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Recent Estimates
of Adult Spawning Stock Biomass
Off the Northeastern United States
from MARMAP Ichthyoplankton Surveys

Peter Berrien[1], Wallace Morse[1], and Michael Pennington[2]

[1] Sandy Hook Lab., National Marine Fisheries Serv., Highlands, NJ 07732
[2] Woods Hole Lab., National Marine Fisheries Serv., Woods Hole, MA 02543

U.S. DEPARTMENT OF COMMERCE
Malcolm Baldridge, Secretary
National Oceanic and Atmospheric Administration
John V. Byrne, Administrator
National Marine Fisheries Service
William G. Gordon, Assistant Administrator for Fisheries
Northeast Fisheries Center

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INTRODUCTION

Major factors controlling year class success of coastal fish populations act during the early life stages of development. To further our understanding of recruitment processes in the early life stages and to improve our potential for forecasting future yields to the fisheries, NEFC scientists initiated in 1977 an intensive field program known as MARMAP. An integral part of MARMAP involves mesoscale ichthyoplankton surveys which are conducted at bimonthly intervals to collect biological and environmental information in continental shelf waters between Cape Hatteras, North Carolina and Cape Sable, Nova Scotia, an area of nearly 260,000 km².

These surveys provide an alternative to virtual population analysis (VPA) for estimating adult spawning biomass of commercially exploited species. Because ichthyoplankton-based population assessments do not utilize fishery catch statistics, i.e. they are fishery independent, they provide the sole source of information for deriving biomass estimates of species for which there are no commercial landing records. This gives an added dimension to the importance of egg and larva surveys as they can be used effectively to monitor population levels of underutilized resources. Population estimates based on repeated broadscale surveys of eggs and/or larvae have been applied widely and include the following species: Atlantic mackerel, Scomber scombrus (Sette 1943, Iversen 1977, Lockwood et al. 1981, Walsh et al. 1983, Iversen and Eltink 1983); pilchard, Sardina pilchardus (Cushing 1957); herring, Clupea harengus (Parrish and Saville 1962, Hardwick 1973); haddock, Melanogrammus aeglefinus (Saville 1964); Argentine anchovy, Engraulis anchoita (deCiechomski and Capezzani 1973); horse mackerel, Trachurus trachurus (Macer 1974); plaice, Pleuronectes platessa (Houghton and Harding 1976); round herring, Etrumeus teres (Houde 1977a); Atlantic thread herring, Opisthonema oglinum (Houde 1977b); scaled sardine, Harengula jaguana (Houde 1977c); blue whiting, Micromesistius poutassou (Coombs 1979); snapper, Chrysophrys auratus (Crossland 1980); and northern anchovy, Engraulis mordax (Ahlstrom 1968, Smith 1972, Parker 1980, Stauffer 1980, Picquelle and Hewitt 1983). These studies were conducted in areas around the world including the Gulf of Mexico, the North Sea, the eastern and western Atlantic Ocean, in the north, east, southeast and southwest Pacific Ocean and assessed both demersal and pelagic species.

Off northeastern United States fish eggs and larvae are collected at 177 stations by towing fine-meshed nets through the water column from surface to bottom or to a maximum depth of 200 m to monitor spatial and temporal variability in the distribution, abundance, production and survival of fish eggs and larvae. Measurements of other key components of the marine ecosystem include: nutrients, phytoplankton, zooplankton, sea birds, marine mammals, water temperature, salinity and dissolved oxygen. In order to use plankton surveys for assessment purposes, certain conditions must be met. Surveys should sample the entire area of spawning and the entire season must be sampled frequently enough to permit an estimation of the egg production rate over time. These criteria are generally met by the MARMAP program.

This paper contains results of five recently completed stock assessments based on eggs or larvae collected on MARMAP surveys. In direct comparison with fishery-dependent assessments, three of the five population estimates, those for Atlantic mackerel, Scomber scombrus; silver hake, Merluccius bilinearis; and haddock, Melanogrammus aeglefinus, were found to be in close agreement. In the case of yellowtail flounder, Limanda ferruginea, a VPA was not available for the year in question because fisheries data were inadequate for the analysis. A VPA is not possible for sand lance, Ammodytes sp., because, with the exception of a limited bait fishery, this small forage species is not fished commercially nor is it caught efficiently on NEFC research trawl surveys. Thus the MARMAP ichthyoplankton surveys provide the only available means for estimating spawning stock size.

The manuscript by Pennington and Berrien analyzes the precision of spawning stock size estimates based on egg surveys. It is shown that egg surveys provide estimates of stock abundance which are sufficiently accurate to detect major population trends. We are now conducting computer simulations based on actual survey frequencies to determine the variability associated with methods using larvae for back calculations. These simulations will concentrate on: 1) effects of survey timing and frequency relative to larva production curves; 2) variability of larva mortality estimates; 3) effects of within-survey variances in catches; 4) effects of changing water temperature on the within-season growth rates of larvae; and 5) effects of non-random distribution of larvae by size or age within the survey area.

When using survey collections of eggs to derive estimates of spawning stock biomass we begin by separating the eggs of a species into two or three developmental stages. Catches of these staged eggs are adjusted to become the numbers per 10 m^2 of sea surface area. Eggs in each stage are aged according to temperature-dependent incubation rates. Numbers at age are integrated and expanded over space and time so as to derive total season-long survey-wide estmates of abundance at each stage. Egg mortality rates are calculated from the exponential decrease in numbers at age. Using these mortality rates described by the data, numbers of eggs spawned are back-calculated from each occurrence of early-stage eggs. These numbers of eggs spawned are expanded over time and area and integrated with similar values from all surveys to calculate an estimate of total egg production for the spawning season within the total survey area. Total egg production is then used to calculate a spawning population estimate by the formula:

$$N = \frac{P}{FR}$$

where: N = total number of mature fish in the stock,
        P = total annual egg production of the population,
        F = fecundity, the number of eggs produced per female, and
        R = the proportion of mature females in the population.

Catches of larvae can also be used to calculate spawning stock biomass. First each larva is aged by applying temperature-dependent growth equations or

an estimate of average larva growth rate which converts lengths to ages. The age frequency is then used to estimate larva "mortality" from the exponential rate of decrease in abundance with increasing age. The "mortality" rate is applied to the age frequency to back-calculate the number of larvae hatched during the entire spawning season. An estimate of egg mortality and the total number of larvae at hatching yields a total estimate of egg production. The final steps are then identical to those presented above for spawning population estimates using eggs.

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ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, EGG PRODUCTION AND SPAWNING POPULATION ESTIMATES FOR 1977 IN THE GULF OF MAINE, GEORGES BANK, AND MIDDLE ATLANTIC BIGHT

P. L. BERRIEN and N. A. NAPLIN
U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Sandy Hook Laboratory
Highlands, New Jersey 07732, USA

and

M. R. PENNINGTON
U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543, USA

The total seasonal egg production of Atlantic mackerel was used to estimate the spawning population for 1977. Seven ichthyoplankton surveys were made from 5 March to 30 August. The survey area was divided into eight strata, for each of which the total number of eggs spawned during the season was calculated. The sum of eggs produced in all strata (3.032 x 10^{14} eggs) was related to the theoretical egg production of the commercial catch to obtain an estimate of the number of spawning females. Assuming a 1 : 1 sex ratio, the spawning population estimate was 1.2247 x 10^9 fish. This estimate, which applies roughly to ICNAF areas 5 and 6, amounts to 88.8% of, and thus compares favorably with, the population estimate of 1.3786 x 10^9 fish derived from cohort analysis of commercial catches and research trawl sampling in ICNAF areas 3 to 6, Newfoundland to Cape Hatteras (Anderson and Overholtz, 1978).

INTRODUCTION

The present report provides a population size estimate of Atlantic mackerel (*Scomber scombrus*), based on egg abundance data. Catch-based estimates were compared favorably with this fisheries independent assessment of population size using ichthyoplankton data.

A previous attempt to estimate the egg production and corresponding spawning population of mackerel has been made in the western North Atlantic. Sette (1943) presented a classic study on eggs and larvae of the 1932 year-class, including abundance and mortality estimates for eggs and larvae, growth rate of larvae, observations on dispersion and the subsequent fate of that year-class, and a spawning population size estimate. Berrien and Anderson (1976) reported on egg production and the number of spawners in the New

York Bight in May 1975. This population estimate was not satisfactory because of the restricted nature of the survey. The estimate was based on one cruise within the Bight and depended on assumptions regarding spawning behavior that could not be definitely substantiated. Anderson and Overholtz (1978) have reported on the 1977 population size of mackerel, using cohort analysis of trawl catches.

METHODS

The total ichthyoplankton survey included the Gulf of Maine, part of the Nova Scotian continental shelf, Georges Bank, and continental shelf waters southward to Cape Hatteras, North Carolina (Fig. 1). Because sampling locations were based on the sampling design of the spring 1977 NMFS trawl survey, the extreme offshore and inshore boundaries of that survey were

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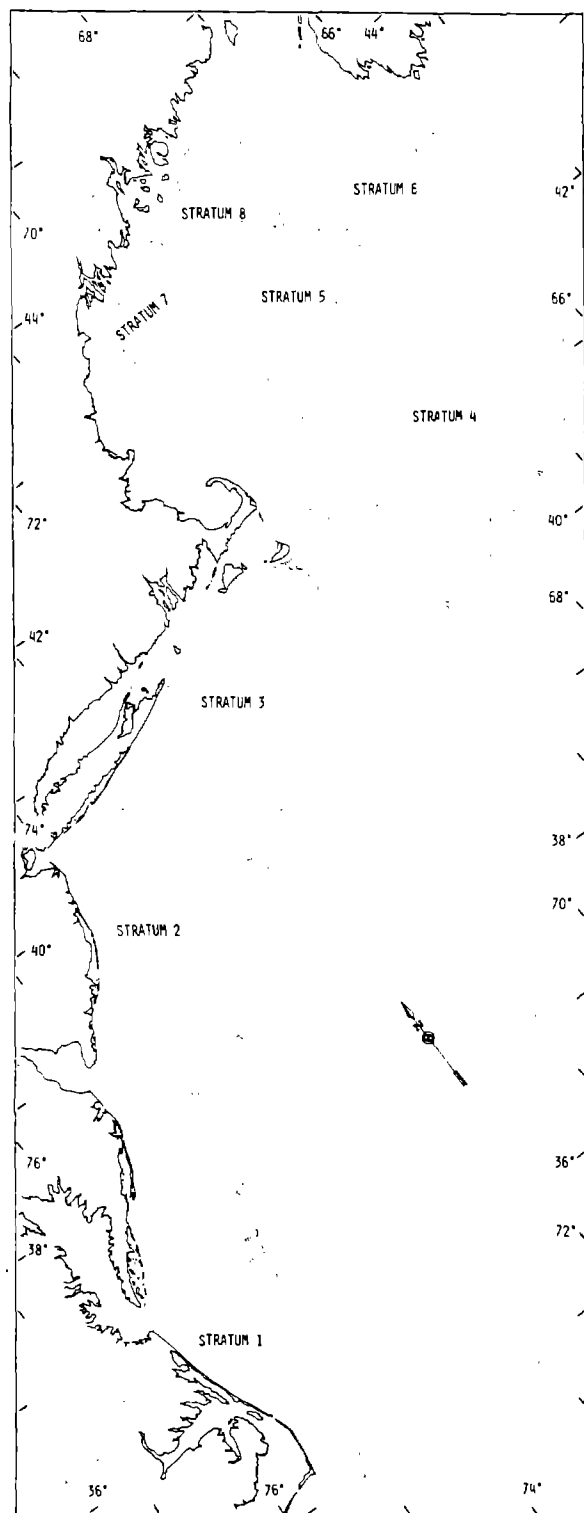
Figure 1. Total area and stratum boundaries for seven ichthyoplankton surveys, 1977.

used for the plankton survey; that is the offshore boundary was the 200-fm (365-m) contour, the inshore boundary south and west of Nantucket was the shoreline, and north and east of Nantucket it followed the division between the inshore trawl survey strata (not sampled) and the offshore strata. The total area defined was about 251 000 km^2.

Seven distinct ichthyoplankton surveys covered all, or part of, the total area. Of these, six are shown on distribution charts (Fig. 3–5); the first survey (cruises GO-77-1 and DE-77-3), made from 5 March to 8 April, apparently before mackerel were spawning did not reveal any eggs. Table 1 summarizes the sampling dates and areas surveyed. Strata referred to in the tables and figures were made necessary by the varying effort, i.e., the number of cruises, within the eight strata shown. This varying effort resulted from vessel scheduling and, in some cases, from restrictions on European vessel operations in U. S. and Canadian waters. Plankton was sampled with 61-cm bongo frames fitted with 0.505-and 0.333-mesh nets. The 0.505-mm mesh net was used for ichthyoplankton analysis. A flowmeter was suspended within the mouth of each sampler for volume-filtered determination, and a bathykymograph was attached next to the sampler to monitor the tow profile and maximum depth attained. A 45-kg ball suspended beneath the bongo depressed the sampler during the tow.

A double-oblique plankton haul was made at each station according to standard MARMAP I procedures (Jossi et al., 1975). The vessel speed was adjusted to maintain a 45° wire angle throughout the haul, and sufficient wire was payed out to sample to a maximum depth of 200 m, or to within 5 m of the bottom at depths less than 205 m. Plankton samples were preserved in a 5% formalin and seawater solution. Surface temperatures were measured with a stem thermometer.

All fish eggs and larvae were removed from the samples; eggs of selected species (including mackerel) were identified and sub-divided according to developmental stage. Three stages were used: fertilization to blastopore closure, blastopore closure to tail free, and tail free to hatching. Eggs were staged so that we could use early stage eggs only (to minimize any mortality-induced bias) for the total egg production calculations, and to determine the mortality rate experienced by mackerel eggs in 1977. The mortality rate was calculated by regressing the log$_e$ (total season's abundance of each of the three stages) on the weighted mean age of these stages; since, if the mortality rate is fairly constant, the population will decline exponentially. The resulting mortality rate (Z = 0.8840) was then used *

*Please note; the correct value for Z is 0.1233.

Table 1. Ichthyoplankton survey dates (1977) and coverage.

Survey	Cruise	No. of samples	Sampling dates	Strata
1	GO-77-01	102	5 Mar–6 Apr	3,4,5
	DL-77-03	69	19 Mar–8 Apr	1,2
2	DL-77-04(pt. 1)	93	13–22 Apr	1,2,3
3	AL-77-02	105	14 Apr–13 May	3,4,5,6,7,8
	DL-77-04(pt. 2)	57	24–29 Apr	2
4	DL-77-05(pt. 1)	90	4–13 May	1,2,3
5	NO-77-02	75	24 May–5 Jun	4(part),7
	DL-77-07(pt. 1)	33	12–16 Jun	4(part),6
	DL-77-05 (pt. 2)	77	18–27 May	2,3
6	DL-77-07(pt. 2)	94	21–30 Jun	1,2,3
7	YU-77-02	143	31 Jul–30 Aug	1(part),2(part),3,4,5,7,8
	DL-77-09	15	30 Jul–3 Aug	1(part),2(part)

NOTE: AL = "Albatross IV", DL = "Delaware II", GO = "Goerlitz", NO = "Nogliki", YU = "Yubileiny".

to adjust the numbers of early-stage eggs sampled/m^2/day to the numbers of eggs spawned/m^2/day. This procedure required knowledge of the duration of each stage at various incubation temperatures; this has been reported by Worley (1933).

The number of early stage eggs at each station was standardized by correcting for the volume filtered and the maximum depth sampled, and expressed as the number of early stage eggs/m^2. Then, using the incubation rate at the surface temperature encountered on the station, and adjusting for mortality we calculated, for each station, the number of eggs spawned/m^2/day.

From Figure 2 it can be seen that, even with the zero values omitted, the distribution of the number of eggs spawned/m^2/day is highly skewed. There is a large proportion of zeros and low values inherent in data of this kind. Inclusion of the zeros produces greater skewness than that shown and adds a certain arbitrariness to the analysis. The proportion of zeros is determined to a great extent by the initial choice of the area to be surveyed. If the precise spawning areas were known, then the distribution of sampling could be tailored to those areas and the number of zeros would be minimal. However, the spawning areas are not known beforehand; furthermore such surveys are generally not designed to sample only one species or confined to sampling ichthyoplankton. Hence most surveys cover a region, part of which is not suitable for spawning by a particular species or where spawning just does not occur. The proportion of zeros in these data was thus used to estimate the percentage of the area surveyed where spawning occurred. The observed distribution of the non-zero values (Fig. 2) was found

to be well approximated by a log-normal distribution. A distribution that has a non-zero probability of zero values and whose conditional distribution of non-zero values is log-normal is called a Δ-distribution (Aitchison, 1955). The minimum variance unbiased estimator of the arithmetic mean (k) is given by:

$$k = \frac{n_1}{n} [\exp (\bar{y})] \Psi_{n_1}\left(\frac{s^2}{2}\right)$$

where n   is the sample size,

n_1 is the number of non-zero values,

n_0 is the number of zero values,

$\bar{y}$ is the sample mean of $\log_e$ (eggs spawned /m^2/day) for non-zero values,

s^2 is the sample variance of the log values, and

ψ_{n_1} is given by an infinite series and can be found in Aitchison and Brown (1957).

For larger values of the population variance s^2, k is a much more efficient estimator than the sample mean of the untransformed data (Pennington, 1979 ms). Furthermore, for large values of s^2 and/or small values of n_1 the factor ψ_{n_1} should be used rather than using the usual approximations

$$\exp\left(\frac{s^2}{2}\right) \text{ or } \exp\left(\frac{n-1}{n} \cdot \frac{s^2}{2}\right)$$

either of which give, as we found in this situation, highly biased estimators. For our analysis ψ_{n_1} was

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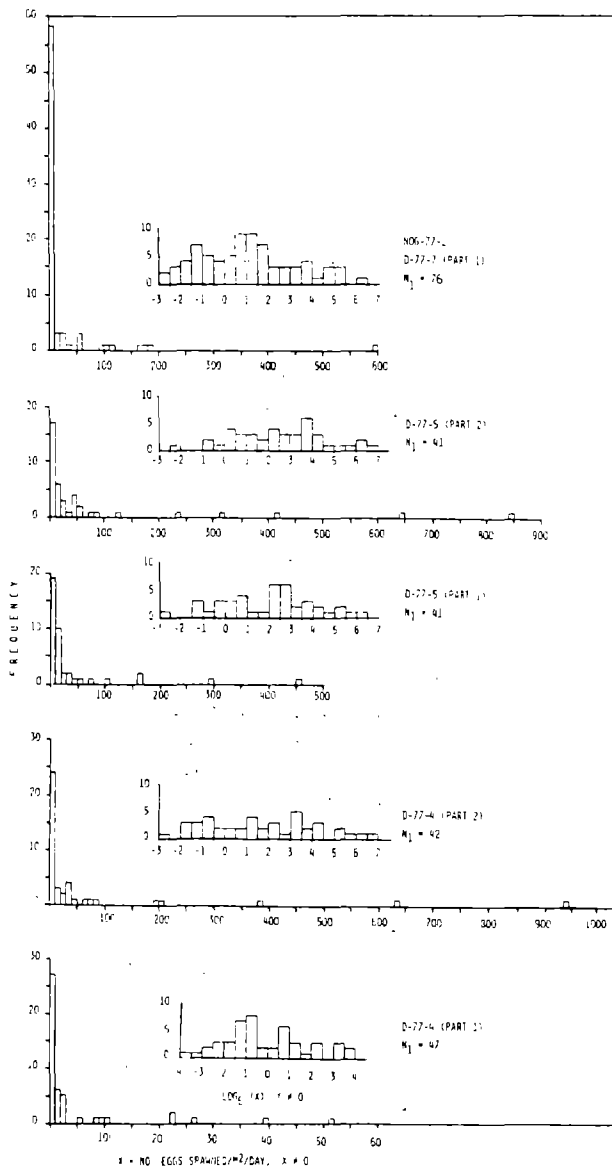
Figure 2. Frequency distributions of non-transformed and log. — transformed values of eggs spawned/m²/day.

calculated by a program written for this purpose. The variance of k is estimated by:

$$var\ (k) = \left[\left(\frac{n}{n_1} \cdot k\right)^2 \div n\right] \cdot$$

$$\left[\frac{n_0\,n_1}{n^2} + \frac{n_1}{n} \cdot \left(s^2 + \frac{s^4}{2}\right)\right]$$

This formula, though approximate, takes into account the fact that k is a function not only of $\bar{y}$ but also of s^2 and n_1. Confidence intervals can be generated by

assuming k (or a weighted sum of the k's when estimating total) is approximately normally distributed with standard error equal to $\sqrt{}$ (var k). It should be noted that, when the proportion of zeros is zero, the Δ-distribution is log-normal and the above estimators may still be used.

The re-transformed mean density (k) was raised to the number of eggs spawned in each stratum per day, then multiplied by the number of days represented by each survey in each stratum. The stratum estimates were summed over time, resulting in the total number of mackerel eggs spawned in 1977 in the area surveyed.

The number of days represented by a survey within a stratum was determined by first calculating the midpoint in time of sampling within each stratum, each time it was surveyed. Then, for each midpoint, half the days between the preceding midpoint and half between the following midpoint were summed to produce the number of days represented by that particular survey in that stratum.

The estimate of total egg production for the season was used to estimate the population size of mature mackerel. A theoretical number of eggs spawned by the mature females in the commercial fishery catch was calculated. This theoretical egg production was divided into the total season's estimate of egg production to derive a factor by which the commercial catch could be multiplied to give an estimate of the total spawning population.

RESULTS

Figures 3–5 show the densities of eggs spawned per day during the 2nd through 7th surveys. No mackerel eggs were taken during the first survey (5 March–8 April) given in Table 1. Generally, the greatest concentrations of spawning occurred in near-shore waters in strata 7 and 4 and in the inner half of continental shelf waters in strata 2 and 3. Throughout the spawning season, the greatest spawning intensity shifted toward the north and east, occurring off New Jersey in late April, off New Jersey and Long Island in early May, and from Long Island to Nantucket in late May and early June (Fig. 3 and 4).

Table 2 summarizes the results from calculations used in deriving egg production estimates for individual strata as well as for the entire survey area and season. The low rate of spawning (3.3 eggs/m²/day) indicated by the second survey (mid-April) for most of the Middle Atlantic Bight increased rapidly (to 76.3 eggs/m²/day) by the time of the third survey (late April). The spawning rate decreased to slightly over half that value and remained so throughout May, then decreased during June to a very low level (0.36 eggs/m²/day).

In the more northeastern strata (nos. 3, 4, and 7) the peak in spawning intensity occurred slightly later in
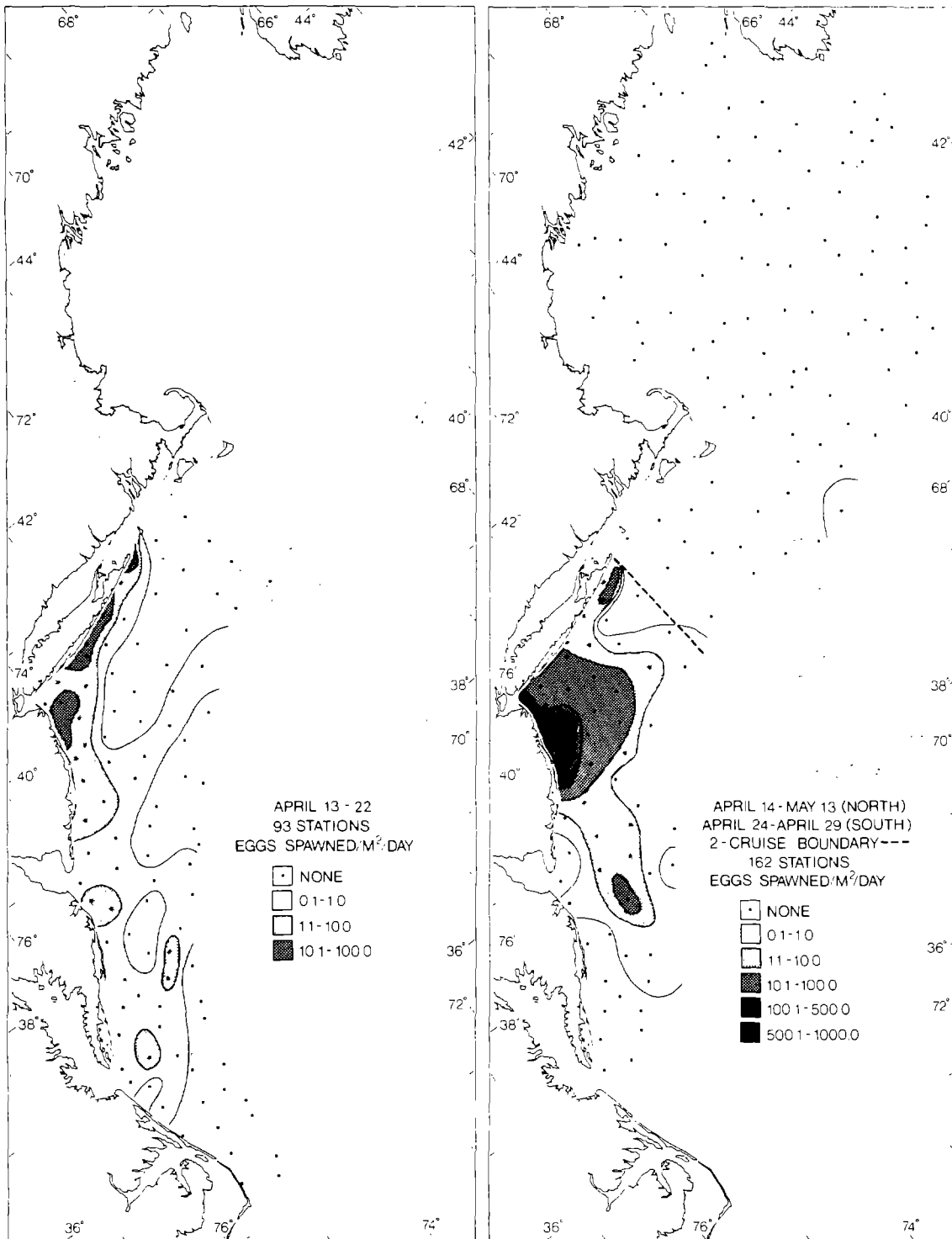
Figure 3. Distribution of Atlantic mackerel eggs during the second and third ichthyoplankton surveys, 1977.

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MAY 4-13
90 STATIONS
EGGS SPAWNED/M²/DAY

· NONE
☐ 0.1-1.0
░ 1.1-10.0
■ 10.1-100.0
■ 100.1-500.0

JUNE 12 -JUNE 16(NORTH)
MAY 24 -JUNE 5(CENTRAL)
MAY 18 - MAY 27 (SOUTH)
2-CRUISE BOUNDARY - - -
185 STATIONS
EGGS SPAWNED M²/DAY

· NONE
☐ 0.1-1.0
☐ 1.1-10.0
▒ 10.1-100.0
■ 100.1-500.0
■ 500.1-1000.0
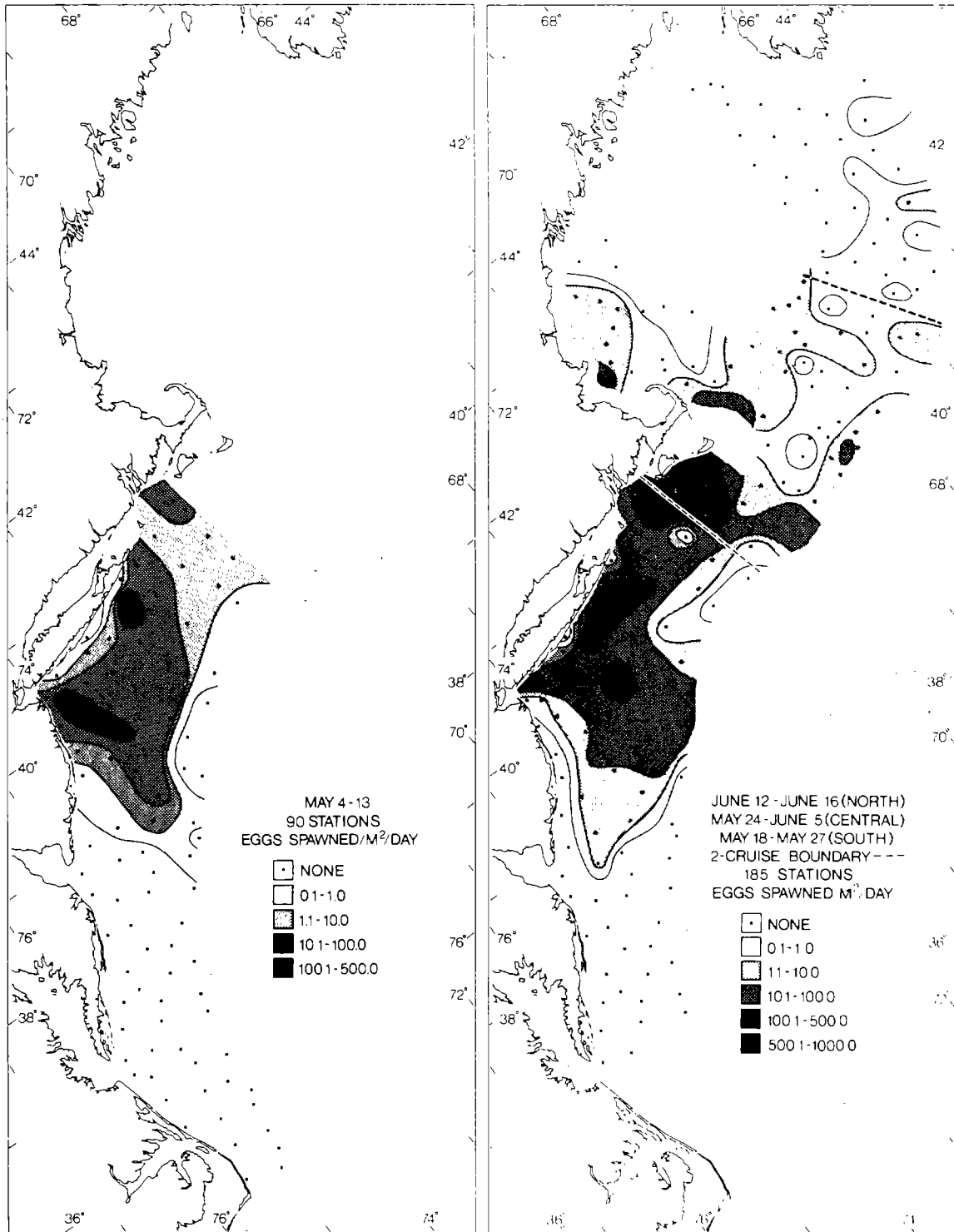
Figure 4. Distribution of Atlantic mackerel eggs during the fourth and fifth ichthyoplankton surveys, 1977
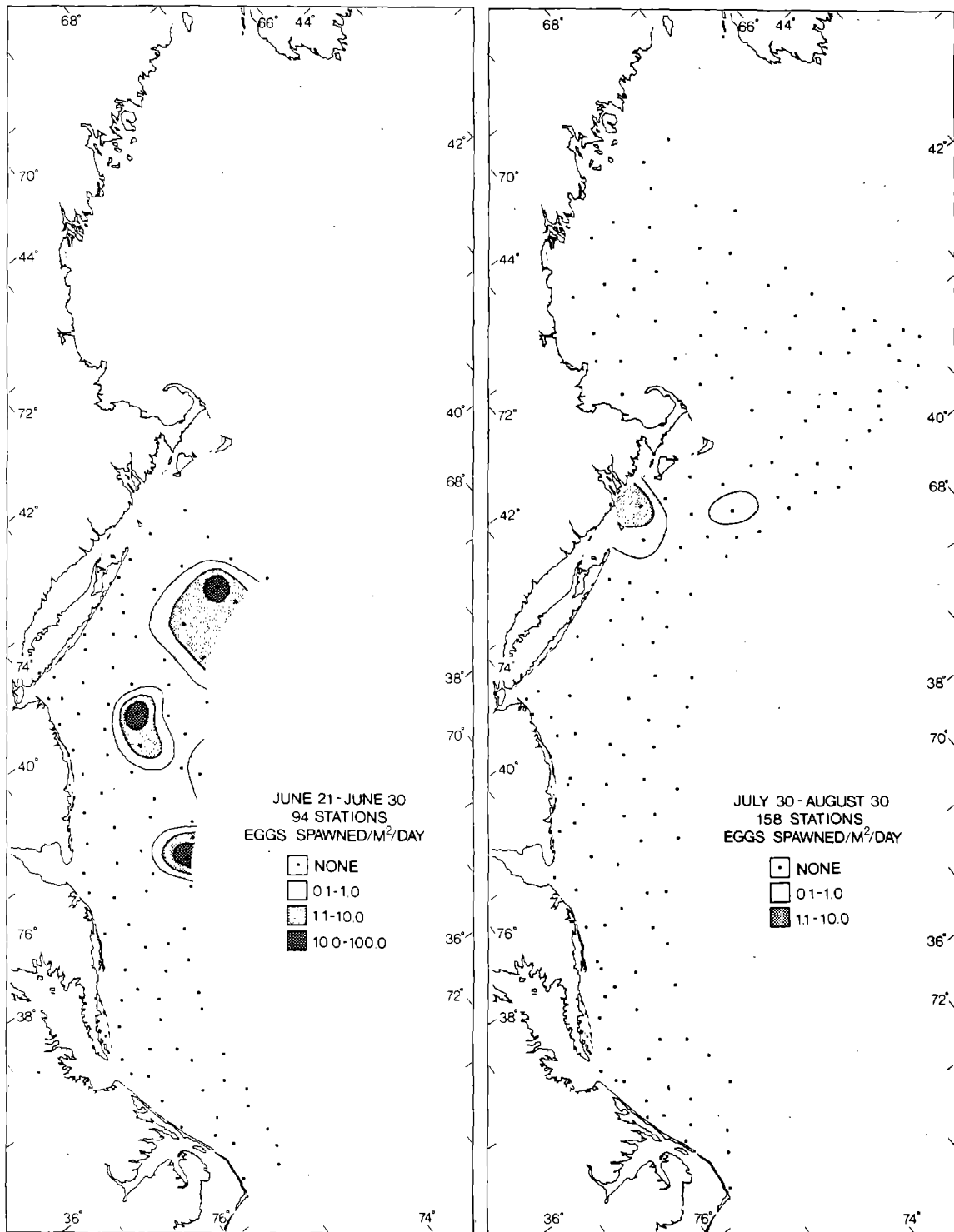
Figure 5. Distribution of Atlantic mackerel eggs during the sixth and seventh ichthyoplankton surveys, 1977.

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Table 2. Atlantic mackerel egg production estimate.

Stratum	Cruise	n	n₁	n₀	$\bar{y}$	s^2	k'	Std. error of k'	Area (km²)	Eggs spawned in stratum per day (No. x 10¹²)	Sampling midpoint date	Days represented	Eggs spawned, represented by this effort in this stratum (No. x 10¹²)
1	DL-77-3	15	0	15					16 560	0	23 Mar	21.628	0
1	DL-77-4(pt. 1)	17	3	14	-1.744076	1.060294	0.0427	0.0386	16 560	0.0007	14 Apr	21.1875	0.0150
1	DL-77-5(pt. 1)	17	0	17					16 560	0	5 May	34.5	0
1	DL-77-7(pt. 2)	17	0	17					16 560	0	22 Jun	49.25	0
1	YU-77-2 / DE-77-9	17	0	17					16 560	0	11 Aug	50.25	0
2	DL-77-3	54	0	54					67 288	0	29 Mar	20.5	0
2	DL-77-4(pt. 1)	68	44	24	-0.040103	3.553738	3.3292	1.6044	67 288	0.2240	19 Apr	14.1875	3.1782
2	DL-77-4(pt. 2)	57	42	15	1.709243	6.402071	76.2885	61.3461	67 288	5.1333	26 Apr	10.25	52.6163
2	DL-77-5(pt. 1)	66	34	32	2.149910	4.928335	42.0080	30.1872	67 288	2.8266	9 May	12.9375	36.5696
2	DL-77-5(pt. 2)	69	35	34	2.590489	4.041763	43.7950	26.3836	67 288	2.9469	22 May	23.5625	69.4358
2	DL-77-7(pt. 2)	69	7	62	1.636568	1.680508	1.0140	0.7700	67 288	0.0570	25 Jun	42.1875	2.8783
2	YU-77-2 / DL-77-9	58	0	58					67 288	0	15 Aug	50.5	0
3	GO-77-1	18	0	18					14 131	0	6 Mar	39.625	0
3	AL-77-2	8	0	8					14 131	0	15 Apr	23.5	0
3	DL-77-4(pt. 1)	8	0	8					14 131	0	22 Apr	7.375	0
3	DL-77-5 (pt. 1)	7	7	0	1.217970	1.098071	5.2838	2.6046	14 131	0.0747	11 May	22.25	1.6613
3	DL-77-5(pt. 2)	8	6	2	2.418879	7.586451	90.7456	224.1528	14 131	1.2823	26 May	24.375	31.2567
3	DL-77-7(pt. 2)	8	2	6	2.489205	3.077634	7.5254	5.9276	14 131	0.1063	29 Jun	40.8125	4.3400
3	YU-77-2	9	2	7	0.277717	1.204928	0.3863	0.4493	14 131	0.0055	15 Aug	47.25	0.2579
4	GO-77-1	70	0	70					84 794	.0	21 Mar	39.625	0
4	AL-77-2	54	1	53	n.a.	n.a.	0.0110	0.0110	84 794	0.0009	29 Apr	37.8125	0.0353
4	NO-77-2 / DL-77-7(pt. 1)	81	67	14	0.927658	5.005552	22.6866	11.7406	84 794	1.9237	4 Jun	50.0	96.1850
4	YU-77-2	54	1	53	n.a.	n.a.	0.0074	0.0074	84 794	0.0006	7 Aug	64.0	0.0402
5	GO-77-1	14	0	14					19 137	0	1 Apr	26.125	0
5	AL-77-2	12	0	12					19 137	0	27 Apr	65.625	0
5	YU-77-2	10	0	10					19 137	0	10 Aug	105.125	0
6	AL-77-2	19	0	19					29 837	0	6 May	38.625	0
6	DL-77-7(pt. 1)	18	2	16	-1.223048	0.099645	0.0335	0.0236	29 837	0.0010	14 Jun	38.625	0.0386
7	AL-77-2	5	0	5					9 299	0	12 May	23.0	0
7	NO-77-2	9	7	2	1.799050	2.630087	11.5437	11.6128	9 299	0.1073	4 Jun	43.8125	4.7030
7	YU-77-2	7	0	7					9 299	0	8 Aug	64.625	0
8	AL-77-2	7	0	7					9 734	0	9 May	91.75	0
8	YU-77-2	3	0	3					9 734	0	8 Aug	91.75	0

The estimated total egg production is 3.032 x 10¹⁴ eggs (std. error = 1.1267 x 10¹⁴).

'For $n_1 = 1$, the mean is estimated by $\frac{x}{n}$, and its variance by $\frac{x^2}{n^2}$, where x is the single non-zero value; both are unbiased estimators.

NOTE: AL = "Albatross IV", DL = "Delaware II", GO = "Goerlitz", NO = "Nogliki", YU = "Yubileiny".

the season, around the beginning of June, then decreased to a negligible amount during that month.

In all, stratum 2 accounted for the greatest amount of spawning in the whole survey (54.3% of all eggs produced). Other areas contributed, in decreasing abundance, stratum 4 — 31.7%, stratum 3 — 12.4%, stratum 7 — 1.6%, — and strata 6 and 1 — together less than 0.02%. The total mackerel egg production for the season was estimated as 3.032 x 10¹⁴ eggs (std. error = 1.1267 x 10¹⁴ eggs).

Egg production over time, in the whole survey area, is shown in Figure 6. The bimodality of the cumulative production curve implies discrete peak spawnings in stratum 2 and in strata 3 and 4. This may be a reflection of two major spawnings, perhaps caused by two waves of spawners entering the area (such as two age groups or two groups which had over-wintered in different localities); or the bimodality may have resulted from the sampling scheme and cruise schedule. We may have missed many eggs in early or mid-May in southern New England waters not sampled, such as Massachusetts Bay; Nantucket Shoals;

and Nantucket, Vineyard, Block Island, and Long Island Sounds. Strata 1 and 6 are not shown in Figure
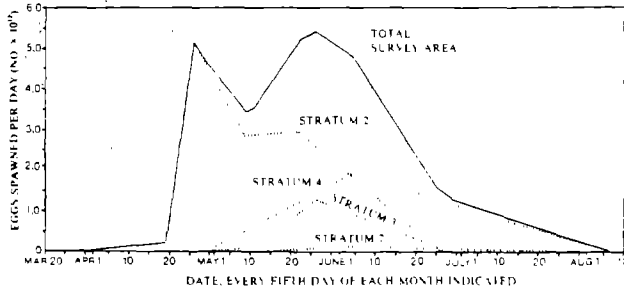
Figure 6. Estimated daily egg production in four strata and in the total Survey Area; Strata 1 and 6 are not shown, their contributions are insignificant.

6 as they would be represented by horizontal lines extremely close to the zero-eggs/day line from 23 March to 5 May and 6 May to 2 July, respectively. The inclusion of these insignificant abundances would clutter the graph, obscuring the overall pattern.

Table 3 summarizes calculations used in estimating the spawning population size. The total commercial catch of mackerel by size and an assumed 1 : 1 sex ratio was used to calculate the number of females in the catch. The length frequencies of the mature mackerel in the commercial catch were assumed to be proportional to those of the spawning population. Using percent-mature-at-length (Morse, pers. comm.) and fecundity-at-length data (Morse, 1978), we calculated the theoretical numbers of eggs spawned by the females in the commercial catch (25.0608 x 10^{12} eggs).

Table 3. Calculations for Atlantic mackerel spawning population estimate.

Fork length (cm)	Total catch[a] of fish (No. x 10^3)	Females[b] in catch (No. x 10^3)	Percent[c] females mature	Mature females in catch (No. x 10^3)	Fecundity[d]	Theoretical egg production by catch (No. x 10^{12})	Mature females in population (No. x 10^6)
14	16	8.0					
15	8	4.0					
16	8	4.0					
17	27	13.5					
18	100	50.0					
19	194	97.0					
20	231	115.5					
21	157	78.5					
22	124	62.0					
23	237	118.5					
24	890	445.0					
25	2 320	1 160.0					
26	4 660	2 330.0					
27	4 961	2 480.5					
28	4 860	2 430.0					
29	6 696	3 348.0	1.6	53.6	202 085	0.0108	0.6485
30	16 758	8 379.0	13.4	1 122.8	243 871	0.2738	13.5843
31	27 279	13 639.5	45.2	6 165.1	292 489	1.8032	74.5889
32	26 749	13 374.5	80.0	10 699.6	348 780	3.7318	129.4499
33	21 221	10 610.5	96.2	10 207.3	413 658	4.2223	123.4938
34	15 803	7 901.5	99.6	7 869.9	488 112	3.8414	95.2146
35	8 351	4 175.5	100.0	4 175.5	573 209	2.3934	50.5176
36	6 161	3 080.5	100.0	3 080.5	670 102	2.0642	37.2697
37	5 769	2 884.5	100.0	2 884.5	780 028	2.2500	34.8983
38	3 997	1 998.5	100.0	1 998.5	904 316	1.8073	24.1790
39	2 742	1 371.0	100.0	1 371.0	1 044 389	1.4319	16.5871
40	1 517	758.5	100.0	758.5	1 201 768	0.9115	9.1768
41	383	191.5	100.0	191.5	1 378 078	0.2639	2.3169
42	70	35.0	100.0	35.0	1 575 049	0.0551	0.4235
Sum	162 289			50 613.3		25.0608	612.3489

[a] First quarter 1977 catch in ICNAF Subareas 5 and 6, submitted to ICNAF; E. Anderson, pers. comm.
[b] Calculated from total catch assuming a 1:1 sex ratio.
[c] Based on 1978 NMFS, NEFC spring trawl survey data; W. Morse, pers. comm.
[d] From Morse (1978).

Dividing the estimated total eggs spawned (3.032 x 10^{14}) by those spawned by the commercial catch gives a factor (12.0986), which when doubled (to adjust for the sex ratio), and multiplied by the number of mature females caught, produces the estimated population of spawners (1.2247 x 10^9 fish). This spawning population estimate, which applies roughly to ICNAF areas 5 and 6, Nova Scotia to Cape Hatteras, is 88.8% of the spawning stock estimate (1.3786 x 10^9 fish) given by Anderson and Overholtz (1978) for ICNAF areas 3 to 6, Newfoundland to Cape Hatteras.

DISCUSSION

In order to obtain an accurate estimate of the total egg production of a species during a spawning season it is necessary to plan survey cruises which sample throughout the entire spawning season and area; and one should sample often enough to be able to describe changes in spawning intensity during the season. Shortcomings in the sampling scheme, especially those concerning seasonal and areal coverage, can easily introduce bias into the egg production estimate which would be hard, or impossible, to detect.

In this study, the distribution charts and production curve show that the spawning season was adequately covered in time. However, the areal coverage was apparently not so complete. We may have missed some areas of low egg density offshore, beyond the survey area. We believe this to be a minor fault, as spawning appeared to be much more intense in the inner, or shoreward portion of the continental shelf water than offshore. We may have missed some eggs by not sampling close enough to shore from Block Island Sound to the western Gulf of Maine, an area of approximately 1600 km^2. Allowing for this bias by assuming similar egg densities to those found in the adjacent areas surveyed would increase the egg production and spawning population estimates by 0.54%, giving values of 3.0485 x 10^{14} eggs produced by 1.2313 x 10^9 mature fish. Our cruise frequency varied with stratum. We sampled more often in southern strata (5–7 times) than in the north (2–4 times). This clearly influences the precision of the estimates, but we are uncertain about both the magnitude and direction of any bias so introduced.

The resulting coefficient of variation (c.v. = 0.37) indicates a relatively low level of precision in the egg production estimate, despite the rather extensive effort reported here. The effectiveness of the technique is better when you consider that the level of effort (7 surveys within 251 000 km^2) was not directed solely toward mackerel egg sampling, but also toward yellowtail flounder (*Limanda ferruginea*), whose spawning does not necessarily coincide in space or time with that of mackerel. If we were to sample, at a similar level of effort, only for mackerel eggs on future surveys, we could certainly improve the precision. By using the knowledge gained on this series of surveys, and by restratifying over time and area, we could probably decrease the coefficient of variation. The probability of conducting a single-species oriented series of cruises, however is remote, leading to the conclusion that the precision level presented here is probably typical of such ichthyoplankton surveys. However, even with a multispecies approach, some improvement in precision of mackerel egg production estimates might result from changing the area stratification to reflect the inshore vs. offshore egg density difference noted here. Such restratification would not be detrimental to the precision of estimates for other species.

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YELLOWTAIL FLOUNDER, LIMANDA FERRUGINEA, ESTIMATES OF EGG ABUNDANCE
AND POPULATION SIZE DURING SPRING 1977 IN GULF OF MAINE,
GEORGES BANK, SOUTHERN NEW ENGLAND AND MIDDLE ATLANTIC BIGHT WATERS

by

Peter Berrien

U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Sandy Hook Laboratory
Highlands, New Jersey 07732 USA

ABSTRACT

The total season's egg production of yellowtail flounder was used to
estimate the total population and female spawning population for 1977. Seven
MARMAP (Marine Resources Monitoring, Assessment and Prediction) ichthyoplankton
surveys were made from March 5 to August 30. Based on sampling effort the survey
area was divided into eight subareas, for each of which a total number of eggs
spawned during the season was calculated. The sum of eggs spawned in all subareas
(56.8616×10^{12} eggs) was related to the theoretical egg production of a reference
catch of adults to obtain estimates of the female spawning population and the
total population. An estimate of 138.1×10^{6} fish, age 2 and greater, of both
sexes was calculated.

INTRODUCTION

Yellowtail flounder (Limanda ferruginea) is a desirable food fish which
historically has sustained significant fishery catches on Georges Bank and
in southern New England waters. Landings reached a peak in the late 1960's
due to large increases in fishing effort, including that from a considerable
influx of foreign ships. There were subsequent drastic reductions in populations
and catches during the early 1970's in southern New England and mid-1970's on
Georges Bank (Clark et al. 1981).

MARMAP plankton surveys have been conducted since autumn 1976 to present,
generally six per year, at various seasons in Gulf of Maine, Georges Bank,
southern New England, and Middle Atlantic Bight waters out to the edge of the
continental shelf (Sherman 1980). Given a favorable cruise sequence, i.e.,
closely spaced in time, one objective of these surveys is to estimate the total
season-long abundance of eggs spawned by certain fish species of interest.
From this egg abundance estimate, in conjunction with knowledge of such biological
features as sex ratio, fecundity, percent mature at length, length frequency
structure of a representative catch of adults, and incubation rates of eggs at

various temperatures, we can calculate the population size of adults. This
approach was utilized for Atlantic mackerel, Scomber scombrus, on the same
data base used here (Berrien et al., in press).

The egg survey approach to population assessments is used to augment
the conventional assessment techniques (by research trawl survey or by analysis
of commercial fishery data) and thereby add support to these conventional and
more timely methods. Although plankton sampling gear operates in a relatively
predictable fashion, patchiness of eggs adds to the variance estimates around
abundance values; but this is a factor to be reckoned with in virtually all
biological sampling.

Additional discussion of the theory and techniques for egg survey work
can be found in papers by Saville (1964), and Smith and Richardson (1977).
Previous population estimates based directly on plankton survey data have been
made on pilchard, Sardina pilchardus (Cushing 1957), Pacific sardine, Sardinops
caerulea (Murphy 1966), northern anchovy, Engraulis mordax (Ahlstrom 1968), round
herring, Etrumeus teres (Houde 1977a), thread herring, Opisthonema oglinum
(Houde 1977b), and Atlantic mackerel, Scomber scombrus (Sette 1943, Lockwood et al.
1981, and Berrien et al., in press).

PROCEDURES

The total ichthyoplankton survey area included the Gulf of Maine, part of
the Nova Scotian continental shelf, Georges Bank, and continental shelf waters
southward to Cape Hatteras, North Carolina (Figure 1). Because sampling locations
were based on the sampling design of the spring 1977 NMFS trawl survey, the
extreme offshore and inshore boundaries for that effort were used for the plankton
survey. That is, the offshore boundary was the 200-fm (365-m) contour; the
inshore boundary south and westward of Nantucket was the shoreline; and north
and eastward of Nantucket it followed the division between the inshore trawl
survey strata (not sampled) and the offshore strata. The total area defined is
about 251,000 km^2. Seven ichthyoplankton surveys from March to August covered
all or part of the total area. These are portrayed on distribution charts
(Figures 1 to 4).

Table 1 summarizes the sampling dates and areas surveyed. Subareas referred
to in tables and figures were made necessary by the varying effort (i.e., the
number of cruises) within the eight subareas shown. This varying effort resulted
from vessel scheduling and operations and, in some cases, from restrictions on
European vessel operations in U. S. and Canadian waters.

Plankton was sampled with 61-cm bongos fitted with 0.505- and 0.333-mm
mesh nets. The 0.505-mm mesh net was used for ichthyoplankton analysis. A
flow meter was suspended within the mouth of each sampler for volume-filtered
determination, and a bathykymograph was attached next to the sampler to monitor
the tow profile and maximum depth attained. A 45-kg ball suspended beneath
the bongo depressed the sampler during the tow.

A double-oblique plankton haul was made at each station according to
standard MARMAP I procedures (Jossi et al. 1975), i.e., the vessel speed was
adjusted so as to maintain a 45° wire angle throughout the haul, and sufficient

wire was paid out to sample to a maximum depth of 200 m, or to within 5 m of the bottom at depths less than 205 m. Surface temperatues were measured with a stem thermometer. Temperatures to the bottom were recorded by expendable bathythermograph probes.

All fish eggs and larvae were removed from the samples; eggs of selected species (including yellowtail flounder) were identified and separated according to developmental stage. Three stages were used: fertilization to blastopore closure; blastopore closure to tail free; and tail free to hatching. Eggs were staged so that we could determine the mortality rate experienced by yellowtail flounder eggs in 1977, and so that we could use early-stage eggs only (to minimize any mortality-induced bias) for the total egg production calculations. The mortality rate was calculated by regressing the $\log_e$ (total season's abundance of each of the three stages) on the weighted mean age of these stages; since, if the mortality rate is fairly constant, the population will decline exponentially (Figure 5). The resulting mortality rate (16.156% per day) was then used to adjust the numbers of early-stage eggs sampled/10m^2/day to become the numbers of eggs spawned/10m^2/day. This procedure required knowledge of each stage's duration at various incubation temperatures, which were determined at NEFC's Narragansett Laboratory by G. Laurence (pers. comm.). Incubation temperatures associated with yellowtail flounder eggs from plankton samples were determined as the mean of the surface and bottom temperatures at each station.

The number of early-stage eggs at each station was standardized by allowing for the water volume filtered by the net and the maximum depth sampled, and expressed as the number of early stage eggs sampled/10m^2. Then, using the known incubation rate at the temperature encountered on station, and adjusting for mortality I calculated, for each station, the number of eggs spawned/10m^2/day:

$$Eo = e_\chi \left(\frac{1}{1+m}\right)^\chi$$

where   Eo   is the number of eggs spawned/10m^2/day, at age zero,

e_χ is the number of eggs sampled/10m^2/day, at age χ days,

χ is the age, in days, determined by temperature, and

m   is the daily mortality rate (m = -0.16156).

From Figure 6 it can be seen that the sampled distribution of the number of eggs spawned/10m^2/day is highly skewed; inclusion of the zero values would have produced an even greater skewness. However, the observed distribution of the non-zero values was found to be well approximated by a lognormal distribution. A distribution with a non-zero probability of zero values and whose conditional distribution of non-zero values is lognormal is called a Δ-distribution (Aitchison 1955). The minimum variance unbiased estimator of the arithmetic mean (k) is given by:

$$k = [n_1 \div n] \cdot [\exp(\bar{y})] \cdot [G_{n_1}(s^2 \div 2)]$$

where   n   is the sample size

n_1 is the number of non-zero values

$\bar{y}$ is the sample mean of $\log_e$ (eggs spawned/$10m^2$/day) for non-zero values

s^2 is the sample variance of the log values, and

G_{n_1} is given by an infinite series and can be found in Aitchison and Brown (1957).

For our analysis, G_{n_1} was calculated by a program written for this purpose. The variance of k, given by Pennington (ms. 1980), is estimated by:

$$\text{var}(k) = \frac{n_1}{n} \cdot \exp(2\bar{y}) \cdot \frac{n_1}{n} \cdot [G_{n_1}(\frac{s^2}{2})]^2 - \frac{n_1-1}{n-1} \cdot [G_{n_1}(\frac{n_1-2}{n_1-1} \cdot s^2)]$$

which is a more efficient estimator of var(k) than that used by Berrien et al., in press). Confidence intervals can be generated by assuming k (or a weighted sum of the k's when estimating totals) is approximately normally distributed with standard error equal to $\sqrt{(\text{var } k)}$. The retransformed mean density (k) was raised to the number of eggs spawned in each subarea per day, then multiplied by the number of days represented by each effort in each subarea. The subarea estimates were summed over time, resulting in the total number of yellowtail flounder eggs spawned in 1977 in the area surveyed.

The number of days represented by an effort (part of a cruise) within a subarea was determined by first calculating the midpoint of time of sampling within each subarea, each time it was surveyed. Then, for each midpoint, half the days between the preceding midpoint and half between the following midpoint were summed to produce the number of days represented by that particular effort in that subarea.

The estimate of total egg production for the season, in conjunction with the spring 1977 groundfish trawl survey length-frequency distribution of the mean catch per tow, was used to estimate the population size of mature yellowtail flounder. The trawl survey results were used, rather than commercial fishery data, so as to be sure that all potential spawners were represented. A theoretical number of eggs spawned by the mature females in the trawl survey catch was calculated. This theoretical egg production by the catch was divided into the total season's egg production (based on the plankton survey) to derive a factor by which the trawl survey catch could be multiplied to give an estimate of the entire "catchable" (including spawning) population.

RESULTS

Seven distribution charts show the densities of eggs spawned per day during the series of surveys (Figures 1-4). Judging from the egg occurrences during the first survey and their incubation rates at prevailing temperatures, spawning began at least as early as during the last week of February (27th) in southern New England waters, by the first week of March (3rd) on western Georges Bank,

by the second week of March (11th) in the New York Bight, and by the third week of March (19th) on eastern Georges Bank. These results differ only slightly from previous reports. The onset of spawning has been reported as: mid-March near Gloucester, Massachusetts (Bigelow and Welsh 1925); during March in the Mid-Atlantic Bight (Smith et al. 1975); and by early April at the latest in southern New England waters (Royce et al. 1959). Bottom temperatures associated with eggs taken on our first survey in 1977 ranged from 1.6 to 6.2°C with a mean of 4.5°C (std. dev., 1.0°C). This is somewhat cooler than the implied minimum spawning temperatures of 5 to 7°C given by Royce et al. (1959).

As revealed by the results of these surveys, the general area of spawning changed little over the season, occurring principally over extreme eastern and western Georges Bank, and over the shoreward half of continental shelf waters west and south of Nantucket Shoals and south of Long Island, New York, with lesser but consistent spawning in adjacent areas extending from the Nova Scotia continental shelf southward to off New Jersey. We apparently sampled only the eastern edge of the spawning area in the western Gulf of Maine referred to by Bigelow and Schroeder (1953).

Table 2 summarizes the results from calculations used in deriving egg production estimates for individual subareas as well as for the entire survey area and season. Figure 7 portrays the spawning intensity over time for the entire survey area and subareas. Subarea 3, part of southern New England waters, contained the highest mean spawning density (123 eggs/10m^2/day during the fourth survey). However, due to the difference in area measurement the greatest contributor (with 595 x 10^9 eggs per day) to the overall daily egg production was Subarea 4, including Georges Bank and parts of southern New England and Gulf of Maine waters. The greatest individual station spawning density was 1042 eggs/10m^2/day on eastern Georges Bank during survey 5. Peaks in spawning intensity can be seen to occur earlier in Subareas 2 and 3, during the last week of April and first two weeks of May, than in Subarea 4 where it occurred around the first week of June in 1977.

Over the course of the entire spawning season Subarea 4 contributed the greatest amount of spawning (67.9% of all eggs produced). In decreasing order of abundance the other subareas contributed lesser amounts: Subarea 3, 13.7%; Subarea 2, 13.3%; Subarea 5, 3.6%; and Subareas 6 and 7, 1.0 and 0.5% respectively. The relatively minor abundances from Subareas 6 and 7 were not included individually on Figure 6 because their portrayal would have confused the graph. The total yellowtail flounder egg production for 1977 was estimated as 56.862 x 10^{12} eggs (std. error = 10.359 x 10^{12} eggs, coef. var. = 0.182).

Calculations used in estimating population sizes of adult, or "catchable" yellowtail flounder, are summarized in Table 3. Length frequencies of fish in the reference catch were assumed proportional to those of the population. Using the percent-female-at-length (S. Clark, pers. comm.), percent-mature-at-length (Royce et al. 1959), and fecundity-at-length (Howell and Kesler 1977), I calculated the theoretical number of eggs which could be spawned by females in the reference catch (1.4977 x 10^{12} eggs). Dividing the estimated total eggs

spawned (56.862×10^{12}) by those theoretically spawned by the reference catch gives a factor (37.967) which when multiplied by either the reference catch, the number of females, or the number of mature females in the reference catch produces an estimate of that population (Table 3). By these methods total population estimates of mature females (49.349×10^6), all females (100.707×10^6) and all fish (200.881×10^6) were calculated. A total male population of 100.174×10^6 fish was determined by subtraction, resulting in an overall sex ratio of 49.87% male to 50.13% female.

DISCUSSION

The estimates in Table 3 include fish as small as 6 cm in length. Therefore, to compare these results with virtual population assessments (VPA) based on commercial catch statistics, it is necessary to eliminate smaller fish not yet recruited to the fishery. By subtracting those less than 27 cm, which is the mean length of age 2 yellowtail flounder, approximately the size at which 50% recruitment occurs (Brown and Hennemuth 1971), an estimate of 138.1×10^6 fish is provided. Population estimates from 1960-1964 as well as commercial landings and trawl survey catch-per tow statistics have been used to compare my results with earlier estimates (Table 4). From these data it is clear that landings and catch-per-tow values were considerably lower in 1977 than in the early 1960's indicating a smaller population in 1977 than earlier. Had a similar VPA estimate based on commercial fishery data been available for the 1977 yellowtail flounder population, it would undoubtedly have been less than 237×10^6 fish reported by Brown and Hennemuth (1971) as the average population in southern New England and Georges Bank waters for 1960-1964. Therefore my value of 138.1×10^6 fish (which is 58.2% of 237.2×10^6) which applied to waters between Nova Scotia and Cape Hatteras, seems quite reasonable.

Due to insufficient data I could not determine the percent-mature-at-length for male yellowtail flounder. Therefore I could not calculate an estimate of the total spawning population, rather only that for spawning females, as well as for all yellowtail flounder capable of being caught in the otter trawl during the spring groundfish survey. Estimates reported here can be converted from length frequencies to age frequencies with the appropriate length-age key.

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Table 1. Ichthyoplankton survey dates (1977) and coverage.

Survey	Cruise	No. of Samples	Sampling Dates	Subareas
1	GO-77-01	102	5 Mar-6 Apr	3,4,5
	DE-77-03	69	19 Mar-8 Apr	1,2
2	DE-77-04 (pt. 1)	93	13-23 Apr	1,2,3
3	AL-77-02	105	14 Apr-13 May	3,4,5,6,7,8
	DE-77-04 (pt. 2)	57	24-29 Apr	2
4	DE-77-05 (pt. 1)	90	4-13 May	1,2,3
5	DE-77-05 (pt. 2)	77	18-27 May	2,3
	NO-77-02	76	24 May-5 Jun	4(pt.),7
	DE-77-07 (pt. 1)	32	12-16 Jun	4(pt.),6
6	DE-77-07 (pt. 2)	94	21-30 Jun	1,2,3
7	YU-77-02	144	31 Jul-30 Aug	1(pt.),2(pt.),3,4,5,7,8
	DE-77-09	15	30 Jul- 3 Aug	1(pt.),2(pt.)

Table 2. Yellowtail flounder egg production estimate.

Subarea	Survey	n	n_1	$\bar{y}$	s^2	k^a	Std. Error of k^a	Area (km^2)	Eggs Spawned in Subarea Per Day ($\times 10^{-9}$)	Sampling Midpoint Date	Days Represented	Eggs Spawned Represented by this Effort in this Subarea ($\times 10^{-12}$)
1	1	15	0					16560	0	24 Mar	21.47	0
1	2	17	0					16560	0	14 Apr	21.09	0
1	4	17	0					16560	0	5 May	34.48	0
1	5	17	0					16560	0	22 Jun	49.28	0
1	7	17	0					16560	0	11 Aug	50.32	0
2	1	54	15	2.47529	1.79704	7.3429	3.2372	67288	49.4090	29 Mar	20.58	1.0168
2	2	58	22	2.99793	2.01189	16.3336	6.5099	67288	109.9054	19 Apr	14.20	1.5612
2	3	57	28	2.56954	2.37508	19.3472	7.5061	67288	130.1831	26 Apr	10.26	1.3363
2	4	66	24	2.40451	2.20831	11.1384	4.4725	67288	74.9478	9 May	13.18	0.9874
2	5	69	22	2.99576	2.09949	16.6960	6.7946	67288	112.3443	23 May	23.54	2.6446
2	6	69	0					67288	0	25 Jun	41.95	0
2	7	58	0					67288	0	15 Aug	50.47	0
3	1	18	3	0.37156	0.93012	0.3226	0.2214	14131	0.4559	7 Mar	39.57	0.0180
3	2	8	3	3.43819	0.69344	14.5323	9.0516	14131	20.5356	22 Apr	13.04	0.2678
3	3	8	6	3.41184	2.12710	50.4353	29.8236	14131	71.2701	15 Apr	23.42	1.6691
3	4	7	5	4.22099	2.67768	123.0481	82.9708	14131	173.8792	11 May	16.60	2.8873
3	5	8	3	5.00699	1.26764	92.3491	57.1399	14131	116.3675	26 May	24.40	2.8388
3	6	8	1	n.a.	n.a.	2.0588	2.0588	14131	2.9092	29 Jun	40.84	0.1188
3	7	9	0					14131	0	15 Aug	47.29	0
4	1	70	15	2.31562	2.55894	6.6399	3.4207	84794	56.3027	21 Mar	39.73	2.2352
4	3	54	24	2.49982	2.33162	19.6971	8.9085	84794	167.0197	30 Apr	37.81	6.3150
4	5	81	50	3.58450	2.39818	70.2166	21.4594	84794	595.3949	1 Jun	49.98	29.7608
4	7	55	3	2.19381	0.52486	0.5786	0.3776	84794	4.9066	8 Aug	64.05	0.3143
5	1	14	1	n.a.	n.a.	0.1229	0.1229	19137	0.2351	1 Apr	26.08	0.0061
5	3	12	2	3.06265	9.68158	16.2830	16.0688	19137	31.1608	27 Apr	65.57	2.0432
5	7	10	0					19137	0	10 Aug	105.06	0
6	3	19	2	1.42497	1.32494	0.5908	0.4980	29837	1.7628	6 May	38.43	0.0677
6	5	17	5	2.00359	2.00446	4.4649	2.9390	29837	13.3220	14 Jun	38.43	0.5120
7	3	5	0					9299	0	12 May	23.00	0
7	5	9	4	1.56137	0.65554	2.6784	1.4214	9299	2.4906	4 Jun	43.87	0.1093
7	7	7	2	1.86779	1.37042	2.5204	2.0873	9299	2.3438	8 Aug	64.74	0.1517
8	3	7	0					9734	0	9 May	91.82	0
8	7	3	0					9734	0	9 Aug	91.82	0

The estimated total egg production is 56.8616 $\times 10^{12}$ eggs (std. error = 10.3592 $\times 10^{12}$).

[a] For $n_1 = 1$, the mean is estimated by $\frac{x}{n}$, and its variance by $(\frac{x}{n})^2$, where x is the single non-zero value; both are unbiased estimators.

Table 3. Calculations for yellowtail flounder population estimate.

Total Length (cm)	Reference[a] Catch of Fish	Percent[b] Females in Catch	Females in Catch	Percent[c] Females Mature	Mature Females in Catch	Fecundity[d]	Theoretical Egg Production by Catch (x 10⁻⁶)	Mature[e] Females in Population (x 10⁻³)	Females[e] in Population (x 10⁻³)	Fish[e] in Population (x 10⁻³)
5	0	50.0								
6	44000	50.0	22000						835.3	1670.5
7	100000	50.0	50000						1898.3	3796.7
8	248000	50.0	124000						4707.9	9415.7
9	220000	50.0	110000						4176.3	8352.7
10	253000	50.0	126500						4802.8	9605.5
11	59000	50.0	29500						1120.0	2240.0
12	12000	50.0	6000						227.8	455.6
13	0	50.0								
14	17000	50.0	8500						322.7	645.4
15	20000	50.0	10000						379.7	759.3
16	10000	50.0	5000						189.8	379.7
17	0	50.0								
18	17000	50.0	8500						322.7	645.4
19	20000	50.0	10000						379.7	759.3
20	31000	50.0	15500						588.5	1177.0
21	94000	50.0	47000						1784.4	3568.9
22	96000	50.0	48000	1.4	664	148871	99	25.2	1822.4	3644.8
23	68000	50.0	34000	6.6	2251	176722	398	85.5	1290.9	2581.7
24	68000	50.0	34000	11.9	4031	208257	840	153.1	1290.0	2581.7
25	150000	52.4	78532	17.1	13424	243780	3273	509.7	2981.6	5695.0
26	127000	47.9	60846	22.3	13587	283604	3853	515.9	2310.1	4821.8
27	205000	46.5	95330	27.6	26280	328055	8621	997.7	3619.4	7783.2
28	153000	44.6	68171	32.8	22363	377468	8441	849.0	2588.2	5808.9
29	113000	44.4	50219	38.0	19104	432192	8257	725.3	1906.7	4290.2
30	133000	40.2	53479	43.3	23145	492582	11401	878.7	2030.4	5049.6
31	136000	41.6	56641	48.5	27480	559008	15361	1043.3	2150.5	5163.5
32	341000	42.4	144679	53.8	77768	631849	49138	2952.6	5493.0	12946.6
33	354000	44.5	157466	59.0	92888	711494	66089	3526.6	5978.5	13440.2
34	387000	45.8	177424	64.2	113952	798345	90973	4326.4	6736.2	14693.1
35	399000	46.7	186421	69.5	129493	892810	115613	4916.4	7077.8	15148.7
36	320000	48.6	155533	74.7	116103	995313	115638	4411.1	5905.1	12149.3
37	322000	52.6	169263	79.9	135303	1106285	149684	5137.0	6426.3	12225.2
38	190000	55.4	105252	85.2	89647	1226168	109922	3403.6	3996.1	7213.7
39	172000	59.5	102402	90.4	92582	1355414	125486	3515.0	3887.9	6530.3
40	98000	63.3	62018	95.6	59319	1494487	88651	2252.1	2354.6	3720.7
41	91000	67.3	61210	100.0	61210	1643860	100621	2323.9	2323.9	3455.0
42	52000	70.2	36506	100.0	36506	1804017	65858	1386.0	1386.0	1974.3
43	54000	74.8	40396	100.0	40396	1976450	79801	1533.7	1533.7	2050.2
44	38000	79.6	30266	100.0	30266	2158665	65335	1149.1	1149.1	1442.7
45	22000	84.9	18684	100.0	18684	2354174	43985	709.4	709.4	835.3
46	10000	88.3	8834	100.0	8834	2562504	22637	335.4	335.4	379.7
47	19000	91.6	17410	100.0	17410	2784186	48472	661.0	661.0	721.4
48	0	94.8								
49	8000	95.5	7640	100.0	7640	3269800	24983	290.1	290.1	303.7
50	10000	96.0	9598	100.0	9598	3534850	33929	364.4	364.4	379.7
51	0	97.5								
52	10000	98.0	9804	100.0	9804	4112308	40316	372.2	372.2	379.7
53	0	98.0								
Sum	5289000						1497674	49349.5	100707.4	200881.3

[a]Reference catch is the stratified catch per tow (multiplied by 1 x 10⁶) from the NMFS spring groundfish survey; M. McBride, pers. comm.

[b]Percent females based on NMFS port sampling data from New Bedford, Massachusetts during first two quarters of 1976, 1977, and 1978; S. Clark, pers. comm.

[c]Percent females mature based on regression of data from Royce et al. (1959).

[d]Fecundity from Howell and Kesler (1977).

[e]These population estimates relate to those sizes caught during NMFS spring groundfish survey.

Table 4. Yellowtail flounder population and catch statistics.

Year	Fishery[a] Landings (m.t. x 10^{-3})	V.P.A.[b] Population Estimate (no. x 10^{-6})	Summer Trawl Survey[a] mean no. per tow	
			Southern New England	Georges Bank
1960	19.4	199.7	ND	ND
1961	25.1	284.6	ND	ND
1962	31.5	292.7	ND	ND
1963	49.2	203.1	28.2	18.4
1964	53.0	205.7	24.5	11.2
1977	16.9	ND	9.0	2.0

[a]Clark et al. (1981)

[b]Brown and Hennemuth (1971)
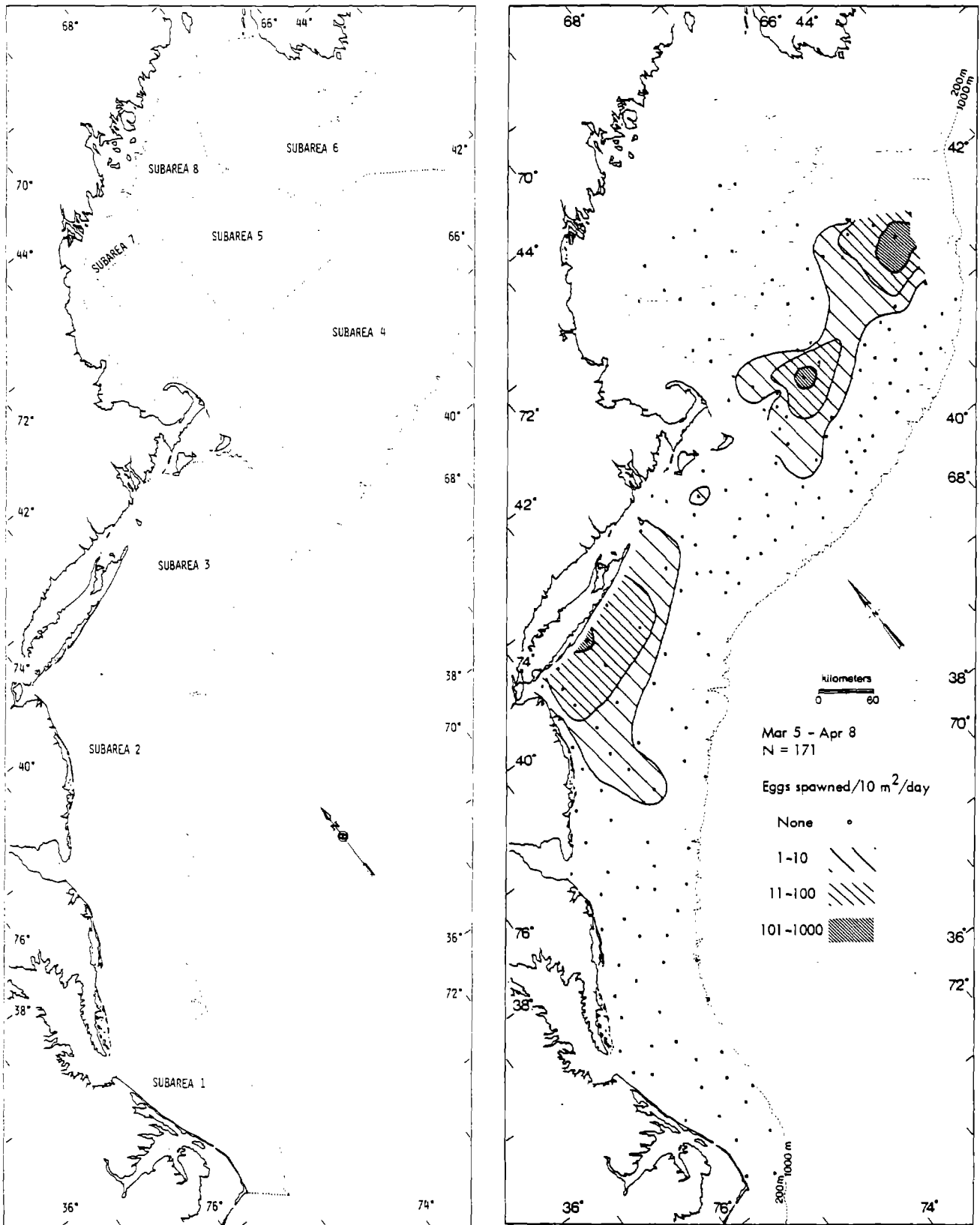
Figure 1.   Left; total survey area and subarea boundaries for seven ichthyo-
plankton surveys, 1977.   Right; distribution of yellowtail flounder
eggs during the first survey, 1977.
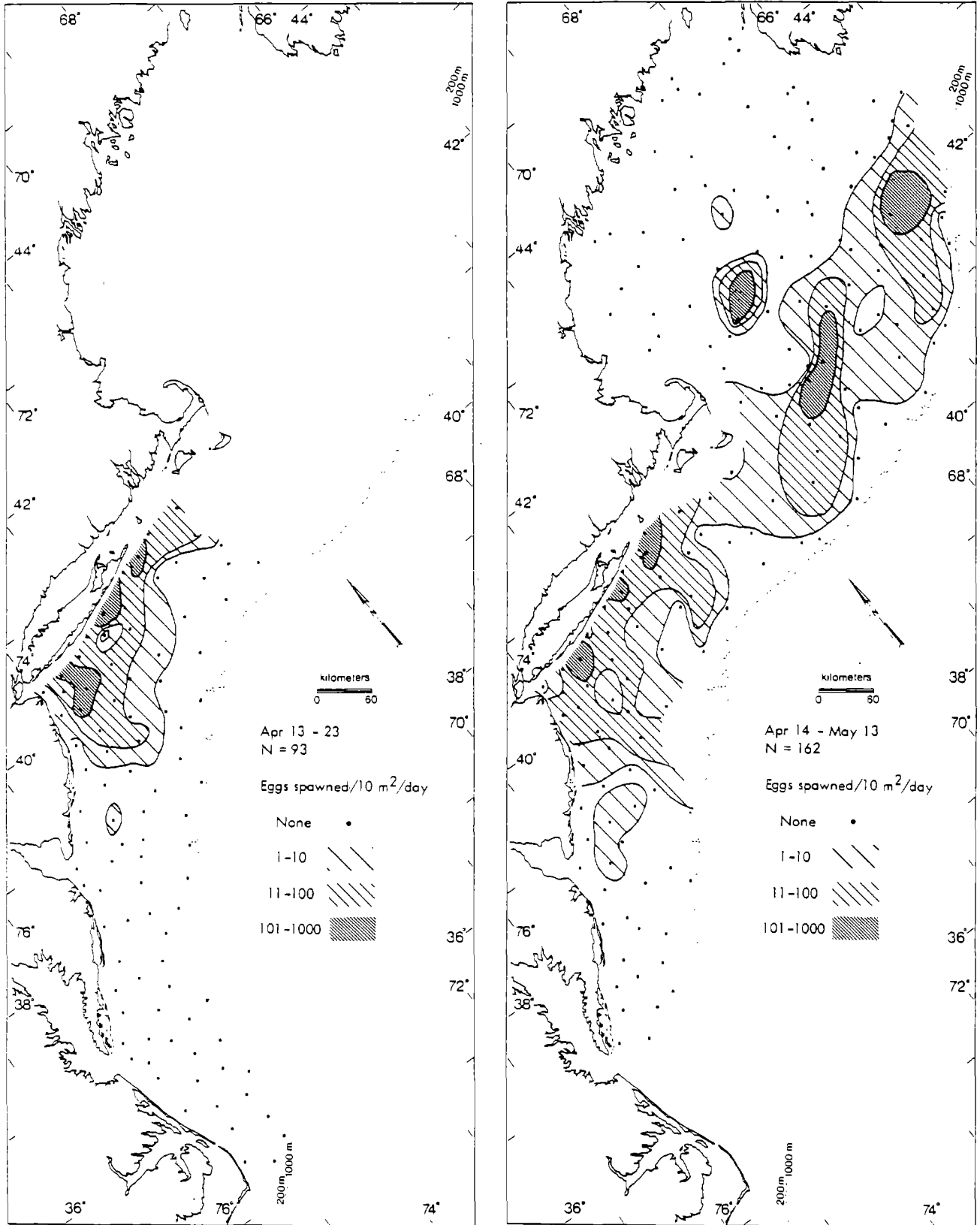
Figure 2.   Distribution of yellowtail flounder eggs during the second and third ichthyoplankton surveys, 1977.
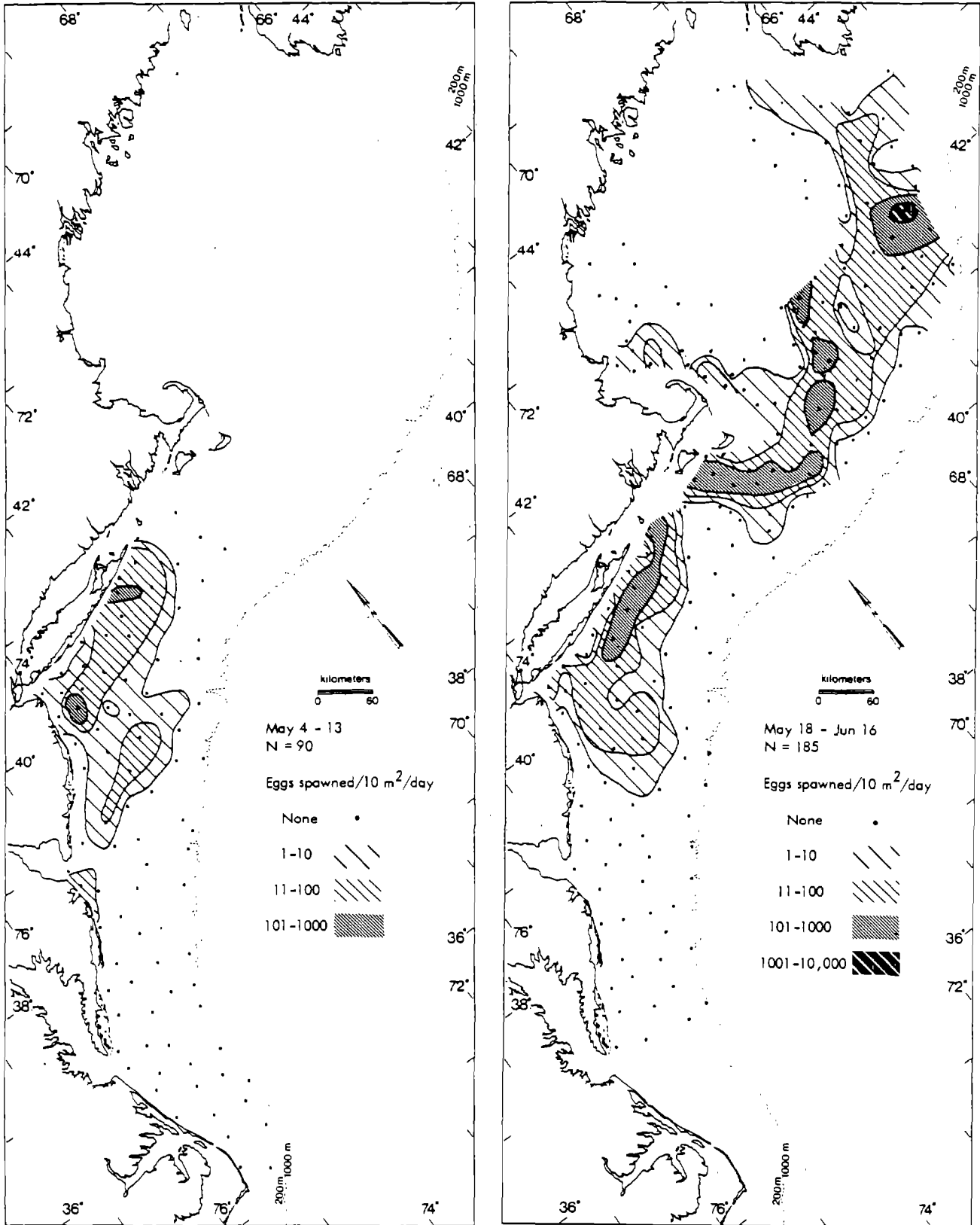
Figure 3.   Distribution of yellowtail flounder eggs during the fourth and fifth ichthyoplankton surveys, 1977.
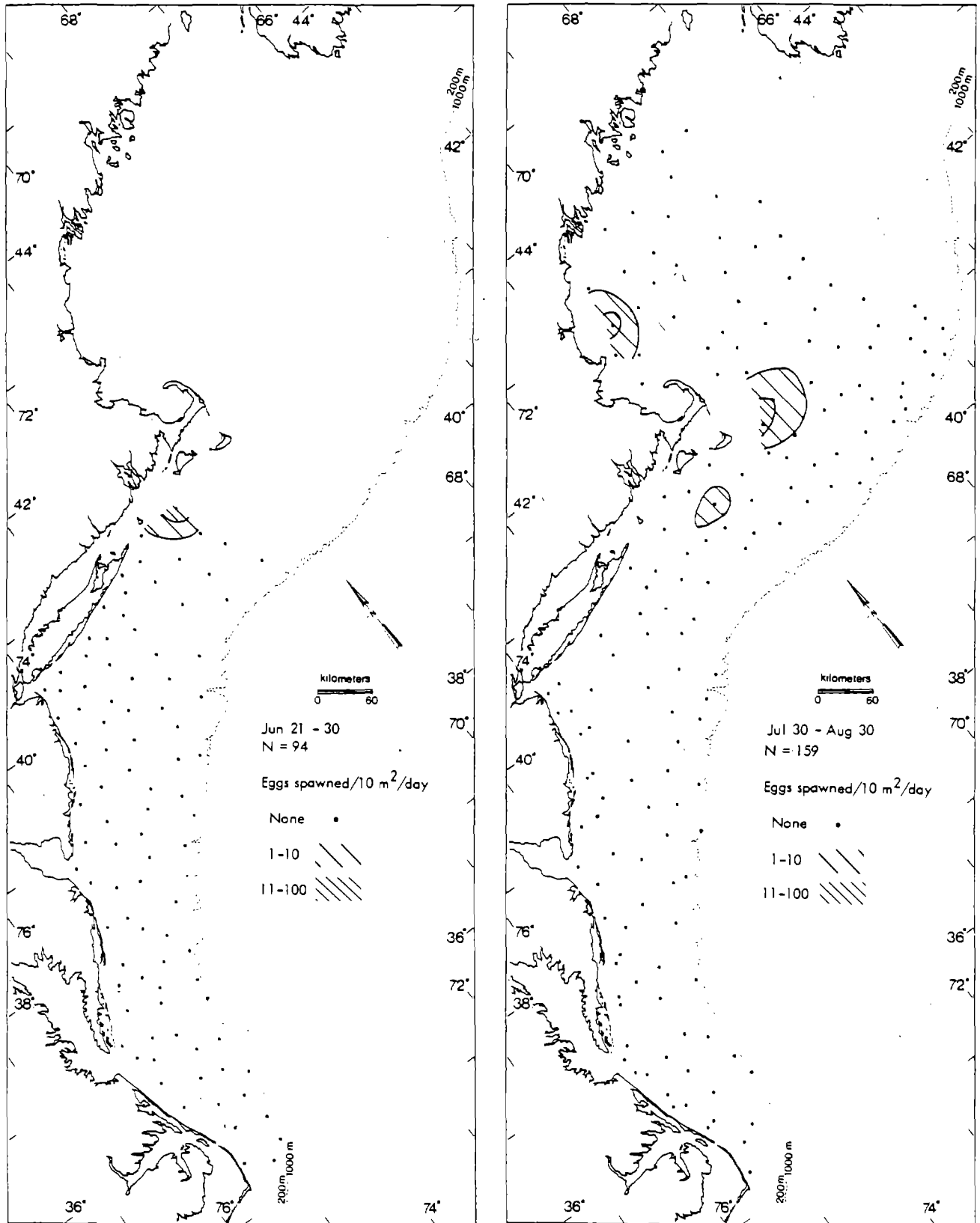
Figure 4. Distribution of yellowtail flounder eggs during the sixth and seventh ichthyoplankton surveys, 1977.
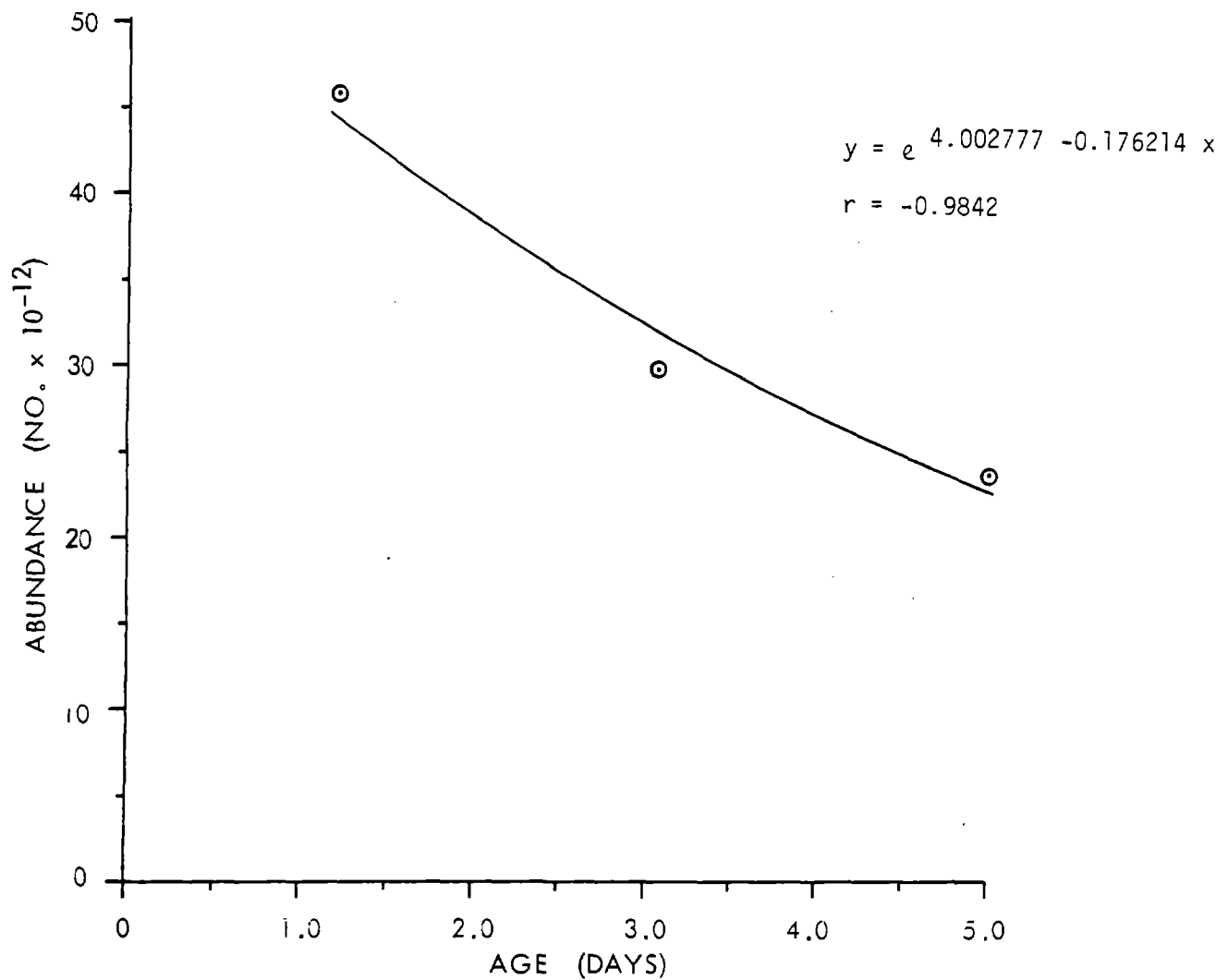
Figure 5. Regression of stage-abundance on the weighted mean age; used
to calculate season-long mortality rate for <u>Limanda ferruginea</u>
eggs, 1977; y is egg abundance at age (x=no. of days), r is the
regression coefficient.
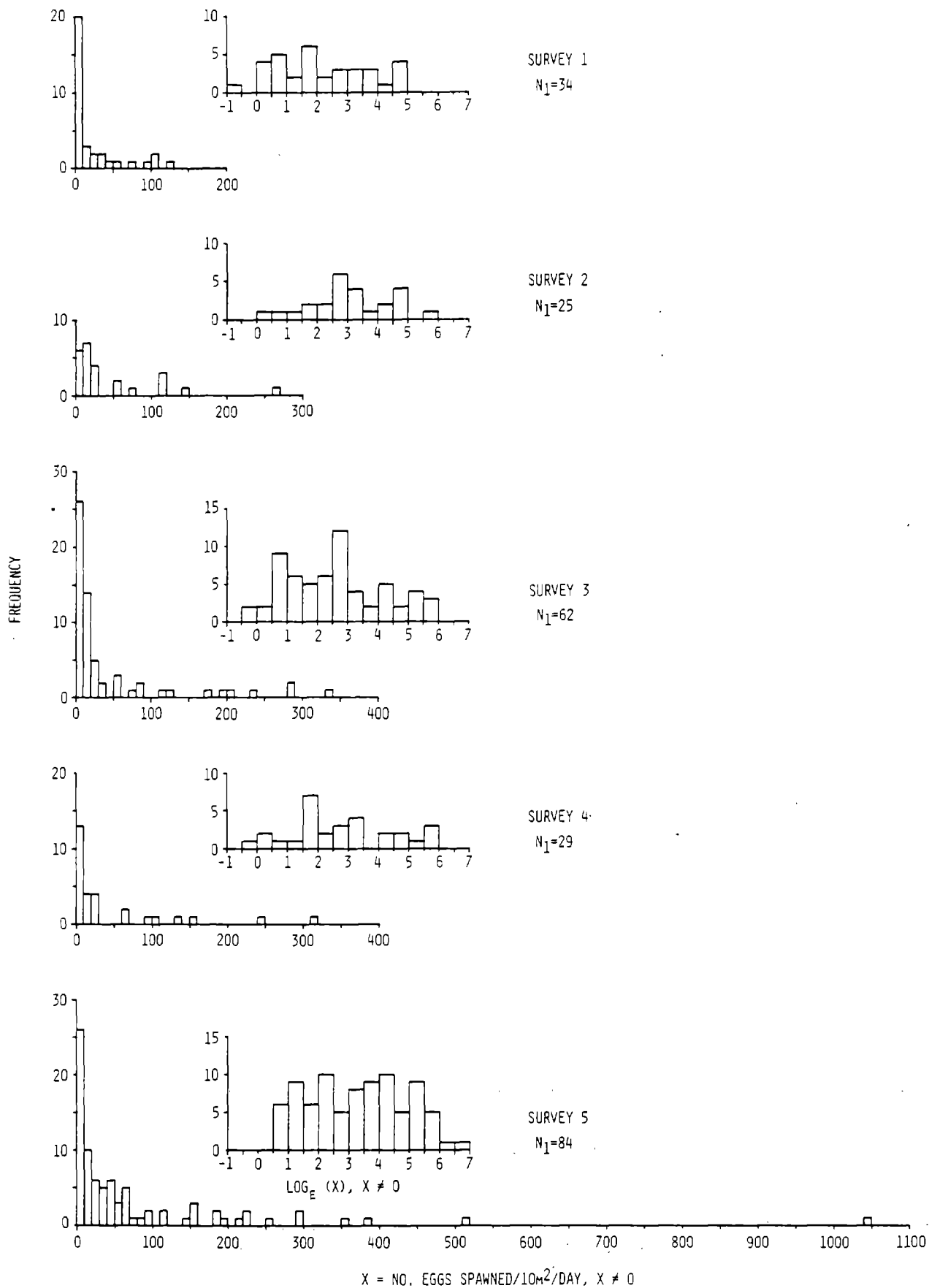
Figure 6. Frequency distributions of non-transformed and log$_e$-transformed values of eggs spawned/10m^2/day.
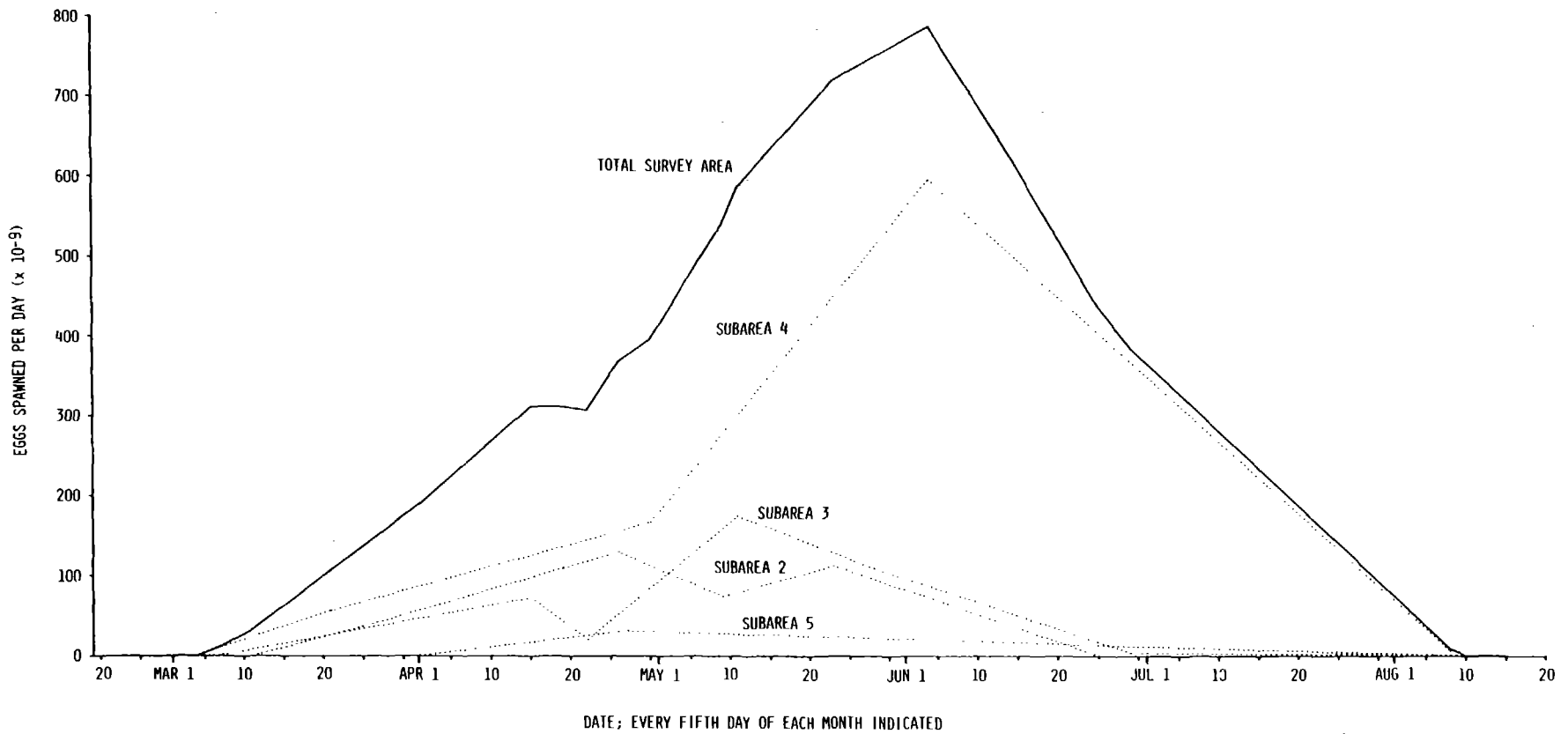
Figure 7. Estimated daily egg production in four subareas and in the total survey area; Subareas 6 and 7 not shown, but are included in the total.

This paper not to be cited without prior reference to the author

SILVER HAKE, Merluccius bilinearis, EGG CENSUS AND ADULT
POPULATION ESTIMATE FOR 1979 IN WATERS OFF EASTERN UNITED STATES

Peter Berrien

U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Sandy Hook Laboratory
Highlands, New Jersey 07732 USA

ABSTRACT

Seasonal egg production of silver hake, Merluccius bilinearis, is
calculated from broadscale ichthyoplankton surveys off eastern United States
in 1979 and used to derive biomass estimates of the adult population.
Spawning occurred from late March to mid-December, reaching a peak in the
first half of July; it occurred from North Carolina to the Gulf of Maine and
western Scotian Shelf and was most abundant on Georges Bank and in southern
New England waters. The sum of eggs spawned (208.7049×10^{12} eggs) is related
to the theoretical egg production of a reference catch of adults to obtain
estimates of all spawners and of the total "catchable" population. An
estimate of 1.54755×10^9 spawners, with a biomass of 364.4×10^3 metric tons,
is calculated.

INTRODUCTION

Silver hake, Merluccius bilinearis, is an economically important species
which occurs in shelf waters of eastern North America. It is found as far
north as southern and eastern Gulf of St. Lawrence, southern Newfoundland and
Grand Banks, and as far south as South Carolina. It is most abundant from
Nova Scotia to New York (Nichols and Breder 1927; Bigelow and Schroeder 1953;
Inada 1981).

Previous studies have indicated that the population consists of separate
stocks (Conover et al. 1961; Konstantinov and Noskov 1969; Nichy 1969;
Anderson 1974; Almeida 1978). As a result of these studies, population
estimates and management measures for silver hake have been reported for three
areas which are roughly in accordance with ICNAF (International Commission for
the Northwest Atlantic Fisheries) and NAFO (Northwest Atlantic Fisheries
Organization) divisions and subdivisions: 1) Gulf of Maine, 2) Georges Bank,
and 3) southern New England-Middle Atlantic stocks (Anderson et al. 1980).

The fishery for silver hake was almost exclusively that of the United
States until 1962 when fleets from European countries, notably the USSR, began

fishing on Georges Bank. Catches increased markedly until the mid-1970's when, due to declining populations and ensuing restrictions on fishing, they decreased rapidly (Clark and Brown 1977, Almeida and Anderson 1981). In the Gulf of Maine the population of age 2+ silver hake, estimated from Virtual Population Analysis (VPA) at 145 to 152 x 10^3 metric tons (MT) in the early 1960's, decreased to a low of approximately 15 to 30 x 10^3 MT in the early 1970's, then subsequently increased to between 25 and 40 x 10^3 MT in the late 1970's. On Georges Bank the decline was even greater, from about 550 to 600 x 10^3 MT in the early 1960's to a low of 20 to 30 x 10^3 MT during 1978 to 1981. Similarly silver hake in southern New England-Middle Atlantic area declined from 320 to 370 x 10^3 MT in the mid-1960's to between 60 and 80 x 10^3 MT in 1978 to 1981 (Almeida and Anderson 1981).

Additional population estimates useful for comparative purposes can be made based on plankton samples. These estimates, which are independent of fishery statistics, are derived from total egg production numbers as determined by plankton surveys, along with ancillary biological information such as representative length-frequency distributions and fecundity, sex ratio and maturation by size, taken on research trawl surveys. Population estimates of adults, based on ichthyoplankton survey results, are now possible for species off northeastern United States because of the inception of National Marine Fisheries Service, MARMAP (Marine Resource Monitoring, Assessment and Prediction) cruises in 1976. Within the framework of this program bi-monthly surveys are conducted to sample ichthyoplankton, zooplankton and phytoplankton and measure nutrients, primary production, chlorophyll, salinity and temperature (Sherman 1980). These surveys constitute the field work needed in order to measure seasonal and annual variability in the structure, function and rates of change in biological and environmental components of the shelf ecosystem, with principal emphasis on fish population levels. The purpose of this paper is to report on a silver hake egg census and corresponding adult population estimate from MARMAP surveys in 1979.

PROCEDURES

The total MARMAP area includes the Gulf of Maine, the western part of the Scotian Shelf, Georges Bank and shelf waters southward to Cape Hatteras, an area of 258,067 km^2. During February to December 1979 seven surveys each covered all or part of the area.

The total area is divided into four subareas, based on oceanographic and biological considerations, these are: Gulf of Maine, Georges Bank, southern New England and Middle Atlantic (see Fig. 1). Data are summarized according to this subdivision, then for the purpose of comparison with adult catch statistics and research trawl surveys, the southern New England and Middle Atlantic subareas, are combined in the adult population estimate. This conforms to areas designated by the Resource Assessment Division of the Northeast Fisheries Center for research trawl surveys, but only approximately with the same three nominal areas designated for management purposes (Anderson et al. 1980) which follow ICNAF subarea delineations.

Plankton was sampled with 61-cm bongo nets fitted with 0.505 and 0.333-mm mesh nets. The 0.505-mm side was used for ichthyoplankton collections. A flowmeter in the net mouth determined water volume filtered and a bathykymograph recorded tow profile and maximum depth sampled. Smooth, double

oblique tows were made by adjusting the vessel speed to maintain a 45° wire angle throughout the haul and paying out enough wire to sample to within 5 m of the bottom, or to a maximum sampling depth of 200 m. Usually the vessel speed was around 1.5 kt (2.8 km/hr) but varied from about 1.0 to 2.0 kts. See Jossi et al. (1975) for a detailed description of sampling procedures.

All fish eggs and larvae were removed from samples. The eggs of selected species, including silver hake, were identified, then further separated into developmental stages. Eggs were staged to determine mortality rate. Two egg stages were used for silver hake: just spawned to tail free, and tail free to hatch. Using early-stage data for census calculations minimizes any bias which might be introduced by an inaccurate mortality rate. The instantaneous daily mortality rate (Z) was derived using the expression:

$$N_0 = \frac{N_t}{e^{-Zt}}$$ (Gulland 1969)

which becomes:

$$Z = \frac{\ln N_0 - \ln N_t}{t}$$

where: Z is the instantaneous daily mortality rate,

N_0 is the number of eggs at the beginning of time interval t, and

N_t is the number of eggs at the end of t.

In this case the values N_0 and N_t were the season-long abundances of eggs in the two above-mentioned stages and t was the difference between their weighted mean ages. The resulting instantaneous mortality rate (Z = .6344) was used to adjust the numbers of early-stage eggs sampled/10m^2/day to become the numbers of eggs spawned/10m^2/day. This procedure required knowledge of each stage's incubation time at various temperatures. Only limited information on this exists for silver hake, but that which is available indicates a very similar incubation rate as for its congener the Pacific hake, Merluccius productus. Incubation time versus temperature for Pacific hake has been reported (Zweifel and Lasker 1976); and since the two species appear to be similar in this relationship, incubation time versus temperature for Pacific hake was used for silver hake. Surface water temperature associated with each silver hake egg collection was used as incubation temperature.

The number of eggs sampled at each station was standardized by allowing for the volume of water filtered by the net, and the maximum depth sampled, and expressed as the number of eggs sampled/10m^2. Then using the incubation rate at the temperature on station and adjusting for mortality, the number of eggs spawned/10m^2/day was calculated, using the equation from Gulland (1969) noted above, where:

N_0 is the number of eggs spawned/10 m^2/day at age zero,

N_t is the number of eggs sampled/10 m^2/day with mean age t, and

Z is the instantaneous daily mortality rate (Z = .6344).

Although frequency distributions of the numbers of eggs spawned/$10m^2$/day were found to be highly skewed, ln-transformation of non-zero densities produced normal distributions. A data set which has a proportion of zero values and which has a lognormal distribution is referrable to the Δ-distribution, as described by Aitchison (1955). Mean densities and associated variances were calculated using equations applicable to the Δ-distribution (Pennington 1983, in press). Re-transformed mean densities were raised to the number of eggs spawned in each subarea per day, then multiplied by the number of days represented by each survey in each subarea. The subarea estimates were summed over time to calculate the total number of silver hake eggs spawned in 1979 in the entire area surveyed.

The number of days represented by a survey within a subarea was determined by first calculating the midpoint in time of spawning (as represented by early-stage collections) within each subarea, each time it was surveyed. Then, for each midpoint, half the days between the preceding and the following midpoints were summed and assumed to be the number of days represented by that particular effort in that subarea. When no early-stage collections were obtained within a subarea, the sampling mid-point was used.

The estimate of total eggs produced for the season, in conjunction with the fall 1979 groundfish trawl survey length-frequency distribution of mean catch per tow, was used to estimate the population size of mature silver hake within each subarea. A theoretical number of eggs which could have been spawned by the mature females in the trawl survey catch was calculated. This theoretical egg production was divided into the total season's egg production, based on the plankton survey, to derive a factor by which the trawl survey catch was multiplied. This produced an estimate of the entire catchable population, including spawners.

RESULTS

Silver hake eggs were taken during six of the seven plankton surveys conducted in 1979. They did not occur on the first survey which was made on 3 February to 14 March. Judging from collection dates, ages of eggs at collection and incubation rates, I found that eggs were first spawned on the southern edge of Georges Bank as early as 30 March, and in inshore as well as offshore southern New England waters as early as 14 April (Fig. 1). Spawning rapidly increased during May and June in area and intensity, spreading throughout Georges Bank, southern New England and Middle Atlantic waters. Eggs were most concentrated offshore in May, then in mid-shelf waters during June and July (Fig. 1). The peak in spawning intensity occurred during the first half of July (Fig. 3). Unfortunately our survey at that time failed to sample most of the Gulf of Maine (Fig. 1) where silver hake spawn during the summer (Bigelow and Schroeder 1953). Spawning remained widespread throughout August although at a lesser intensity than during the previous survey (Fig. 2). By the time of the October survey spawning had virtually ceased in the Gulf of Maine, was significantly reduced in area and intensity in Middle Atlantic and Georges Bank waters and had decreased in intensity off southern New England (Fig. 2). By November and December, spawning was so reduced as to be almost terminated, although eggs were scattered in offshore waters of southern New England and Georges Bank in the first two weeks of December. Whether or not spawning continued at this time offshore in the Middle Atlantic waters was not determined.

Calculations of egg production estimates for subareas and the total area were summarized (Table 1). Resulting values plotted over time for the total area indicate that spawning intensity increased steadily and rapidly from late March to July, reached a peak in the second week of July, then similarly declined so as to end early in December (Fig. 3). The time lag of over one month between peaks in spawning, in Georges Bank and southern New England waters on one hand, and in the Gulf of Maine on the other, may represent a seasonal progression in spawning intensity between the areas. However, this lag may have reflected our low level of sampling in the Gulf of Maine in July, especially in the western and southwestern portions where spawning has been reported as significant (Bigelow and Schroeder 1953). MARMAP collections of larval silver hake during the last week of August 1979 (Silverman 1982) indicate that western Gulf of Maine was an important spawning area during late July and/or early August.

Despite being the smallest of the four subareas, comprising only 16.2% of the total survey area, Georges Bank produced the most silver hake eggs. Over the whole season 85.4 x 10^{12} eggs, or 40.9% of the total, were spawned there. Peak spawning occurred during the second week of July when the mean density was 224.9 eggs spawned/$10m^2$/day. One locality on Georges Bank produced the two highest spawning densities sampled; the values of 6617 and 1860 eggs spawned/$10m^2$/day were sampled on 23 May and 13 July respectively (Fig. 1). Southern New England waters ranked second in egg production, contributing 33.8% of the total while the Gulf of Maine and Middle Atlantic waters produced 17.4 and 7.9% respectively. Total production, for the entire season was calculated as 208.7049 x 10^{12} eggs (std. error = 45.6339 x 10^{12}, coef. var. = 0.2187).

Calculations used in estimating population sizes of catchable and mature silver hake are summarized in Tables 2 to 5. Length frequencies of fish in the reference catches were assumed proportional to those of the population. The reference catch is the subarea mean catch per tow from the fall 1979 bottom trawl survey (Almeida unpubl. data)[1]. Theoretical numbers of eggs which could have been spawned by the reference catches were calculated for each subarea using percent-female-at-length (Almeida unpubl. data)[1], percent-mature-at-length (Morse unpubl. data)[2], both from the 1979 fall bottom trawl survey, and fecundity-at-length (Mari and Ramos 1979). Dividing the estimates of total eggs spawned, by those theoretically spawned by the reference catches, produced factors which when multiplied by the reference catches produced population estimates for each subarea. A total spawning population of 1.54755 x 10^9 fish results from summing all subarea estimates. This is equivalent to a spawning biomass of 364.4 x 10^3 MT (Table 6).

DISCUSSION

The following conditions should be met in order for a series of plankton surveys to produce an accurate egg census: the entire spawning area should be sampled, the entire spawning season should be sampled, and sampling should be frequent enough to be able to describe spawning intensity over time (Saville 1964). The latter two conditions were met during 1979 for silver hake off the United States east coast. However, there were instances of incomplete areal coverage. Lack of sampling on eastern Georges Bank during surveys in July and August-September was not felt to be a major problem, assuming that the portion we did sample was representative of the area missed. Previous reports of

silver hake spawning on Georges Bank, based on egg samples in 1959-62 (Sauskan and Serebryakov 1968), and abundances of larvae in 1971 (Colton and Byron 1977) and 1979 (Silverman 1982) indicate considerable variation in the relative importance of western versus eastern Georges Bank silver hake spawning between years. Patterns of egg densities described for western and central Georges Bank during summer 1979 show the highest spawning levels on central rather than on western Georges Bank (Fig. 1). And although Silverman (1982) illustrated somewhat greater concentrations of larvae on southwestern rather than on eastern Georges Bank during October, he also noted advective circulation which would tend to move larvae from spawning areas farther east. Lack of sampling in the western Gulf of Maine in July, and in Middle Atlantic waters in April and November-December may have biased the estimate downward. Overall I feel the estimate of egg production is conservative, slightly lower than it probably would have been if we had covered all the area every time.

Spawning population estimates derived from these egg production numbers were consistently greater than the estimates from VPA as reported by Almeida and Anderson (1981) (Table 6). Moreover, as noted above, had we been able to fully sample all areas on all surveys the discrepancies would probably be even greater than those noted here.

Silver hake catches have undergone sharp declines in recent years due to reductions in biomass and, since the implementation of extended jurisdiction in 1977, restrictions placed on the foreign fishery. Consequently, population estimates from VPA for the most recent years must be considered tentative due to the VPA's tendency to underestimate population sizes in a fishery with declining catches (Almeida pers. comm.)[1].

One reason for the disparate population estimates may lie in the use of different size (age) at maturity information. Almeida and Anderson (1981) and Anonymous (1982) used a spawner age definition of age 2+ for all years calculated. This assumes that no one-year-olds are spawners and all two-year-olds and older are spawners. However, the size at maturation can vary between years. The length at 50% mature for female silver hake was observed to vary by as much as 3.7 cm between adjacent years during the period 1977 to 1980 (W. Morse unpubl. data)[2]. The use of the "age 2+" definition, in conjunction with growth relationships described by Almeida (1978) would exclude many fish which I calculate as spawners in 1979 based on the percent mature-at-length. Had I used the criterion of age 2.8+ year to define spawners (as would apply to autumn data rather than age 2.0+ year) then my calculated estimates of spawners would be closer to the VPA estimates (1.155×10^9 spawners with a biomass of 342.4×10^3 MT).

Another possible source of bias in my population estimate could be in the use of Mari and Ramos' (1979) fecundity data. If their determination of total fecundity was based, even partially, on gonad samples taken after the beginning of spawning, then the fecundity estimates would be biased downward. This appears to be a possibility in their study, since they note that gonad samples were taken off Nova Scotia during July and August. Resulting population estimates on my part would be biased upwards.

FOOTNOTES

[1]F. Almeida, unpubl. data, pers. comm., NMFS, Woods Hole, Massachusetts.

[2]W. Morse, unpubl. data, pers. comm., NMFS, Sandy Hook Laboratory, Highlands, New Jersey.

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Table 1. Silver hake egg production by subarea, 1979; N = no. samples in subarea; N_1 = no. samples containing silver hake eggs and k = mean density of eggs spawned per $10m^2$ per day.

Subarea	Sampling dates	N	N_1	k	Std. error (k)	Eggs spawned in subarea/day $(x10^{-9})$	Days repr. by survey	Eggs spawned in subarea, indicated by survey $(x10^{-12})$
Gulf of Me.	10-14 Mar	9	0	0	-	0	21.025	0
	8 Apr-7 May	39	0	0	-	0	36.190	0
(98026 km^2)	19-29 May	50	4	1.0633	0.6183	10.4228	39.045	0.4070
	9-12 July	11	3	13.3779	10.5182	131.1381	48.365	6.3425
	25 Aug-2 Sep	39	12*	54.9474	29.1356	538.6273	54.620	29.4198
	20-28 Oct	38	1*	0.1889	0.1889	1.8521	46.775	0.0866
	15 Nov-14 Dec	45	0	0	-	0	16.640	0
							Gulf of Maine total =	36.2559
Geo. Bank	10-14 Mar	5	0*	0	-	0	9.000	0
	1-22 Apr	32	1*	0.1492	0.1492	0.6238	35.320	0.0220
(41809 km^2)	19-24 May	27	6	148.6222	130.5056	621.3746	51.690	32.1189
	9-13 Jul	19	14	224.8977	107.9549	940.2747	49.300	46.3555
	24 Aug-2 Sep	19	13*	31.1972	11.3595	130.4323	52.475	6.8444
	20-25 Oct	29	1*	0.1875	0.1875	0.7840	54.025	0.0424
	17 Nov-17 Dec	29	1*	0.1848	0.1848	0.7727	25.480	0.0197
							Georges Bank total =	85.4029
So. N. Eng.	2-11 Mar	40	0	0	-	0	20.225	0
	11-20 Apr	25	4	1.0637	0.5724	6.3722	34.825	0.2219
(59906 km^2)	12-21 May	44	24	63.4199	26.8508	379.9231	41.170	15.6414
	4-10 Jul	43	19	130.0935	69.5369	779.3379	48.865	38.0823
	17-24 Aug	38	21	38.2218	14.2961	228.9716	50.090	11.4692
	10-21 Oct	42	23	18.8596	6.0945	112.9805	45.085	5.0937
	19 Nov-20 Dec	27	3	0.9946	0.6619	5.9582	17.290	0.1030
							Southern New England total =	70.6116
Mid. Atlantic	25 Feb-3 Mar	48	0	0	-	0	22.235	0
	13 Apr	2	0	0	-	0	34.605	0
(58326 km^2)	6-12 May	49	16	30.6774	14.7907	178.9288	36.605	6.5497
	17 Jun-4 Jul	50	7	24.4127	17.6317	142.3894	50.240	7.1536
	11-18 Aug	49	10	7.6297	3.7004	44.5013	52.645	2.3428
	4-11 Oct	48	5	2.4995	1.8963	14.5785	26.640	0.3884
	Nov-Dec	0	-	-	-	-	-	-
							Middle Atlantic total =	16.4345
							Entire survey area total =	208.7049

*When N_1 = 1 the value given under K is $\bar{x}$, $(=x_i \div N)$, and std. error (k) is $\sqrt{x_i^2 \div N^2}$

Table 2. Silver hake population estimate, Gulf of Maine, 1979; numbers in parentheses are estimated.

Length (cm)	Reference catch	% female	% females mature	Fecundity	Theoretical egg production by ref. catch	% males mature	Total population estimate*	Spawners, both sexes
1.0								
2								
3								
4	0.039	(50.0)	(0)			(0)	831957	
5	0.047	(50.0)	(0)			(0)	1002615	
6	0.102	(50.0)	(0)			(0)	2175888	
7	0.111	(50.0)	(0)			(0)	2367878	
8	0.082	(50.0)	(0)			(0)	1749243	
9	0.091	(50.0)	(0)			(0)	1941233	
10	0.124	(50.0)	(0)			(0)	2645197	
11	0.034	(50.0)	(0)			(0)	725296	
12	0.006	(50.0)	(0)			(0)	127993	
13	0.046	(50.0)	(0)			(0)	981283	
14	0.096	(50.0)	(0)			(0)	2047894	
15	0.235	38.6	(0)				5013075	
16	0.394	51.1	(0)			(0)	8404900	
17	0.783	50.4	(0)			(0)	16703138	
18	1.270	39.5	(0)			(0)	27091935	
19	2.062	48.5	(1.8)	47579	855.776	(7.1)	43987063	1993327
20	3.652	49.1	10.5	54703	10291.028	10.2	77905312	8061003
21	4.541	45.9	14.2	62466	18496.324	14.5	96869667	13912654
22	5.878	45.5	22.8	70892	43200.285	14.8	125390862	23119066
23	6.691	45.1	19.9	80003	48074.604	19.2	142733966	27855832
24	6.368	47.2	27.7	89822	74815.490	29.2	135843656	38704167
25	4.761	48.6	32.5	100370	75447.174	33.3	101562758	33425685
26	3.802	47.4	43.3	111669	87065.145	48.0	81105147	37125135
27	2.390	48.5	54.6	123742	78283.509	63.1	50984035	30069976
28	1.344	49.5	62.5	136608	56767.181	80.1	28670520	20468825
29	1.064	50.2	69.4	150290	55688.028	87.7	22697495	17821406
30	0.837	49.1	73.5	164807	49751.309	90.4	17855078	14660300
31	0.598	49.2	80.8	180182	42799.217	93.8	12756675	11150508
32	0.646	50.0	89.6	196433	56860.652	93.9	13780622	12643662
33	0.770	51.3	96.0	213582	81023.921	94.2	16425819	15624857
34	0.889	50.0	(99.0)	231648	101999.023	94.1	18964355	18310363
35	0.777	53.4	(100.0)	250652	103961.075	97.5	16575145	16381961
36	0.688	61.3	(100.0)	270613	114129.409	98.5	14676576	14591378
37	0.518	70.4	(100.0)	291551	106380.896	93.3	11050096	10831247
38	0.385	77.4	(100.0)	313486	93403.624	93.3	8212909	8088495
39	0.367	85.6	(100.0)	336436	105667.348	(93.3)	7828929	7753291
40	0.195	92.8	(100.0)	360421	65235.841	(100.0)	4159785	4159785
41	0.138	96.7	(100.0)	385459	51422.004	(100.0)	2943848	2943848
42	0.102	96.7	(100.0)	411571	40582.300	(100.0)	2175888	2175888
43	0.035	98.7	(100.0)	438774	15152.841	(100.0)	746628	746628
44	0.034	100.0	(100.0)	467087	15880.958		725296	725296
45	0.019	100.0	(100.0)	496529	9434.051		405312	405312
46	0.021	100.0	(100.0)	527118	11069.478		447977	447977
47	0.013	100.0	(100.0)	558872	7265.336		277319	277319
48	0.013	100.0	(100.0)	591810	7693.530		277319	277319
49	0.003	100.0	(100.0)	625950	1877.850		63997	63997
50	0.005	100.0	(100.0)	661310	3306.550		106661	106661
51								
52								
53	0.010	100.0	(100.0)	774884	7748.840		213322	213322
54	0.015	100.0	(100.0)	815300	12229.500		319983	319983
55	0.003	100.0	(100.0)	857024	2571.072		63997	63997
56								
57	0.003	100.0	(100.0)	944465	2833.395		63997	63997
58	0.010	100.0	(100.0)	990218	9902.180		213322	213322
59								
60	0.003	100.0	(100.0)	1085870	3257.610		63997	63997
61								
62								
63	0.007	100.0	(100.0)	1239975	8679.825		149326	149326
64								
65	0.003	100.0	(100.0)	1349991	4049.973		63997	63997
66	0.007	100.0	(100.0)	1407233	9850.631		149326	149326
67								
68	0.003	100.0	(100.0)	1526268	4578.804		63997	63997
					Totals =		1333381504	396288428

*Dashed line within "Total population estimate" column indicates size at age 2.8 yr, see discussion.

Table 3. Silver hake population estimate, Georges Bank, 1979; numbers in parentheses are estimated.

Length (cm)	Reference catch	% female	% females mature	Fecundity	Theoretical egg production by ref. catch	% males mature	Total population estimate*	Spawners, both sexes
1.0								
2	0.189	(50.0)	(0)			(0)	22996214	
3	3.586	(50.0)	(0)			(0)	436319691	
4	5.537	(50.0)	(0)			(0)	673703884	
5	4.167	(50.0)	(0)			(0)	507011755	
6	2.673	(50.0)	(0)			(0)	325232162	
7	1.389	(50.0)	(0)			(0)	169003918	
8	0.882	(50.0)	(0)			(0)	107315663	
9	0.730	(50.0)	(0)			(0)	88821354	
10	0.388	(50.0)	(0)			(0)	47209158	
11	0.166	(50.0)	(0)			(0)	20197732	
12	0.012	(50.0)	(0)			(0)	1460077	
13	0.008	(50.0)	(0)			(0)	973385	
14	0.004	(50.0)	(0)			(0)	486692	
15	0.004	(50.0)	(0)			(0)	486692	
16	0.004	(50.0)	(0)			(0)	486692	
17	0.011	(50.0)	(0)			(0)	1338404	
18	0.032	41.3	(0)			(0)	3893539	
19	0.038	(47.0)	(1.8)	47579	15.309	(7.1)	4623577	213003
20	0.059	52.8	10.5	54703	178.796	10.2	7178712	743591
21	0.089	44.2	14.2	62466	348.856	14.5	10828905	1555835
22	0.205	51.1	22.8	70892	1693.526	14.8	24942983	4711430
23	0.270	50.8	19.9	80003	2182.809	19.2	32851734	6424308
24	0.359	49.2	27.7	89822	4395.520	29.2	43680638	12432318
25	0.435	46.9	32.5	100370	6650.763	33.3	52927793	17426497
26	0.645	46.1	43.3	111669	14380.546	48.0	78479141	35969211
27	0.474	49.6	54.6	123742	15890.768	63.1	57673043	33959214
28	0.438	43.0	62.5	136608	16087.948	80.1	53292812	38652467
29	0.274	39.6	69.4	150290	11302.815	87.7	33338426	26824881
30	0.457	39.6	73.5	164807	21938.315	90.4	55604601	46542458
31	0.316	39.0	80.8	180182	17923.747	93.8	38448696	34117527
32	0.442	40.5	89.6	196433	31529.808	93.9	53779505	49561691
33	0.358	43.6	96.0	213582	32004.084	94.2	43558965	41374396
34	0.307	53.6	(99.0)	231648	37722.879	94.1	37353638	36130463
35	0.305	58.9	(100.0)	250652	44997.799	97.5	37110292	36728612
36	0.240	66.6	(100.0)	270613	43280.761	98.5	29201541	29055416
37	0.263	71.8	(100.0)	291551	55039.406	93.3	32000022	31394985
38	0.124	82.3	(100.0)	313486	31995.760	93.3	15087463	14908642
39	0.107	89.4	(100.0)	336436	32168.395	(93.3)	13019020	12926210
40	0.091	94.9	(100.0)	360421	31132.157	(100.0)	11072251	11072251
41	0.069	97.1	(100.0)	385459	25836.006	(100.0)	8395443	8395443
42	0.039	100.0	(100.0)	411571	16051.269	(100.0)	4745250	4745250
43	0.043	100.0	(100.0)	438774	18867.282	(100.0)	5231943	5231943
44	0.034	95.0	(100.0)	467087	15086.910	(100.0)	4136885	4136885
45	0.035	95.0	(100.0)	496529	16509.589	(100.0)	4258558	4258558
46	0.038	95.0	(100.0)	527118	19028.960	(100.0)	4623577	4623577
47	0.025	95.0	(100.0)	558872	13273.210	(100.0)	3041827	3041827
48	0.021	(95.0)	(100.0)	591810	11806.610	(100.0)	2555135	2555135
49	0.020	95.0	(100.0)	625950	11893.050	(100.0)	2433462	2433462
50	0.010	(100.0)	(100.0)	661310	6613.100		1216731	1216731
51	0.022	100.0	(100.0)	697907	15353.954		2676808	2676808
52	0.013	100.0	(100.0)	735759	9564.867		1581750	1581750
53	0.015	100.0	(100.0)	774884	11623.260		1825096	1825096
54	0.010	100.0	(100.0)	815300	8153.000		1216731	1216731
55	0.010	100.0	(100.0)	857024	8570.240		1216731	1216731
56								
57	0.003	100.0	(100.0)	944465	2833.395		365019	365019
58	0.010	100.0	(100.0)	990218	9902.180		1216731	1216731
59	0.004	100.0	(100.0)	1037347	4149.388		486692	486692
60	0.011	100.0	(100.0)	1085870	11944.570		1338404	1338404
61	0.004	100.0	(100.0)	1135805	4543.220		486692	486692
62								
63	0.006	100.0	(100.0)	1239975	7439.850		730039	730039
Totals =							3226770275	576504911

*Dashed line within "Total population estimate" column indicates size at age 2.8 yr, see discussion.

Table 4. Silver hake population estimate, southern New England, 1979; numbers in parentheses are estimated.

Length (cm)	Reference catch	% female	% females mature	Fecundity	Theoretical egg production by ref. catch	% males mature	Total population estimate[*]	Spawners, both sexes
1.0								.
2								
3	0.547	(50.0)	(0)			(0)	24158174	
4	4.075	(50.0)	(0)			(0)	179971772	
5	8.145	(50.0)	(0)			(0)	359722719	
6	7.101	(50.0)	(0)			(0)	313614614	
7	4.461	(50.0)	(0)			(0)	197019404	
8	1.178	(50.0)	(0)			(0)	52026196	
9	0.189	(50.0)	(0)			(0)	8347157	
10	0.097	(50.0)	(0)			(0)	4283991	
11	0.010	(50.0)	(0)			(0)	441649	
12	0.039	(50.0)	(0)			(0)	1722429	
13								
14	0.021	(50.0)	(0)			(0)	927462	
15	0.011	(50.0)	(0)			(0)	485813	
16	0.134	(50.0)	(0)			(0)	5918090	
17	0.291	(50.0)	(0)			(0)	12851972	
18	0.294	50.5	(0)			(0)	12984466	
19	0.201	47.8	(1.8)	47579	82.301	(7.1)	8877135	405336
20	0.251	48.0	10.5	54703	692.592	10.2	11085378	1146685
21	0.279	51.1	14.2	62466	1265.106	14.5	12321994	1767792
22	0.388	53.4	22.8	70892	3349.549	14.8	17135963	3268308
23	0.422	51.4	19.9	80003	3452.633	19.2	18637568	3645458
24	0.563	50.7	27.7	89822	7106.172	29.2	24864812	7071316
25	0.476	51.8	32.5	100370	8050.873	33.3	21022470	6913281
26	0.395	46.3	43.3	111669	8835.340	48.0	17445117	7994361
27	0.407	44.4	54.6	123742	12211.948	63.1	17975095	10663752
28	0.494	42.3	62.5	136608	17828.522	80.1	21817437	15852654
29	0.625	39.7	69.4	150290	25879.750	87.7	27603032	22202472
30	0.908	32.5	73.5	164807	35768.389	90.4	40101686	34047983
31	1.001	35.3	80.8	180182	51472.770	93.8	44209017	39438157
32	1.376	39.2	89.6	196433	94862.478	93.9	60770836	56040246
33	1.085	42.8	96.0	213582	95238.128	94.2	47918864	45508823
34	0.991	47.7	(99.0)	231648	108383.888	94.1	43767368	42207854
35	0.746	55.8	(100.0)	250652	104263.612	97.5	32946980	32582586
36	0.653	66.0	(100.0)	270613	116664.133	98.5	28839648	28692653
37	0.550	71.4	(100.0)	291551	114492.078	93.3	24290669	23825211
38	0.306	77.8	(100.0)	313486	74592.614	93.3	13514445	13313069
39	0.326	85.5	(100.0)	336436	93730.935	(93.3)	14397742	14257482
40	0.248	90.7	(100.0)	360421	81089.535	(100.0)	10952883	10952883
41	0.198	92.7	(100.0)	385459	70718.929	(100.0)	8744641	8744641
42	0.177	97.3	(100.0)	411571	70859.315	(100.0)	7817179	7817179
43	0.180	100.0	(100.0)	438774	78979.320		7949673	7949673
44	0.155	100.0	(100.0)	467087	72398.485		6845552	6845552
45	0.103	100.0	(100.0)	496529	51142.487		4548980	4548980
46	0.040	100.0	(100.0)	527118	21084.720		1766594	1766594
47	0.040	100.0	(100.0)	558872	22354.880		1766594	1766594
48	0.043	100.0	(100.0)	591810	25447.830		1899089	1899089
49	0.007	100.0	(100.0)	625950	4381.650		309154	309154
50	0.022	100.0	(100.0)	661310	14548.820		971627	971627
51	0.011	100.0	(100.0)	697907	7676.977		485813	485813
52	0.011	100.0	(100.0)	735759	8093.349		485813	485813
53								
54								
55	0.055	100.0	(100.0)	857024	47136.320		2429067	2429067
56								
57	0.022	100.0	(100.0)	944465	20778.230		971627	971627
58								
59	0.011	100.0	(100.0)	1037347	11410.817		485813	485813
60								
61	0.011	100.0	(100.0)	1135805	12493.855		485813	485813
					Totals =		1782935073	469761390

[*]Dashed line within "Total population estimate" column indicates size at age 2.8 yr, see discussion.

Table 5. Silver hake population estimate, Middle Atlantic, 1979; numbers in parentheses are estimated.

Length (cm)	Reference catch	% female	% females mature	Fecundity	Theoretical egg production by ref. catch	% males mature	Total population estimate	Spawners, both sexes
1.0								
2								
3	0.194	(50.0)	(0)			(0)	23737965	
4	1.443	(50.0)	(0)			(0)	176566406	
5	1.717	(50.0)	(0)			(0)	210093222	
6	1.818	(50.0)	(0)			(0)	222451647	
7	0.225	(50.0)	(0)			(0)	27531144	
8	0.070	(50.0)	(0)			(0)	8565245	
9	0.002	(50.0)	(0)			(0)	244721	
10								
11								
12								
13	0.007	(50.0)	(0)			(0)	856524	
14	0.007	(50.0)	(0)			(0)	856524	
15	0.002	(50.0)	(0)			(0)	244721	
16	0.027	(50.0)	(0)			(0)	3303737	
17	0.027	(50.0)	(0)			(0)	3303737	
18	0.020	50.5	(0)			(0)	2447213	
19	0.022	47.8	(1.8)	47579	9.008	(7.1)	2691934	122916
20	0.022	48.0	10.5	54703	60.705	10.2	2691134	278457
21	0.015	51.1	14.2	62466	68.016	14.5	1835410	263320
22	0.032	53.4	22.8	70892	276.252	14.8	3915541	746803
23	0.011	51.4	19.9	80003	89.998	19.2	1345967	263268
24	0.119	50.7	27.7	89822	1502.015	29.2	14560916	4140986
25	0.036	51.8	32.5	100370	608.890	33.3	4404983	1448588
26	0.029	46.3	43.3	111669	648.670	48.0	3548459	1626109
27	0.087	44.4	54.6	123742	2610.416	63.1	10645376	6315385
28	0.015	42.3	62.5	136608	541.352	80.1	1835410	1333617
29	0.031	39.7	69.4	150290	1283.636	87.7	3793180	3051040
30	0.033	32.5	73.5	164807	1299.952	90.4	4037901	3428344
31	0.004	35.3	80.8	180182	205.685	93.8	489443	436624
32	0.110	39.2	89.6	196433	7583.483	93.9	13459671	12411928
33	0.103	42.8	96.0	213582	9041.039	94.2	12603146	11969281
34	0.050	47.7	(99.0)	231648	5468.410	94.1	6118032	5900035
35	0.079	55.8	(100.0)	250652	11041.321	97.5	9666491	9559579
36	0.029	66.0	(100.0)	270613	5181.102	98.5	3548459	3530372
37	0.100	71.4	(100.0)	291551	20816.741	93.3	12236064	12001597
38	0.075	77.8	(100.0)	313486	18282.504	93.3	9177048	9040303
39	0.005	85.5	(100.0)	336436	1437.591	(93.3)	611803	605843
40	0.065	90.7	(100.0)	360421	21253.306	(100.0)	7953442	7953442
41	0.070	92.7	(100.0)	385459	25001.642	(100.0)	8565245	8565245
						Totals =	819938661	104993082

[*]Dashed line within "Total population estimate" column indicates size at age 2.8 yr, see discussion.

Table 6. Spawning population estimates for three subareas, 1979; numbers in parentheses are comparable values from VPA estimates (Almeida[1]).

	Population (no. x 10^{-6})	Wtd. mean length per spawner (cm)	Weight per spawner (kg)	Weight of spawning population (MT x 10^{-3})
Gulf of Maine	396.288 (120.1)	28.5	0.163	64.5 (31.7)
Georges Bank	576.505 (302.9)	32.8	0.249	143.8 (69.6)
So. New England-Middle Atlantic	574.754 (345.5)	33.7	0.272	156.1 (92.7)
Total survey area	1547.547 (768.5)	32.0	0.231	364.4 (194.3)
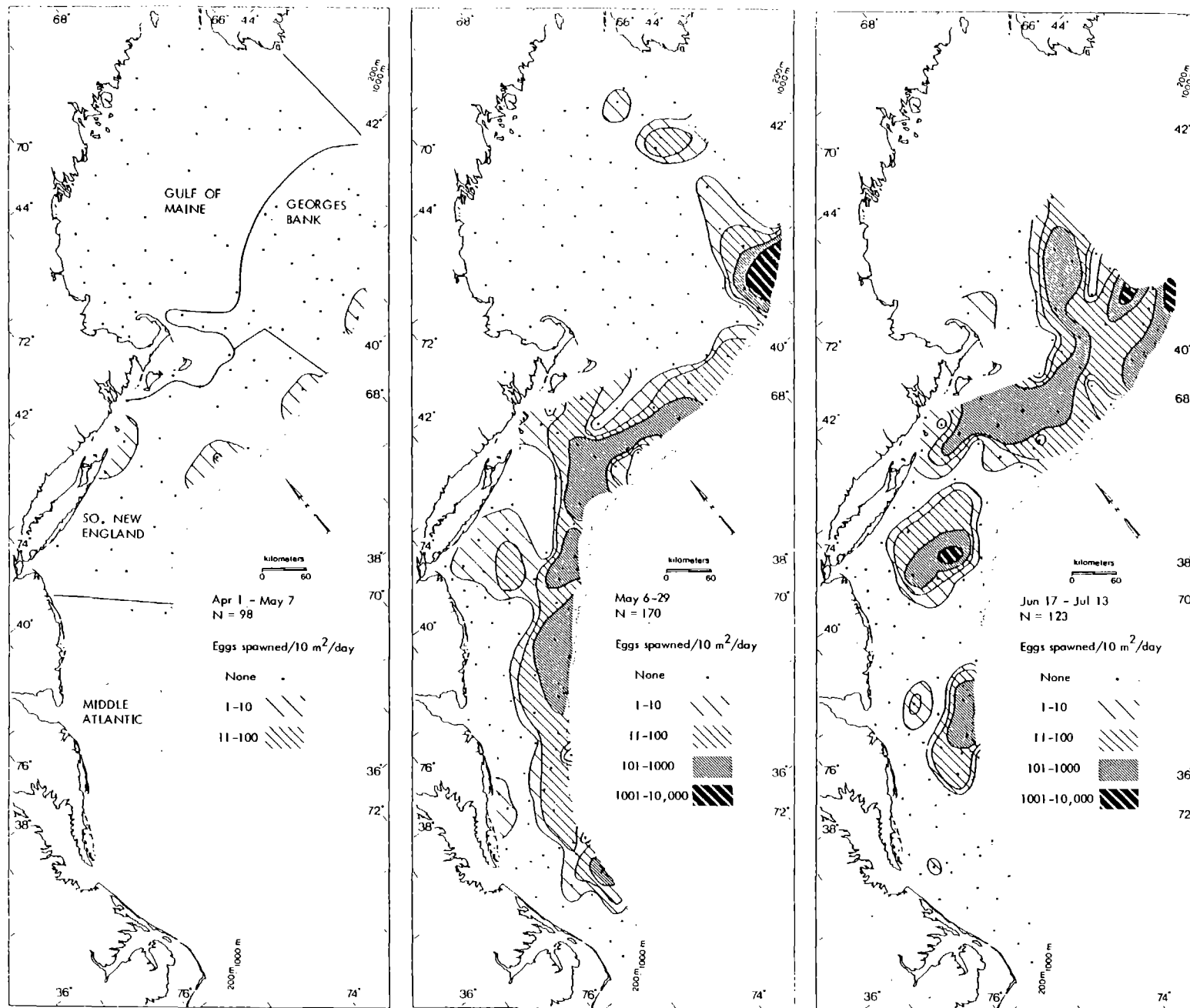
Figure 1. Distribution of silver hake eggs during the second, third, and fourth MARMAP ichthyoplankton surveys, 1979. Subarea boundaries shown on left apply to all surveys.

51
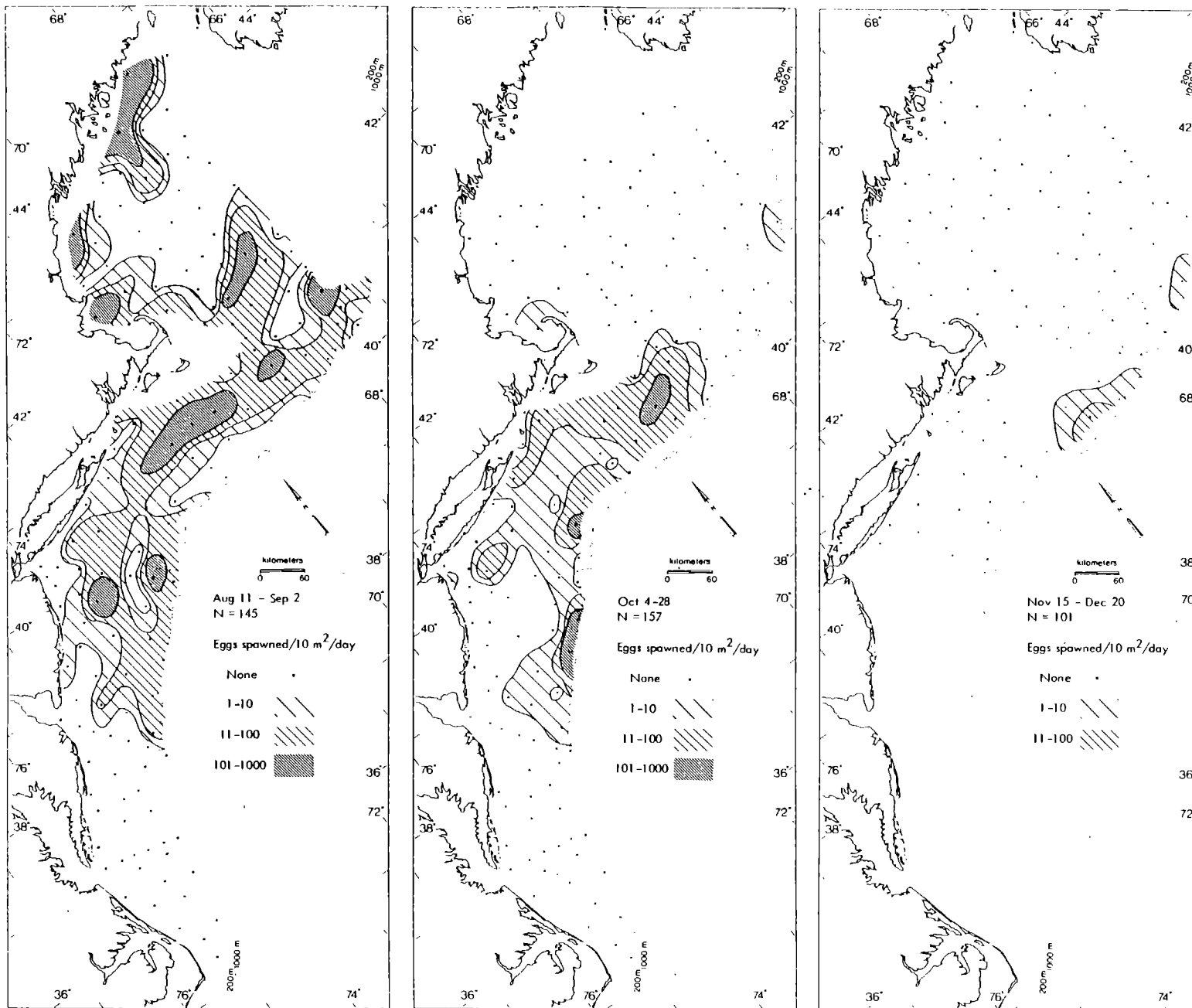
Figure 2. Distribution of silver hake eggs during the fifth, sixth, and
seventh MARMAP ichthyoplankton surveys, 1979.

Figure 3. Estimated daily silver hake egg production in four subareas and in the total survey area, 1979.

SPAWNING STOCK BIOMASS ESTIMATES OF SAND LANCE,
AMMODYTES SP., OFF NORTHEASTERN UNITED STATES,
DETERMINED FROM MARMAP PLANKTON SURVEYS, 1974-1980

by

Wallace Morse

U. S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Sandy Hook Laboratory
Highlands, New Jersey 07732 USA

ABSTRACT

Sand lance, Ammodytes sp., larvae from 18 MARMAP (Marine Resources
Monitoring, Assessment and Prediction) surveys from 1974-1980 were used
to estimate spawning stock biomass from Cape Hatteras, North Carolina to
Nova Scotia. A dramatic 50-fold increase in biomass occurred between 1974
to 1978 and then decreased to approximately one-third of the 1978 level in
1980. Changes in the species composition of the pelagic finfish community
suggest sand lance replaced Atlantic mackerel and Atlantic herring through
changes in energy flow within the ecosystem.

INTRODUCTION

Marine fish stocks off the northeastern United States were subjected
to intense fishing pressure during the late 1960's and early 1970's. By
1975 the fish biomass of the principal finfishes and squids found in shelf
waters between Cape Hatteras, North Carolina and Nova Scotia had been reduced
by approximately 50% (Clark and Brown 1977). During the period of reduced
biomass, 1974-1979, scientists at the Northeast Fisheries Center's Sandy
Hook Laboratory found evidence of a significant change in the ichthyofaunal
structure when they discovered a tremendous increase in sand lance larvae
abundance during winter MARMAP surveys (MARMAP is an acronym for Marine
Resources Monitoring, Assessment and Prediction; see Sherman (1980) for a
detailed description of the program). Abundance estimates of sand lance
larvae increased 20-fold from 490 x 10^9 in 1974, when they accounted for
less than 50% of the winter larval assemblage, to 9640 x 10^9 in 1979, when
they accounted for nearly 90% of the winter ichthyoplankton (Sherman et al.
1981). The increase in larval abundance and evidence from other MARMAP
studies (e.g. bottom trawl surveys, diver observations and a significant
increase in sand lance as a predator food item) indicate that adult popula-
tions of sand lance larvae increased sharply since 1976.

Prior to the increase in sand lance, both Atlantic herring, Clupea harengus, and Atlantic mackerel, Scomber scombrus, stocks decreased to extremely low levels between 1964-1975. Northeast Fisheries Center scientists are currently attempting to determine the consequences of this structural change in the shelf ecosystem. As part of this effort, I have derived estimates of the annual spawning stock biomass of sand lance using fishery independent data. Because the taxonomy of sand lance in the northwest Atlantic remains confused, the larvae were classified as Ammodytes sp. and considered a single taxon.

METHODS

Ammodytes sp. larvae were collected during 18 surveys conducted by the National Marine Fisheries Service of the continental shelf waters between Nova Scotia and North Carolina from 1974-1980 (Table 1). This analysis is based on information from these subareas: Georges Bank, southern New England and Middle Atlantic (Figure 1). The Gulf of Maine subarea was not included because catches of sand lance larvae were either nonexistent or relatively insignificant.

Standard MARMAP I double-oblique tows were made at each station (Jossi et al. 1975). Paired 60-cm bongo net frames, fitted with 0.505 and 0.333-mm mesh nets, were towed at approximately 1.5 knots. Net catches were preserved aboard ship in a 5% formalin solution. The ichthyoplankton in each 0.505-mm sample were sorted, identified, enumerated and larvae were measured to ±0.1 mm at the Morski Instytut Rybacki, Szczecin, Poland. For analysis, lengths were combined to whole millimeters, e.g. lengths between 8.0-8.9 mm were combined into 8 mm. The number of larvae per mm interval at each station was standardized to the number under 10 m^2 surface area to the depth of tow. This was calculated using the volume of water filtered and maximum tow depth by the equation:

$$S_{Lx} = 10 \ (\pi r^2)^{-1} (C \cdot T)^{-1} (D)(L_x) \qquad (1)$$

where S_{Lx} is number of larvae at length x under 10 m^2, r is the radius of the bongo net mouth opening in meters, C is the calibration factor for the flow meter in meters per revolution, T is flow meter revolutions, D is maximum tow depth and L is number of larvae at length x. Total larval abundance at a station is the sum of all S_{Lx}.

The instantaneous mortality rate (Z) was defined as:

$$\frac{N_L}{N_x} = Exp(-ZL) \qquad (2)$$

where N_x is the number of larvae at hatching and N_L is the number of larvae surviving to length L. Length at hatching was assumed to be 5 mm and the maximum length considered fully vulnerable to the sampling was 27 mm, the approximate length at which metamorphosis begins (Cameron 1958; Macer 1965). The 27 mm length was chosen because the standardized length frequencies become erratic at lengths greater than 28 mm. This indicates net avoidance

or length specific mortality becomes a factor at about 28 mm. Z was estimated from the exponential regression coefficient of the decline in catch with increasing length in the interval 5-27 mm (Figures 2 and 3).

Larval production curves were determined for each survey by backcalculating over time the number of larvae hatched. The lengths at each station between 5 and 27 mm were converted to ages (days old) by the relationship:

$$Age\ (days) = \frac{L_t - L_o}{G} \qquad (3)$$

where L_t is length at capture, L_o is length at hatching (5 mm) and G is growth rate in mm per day. Estimates of larval growth rates ranged from 11.6 mm per month by Norcross et al. (1961) off Chesapeake Bay to 5.9 mm per month for larvae on the Scotian Shelf (Scott 1972). An "average" growth rate (G) of 0.33 mm per day was used for larvae throughout the survey area for the entire spawning season. Thus by applying equations 2 and 3 to the standardized length frequencies of each station, daily larval production was estimated and a curve was fitted to the data by eye to define the shape of the larval production curve for each survey. For each year when surveys were made in the same area at different times, a size overlap often occurred in the production curves. Those fish contributing to the overlap in the second or later survey in a given year were eliminated from the total larval abundance estimates because those larvae were present in the first survey and would be counted twice. Larval production curves were usually incomplete due to the timing of the surveys or insufficient coverage during the entire spawning season. In such cases, I estimated the beginning and/or end of hatching and completed the production curve by fitting the remainder of the curve by eye. The percentage of area estimated in this way was used to correct the total larval abundance.

Larval production, measured as the number of newly hatched larvae (5 mm) represented in the catches, was determined for each station as the sum of N_x for each length interval between 5-27 mm. Thus in equation 2, L equals observed length minus 5. Total larval production for the entire survey area was determined by multiplying the mean larval production per 10 m^2 times the total survey area (160,041 km^2). Statistical methods used are given in Aitchison (1955) and Pennington (1982).

Total larval production was converted to spawning stock biomass in metric tons by the relationship:

$$SSB(t) = \frac{LP}{F} \cdot ES^{-1} \cdot PF^{-1} \cdot 10^{-6}$$

where LP is larval production, F is relative fecundity, ES is egg survival and PF is the proportion of females in the spawning stock. Relative fecundity was estimated from data presented by Westin et al. (1979) was 973 eggs per gram of female and the sex ratio was assumed to be 1:1.

RESULTS

Sand lance larvae were captured at 737 stations which accounted for over 61% of the stations occupied during the surveys used in this study. Back-calculated numbers at hatching under 10 m^2 ranged up to 77,000 with the highest densities occurring on Georges Bank and from Nantucket Shoals to Long Island, New York (Sherman et al. 1981). Mean catch per tow was lowest in 1974 at 153.4 larvae per 10 m^2, and highest in 1977 at 6544.4 larvae per tow.

The estimated mortality rates ranged from 0.207 to 0.363 which gives a decrease of 19% to 30% per mm of growth and daily mortality between 6% and 10% for the length interval 5-27 mm.

Spawning stock estimates based on egg survival between 1.0 and 0.05 increased 50-fold between 1974 and 1978, then decreased to approximately one-third of the 1978 level in 1980 (Table 2). Incubation time for Ammodytes sp. eggs is unusually long, greater than 30 days (G. Laurence pers. comm.), indicating egg mortalities could be high. If daily mortality is 5% for just 30 days, then survival is only 22% to hatching and at 45 days survival is 10%.

DISCUSSION

Standard techniques for assessing stock size of pelagic species using fisheries data, e.g. fishing effort and fishing mortality, are being seriously questioned (Saville and Schnack 1981). For those species without a directed fishery or where managers have prohibited fishing there will, of course, be no fisheries related data available to assessment biologists to apply to fisheries models. In such cases, research vessel trawl surveys are often used to provide catch-per-tow data as a measure of catch-per-unit effort when fishing effort of the commercial fleet is inadequate or unavailable.

Sand lance do not support a fishery in the northwest Atlantic nor are research vessel catches adequate for stock assessment due to net avoidance and the burrowing habits of sand lance (Livingstone 1962; Meyer et al. 1979). However, trawl survey indices (stratified mean catch-per-tow) do indicate higher abundance of sand lance in recent years though large annual fluctuations of the index have occurred (Grosslein et al. 1980). For sand lance and many other species, macroscale egg and larval surveys provide a fisheries independent method of assessing spawning stock size as well as monitoring major biotic changes in the marine ecosystem.

The dramatic 50-fold increase in the sand lance spawning stock biomass, following the precipitous decline in Atlantic herring and Atlantic mackerel stocks, indicates a significant change in the species composition of the pelagic finfish community. Clark and Brown (1977) estimated a 6-7 million ton decline in mackerel and herring stocks from 1968 to 1975. Average biomass on Georges Bank declined 42% and production of fish and squid (Kcal/Km^2) declined by 26% from 1964 to 1975 (Grosslein et al. 1980). Assuming the basic productivity of the shelf has not changed, then a surplus of food energy was available during the mid-1970's. Sand lance biomass increased 30-fold from 1974 to 1976 indicating a shift in energy flow within the pelagic component of the ecosystem. Sand lance population levels increased after the herring

and mackerel stocks had reached extremely low levels which suggests replacement (see Daan 1980) rather than competition as predator-prey or as predators of a common food source. It remains to be seen if this shift in species composition is a long-term trend or if, under the present management strategies for mackerel and herring, a return to the pre-1960 species composition and biomass levels will occur.

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Table 1. Summary of surveys used to estimate sand lance, _Ammodytes_ sp., spawning stock, N_0 = total stations sampled, N_1 = stations with sand lance larvae.

Year	Survey	Dates		N_0	N_1
1974	ALB 74-02	Feb 11-22		58	41
	ALB 74-04	Mar 13-Apr 2		19	11
	ATW 74-02	Apr 2-22		22	9
			TOTAL	99	61
1975	ALB 75-02	Feb 12-28		73	44
	CWL 75-02	Mar 5-11		17	11
	ALB 75-03	Mar 3-17		26	16
			TOTAL	116	71
1976	ALB 76-01	Feb 10-25		103	96
	DEL 76-05	Mar 3-23		75	48
			TOTAL	178	144
1977	GOR 77-01	Mar 3-Apr 7		88	47
	DEL 77-03	Mar 19-Apr 8		68	55
	DEL 77-05	May 17-27		87	21
	NOG 77-02	May 22-Jun 6		57	7
	DEL 77-07	Jun 6-30		31	8
			TOTAL	331	138
1978	DEL 78-02	Feb 14-Mar 17		102	84
	ARG 78-04	Apr 13-May 20		119	48
			TOTAL	221	132
1979	DEL 79-03	Feb 25-Mar 14		101	85
	DEL 79-04	Apr 11-29		34	24
			TOTAL	135	109
1980	ALB 80-02	Feb 27-Apr 5		122	82

Table 2. Spawning stock estimates of sand lance, Ammodytes sp., in metric tons from Georges Bank to Cape Hatteras, 1974-1980. $\overline{X}$ is mean catch per tow and $\overline{Z}$ is larval mortality coefficient.

Year	Survey	X̄/Tow	Std Error of X̄	Z	EGG SURVIVAL 1.00	0.90	0.75	0.50	0.25	0.10	0.05
1974	1	153.4	43.136	0.221	5,489	6,099	7,318	10,978	21,956	54,890	109,780
1975	1	528.1	155.130	0.207	25,547	28,386	34,063	51,094	102,188	255,470	510,940
1976	1	4541.6	1254.084	0.308	207,717	230,797	276,956	415,434	830,868	2,077,170	4,154,340
1977	1	6544.4	2452.655	0.283	246,333	273,703	328,444	492,666	985,332	2,463,330	4,926,660
	2	138.0	94.622								
1978	1	6321.4	2022.060	0.363	264,141	293,490	352,188	528,282	1,056,564	2,641,410	5,282,820
	2	584.0	324.004								
1979	1	3239.4	1257.670	0.288	196,432	218,258	261,909	392,864	785,728	1,964,320	3,928,640
	2	1197.8	260.543								
1980	1	1171.6	361.523	0.229	91,764	101,960	122,352	183,528	367,056	917,640	1,835,280

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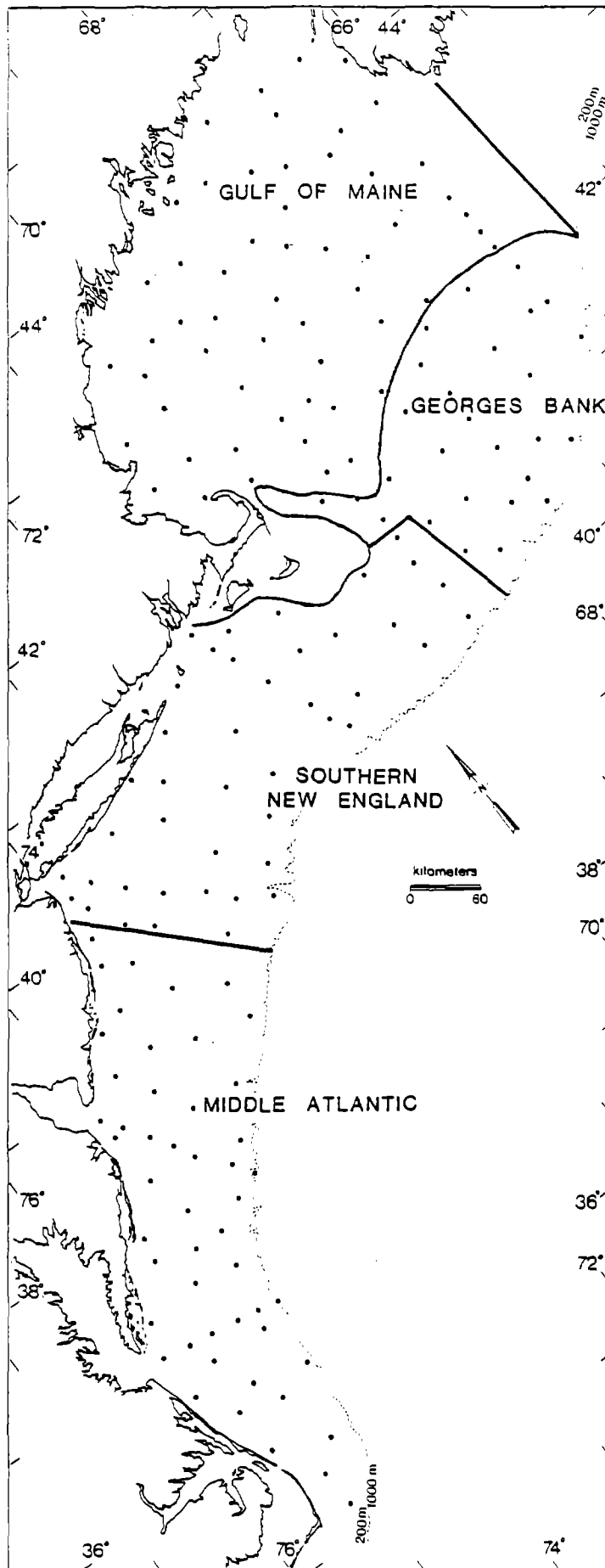
Figure 1. Station locations and analytical
subareas of standard MARMAP
surveys.
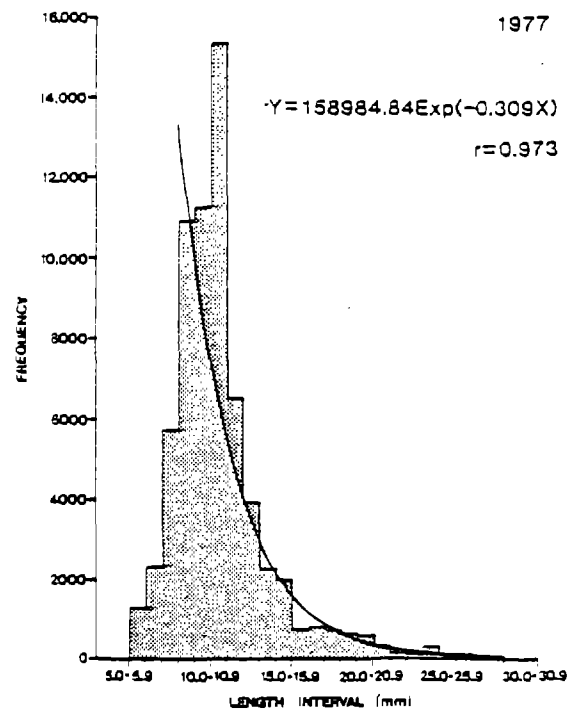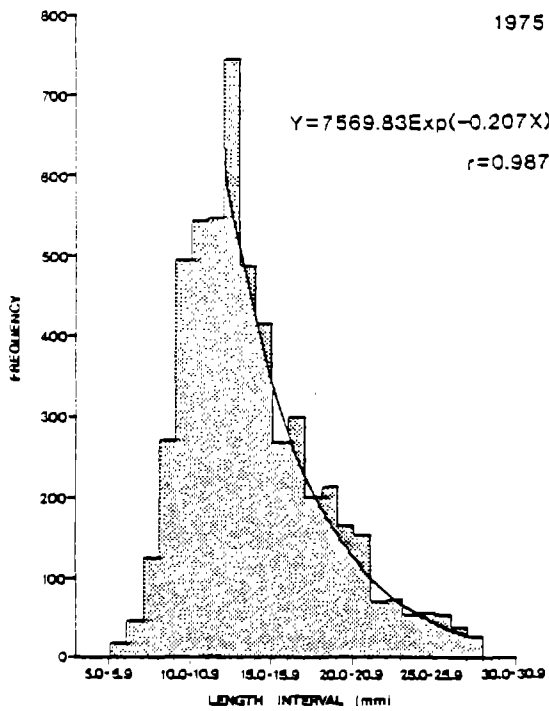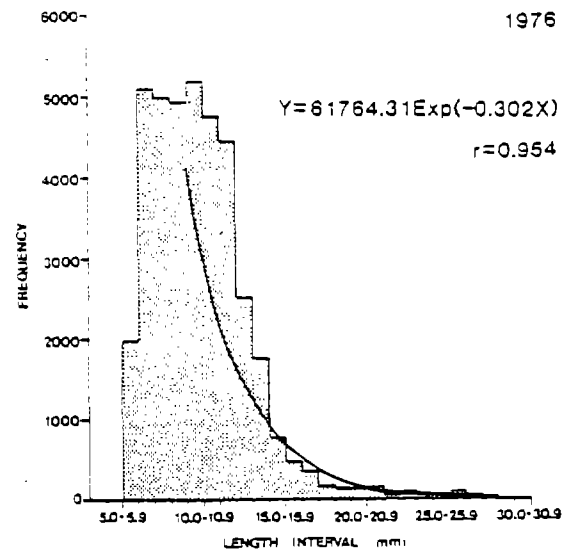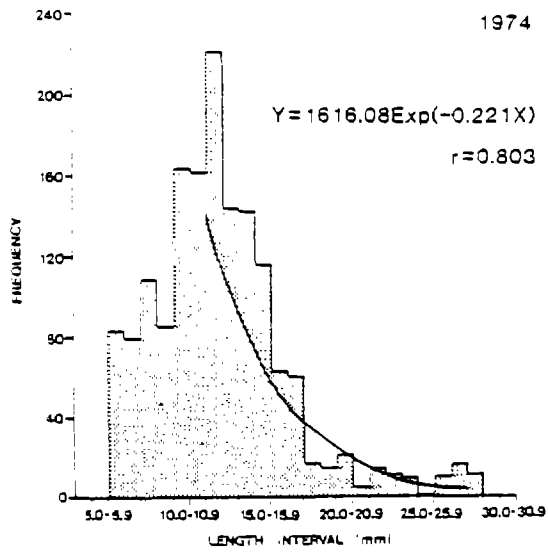
Figure 2. Length frequencies and fitted regressions for sand lance,
Ammodytes sp., 1974-1977.
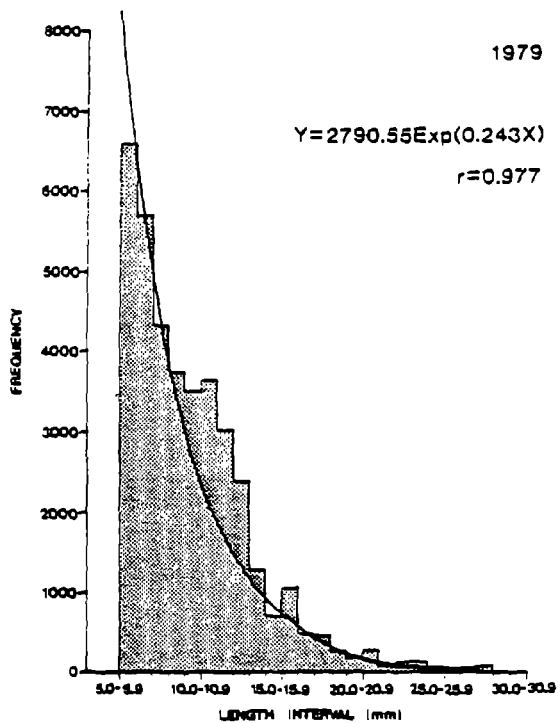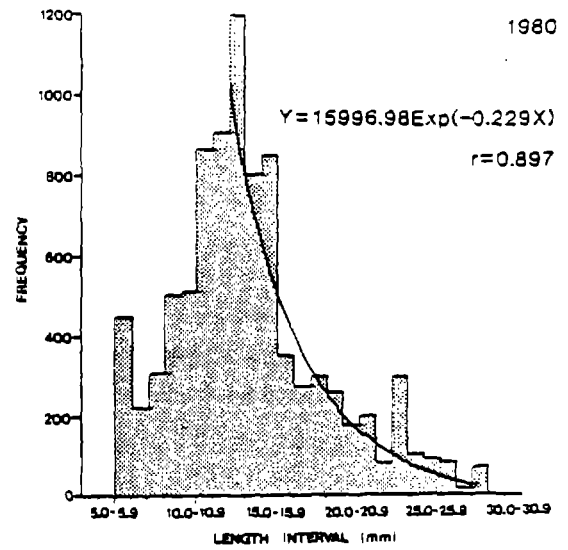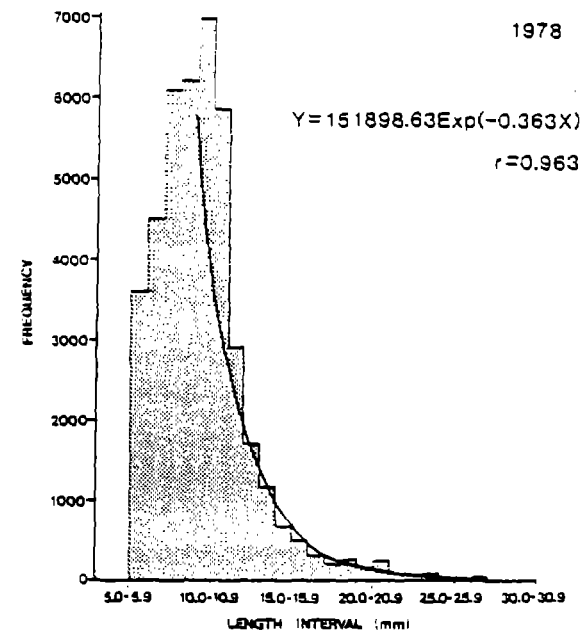
Figure 3. Length frequencies and fitted regressions for sand lance,
          Ammodytes sp., 1978-1980.

AN ASSESSMENT OF THE GEORGES BANK HADDOCK STOCK BASED ON LARVAE

COLLECTED ON MARMAP PLANKTON SURVEYS, 1977-1982

by

Wallace Morse

U. S. Department of Commerce

National Oceanic and Atmospheric Administration

National Marine Fisheries Service

Northeast Fisheries Center

Sandy Hook Laboratory

Highlands, New Jersey   07732

INTRODUCTION

The study of the abundance of fish eggs and larvae to estimate the size of the parental stock that produced them has had a long and often erratic history. In 1895 the Nordsee-Expedition attempted to assess the North Sea fish stocks from plankton egg surveys but not until Sette (1943), working on Atlantic mackerel, Scomber scombrus, in the northwest Atlantic, was an estimate of spawning stock derived from the distribution and abundance of ichthyoplankton. During the next 20 years, as sampling methods and opportunities improved, numerous stock assessments from plankton surveys were made, notably Saville (1956) and Simpson (1959) in the North Sea and Sette and Ahlstrom (1948) in the eastern Pacific. Today, 10+ year data sets useful for stock assessments from early life history stages exist only in the northeast Atlantic and eastern Pacific. Such data sets provide a fisheries independent estimate of spawning stock or at least an index of changes in the parental stock over time.

The impetus for this study resulted from the effects of management of the Georges Bank haddock stock and their impact on the traditional use of the commercial catch-at-age information to derive stock estimates using virtual population analysis (VPA). According to Clark et al. (1982), VPA estimates for 1974-1977 were in some doubt due to the lack of directed fishing effort data as a result of incidental catch regulations. Estimates of stock size in recent years (Overholtz et al. 1983) were derived using estimates of total mortality from research vessel trawl survey catch-at-age data to estimate a terminal F for VPA. A fisheries independent estimate of spawning stock sizes for the 1977-1982 time span was deemed useful for comparison with recent VPA stock estimates.

The MARMAP program is multinational and designed to measure changes in both physical and biological components of the continental shelf ecosystem from Cape Hatteras, North Carolina to Nova Scotia (Sherman 1980). A minimum of six surveys a year provide information about nutrients, primary production, zooplankton, ichthyoplankton and water column temperature and salinity. The MARMAP program provides an opportunity to derive fisheries-independent estimates of spawning biomass from both fish egg and larvae catches.

MATERIALS AND METHODS

Survey Area and Sampling Intensity

MARMAP surveys are conducted in continental shelf and slope waters from Cape Hatteras, North Carolina to Nova Scotia, Canada in depths from about 10-1200 m (Fig. 1). From February 1977 to June 1982, 36 surveys were completed and haddock larvae were captured on 19 surveys (Table 1). A standard survey includes approximately 180 stations at fixed locations (Fig. 1). Nonstandard sampling locations were made during all or part of some surveys, particularly in 1977, to supplement incomplete areal and/or temporal coverage of standard survey stations. Station locations were selected from a stratified random sampling pattern used on Northeast Fisheries Center resource surveys (Grosslein 1969). Sampling intensity was maintained at approximately one station per 1200 km^2.

For analysis of haddock data, the survey area was stratified into three subareas: northern Middle Atlantic Bight (NMAB), Georges Bank (GB) and southwestern Gulf of Maine (SGOM) (Fig. 1). These strata were selected based upon hydrography, topography, and spatial and temporal density gradients of haddock larvae abundance. Haddock larvae captured on western edge of the Scotian Shelf were not included in this analysis.

Ichthyoplankton Sampling and Analysis

Ichthyoplankton was sampled with 61-cm bongo net frames fitted with 505- and 333-μ mesh nets. A double oblique tow was made at each station to a depth of 5 m above the bottom or to a maximum tow depth of 200 m. Vessel speed varied between 1 and 2 kts to maintain a constant 45° tow-wire angle. Calibrated flow meters suspended within the mouth of each net and a bathykymograph were used on each tow to determine water volume filtered and maximum tow-depth, respectively. Details of the net configuration are given by Posgay and Marak (1980) and field sampling methods by Smith and Richardson (1977).

Samples were preserved in a 5% formalin and seawater solution. Fish eggs and larvae from the 505-μ mesh net were sorted and larvae were identified, enumerated and measured to the nearest 0.1 mm SL. For taxa which were abundant in a tow, approximately 50-100 specimens were measured to obtain a representative length frequency. For this study all lengths of haddock larvae were rounded to the nearest mm. The total abundance of each taxon at a station was standardized as the number of larvae under 10 m² of surface area to the maximum tow depth (Smith and Richardson 1977).

The analysis of ichthyoplankton survey data usually includes the calculation of mean catch-per-tow. The data set often contains stations where the species of interest is absent and the frequency of abundances at positive stations is non-normally distributed, usually negative binomially or lognormally distributed. Such data are described by the Δ-distribution (Aitchison 1955). Therefore, the analysis of haddock data was made using the Δ-distribution to determine the mean catch-per-tow and its standard error (Pennington 1983).

Net-Mesh Retention

The bongo net sampler provides suitable samples for analysis of retention rates of larvae at the lower end of the larval length frequency curve. Nets of mesh size 505- and 333-μ are arrayed simultaneously at all standard MARMAP stations. Many of the variables affecting larval catches, e.g. time of day, tow speed, tow depth, etc., are constant for the two nets at a station thus permitting direct comparison of the retention rates of the two nets.

Catches at 18 stations on Georges Bank where larval haddock were abundant were sorted from both nets and compared. Initial comparison of the length frequencies and total number of larvae caught indicated the 333-μ net retained a higher proportion of small (≤6.0 mm) larvae and that total catch was greater (1860 vs 1090 larvae). Approximately 97% of the difference in total catch is accounted for in lengths 3.0-6.0 mm, therefore lengths greater than 6.0 mm were considered fully retained by the 505-μ mesh net.

The relationship of length and proportion retained by the 505-μ net relative to 333-μ net was calculated by applying the linear model of Lenarz (1972) such that $C_i = a + bL$; where C_i equals the relative numbers (percent of total number caught) at length i caught by the 505-μ mesh net divided by the relative numbers caught by the 333-μ mesh net and L_i equals length in mm. The relationship for lengths 3.0-6.0 mm equals $C_i = -1.059 + 0.0452\ L_i$. The length where C_i equals 1 (4.6 mm) indicates the length at equal retention by both nets, therefore C_i at 5.0 mm was assigned a 1 and the regression recalculated. Thus for lengths 3.0, 4.0 and 5.0-mm, C_i equalled 0.272, 0.800 and 1.00, respectively and the linear equation equalled $C_i = -0.765 + 0.0364\ L_i$. The correction factor for extrusion through the 505-μ mesh net is then

$$N_{it} = \frac{N_i}{C_i}$$

where N_{it} is corrected catch at length i and N_i is number caught at length i. Corrections were made for lengths ≤4.8 mm which equals the length at which C_i approaches 1.

Net Avoidance

The ability of fish larvae to actively avoid capture through sensory detection of an approaching net may result in a serious underestimation of total abundance. When visual detection by larvae of an oncoming net is the primary sensory cue then the difference between day- and night-caught larvae should give a measure of avoidance. Clutter and Anraku (1968) reviewed the problem of avoidance and concluded that due to high sampling variability it may be difficult to specify avoidance effects upon catches within useful confidence limits. However, various attempts have been made to account for at least some of the avoidance problem by investigating day-night differences in larval catches (Ahlstrom 1954, Farris 1961, Lenarz 1973). Lenarz studied four species and developed an exponential equation to relate catch rates to larval length and time of day. He found night catches exceeded day catches and the ratio of night to day increased with increasing length of the larvae. This is expected if vision and swimming ability improved as larvae grow.

I investigated the day-night differences in catches of larval haddock from eight surveys of the Georges Bank subarea during the months April-June in 1977-1981. Daytime hours were from 1 hr after sunrise to 1 hr before sunset and night was designated as the time between 1 hr after sunset to 1 hr before sunrise. During these surveys, 142 day-stations and 83 night-stations were sampled. The difference in the number of day and night stations reflects the latitudinal difference in daylight and nighttime hours during the spring months on Georges Bank. The expected ratio of day:night equals 1.63:1 which for exact proportioning of sampling effort day-stations would number 139 and night-stations would number 86.

Before comparing the day catches to night catches, effort must be standardized both spatially and temporally. Preliminary attempts to adjust effort by survey was confounded by the inclusion of stations where the probability of catching haddock larvae was zero. This confounding occurs because a zero tow will affect the day-night comparison when the probability of catching haddock larvae is not zero and thus avoidance is the determining

factor producing a zero tow. It is clear then that zero tows may occur because of: 1) avoidance; 2) the tow was made beyond the areal limits of larval occurrence; or 3) larvae are not at the station because the sample was taken outside the spawning time.

When I analyzed relative abundance (percent abundance), the difference in day-night catches was again misleading because, on a relative scale (%), the total abundance is ignored. Day catches might be 10 times the night catches but when making relative comparisons this important difference is lost in the analysis. It is also evident that large differences in percent abundance at a few length increments between the day and night catches, usually the smallest lengths of the compared length frequencies, will determine the relationship of percentage of all subsequent lengths. This relationship is evident in the length frequencies (%) of Lenarz (1973). His catch curves for northern anchovy by day and night show approximately 80% of the day catches occur in the first two length intervals and only about 45% for the night catches. This leaves 20% and 55% to be apportioned throughout the remaining length intervals, thus producing the characteristic length-percent curves where night catches exceed day catches in the larger size intervals.

Since both night and day catches of haddock larvae appeared to conform to the Δ-distribution, I calculated the Δ-mean catch-per-tow for each mm length interval for day and night catches to determine if avoidance could be detected in the length frequencies. This approach eliminates the problems introduced when using a relative scale and zero tows are included in the calculated Δ-mean.

Shrinkage

The application of laboratory reared growth parameters to field collected larvae requires intercalibration to acount for morphological differences due to preservation and net treatment (Theilacker 1980). The factors of interest here are larval length (SL) and the determination of differences between the measured length of haddock larvae following collection and preservation from surveys and the lengths of live, laboratory reared larvae at the same development stage.

Preservation shrinkage was determined by measuring 25 (4.4-12.7 mm SL) larvae immediately after capture, one day after preservation in 5% buffered formalin solution and again seven days after capture. Mean shrinkage after one day was 3.9% (S = 2.7) and after seven days total shrinkage was 4.2% (S = 3.1). From these data it is clear that over 90% of the preservation shrinkage occurred after one day. The maximum shrinkage between days one and seven was only 1.9%. Mean shrinkage for length <7.9 mm was 5.0% and for lengths >8.0 mm the mean was 1.9%. This is expected because shrinkage is probably related to the degree of ossification (Theilacker 1980) and the ratio of length after preservation to live length should reach an asymptote of one when ossification is complete.

Both the mechanical damage during net collecting and death upon larval length were documented by Blaxter (1971) and Theilacker (1980). Estimates of shrinkage from these factors ranged from 19% for larvae 6 mm or less to between 3% and 8% (depending upon the length of time in the net) for larvae 26 mm or greater. Theilacker (1980) developed an exponential formula to

describe net-treatment shrinkage for northern anchovy, Engraulis moradx, from 4 to about 35 mm long, at which time ossification is complete. Her formula was adopted for a mean net-treatment time of 10 min and adjusted to lengths between 4 mm, the approximate length at hatching, to 15 mm when ossification is essentially complete. Thus shrinkage was maximum at 4 mm and decreased exponentially to near zero at 15 mm. The equation describing the relationship of preserved and net-treated larval length (P_L) to live length (L_L) was:

$$L_L = 1.78369 \, P_L^{0.88979}$$

where lengths are mm x 10.

Temperature-Dependent Larval Growth

Changes in larval growth rate, both between samples during a cruise and between seasons or years, affect the time (days) a larva spends within a given length interval. The greater the change in larval growth due to temperature, the more serious will be the bias upon estimates of larval production and mortality (Saville 1956, Zweifel and Smith 1981). Therefore, the age of each larva was determined using growth rates and length-weight relationships given by Laurence (1978, 1979).

The growth rate of larval haddock was assumed to be curvilinear in relation to temperature where the maximum rate occurs at an optimum temperature and decreases as the temperature varies above or below the optimum. Thornton and Lessem (1978) developed an algorithm for modifying growth rates relative to environmental temperature which uses as input the temperature (t) and growth rate multiplier (K_t) at t. Information presented by Laurence (1978) showed optimum growth occurred at 9°C under laboratory conditions and 4°C was near the lower threshold temperature. By converting growth per week in weight to growth in mm per day from length-weight relations (Laurence 1979), the average growth rate per day at 4°C was 0.81% and at 9°C it was 2.96%. Thus the age of larvae can be calculated as:

$$\text{Age (days)} = \frac{\ln(\frac{L_t}{L_0})}{q}$$

where L_t is observed length, L_0 is length at hatching (4.0 mm) and $q = K_t \, 0.02964$. The value 0.02964 is the optimum instantaneous growth efficient at 9°C for haddock larvae. The growth rate multiplier (K_t) is determined from the growth rate multiplier at t_1 (4°C) which equals 0.274 (0.81/2.96), the observed temperature (t) and r_1, the specific rate coefficient by the formula

$$K_t = \frac{K_1 \, EXP[r_1(t-t_1)]}{1+K_1 \{EXP[r_1(t-t_1)]-1\}}$$

where the specific rate coefficient is

$$r_1 = \frac{1}{t_0 - t_1} \ln \frac{K_0(1-K_1)}{K_1(1-K_0)}$$

As recommended by Thornton and Lessem (1978) K_0 is specified as 0.98 which results in the best fit of data. $t_0 = 9°C$ for haddock, the optimum temperature for growth. Growth rates at temperatures greater than 9°C were assumed to be near the optimum growth rate (i.e. $K_0 > 0.98$ and < 1.0) because information on haddock growth is insufficient to establish the growth rate-temperature relationship at temperatures above 9°C.

Mortality

The estimation of mortality from catch curves assumes: 1) that all individuals in a sample are from one source that has been producing at a constant rate over the time needed to reach the greatest age or length observed, and 2) that mortality is constant over the entire age or length range of the sample. Fishes, in general, do not spawn at a constant rate but rather exhibit an annual spawning peak with spawning intensity decreasing over time before and after the peak. The spawning curve can usually be approximated by a normal distribution. This description is particularly appropriate for temperate and boreal species (Cushing 1975, Wyatt 1980) and certainly describes haddock spawning on Georges Bank (Marak and Livingstone 1970). Assuming a normal curve, spawning mortality will be overestimated from catch curves calculated during the ascending limb of the curve and underestimated on the descending limb. Hewitt and Methot (1982) have shown, through simulation studies, that when larval numbers are accumulated from systematic monthly catch curves that mortality estimation biases tend to cancel out and the calculated mortality from the combined monthly samples estimates the expected larval mortality if mortality is constant.

The assumption of constant mortality over the ages or lengths observed was not verified but rather that the calculated mortalities from accumulated samples for the entire spawning season represent an average value for all lengths or ages in the samples. The yearly catch curves appear to substantiate this because the decrease in numbers at age are not erratic but are reasonably smooth over the entire age range.

The instantaneous "mortality" coefficients (Z) were calculated from age-frequency curves for each year. Lengths were corrected for shrinkage and abundances were corrected for retention (see above) before construction of the frequency curves. The slope of the exponential relationship of abundance on age was used to estimate Z as

$$N = a \, EXP(Z \, t)$$

where N = number of larvae at age t in days.

The exponential decrease in the age frequency of field-sampled larvae, here defined as Z, has two distinct components. One component measures the

death rate of larvae caused by numerous factors including predation, starvation, genetic malformities, disease, etc. This represents the traditional definition of Z and is assumed to be exponential for the purposes of this study. The other component of Z is net avoidance by larvae which can be assumed to increase as larvae grow. The relationship of net avoidance to larval length is probably a power function which increases until 100% avoidance at some length. This seems reasonable because plankton nets are designed to capture only the very youngest life stages of fish and length frequencies of net samples are not continuous. The contribution by each of these two components to the calculated instantaneous "mortality" coefficient cannot be determined from the bongo net samples. An example of avoidance is given by Murphy and Clutter (1972) who found the catches of anchovy (Stolephorus purpureus) larvae over 5.5 mm in length with a purse seine were at least an order of magnitude greater than with towed plankton nets. However, if it is assumed that rate of increase in net avoidance with larval length is constant and that the smallest larvae cannot avoid capture or be extruded, then Z can be used for backcalculating spawning stock size without introducing a systematic bias.

Spawning Stock Biomass Estimates

The relationship of spawning stock biomass to ichthyoplankton is usually expressed as

$$B = \frac{I}{R_I}$$

where B = spawning stock biomass, I = ichthyoplankton abundance and R_I is the production of I per unit weight of the spawning stock. I is determined from survey data and growth or incubation rates of larvae or eggs, respectively. R_I usually represents egg production per unit weight of mature females from fecundity studies adjusted for the ratio of females to males in the spawning stock. Thus by determining the total abundance of eggs produced during the entire spawning season and the production of eggs per gram of spawning stock will give an estimate of total grams of spawning stock.

The use of larval abundance, i.e. the number of larvae at hatching, and an estimate of egg mortality will yield a total egg abundance estimate. In this study, estimates of growth and mortality were applied to shrinkage and extrusion adjusted larval abundances to determine the number of larvae at hatching at each station. Since larval haddock remain vulnerable to sampling for as long as 53 days (see Table 3) and surveys were less than 53 days apart in an area, then newly hatched larvae in a survey could be captured again in the succeeding survey. This double sampling will overestimate spawning stock biomass and must be eliminated before the estimates are made. To accomplish this, the mean sampling date of tows containing haddock larvae in each of the three subareas by survey was determined and any larvae hatched on or before this date in subsequent surveys in the same subareas were dropped from the biomass analysis.

An investigation of cod, Gadus morhua, and haddock eggs collected in April and early May 1979 on Georges Bank and in the Gulf of Maine revealed an average daily egg mortality of 7.5% (P. Berrien, personal communication). Mean surface water temperature in the survey area was 4.6°C which indicates

incubation was 17 days and a total egg survival of 26.8%. Saville (1953), working on haddock eggs at Faroe, found egg mortalities were about 10% per day for the 1950-1953 spawning seasons. Given an average incubation of 14 days, total egg survival at Faroe (22.9%) is remarkably close to that found during 1979 in the Georges Bank-Gulf of Maine area. For this study, egg mortality was assumed to be 10% per day and an average incubation time of 14 days. Thus larval abundances were converted to egg abundances by calculating the number of eggs at each station by applying the assumed egg mortality rate. The Δ-mean eggs per 10 m² were then expanded for each survey using the subarea surface area to give total egg abundance. Subarea and survey totals were summed to give the total eggs spawned in each year.

Relative fecundity (eggs per gram of female) was estimated to be 640 from haddock length-weight relationships (Hodder 1963) and length-fecundity relationships of haddock on Georges Bank (Morse et al. unpublished data). Sex ratio of the spawning stock was approximately 1:1 (Morse unpublished data) and was assumed to be 1:1 for this analysis.

RESULTS

Net Avoidance

A total of 10,966 haddock larvae was captured during both day and night tows; 7,174 during daylight hours and 3,792 at night. Table 2 gives the Δ-mean catch-per-tow by millimeter length intervals for day and night samples as well as the ratio of night to day Δ-means. Two conclusions are obvious from the table: 1) for larval lengths greater than 12 mm and less than 3 mm, the sample size is inadequate for day-night comparisons and 2) the ratio of night to day Δ-means is quite variable - ranging from 0.70 at 4 mm to 3.90 at 12 mm.

If the assumption that visual detection of the approaching net by larvae is a significant factor contributing to net avoidance then the ratio of night to day catches should increase above 1.0 as larval swimming ability increases. The trend in ratios in Table 2 does not support the above hypothesis. In fact, ratios less than 1.0 occur at 4-, 5-, 9- and 11-mm lengths and the only consistent trend of increasing ratios occur between 4- to 8-mm lengths. For lengths greater than 8 mm the ratio fluctuates between 0.80 and 3.90 and this length interval would be expected to show consistently high ratios if visual detection and avoidance were a significant factor affecting the catches. Thus, differential net avoidance could not be detected by examining the difference in day and night catches.

Mortality

Age frequencies were developed for each year using the methods described above. Catches were corrected for extrusion loss through the 505 μm mesh net and preserved lengths were adjusted for shrinkage. The age of each larva was then determined using the surface temperature at the place of capture as the reference temperature to adjust for temperature-dependent growth. Age frequencies for each station were then combined for each year to give the total age frequency (Figure 2). Numbers at age were grouped into 4-day intervals and exponential regressions were calculated for each year. The slope of the regression line was used as an estimate of larval mortality for

all years except 1979. The length frequency for 1979 showed a modal length at 25 mm indicating its unsuitability for mortality estimation. Mortalty for 1979 was estimated as the average mortality of years 1977-1982, minus 1979.

Daily percent mortality ranged from 9.0 (Z = 0.0933) in 1980 to 12.2 (Z = 0.13062) in 1982 (Table 3). The 1982 larval catches were quite small relative to the other years examined and show the magnitude of interannual variability of catches and indicate a possible problem when this variability is not accounted for or is unknown.

Larval Abundance and Spawning Stock Biomass

The Δ-mean catch-per-tow of larvae at hatching was calculated for each subarea by survey (Table 4). The southern Gulf of Maine (SGOM) contributed only small numbers of larvae during 1977 and 1978 and no larvae from 1979-1982. SGOM accounted for 1.4% of all larvae. Georges Bank (GB) subarea contained 86.1% of the larvae and catches there were dominant during all but four surveys. The northern Middle Atlantic Bight (NMAB) subarea contributed 12.5% of the larvae captured with significant numbers caught during 1977, 1979 and 1980.

Total larval production by subarea, survey and year are given in Table 5. These represent expansions of Δ-mean catch-per-tow by the surface area of each subarea. Production increased from approximately 3.6×10^{12} larvae in 1977 to a peak of 9.3×10^{12} in 1979. A 49% decrease occurred from 1979 to 1981 and a precipitous decrease was found in 1982 to only 5.5% of the 1981 level.

Spawning stock biomass estimates shown in Table 5 are a function of larval production and thus follow the same trends. Peak biomass at 127,522 t occurred in 1979 and the lowest estimate was in 1982 of 3,590 t. Other years were between 49 and 94 thousand t.

DISCUSSION

The techniques of using ichthyoplankton for spawning stock biomass estimation have been well documented, e.g. Smith and Richardson (1977) and Zweifel and Smith (1981), although surprisingly few data sets exist which meet even the minimum technical requirements necessary to derive meaningful estimates. The ichthyoplankton sampling of the MARMAP program has provided a unique opportunity to use a 6-year data set in the northwest Atlantic to estimate the spawning biomass of numerous species.

This study of haddock larvae on Georges Bank attempts to address what Zweifel and Smith (1981) call the "effective sampler size" by accounting for some of the most serious biases encountered in larval sampling. These biases include standardization of net catches to the number of larvae under 10 m^2 of surface area, net avoidance, extrusion through the net meshes, temperature-dependent growth and annual changes in larval mortality.

A comparison of spawning stock biomass from larval data and VPA and research vessel catch-per-tow (kg) (Overholtz et al. 1983) shows similar trends for all three values (Table 6). The greatest magnitude of change occurred in the biomass estimates from larval data when 1982 is included.

However, as I mentioned earlier, the 1982 data appears anomolous is not adequate for biomass estimates. Omitting the 1982 larval estimate, there was a 2.6 fold change in spawning stock biomass with a minimum value in 1977 and the peak in 1979. VPA estimates peaked in 1978 and then decreased steadily to a minimum in 1982. The stratified mean catch-per-tow peaked in 1979, as the larval estimates did, and the minimum value occurred in 1982. The catch-per-tow showed the greatest variability with a 6.4 fold decrease from 1979 to 1982. All three values indicate a significant decrease in haddock spawning stock biomass from a peak in either 1978 or 1979 to minimum biomass in 1982.

It is tempting to use a statistical comparison of the three data sets in Table 6 but each estimate contains its own variability and uncertainties which makes comparisons, such as correlation analysis, inappropriate. To illustrate this point, Grosslein (1971) has shown that the research vessel surveys will not detect a change in haddock abundance if the change is less than a factor of 2. This corresponds to a confidence interval of the mean catch-per-tow on the linear scale of ±50%. The standard error of the Δ-mean catch-per-tow of the larval data is often greater than 50% of the mean (Table 6) which again illustrates the degree of sampling error inherent in the larval data. Overholtz et al. (1983) do not give the variance component for their VPA biomass estimates but, given the effects of misreporting of haddock landings in recent years and the sensitivity of VPA to terminal F values, it seems reasonable to assume the VPA estimates contain significant uncertainties.

Although this study has attempted to derive an "effective sampler size" for haddock larvae, much work still needs to be done to reduce uncertainties and increase the reliability of spawning stock estimates from larval surveys. The two most important, and most difficult to define, variables used in this study are larval mortality and temperature-dependent growth. Mortalities estimated from age-frequencies pooled from a number of surveys during a spawning season seems adequate if spawning intensity over time is approximated by a normal curve and samples are collected frequently (monthly?) throughout the spawning season (Hewitt and Methot 1982). However, the interdependence of the growth rate, temperature and food supply and their effects on the derived age-frequency curves need further study. Thus the next steps needed to improve our estimates of spawning stock biomass include larval growth studies, in situ, and vertical distribution studies to define the larval fish habitat in relation to water temperature.

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Table 1.--Summary of survey dates, total number of stations sampled and stations at which haddock larvae were captured by subarea. NMAB = northern Middle Atlantic Bight; GB = Georges Bank; SGOM = southern Gulf of Maine.

Survey	Dates	Number of stations by subarea			Number of stations with haddock by subarea		
		NMAB	GB	SGOM	NMAB	GB	SGOM
77-2	4 Mar-23 Apr	57	32	16	5	3	0
77-3	14 Apr-13 May	26	30	21	2	15	0
77-4	20 May-16 Jun	63	43	20	28	13	3
78-1	16 Feb-17 Mar	47	42	18	0	6	0
78-2	25 Apr-23 May	46	36	18	0	14	0
78-3	29 Jun-16 Jun	45	16	16	1	2	1
79-1	2 Mar-14 Mar	40	5	9	1	0	0
79-2	1 Apr- 7 May	44	33	22	0	16	0
79-3	12 May-29 May	44	30	21	8	14	0
80-1	20 Feb- 4 Apr	45	29	25	1	10	0
80-2	23 Apr-12 May	45	29	24	5	16	0
80-3	29 May-29 Jun	43	23	20	11	8	0
80-4	8 Jul- 9 Aug	44	24	23	0	1	0
81-1	18 Feb-21 Mar	43	30	23	1	6	0
81-2	7 Apr-12 May	45	30	11	0	13	0
81-3	21 May-14 Jun	43	29	24	4	14	0
81-4	1 Jul-19 Jul	35	26	0	1	0	0
82-2	25 Mar- 7 May	42	26	22	0	4	0
82-3	18 May-11 Jun	39	35	14	3	5	0

Table 2.--The Δ-mean catch-per-tow of haddock larvae on Georges Bank by day and night and the ratio of night caught to day caught by length interval.

Length (mm)	Day Caught		Night Caught		
	Number of stations	Δ-mean catch/tow (D)	Number of stations	Δ-mean catch/tow (N)	Ratio N/D
2	1	0.069	1	0.087	1.26
3	17	1.258	9	1.355	1.08
4	36	3.072	21	2.153	0.70
5	22	2.043	15	1.642	0.80
6	21	1.891	11	1.966	1.04
7	21	1.494	10	1.797	1.20
8	17	1.060	13	2.083	1.97
9	17	1.222	8	0.972	0.80
10	15	0.704	10	0.915	1.30
11	10	0.502	5	0.463	0.92
12	3	0.112	5	0.437	3.90
13	5	0.192	1	0.069	0.36
14	1	0.012	1	0.070	5.83
15	6	0.271	-	-	-
16	2	0.045	-	-	-
17	-	-	-	-	-
18	-	-	2	0.142	-

Table 3.--Summary of regression analysis of haddock larvae on Georges Bank
for estimating mortality (Z).

Year	N	Age (days) interval	Regression constants		SE_z	r^2
			a	Z		
1977	14	1-53	2054.54	-0.10206	±0.0391	.91
1978	13	1-49	1708.975	-0.11389	±0.0440	.78
1979	-	-	-	-0.10814[*]	-	-
1980	11	9-49	3285.560	-0.09386	±0.0346	.82
1981	13	1-49	1836.550	-0.10029	±0.0401	.94
1982	6	17-37	245.672	-0.13062	±0.0266	.68

[*]Average Z for 1977-1982

Table 4.--The Δ-mean catch-per-tow of haddock larvae at hatching by subarea and survey, 1977-1982.

| | SUBAREA | | | | | |
| | NMAB | | GB | | SGOM | |
Survey	Δ-mean	Std. error	Δ-mean	Std. error	Δ-mean	Std. error
77-2	6.75	4.41	5.98	3.72	-	-
77-3	3.26	2.61	523.12	372.58	-	-
77-4	124.12	43.94	87.66	35.54	45.57	42.63
78-1	-	-	9.81	7.23	-	-
78-2	-	-	1018.39	700.81	-	-
78-3	2.34	15.71	42.32	29.84	10.98	43.90
79-1	2.70	17.08	-	-	-	-
79-2	-	-	65.40	26.18	-	-
79-3	309.21	204.56	1720.76	952.70	-	-
80-1	8.95	60.03	173.39	95.62	-	-
80-2	202.45	145.28	1018.55	613.12	-	-
80-3	23.58	7.02	115.00	55.69	-	-
80-4	-	-	2.70	13.22	-	-
81-1	2.62	17.18	27.56	12.82	-	-
81-2	-	-	563.52	334.73	-	-
81-3	28.94	15.14	551.15	230.81	-	-
82-2	-	-	38.41	30.32	-	-
82-3	10.13	6.11	9.96	5.46	-	-

Table 5.--Total abundance of haddock larvae (x 10^9) by subarea, survey and yearly total and spawning stock biomass estimates by survey and year.

Survey	Subarea			Larval abundance (x 10^9)	Sp. stock biomass (t)
	NMAB	GB	SGOM		
77-2	40.45	24.99	-	65.44	893.92
77-3	19.52	2187.10	-	2206.62	30142.50
77-4	743.53	366.50	182.28	1292.31	17653.00
			TOTALS	3564.37	48689.42
78-1	-	41.03	-	41.03	560.48
78-2	-	4257.78	-	4257.78	58161.42
78-3	14.02	176.92	43.92	234.86	3208.20
			TOTALS	4533.67	61930.10
79-1	16.17	-	-	16.17	220.88
79-2	-	273.43	-	273.43	3735.06
79-3	1852.33	7194.32	-	9046.65	123577.54
			TOTALS	9336.25	127533.48
80-1	53.62	724.94	-	778.56	10635.16
80-2	1212.78	4258.47	-	5471.25	74737.46
80-3	141.27	480.81	-	622.08	8497.63
80-4	-	11.29	-	11.29	154.22
			TOTALS	6883.18	94024.31
81-1	15.76	115.24	-	131.00	1789.46
81-2	-	2356.03	-	2356.03	32183.45
81-3	173.38	2137.05	-	2310.43	31560.55
			TOTALS	4797.46	65533.46
82-2	-	160.57	-	160.57	2193.39
82-3	60.68	41.64	-	102.32	1397.69
			TOTALS	262.89	3590.08

Table 6.--Spawning stock biomass estimates and stratified mean
catch-per-tow of the Georges Bank haddock stock.

Year	Spawning Stock Biomass (t)		Stratified catch/tow (kg)
	Larvae	VPA	
1977	48,699	60,596	23.13
1978	61,931	90,896	15.18
1979	127,533	78,826	26.87
1980	94,025	87,465	18.47
1981	65,534	40,701	11.77
1982	3,591	39,642	4.17
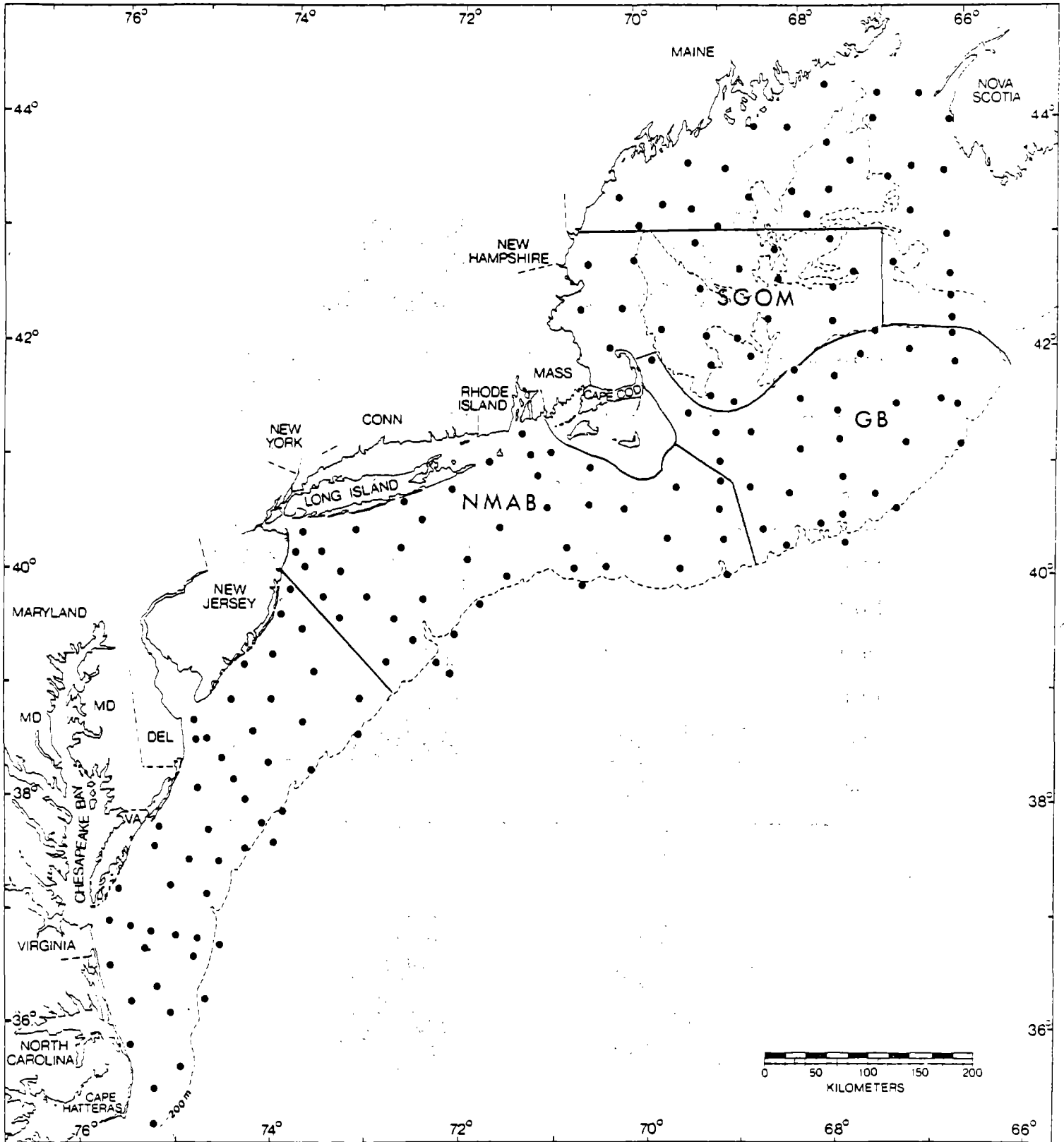
Figure 1. Standard MARMAP sampling locations and boundaries of subareas used for analysis of haddock larvae.
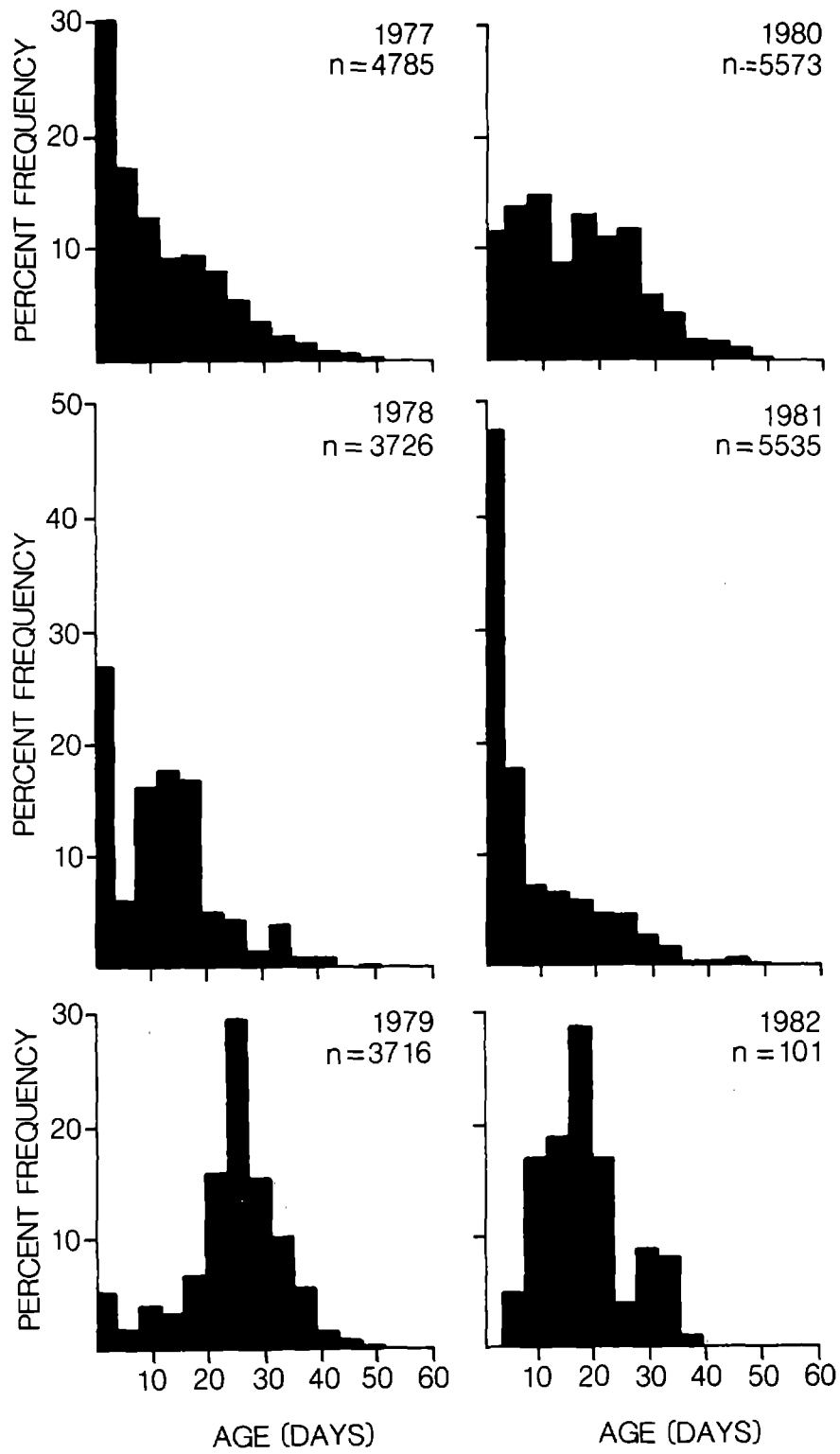
Figure 2. Age frequencies of haddock larvae for years 1977-1982.
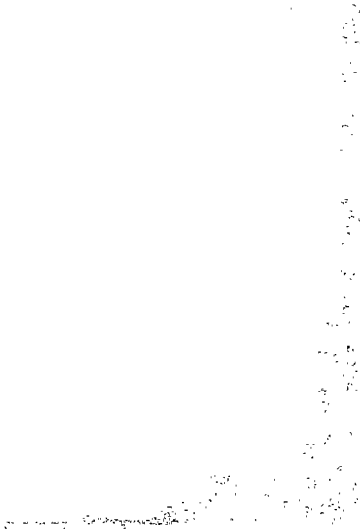
Measuring the Precision of Estimates of Total Egg Production

Based on Plankton Surveys[*]

by

Michael Pennington[1] and Peter Berrien[2]

[1]National Marine Fisheries Service, NOAA
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543

[2]National Marine Fisheries Service, NOAA
Sandy Hook Laboratory
Highlands, New Jersey 07732

ABSTRACT

Methods are given to measure the effects of spatial and temporal differences in fish egg production on the precision of estimates of total seasonal egg production derived from ichythyoplankton surveys. The techniques are applied to the results of large scale plankton surveys conducted in 1977 and 1979 off the northeastern United States. For the three species analyzed (Atlantic mackerel, _Scomber_ _scombrus_; silver hake, _Merluccius_ _bilinearis_; and yellowtail flounder, _Limanda_ _ferruginea_), the surveys produced estimates of total egg production having an average coefficient of variation equal to 31%. Estimates of spawning stock size based on the egg production estimates compared favorably with other independent assessments of stock size.

INTRODUCTION

Large scale plankton surveys have been conducted off the northeast coast of the United States since the autumn of 1976 as part of a long-term monitoring program (MARMAP) of the National Marine Fisheries Service. Generally, six data gathering cruises per year, at various seasons, cover the Gulf of Maine, Georges Bank, Southern New England, and Middle Atlantic Bight waters out to the edge of the continental shelf. One objective of these surveys is to produce an estimate of the total seasonal production of eggs spawned by certain fish species. From egg abundance values, estimates can be made of spawning stock size if other biological information such as the sex ratios, fecundity, percent mature, and length frequencies are available. Egg surveys often produce estimates of spawning stock size which are consistent with estimates derived from other data (see e.g., Saville, 1954; Simpson, 1959; Berrien et al., 1981; Lockwood et al., 1981; Berrien, 1981; Berrien, 1983).

The estimated precision of egg surveys, and hence of the derived spawning stock size estimates, is usually based only on the variability of egg densities over space while the variability due to production changing over time is ignored (Saville, 1964; Lockwood et al., 1981). In this paper a technique is described which measures the effect of varying production over time and space on the precision of estimates of total seasonal egg production. The method is applied to survey results for three species, Atlantic mackerel (Scomber scombus), silver hake (Merluccius bilinearis) and yellowtail flounder (Limanda ferruginea) to ascertain the approximate precision of the estimates of total egg production.

METHODS

The Data

Data analyzed in this paper were collected during MARMAP (Marine Resources Monitoring, Assessment and Prediction) ichthyoplankton surveys in 1977 (mackerel and yellowtail) and 1979 (silver hake). The MARMAP surveys cover much (258,000 km^2) of the continental shelf off the northeast coast of North America from Cape Hatteras, North Carolina to Nova Scotia. Subareas for 1977 (Figure 1) were based on the frequency of survey cruises in each subarea. The unequal effort in each subarea resulted from vessel scheduling problems and, in some cases, from restrictions on European vessel operations in U.S. and Canadian waters (Berrien et al., 1981). Different subareas were used for 1979 data (Figure 1). They were based on oceanographic and biological considerations, and were selected so as to allow direct comparison with population estimates from cohort analysis.

Ichthyoplankton was sampled with 61-cm bongos fitted with 0.505-mm mesh nets. Smooth, double-oblique plankton hauls were made at each station according to standard MARMAP I procedures (Jossi et al., 1975). Sampling extended from the surface to within 5 m of the bottom or to a maximum depth of 200 m and was conducted at a vessel speed of approximately 1.5 kts.

Fish eggs were removed from the samples, identified and separated into developmental stages. Numbers of eggs collected were adjusted to no./day/m^2 of sea surface area. Mortality rates were calculated on the observed decline in numbers with stage mean age. Numbers sampled/m^2/day at each station were then adjusted for mortality to calculate numbers of eggs spawned/m^2/day and

these adjusted values were used to derive the estimates of total egg production for the entire season. For a more detailed account of sampling and analysis procedures, see Berrien et al. (1981) and Berrien (1981, 1983).

Statistical Methods

Data from a cruise was used to estimate the mean number of eggs spawned/m^2/day at the time of each cruise. Only part of each survey area contained the eggs of any particular species, and hence the proportion of nonzeros in the sample estimates the fraction of the area in which eggs occurred. It has been observed (Berrien et al., 1981; Berrien, 1981; Lockwood et al., 1981) that the distribution of the nonzero values is often lognormal for egg data. A distribution with a proportion of zeros such that the nonzero values are lognormally distributed is called a Δ-distribution (Aitchison and Brown, 1957). The estimator (c) of the arithmetic mean (Aitchison and Brown, 1957) and its variance [var(c)] (Pennington, 1983) for the Δ-distribution are:

$$
c = \begin{cases} \dfrac{m}{n} \exp(\bar{y}) G_m(s^2/2), & m > 1, \\[2em] \dfrac{x_1}{n}, & m = 1, \\[2em] 0 & m = 0, \end{cases} \qquad (1)
$$

and

$$
\text{var}(c) = \begin{cases}
\frac{m}{n} \exp(2\bar{y})\{\frac{m}{n} G_m^2(s^2/2) - (\frac{m-1}{n-1}G_m(\frac{m-2}{m-1} s^2))\} , & m>1, \\
\\
(\frac{x_1}{n})^2 & m=1, \\
\\
0, & m=0,
\end{cases} \qquad (2)
$$

where:

n is the sample size,

m is the number of nonzero values,

$\bar{y}$ is the sample mean of the nonzero $\log_e$ values,

s^2 is the sample variance of the $\log_e$ values,

x_1 is for m=1 the single nonzero value,

and

$$
G_m(x) = 1 + \frac{m-1}{m}x + \sum_{j=2}^{\infty} \frac{(m-1)^{2j-1} x^j}{m^j(m+1)(m+3)\ldots(m+2j-3)j!} .
$$

With a computer it is easy to evaluate $G_m(x)$ for given values of x and m. For smaller values of m and/or larger values of x, the usual approximations to $G_m(x)$ such as $\exp[(\frac{m-1}{m})x]$ (Jones, 1956) are poor. For egg surveys, c can be much more efficient in estimating the mean number of eggs spawned/ m^2/day than the ordinary sample mean (Pennington, 1983).

The rate (T_t) of production for a subarea at time t (taken to be the midpoint of sample collection) is then estimated by

$$T_t = Ac,$$

where A is the area of the subarea, and its variance by

$$var(T_t) = A^2 var(c).$$

To calculate an estimate of total seasonal egg production (T), the production rates are integrated over time or

$$T = a_1 T_{t_1} + a_2 T_{t_2} + \ldots + a_k T_{t_k}$$

where $a_1, \ldots a_k$ are constants which depend on the spacing of the cruises and $t_1, \ldots, t_k$ are the times represented by each individual survey cruise.

A sequence of plankton surveys is in effect most often a systematic survey taken over time. For a sequence of k surveys conducted, for example at monthly intervals, let $T_{t_1, t_2, \ldots, t_k}$ denote the estimate of total egg production based on the k surveys. Then the variance of $T_{t_1, t_2, \ldots, t_k}$ is given by (Rao, 1973, p. 97):

$$\text{Var}(T_{t_1, t_2, \ldots, t_k}) = E[\text{Var}(T_{t_1, t_2, \ldots, t_k} \mid t_1, t_2, \ldots, t_k)] +$$

$$\text{Var}[E(T_{t_1, t_2, \ldots, t_k} \mid t_1, t_2, \ldots, t_k)]. \tag{3}$$

The first term on the right hand side of equation (3) is the average variance due to spatial differences in abundance, and the last term is the variance of the expected abundance for a particular sequence taken over all possible sequences of monthly surveys. Now if T_1, T_2, $\ldots$ T_ℓ are estimates of total egg production based on ℓ systematic monthly surveys taken with random starts then

$$\bar{T} = \sum_{i=1}^{\ell} T_i / \ell \tag{4}$$

is an unbiased estimate of total production,

$$\text{var}(\bar{T}) = \sum_{i=1}^{\ell} (T_i - \bar{T})^2 / \ell(\ell-1) \tag{5}$$

is an unbiased estimate of its variance, and $\ell \cdot \text{var}(\bar{T})$ is an unbiased estimate of the variance of a single systematic survey conducted at monthly intervals, i.e., of the left hand side of equation (3).

For the data at hand, since the nonzero values from an individual cruise were distributed lognormally, the production rate for each subarea and cruise was calculated using equation (1). Alternate cruises were then used to calculate two estimates of total production for each subarea (or a combination of subareas if production was low). The average of the two values (equation (4) with $\ell = 2$) estimates egg production in each subarea with an estimated variance given by equation (5). The final estimate of total production for the entire region is the sum of the subarea estimates of production and its variance is the sum of their estimated variances. One reason for calculating subarea estimates is to increase the number of degrees of freedom for the estimate of the total variance. But since the variances of the production estimates for the subareas were considerably different, Satterthwaite's formula (Cochran, 1977, p. 96) was used to estimate the effective number of degrees of freedom.

It was also desired to obtain a rough indication of the proportion of the total variance due respectively to spatial and temporal effects for the surveys. Equation (2) was used to estimate the spatial component of variance, which along with the estimate of the total variance, was used in conjunction with equation (3) to obtain an estimate of the variability due to time for the present survey design.

Finally, estimates of spawning stock size based on total egg production were calculated as described in Berrien et al. (1981), Berrien (1981), and Berrien (1983). It is assumed that the variability of the estimates were due mainly to the variability of the egg production estimates and hence the variance of the spawning stock size estimates reflect solely the variability of the egg data.

RESULTS

Tables I and II summarize the statistics used to estimate the egg production for each subarea at the times represented by the individual surveys. Also given are estimates of the standard error of the estimated rate of production (c) resulting from the spatial variability at the times sampled. The daily egg production curves for each subarea and for the entire region are shown in Figures 2-4.

Table III contains estimates of total seasonal egg production for each species based on treating the series as two alternating systematic samples. In parentheses, under the production estimates, are the estimates of production derived by treating the series as a single systematic sample. Also in Table III are estimates of the components of the sampling variance due to temporal and spatial effects for the surveys as conducted. Column 6 gives the estimated standard error of the total seasonal egg production estimates and in column 7 are its effective number of degrees of freedom.

In Table IV are estimates of spawning stock size for each species based on the egg production estimates. Confidence intervals for these estimates (80% for mackerel and silver hake, 70% for yellowtail) are also presented. Again, it should be noted that the confidence intervals only take into account the variability of the egg estimates.

DISCUSSION AND CONCLUSIONS

In practice the dates at which plankton survey cruises are conducted are spread throughout a season rather than chosen randomly with respect to time. Therefore, the surveys are effectively systematic in time. For natural populations, systematic sampling can be much more efficient than random sampling, particularly so for populations which vary continuously

(Cochran, 1977, p. 221). Egg production for the three species analyzed appears to be fairly continuous over time. That is, though the estimated error of the individual production rates (c) for each subarea is relatively large, the rates (see Tables I and II) do not vary erratically over time, but for most subareas, rise to a peak and then decline.

There are various ways to estimate the variance of the results from a single systematic sample after making some assumptions (Cochran, 1977, p. 223). Where practical, unbiased estimates of the sampling variance can be made by dividing the effort into two (or more) systematic samples with random starts. Though the MARMAP surveys were not designed as two independent series of surveys, logistics and the large area covered produced alternate surveys with starts approximately random in each subarea. A disadvantage of the method used to estimate the total variance is that it may overestimate the true value, especially if the complete survey, being systematic in time, has been effective in reducing the variance.

The relative sizes of the variance components (Table III), though imprecise as reflected by the negative estimate of the time component for silver hake, indicate the sources of variability for the surveys as conducted. For example, the proportion of the total variation due to time was highest for yellowtail flounder and lowest for silver hake. This results from the fact that one cruise in a subarea accounted for 52% of the yellowtail egg production (Table I) as compared with 22% from a single cruise for silver hake (Table II). The high concentration of egg production in a short time period for yellowtail is the reason that the estimate of the total variance has only 1 effective degree of freedom,

as a consequence, the estimate of seasonal egg production for yellowtail
is the least precise of the three.

One way to assess the accuracy of egg surveys is to compare the
estimates of spawning stock size based on the surveys with other available
estimates. Table IV contains estimates of spawning stock size derived
both from the egg surveys and from cohort analysis. For Atlantic mackerel
the spawning stock estimates based on the egg survey (1.20×10^9 fish) com-
pared favorably with cohort analysis ($.96 \times 10^9$ fish). The estimate for
silver hake from cohort analysis ($.77 \times 10^9$ fish), though considerably
lower than the estimate based on the egg survey (1.55×10^9 fish), is just
within the 95% confidence interval for the egg survey estimate. Due to
silver hake catches having sharply declined in recent years, the estimate
based on cohort analysis is considered tentative since cohort analysis
tends to underestimate population sizes in a fishery with declining catches
(Berrien, 1983). The estimate for yellowtail (1.38×10^8 fish) based on
the egg survey appears to be quite reasonable, although no cohort analysis
is available (Berrien, 1981).

There are other possible sources of uncertainty in egg abundance
estimates which have not been addressed here. Errors could result from
insufficient coverage of spawning area and season due either to inadequate
survey design or vessel operations and the vagaries of weather. For in-
stance, an apparently important spawning area of silver hake in the western
Gulf of Maine was not adequately sampled in the summer resulting in egg
estimates that are probably low. Another possible, but less worrisome
source of bias in egg census work, could arise through choice of a water

column temperature which does not accurately reflect conditions experienced by an egg sample in question. The application of an inaccurate mortality rate to egg catches would bias resulting production levels. However, this effect is minimized by the use of the youngest stage eggs to derive the final egg census estimates. Beyond egg production estimates, errors in any of the following parameters on adults could bias the resulting population estimates: the length-frequency distribution, male-female ratio, percent mature at size, and fecundity at size.

For the species considered, the egg surveys provide estimates of sufficient accuracy for detecting large changes in the spawning populations. It should be stressed though, that the data are only from one year for each species. But if the shape of the production curves proves to be similar for other years, then the use of egg surveys to estimate fish abundance would appear to offer a feasible method of monitoring major fluctuations in spawning stocks. It provides a means of estimating the absolute abundance for species for which no fishery exists, and probably is cost effective in cases where fishery statistics are inadequate to provide an accurate cohort analysis.

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Table I. Atlantic Mackerel and Yellowtail Flounder Egg Production Estimates for 1977.

Subarea (Area km²)	Survey Cruise	Sampling Midpoint Date	Days Represented	ATLANTIC MACKEREL					YELLOWTAIL FLOUNDER			
				n	m	c	Standard Error of c	Eggs Spawned in Subarea by Survey (x10⁻¹²)	m	c	Standard Error of c	Eggs Spawned in Subarea by Survey (x10⁻¹²)
1 (16560)	1	24 Mar	22	15	0	0	0	0	0	0	0	0
	2	14 Apr	21	17	3	0.0	0.0	0.0	0	0	0	0
	3	5 May	35	17	0	0	0	0	0	0	0	0
	4	22 Jun	49	17	0	0	0	0	0	0	0	0
	5	11 Aug	50	17	0	0	0	0	0	0	0	0
2 (67288)	1	29 Mar	26	54	0	0	0	0	15	7.3	3.2	1.0
	2	19 Apr	14	68	44	3.3	1.4	3.2	22	16.3	6.5	1.6
	3	26 Apr	10	57	42	76.3	44.9	52.6	28	19.3	7.5	1.3
	4	9 May	13	66	34	42.0	22.8	36.6	24	11.1	4.5	1.0
	5	23 May	24	69	35	43.8	21.1	69.4	22	16.7	6.8	2.6
	6	25 Jun	42	69	7	1.0	0.6	2.9	0	0	0	0
	7	15 Aug	51	58	0	0	0	0	0	0	0	0
3 (14131)	1	7 Mar	40	18	0	0	0	0	3	0.3	0.2	0.0
	2	15 Apr	23	8	0	0	0	0	6	50.4	29.8	1.7
	3	22 Apr	13	8	0	0	0	0	3	14.5	9.1	0.3
	4	11 May	17	7	7	5.3	2.1	1.7	5	123.0	83.0	2.9
	5	26 May	24	8	6	90.9	78.1	31.3	3	82.3	57.1	2.8
	6	29 Jun	41	8	2	5.6	5.2	4.3	1	2.1	2.1	0.1
	7	15 Aug	47	9	2	0.4	0.3	0.3	0	0	0	0
4 (84794)	1	21 Mar	40	70	0	0	0	0	15	6.6	3.4	2.2
	2	30 Mar	38	54	1	0.0	0.0	0.0	24	19.7	8.9	6.3
	3	4 Jun	50	81	67	22.7	9.9	96.2	50	70.2	21.5	29.8
	4	8 Aug	64	55	1	0.0	0.0	0.0	3	0.6	0.4	0.3
5 (19137)	1	1 Apr	26	14	0	0	0	0	1	0.1	0.1	0.0
	2	27 Apr	66	12	0	0	0	0	2	16.3	16.1	2.0
	3	10 Apr	105	10	0	0	0	0	0	0	0	0
6 (29837)	1	6 May	38	19	0	0	0	0	2	0.6	0.5	0.1
	2	14 Jun	38	17	2	0.0	0.0	0.0	5	4.5	2.9	0.5
7 (9299)	1	12 May	23	5	0	0	0	0	0	0	0	0
	2	4 Jun	44	9	7	12.8	7.8	4.7	4	2.7	1.4	0.1
	3	8 Aug	65	7	0	0	0	0	2	2.5	2.1	0.2
8 (9734)	1	9 May	92	7	0	0	0	0	0	0	0	0
	2	9 Aug	92	3	0	0	0	0	0	0	0	0

Table II. Silver Hake Egg Production Estimates for 1979

Subarea (Area km²)	Survey Cruise	Sampling Midpoint Date	Days Represented	n	m	c	Standard Error of c	Eggs Spawned in Subarea by Survey (x10⁻12)
Gulf of Maine (98026)	1	10 Mar	21	9	0	0	0	0
	2	21 Apr	36	39	0	0	0	0
	3	21 May	39	50	4	1.1	0.6	0.4
	4	8 Jul	48	11	3	13.4	10.5	6.3
	5	26 Aug	55	39	12	54.9	29.1	29.4
	6	25 Oct	47	38	1	0.2	0.2	0.1
	7	27 Nov	17	45	0	0	0	0
Georges Bank (41809)	1	10 Mar	9	5	0	0	0	0
	2	28 Mar	35	32	1	0.1	0.1	0.0
	3	19 May	52	27	6	148.6	130.5	32.1
	4	9 Jul	49	19	14	224.9	108.0	46.4
	5	26 Aug	52	19	13	31.2	11.4	6.8
	6	22 Oct	54	29	1	0.2	0.2	0.0
	7	12 Dec	25	29	1	0.2	0.2	0.0
Southern New England (59906)	1	4 Mar	20	40	0	0	0	0
	2	14 Apr	35	25	4	1.1	0.6	0.2
	3	13 May	41	44	24	63.4	26.9	15.6
	4	5 Jul	49	43	19	130.1	69.5	38.1
	5	19 Aug	50	38	21	38.2	14.3	11.5
	6	13 Oct	45	42	23	18.9	6.1	5.1
	7	17 Nov	17	27	3	1.0	0.7	0.1
Middle Atlantic (58326)	1	26 Feb	22	48	0	0	0	0
	2	11 Apr	35	2	0	0	0	0
	3	6 May	37	49	16	30.7	14.7	6.5
	4	23 Jun	50	50	7	24.4	17.6	7.2
	5	14 Aug	53	49	10	7.6	3.7	2.3
	6	7 Oct	27	48	5	2.5	1.9	0.4

Table III. Estimates of Total Seasonal Egg Production and Associated Statistics.

Species	Variation due to time ($\times 10^{-24}$)	Variation due to space ($\times 10^{-24}$)	Total Variation ($\times 10^{-24}$)	Estimated Total Production of Egg ($\times 10^{-12}$)	Standard Error of Total Production ($\times 10^{-12}$)	Effective Number of d.f.
Atlantic mackerel	14067	4974	19041	328 (303)*	138	2.2
Silver hake	---	1936	786	203 (209)*	28	2.5
Yellowtail flounder	407	107	514	58 (57)*	22	1.0

*Estimates based on treating surveys as a single systematic survey (see text).

Table IV. Estimates of spawning stock size based on egg surveys and a cohort analysis.

Species	Estimate of Spawning Stock (egg surveys)	Confidence Interval	Estimate of Spawning Stock Size[+] (cohort analysis)
Atlantic mackerel	1.20×10^9	$(.31 \times 10^9, 2.12 \times 10^9)$*	$.96 \times 10^9$
Silver hake	1.55×10^9	$(1.14 \times 10^9, 1.96 \times 10^9)$*	$.77 \times 10^9$
Yellowtail flounder	1.38×10^8	$(.35 \times 10^8, 2.99 \times 10^8)$**	Not Available

*80% level.

**70% level.

[+]Resource Assessment Division, NMFS, NEFC, Woods Hole, MA.
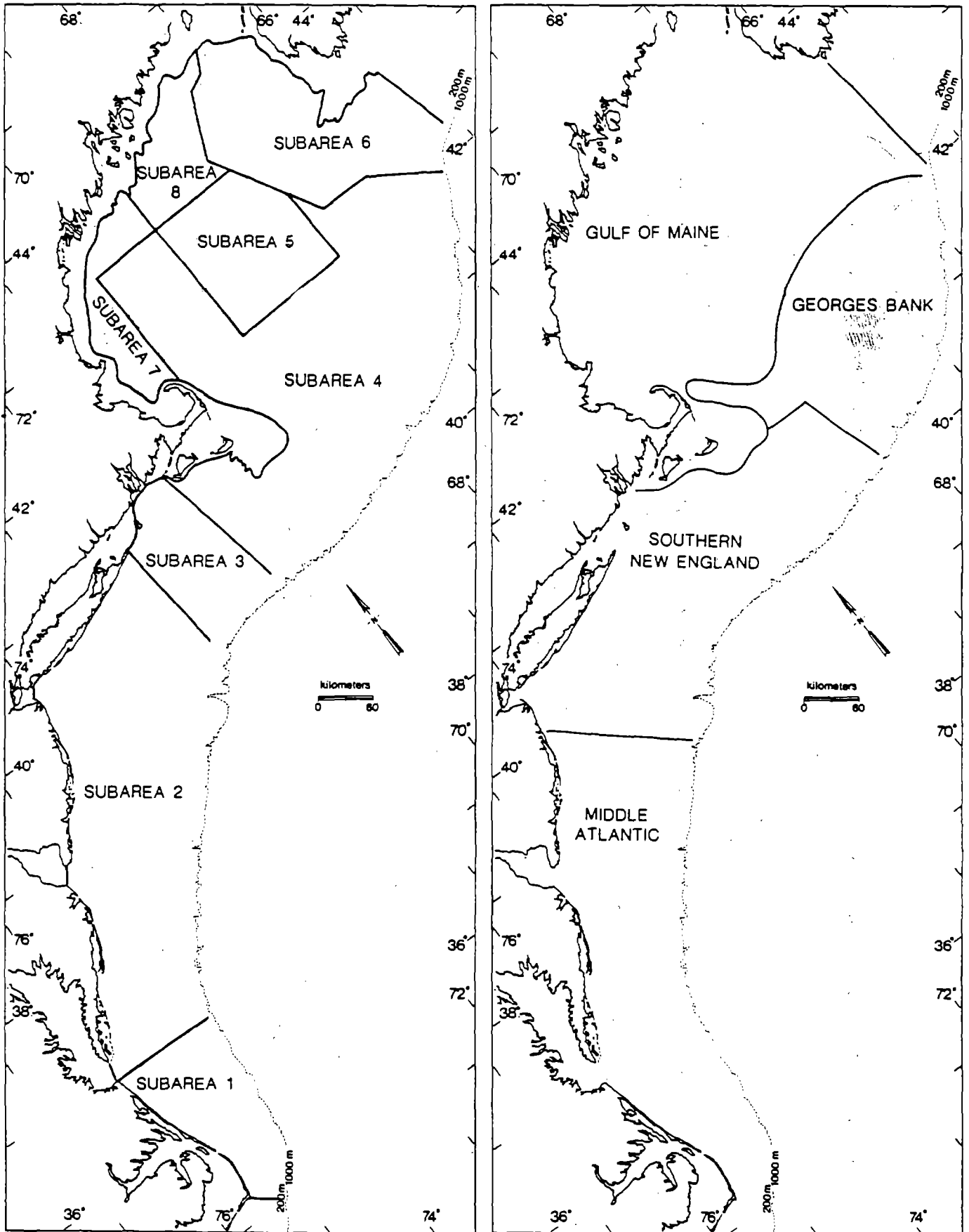
Figure 1. Ichthyoplankton survey area ; subareas for 1977 (left) and 1979 (right).
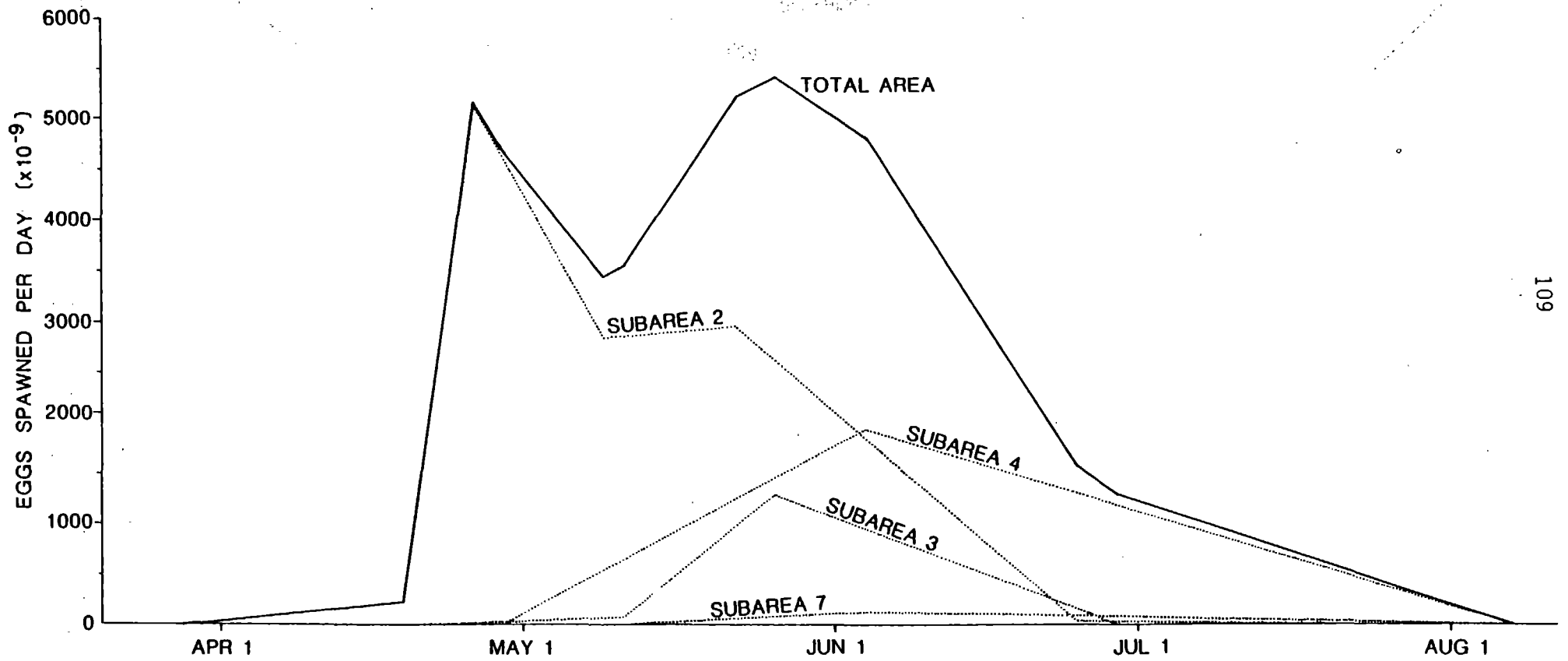
Figure 2. Estimated daily Atlantic mackerel egg production within the MARMAP survey area, 1977.
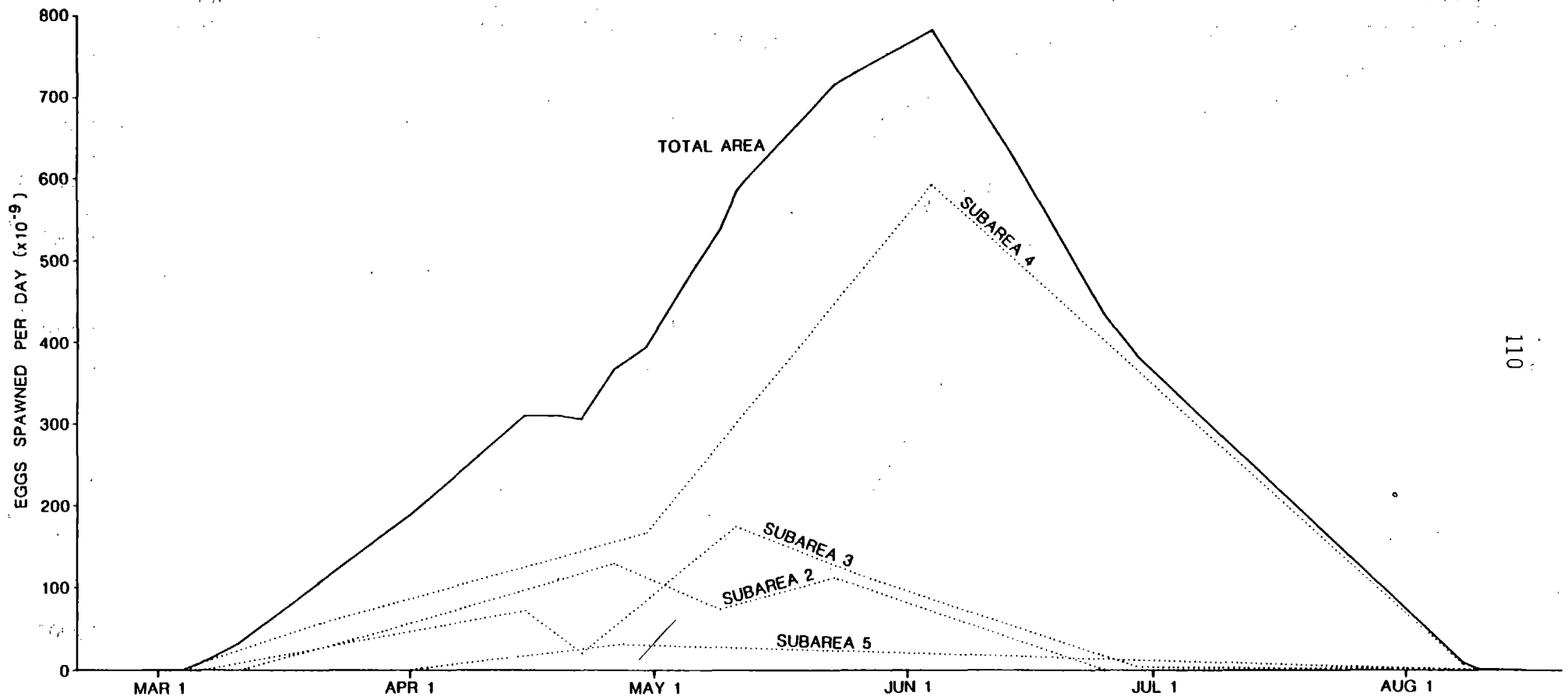
Figure 3. Estimated daily yellowtail flounder egg production within the MARMAP survey area, 1977.
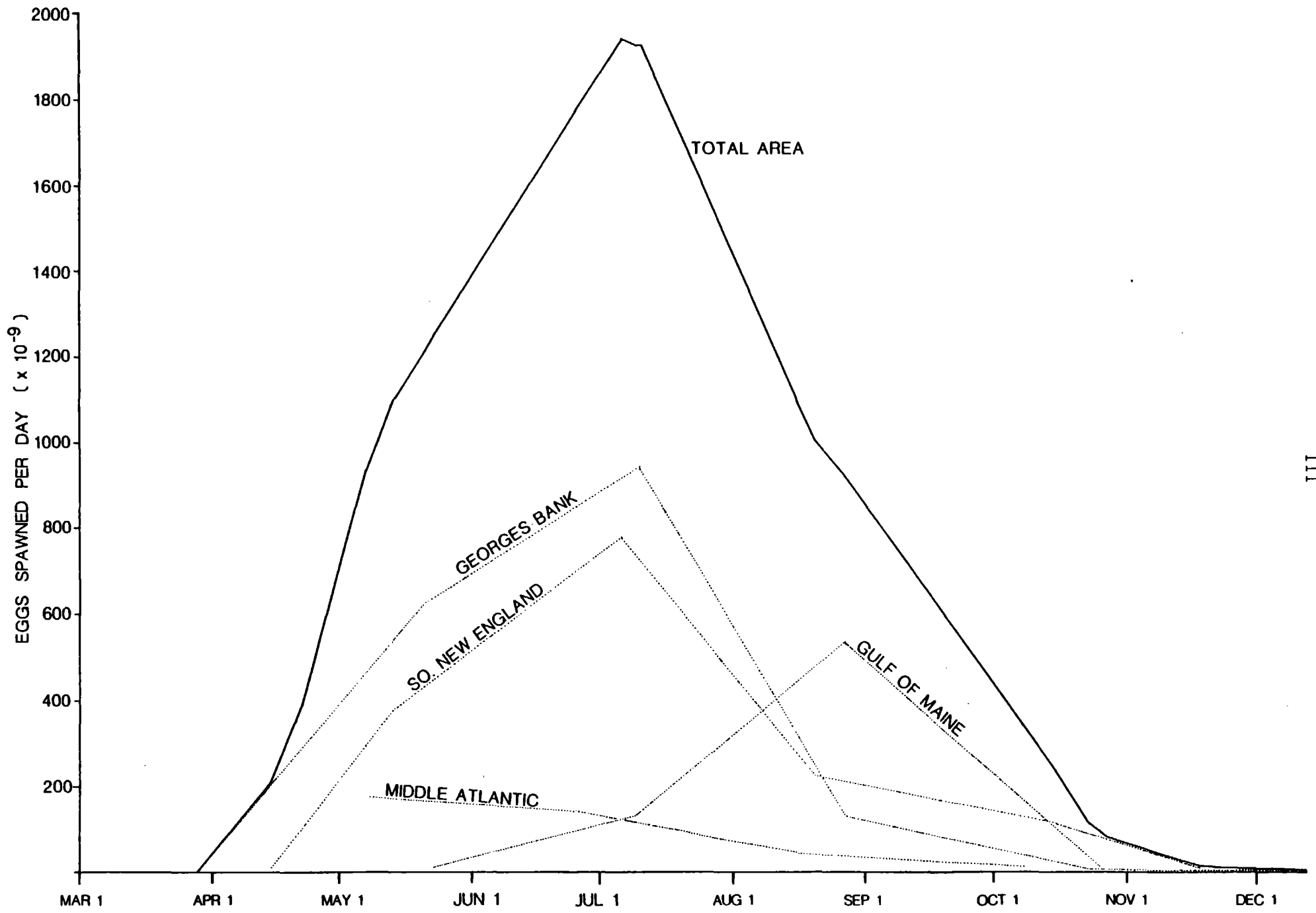
Figure 4. Estimated daily silver hake egg production in four subareas and in the total survey area, 1979.