 3, in 1987.

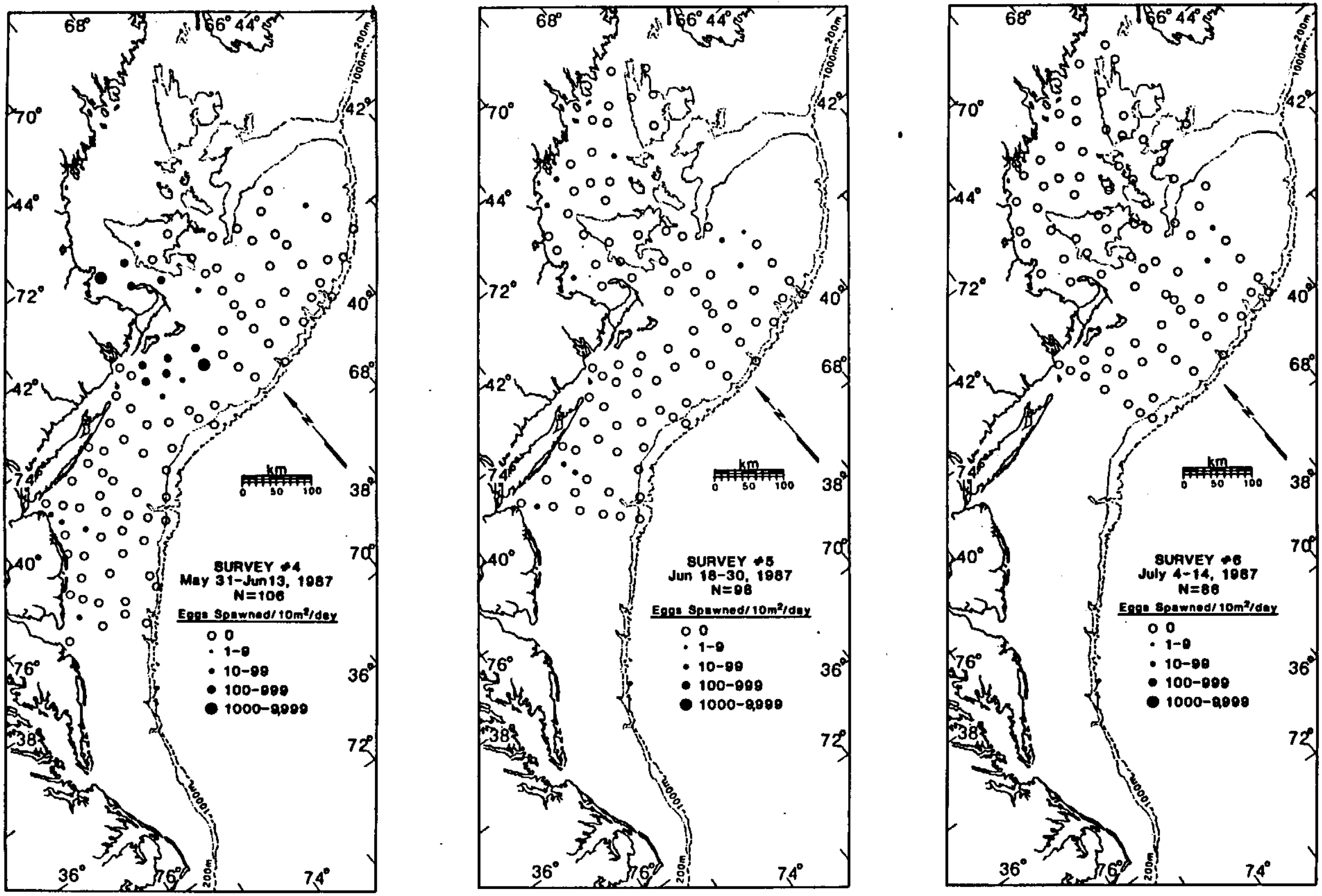
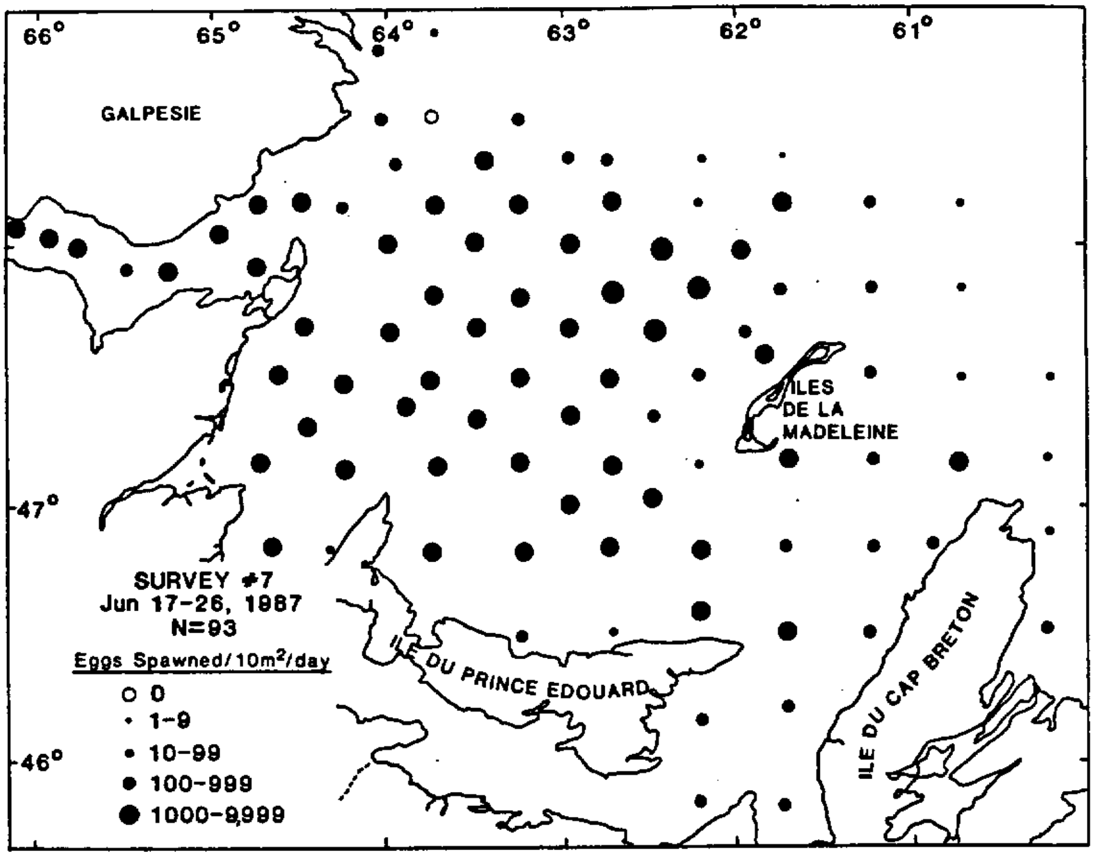


Figure 2. Spawning density of Atlantic mackerel in U.S. waters during surveys 4, 5 and 6, in 1987.



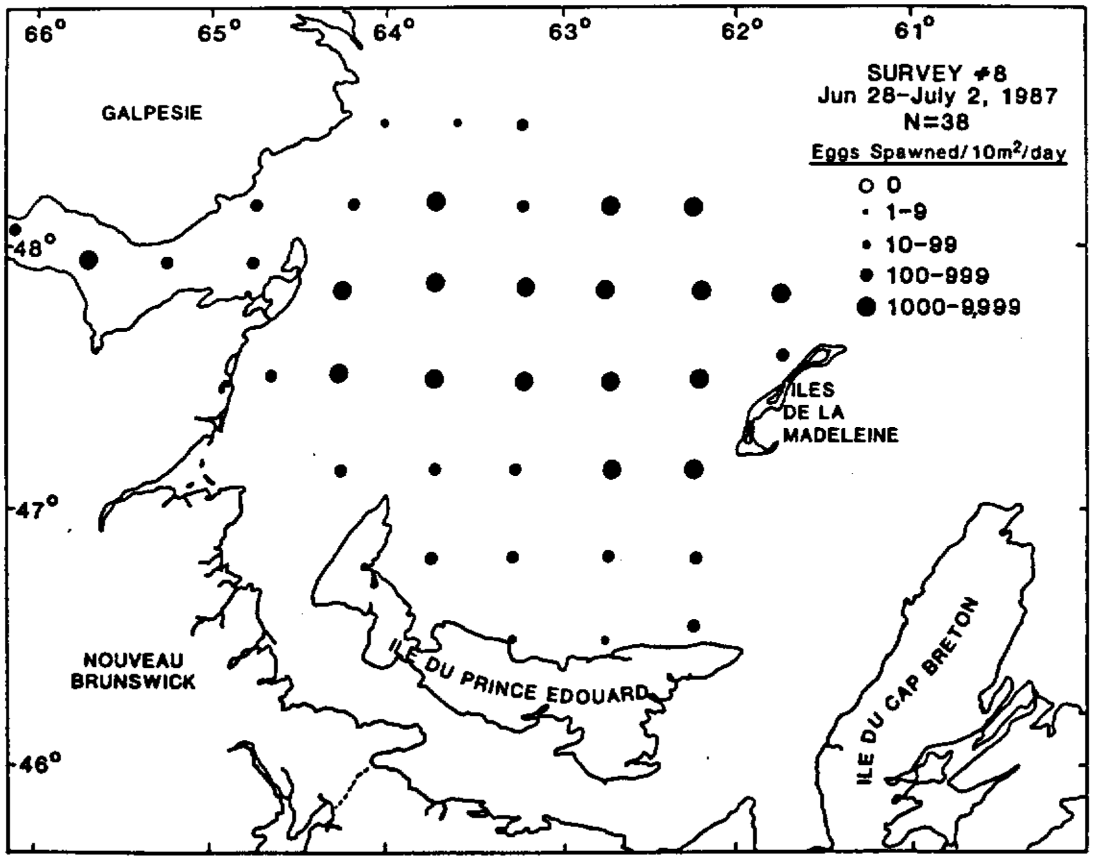


Figure 3. Spawning density of Atlantic mackerel in the Gulf of St. Lawrence during surveys 7 and 8, in 1987.

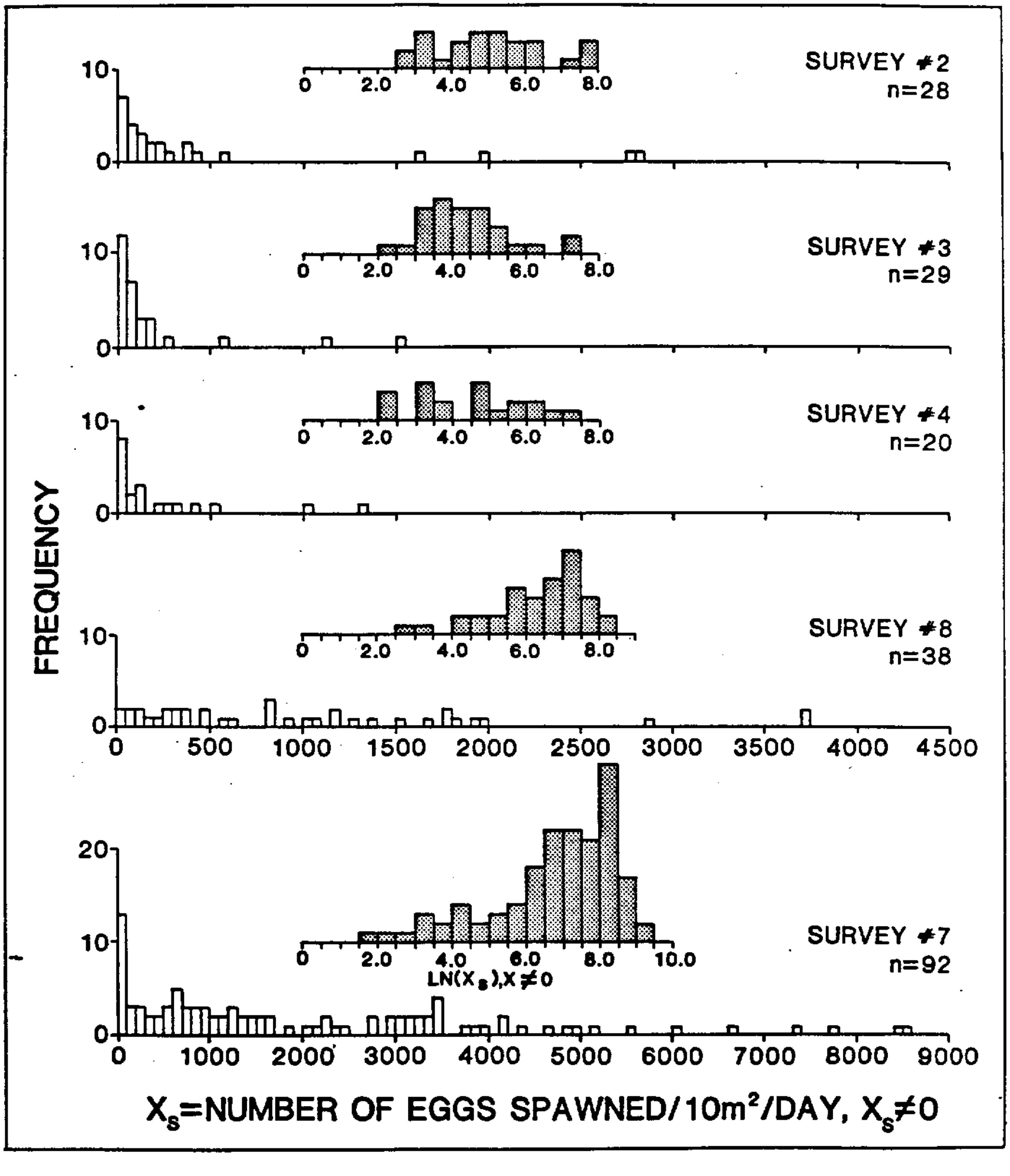


Figure 4. Frequency distributions of non-transformed and ln-transformed values of eggs spawned/$10m^2$/day.

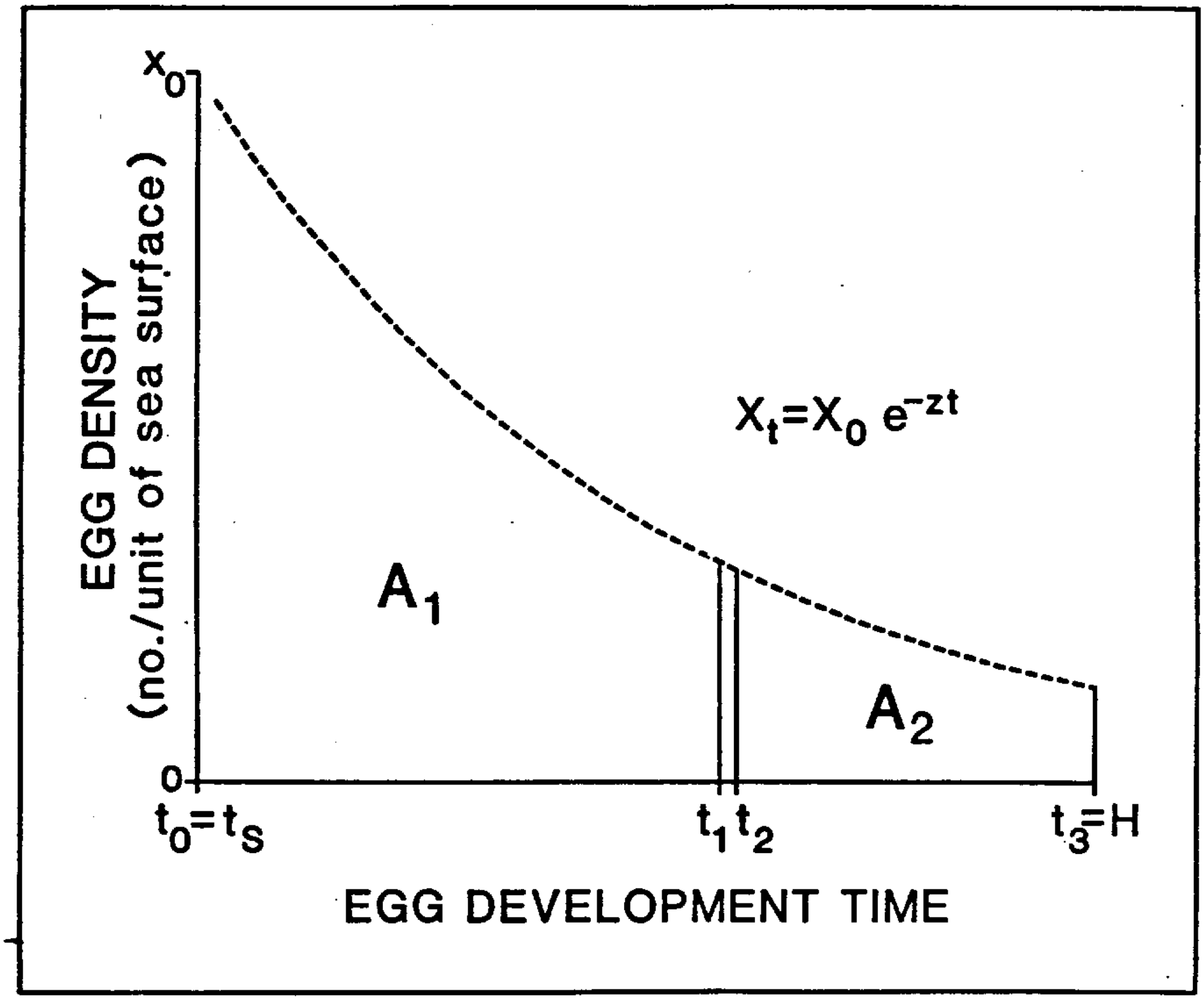


Figure 5. Survival curve. Theoretical change in egg density over time due to mortality. Areas A_1 and A_2 represent observed egg densities which correspond to incubation time intervals (stages) t_o to t_1 and t_2 to t_3 respectively; the dashed line is the calculated value of X at time t as determined by equation 7 and Z; and X_o is egg density at spawning. In this paper t_o = t_s = age 0 (just spawned) and t_3 = H = age at hatching.

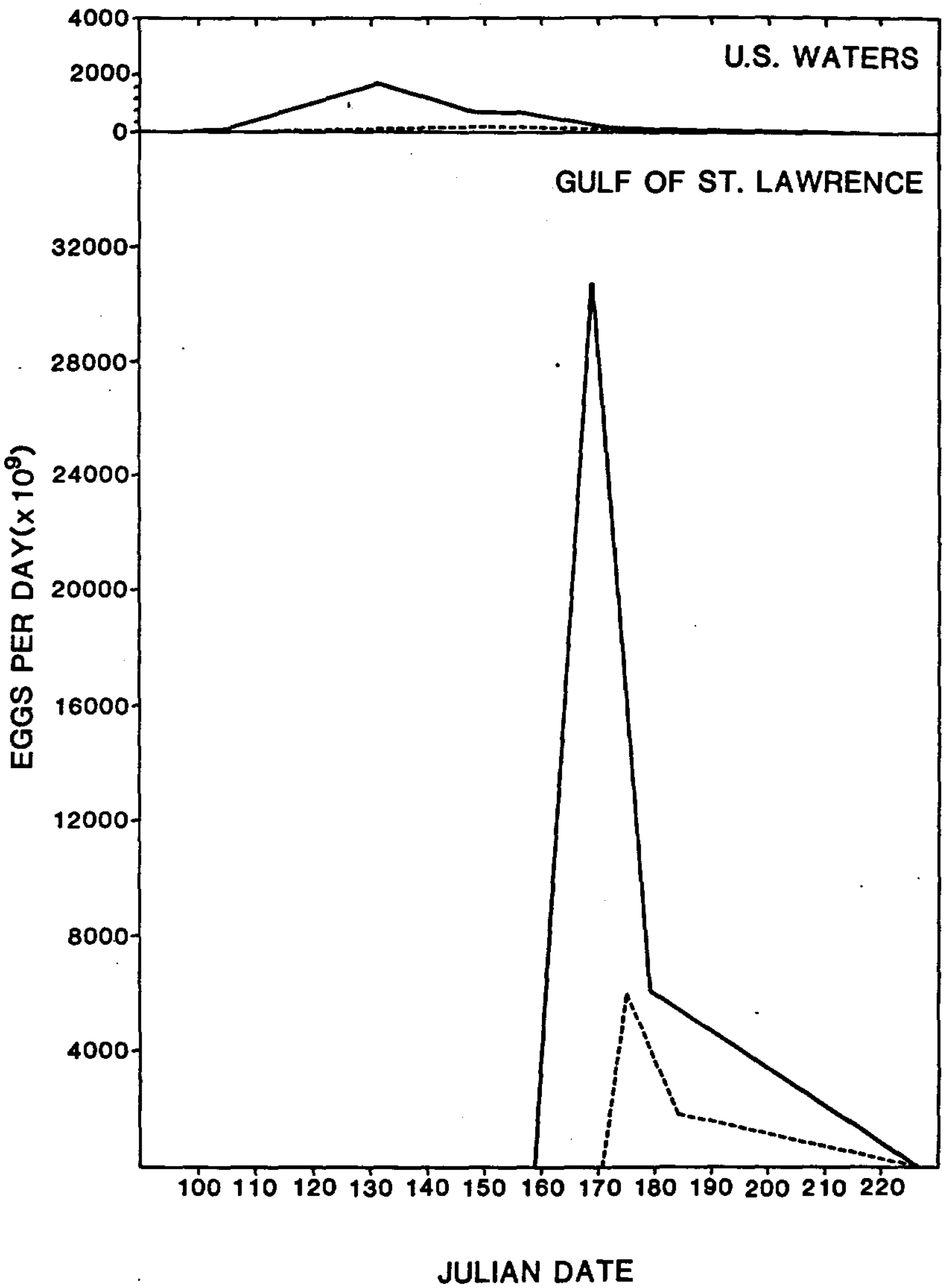


Figure 6. Atlantic mackerel daily egg production (solid lines) and hatching rates (dashed lines) for U.S. and Canadian waters, 1987.

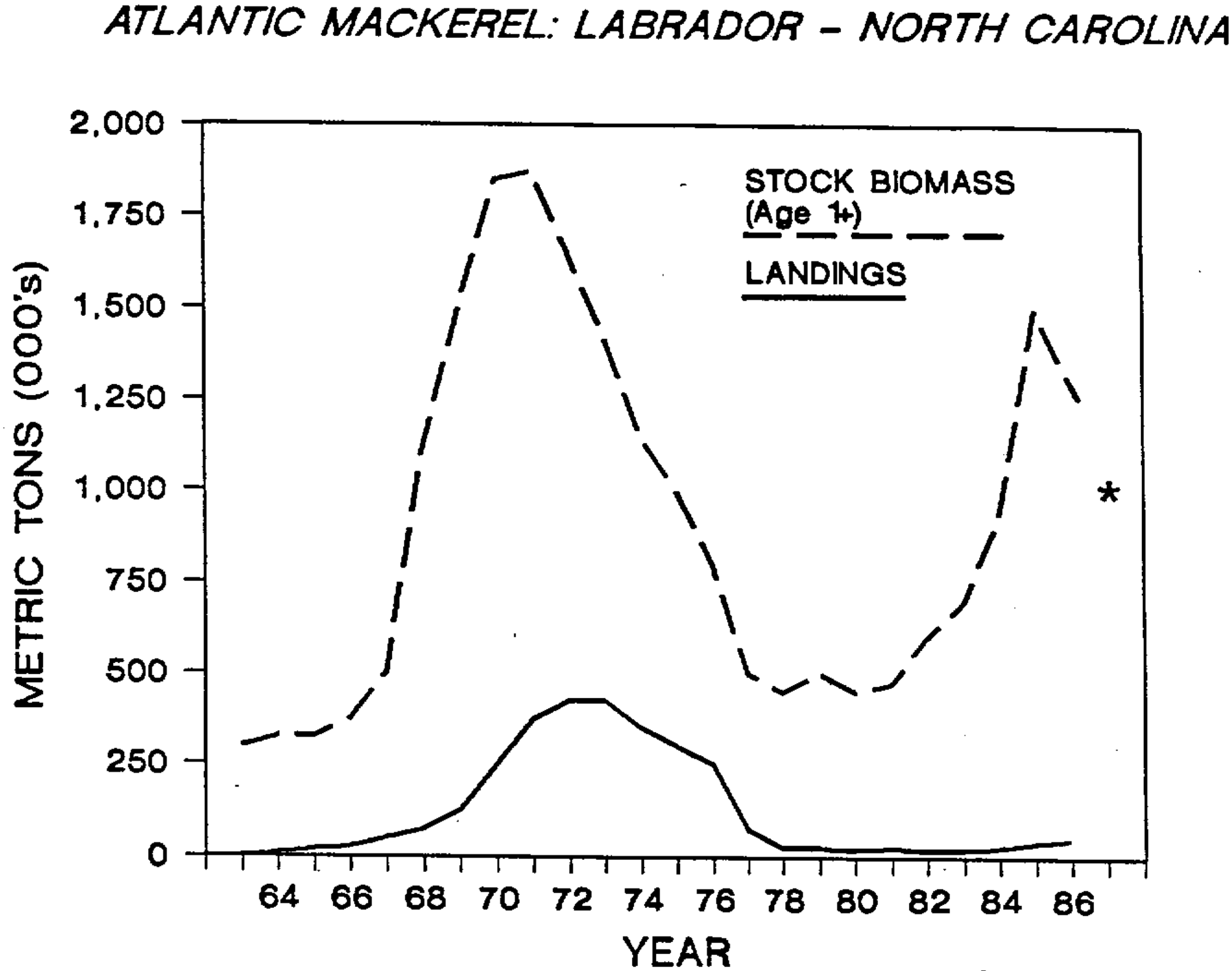


Figure 7. Atlantic mackerel spawner biomass for 1987 (*), for the area between Labrador and North Carolina, based on plankton survey data (this paper) superimposed on Figure 18.1 of Cons. and Util. Div.,NEFC (1987).