Northeast Fisheries Science Center Reference Document 94-08

Atlantic Cod, *Gadus morhua*, Larvae: An Analysis of the MARMAP Time Series, 1977-1987

A Report
to the Office of Global Programs, R/OGP
National Oceanic and Atmospheric Administration

by

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> *The problem is not ignorance, it's what we know that ain't so.*
> Josh Billings

INTRODUCTION

The effects of climate change on Atlantic cod *(Gadus morhua)* stocks off the northeastern United States are expected to alter their distribution, reproduction, growth, and survival during various life stages and on a variety of spatial scales (Frank *et al.* 1990). The fact that cod in this area are the most southerly stocks in the world contributes to the expectation of a significant, and hopefully measurable, effect on various demographic parameters cause by changes in water temperature, salinity, stratification, circulation patterns, *etc.*, particularly on Georges Bank. However, an analysis of trawl data (1967-1990) for the effect of water temperature on 36 finfish and squid distributions off the northeastern United States revealed that adult Atlantic cod distributions were not related significantly to changes in mean surface water temperatures (Murawski and Mountain 1990). It is clear that our expectations about the effects of climate change may not be supported by data and that predicted change in complex systems is dangerous (American Fisheries Society 1990).

This report details an analysis of the MARMAP[1] larval Atlantic cod data set (1977-1987), which encompasses the area from Cape Hatteras, N. C. to Nova Scotia. This historical data set offers an opportunity to present information on cod larvae as a baseline for detection of the effects of climate change. Information is presented on the distribution and abundance of larvae and on abundance in relation to water temperature. Temperature-dependent growth functions are developed and applied to the length data in the MARMAP data set to define larval ages. Mortality rates are then calculated and methods for adjusting mortality for larval production rates are developed. Water temperature is again introduced as an independent variable and its effects on larval mortality rates are given. Larval drift on Georges Bank is shown for all years combined as well as on an annual basis, and is briefly compared to haddock drift. Finally, larval abundance in relation to water column stratification is examined, as is the relationship of larval production and recruitment to age 1 on Georges Bank.

This work was funded in part by the Marine Ecosystems Response Program of the Office of Global Programs, NOAA.

SURVEY METHODS

During 1977-1987, the Northeast Fisheries Science Center MARMAP program surveyed the continental shelf and slope waters off the Northeast United States from six to nine times each year. Approximately 100 to 180 stations were occupied from Cape Hatteras, N. C. to Cape Sable, Nova Scotia on each survey, with sampling conducted around the clock. For analysis, the entire survey area is subdivided into four areas, based on circulation patterns and topography (Figure 1). Of the 81 surveys completed by the MARMAP program, 54 contained cod larvae. The timing and duration of each survey is shown in Figure 2.

Detailed explanations of survey methods and sampling protocols are given in Sibunka and Silverman (1984, 1989). Briefly stated, at each station a 61 cm bongo net was lowered to within a few meters of the bottom or to a maximum depth of 200 m at a rate of 50 m sec^{-1} and retrieved at 20 m sec^{-1}. Vessel speed was adjusted from 1 to 2 kts to maintain a 45° wire angle. Flow meters in the net mouth monitored the amount of water filtered. Plankton sampled from the 0.505 mm mesh net were preserved in 5% buffered formalin.

Plankton samples were then shipped to the Polish Sorting Center in Szczecin, Poland, for sorting, identification, and counting. Up to 50 randomly selected larvae were measured for each taxon. Ichthyoplankton was returned to the Sandy Hook Laboratory for verification, archiving, and data entry. Numbers of larvae caught were adjusted to the number of larvae under 10m^2 of sea surface based on the maximum depth of tow and amount of water filtered by the net and for day-night-twilight catchability (Morse 1989).

DISTRIBUTION

Cod larvae are distributed throughout the study area in depths $\leq$150 m. Centers of abundance shift seasonally. Hatching begins in the Gulf of Maine area in October and by November, larvae are spread along the coast of the western Gulf of Maine and the first indications of spawning on Georges Bank are evident. In December hatching intensifies around Nantucket Shoals, and by January it has nearly stopped in the Gulf

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[1] Marine Resource Monitoring, Assessment, and Prediction.

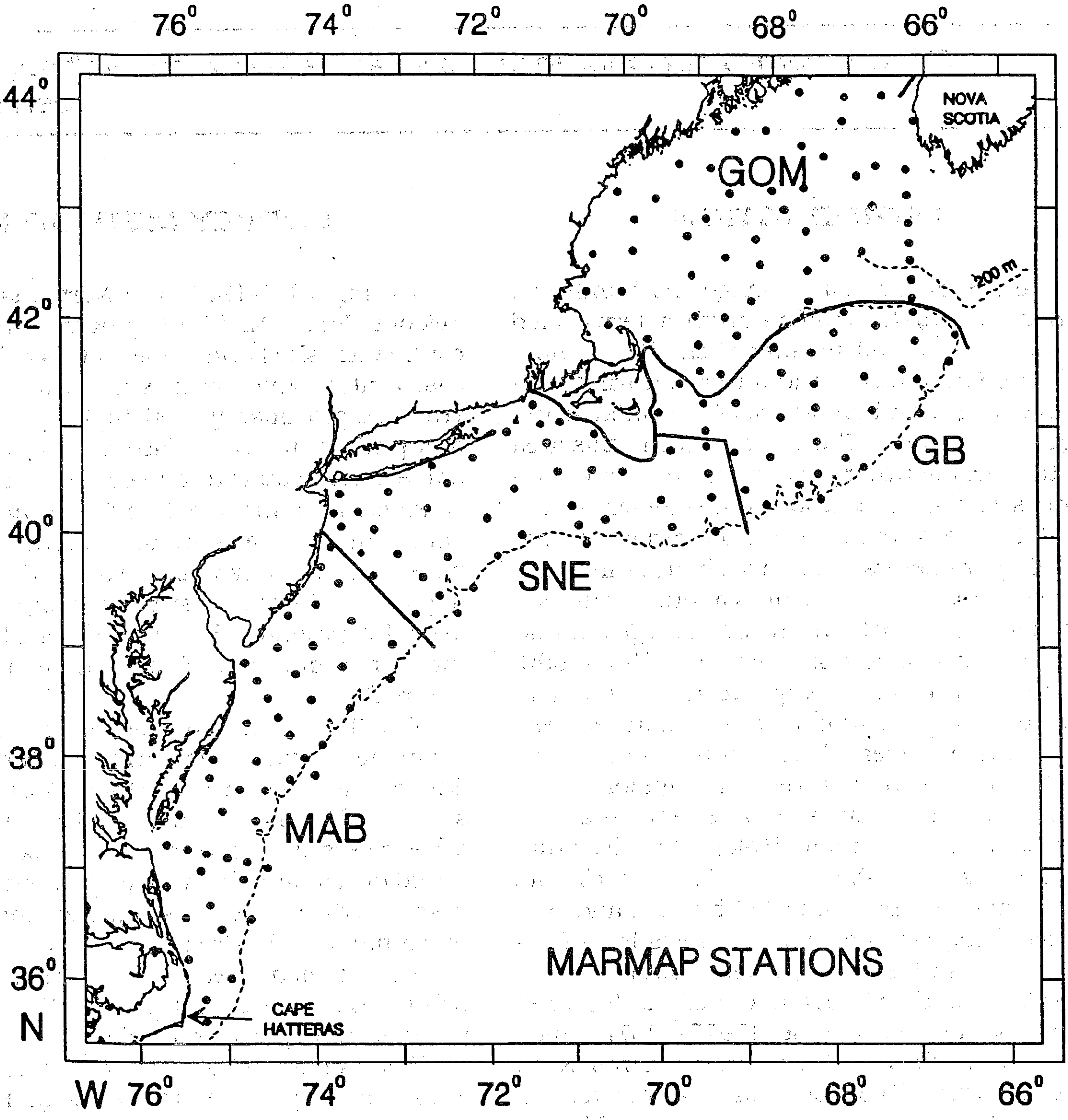


Figure 1. Locations of MARMAP stations and boundaries of areas: MAB=Middle Atlantic, SNE=Southern New England, GB=Georges Bank, GOM=Gulf of Maine.

of Maine. Two centers of distribution occur at this time, one on Georges Bank and the other around Nantucket Shoals. During February, larvae occur from Cape Hatteras, N. C. to Georges Bank, and in March a clear center of distribution is seen on Georges Bank.

April distribution shows an intensification of hatching on Georges Bank, no larvae occurring in the southernmost part of the study area, and larvae are again scattered in the Gulf of Maine. In May and June, hatching activity declines throughout the area, although larvae are still distributed from Cape Henlopen, Del. to Cape Sable, Nova Scotia. Larvae are nearly absent in the study area by July, but a small concentration occurs north of Cape Cod, Mass. In August and September, three are a few patches of larvae on Georges Bank and in the Gulf of Maine.

This seasonal shift in centers of abundance from north to south in the fall and winter and their return north during early spring is clearly seen in monthly composite plots of larvae given in Figure 3a and 3b. Distribution plots by survey are shown in Appendix Figure 1.

ABUNDANCE

Cod larvae were captured during every month, although abundance was very low during August-October. The average abundance by month for all years and areas combined shows a peak

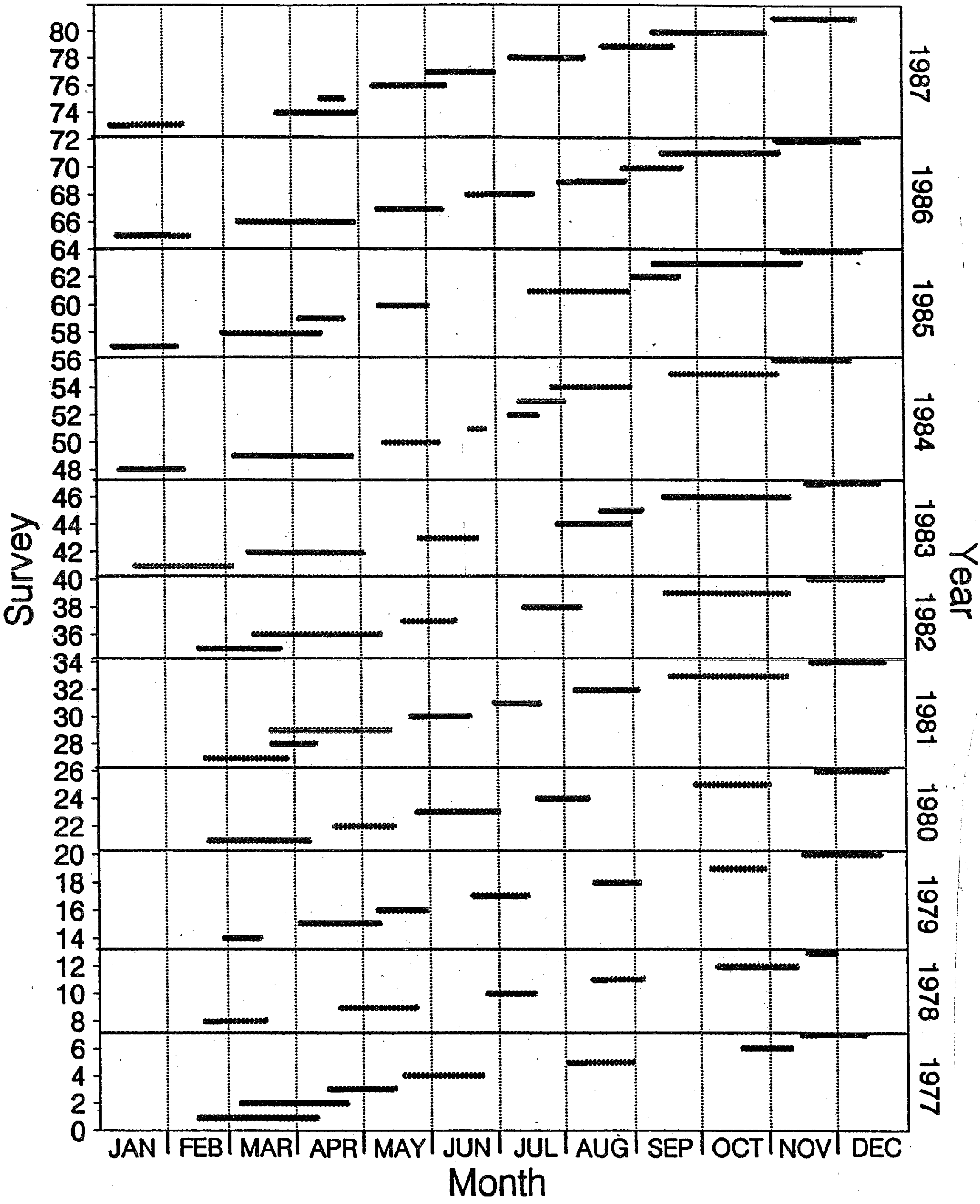


Figure 2. Distribution of sampling effort for MARMAP surveys off the Northeast United States, 1977-1987.

occurring from March to April (Figure 4). The highest abundance occurred in April, slightly smaller numbers in March, and the third-highest abundance in January. The monthly cycles of abundance showed considerable variation within each of the four areas.

In the Middle Atlantic area, cod larvae were captured primarily from January to April, and peak abundance occurred during February. A few larvae were captured here in May, June, and October.

Moving northward, the Southern New England area analysis showed cod larvae occurring during all months except August to October. Peak abundances occurred in December and January and again in April, although April catches are about 66% of the numbers in January.

On Georges Bank, larvae occurred in all

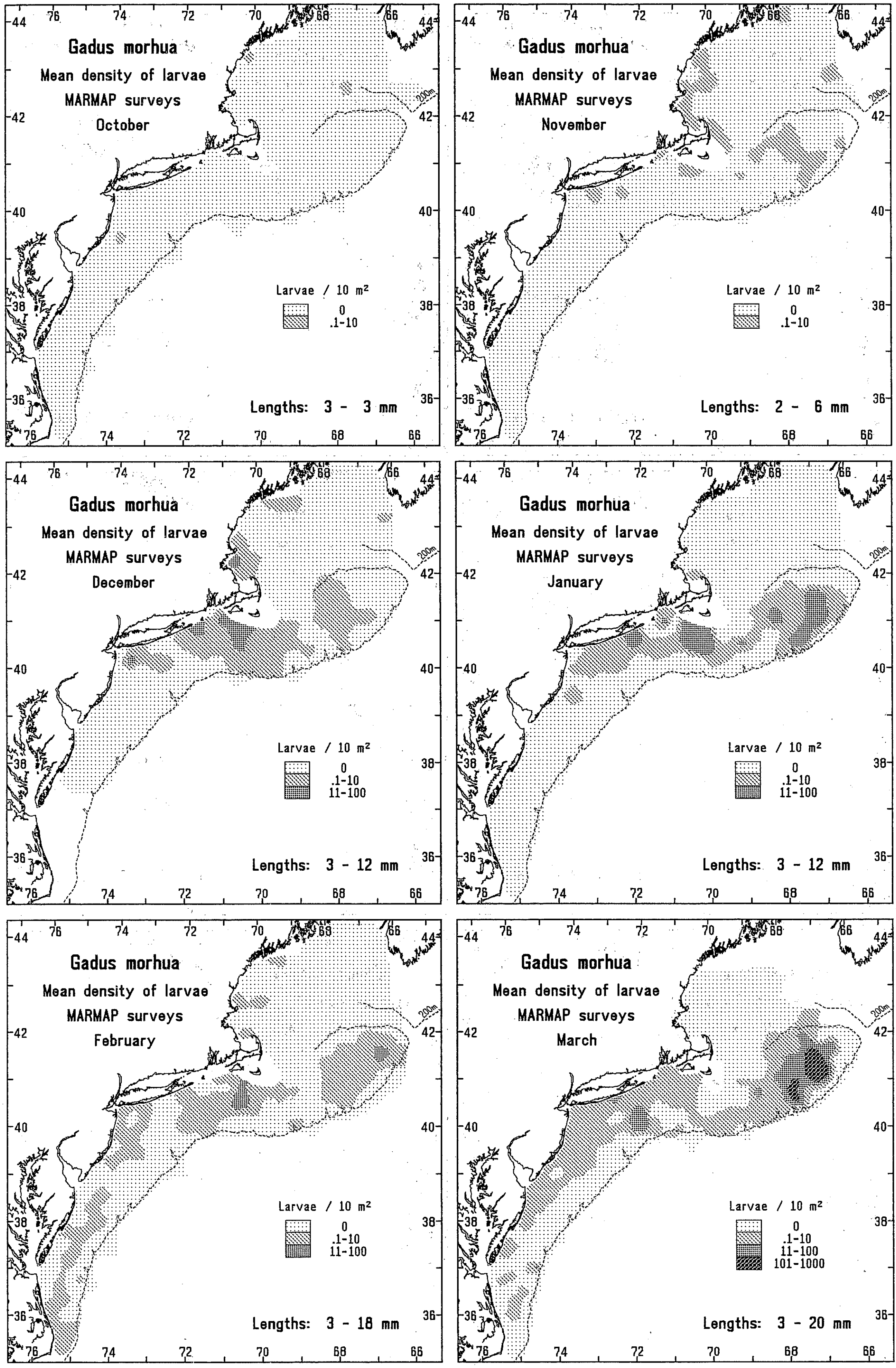


Figure 3a. Monthly composite distribution and abundance of cod larvae from the MARMAP Program, 1977-1987.

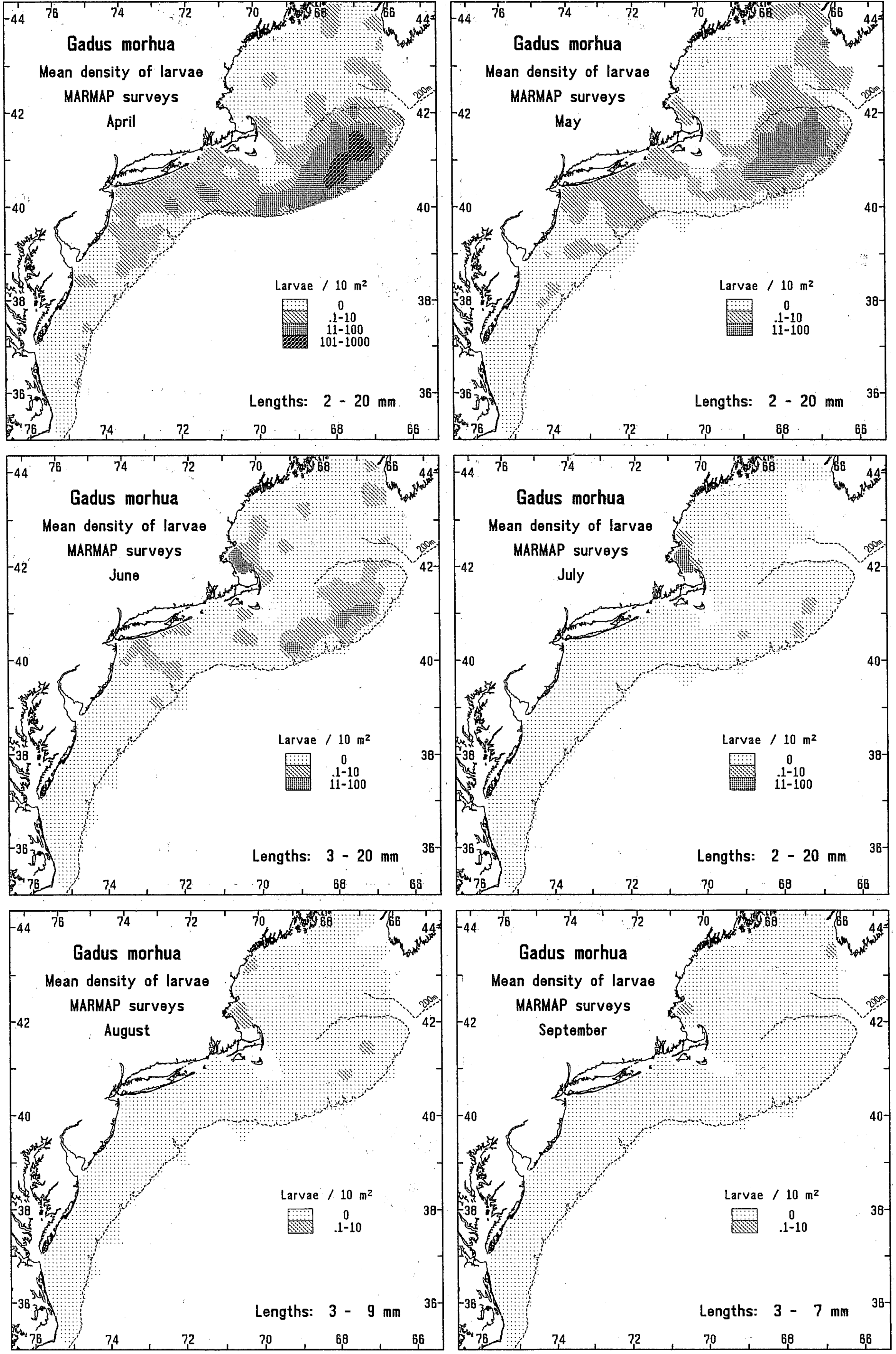


Figure 3b. Monthly composite distribution and abundance of cod larvae from the MARMAP Program, 1977-1987.

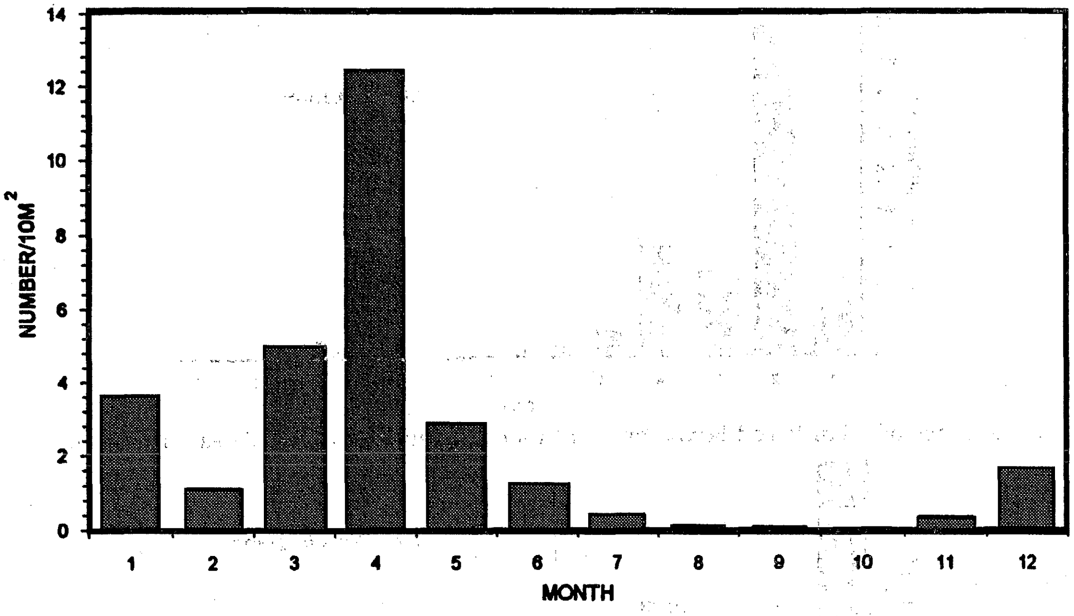


Figure 4. Abundance of Atlantic cod larvae by month for all areas and years combined.

months except September and October. Here the peak abundance is in March in April. In the Gulf of Maine area larvae were captured in all months except March. Larval abundance in this area is low, with a slight peak in May-July. The monthly cycles in abundance for each area are shown in Figures 5a to 5d, and the catch statistics are given in Appendix Table 1.

The mean catches per 10 m^2 clearly show the dominance of Georges Bank as the center cod larvae abundance within the study area (note the change in scales on Figures 5a to 5d). Peak monthly mean catches were only 0.9 in the Middle Atlantic, 7.5 in Southern New England, 58 on Georges Bank, and just 1.5 in the Gulf of Maine.

To investigate the interannual changes in abundance of larvae, the time series of survey mean abundance were plotted for each area (Figures 6a to 6d). Catch statistics for each area by survey are given in Appendix Table 2. The ranges in annual peak abundance throughout the time series span approximately two orders of magnitude in each of the areas. The annual minimum and maximum peak abundances are not coincident in time across areas. For example, the peak abundances occurred on Georges Bank in 1977 and 1983, yet the peak year in Southern New England occurred in 1985 and the lowest catches are seen in 1977. Similarly, peak abundance years in the Gulf of Maine and Middle Atlantic were 1980 and 1984, respectively, and minimum catches occurred in these two areas in 1984 and 1985, respectively. Temporal trends in abundance are evident in Southern New England and in the Gulf of Maine but not in either the Middle Atlantic or on Georges Bank. The trend in Southern New England shows a general increase in abundance during the time series with the last three years (1985-1987) having the highest peak abundances. The Gulf of Maine shows a peak in abundance during 1978-1980, then much lower and relatively constant abundances during 1981-1987. Of special note is the near-absence of cod larvae on Georges Bank in the spring of 1982.

Some caution must be exercised when looking for significant interannual trends in the MARMAP data set of larval cod catches because three factors conspire to obfuscate any true trends in the data. These factors are: 1) the number of stations completed and incomplete coverage on a survey within a particular area may be inadequate to monitor actual abundance of larvae; 2) the timing of the survey in relation to the timing of peak cod hatching and/or abundance varies between years and will affect the maximum abundance observed and; 3) the patchy distribution of larvae is reflected in the often high uncertainty in the mean abundance estimates (see Appendix Table 2).

WATER TEMPERATURE AND ABUNDANCE

The occurrence of cod larvae during every month of the year and their widespread distribu-

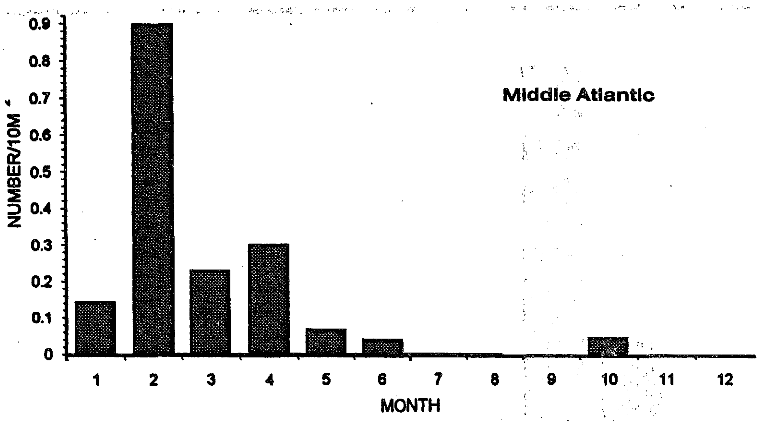


Figure 5a. Abundance of Atlantic cod larvae by month for all years in the Middle Atlantic area.

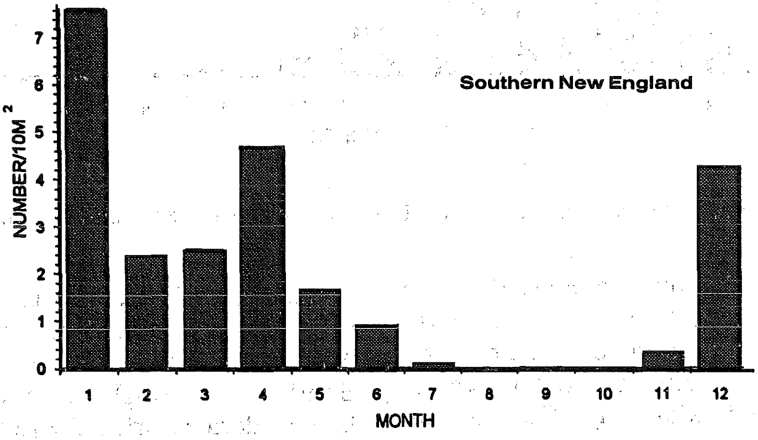


Figure 5b. Abundance of Atlantic cod larvae by month for all years in the Southern New England area.

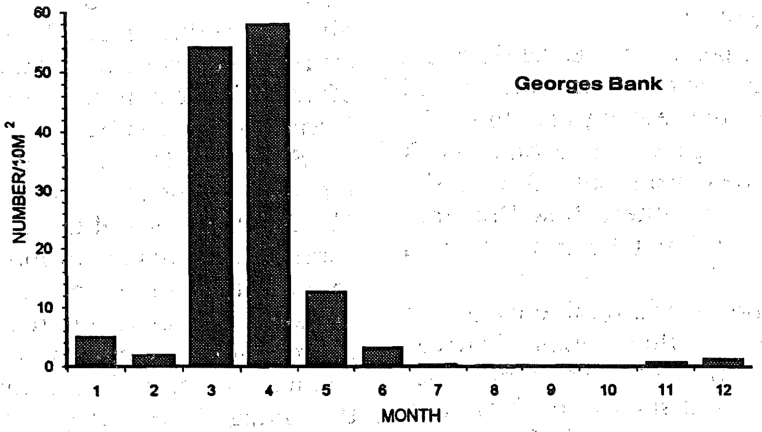


Figure 5c. Abundance of Atlantic cod larvae by month for all years in the Georges Bank area.

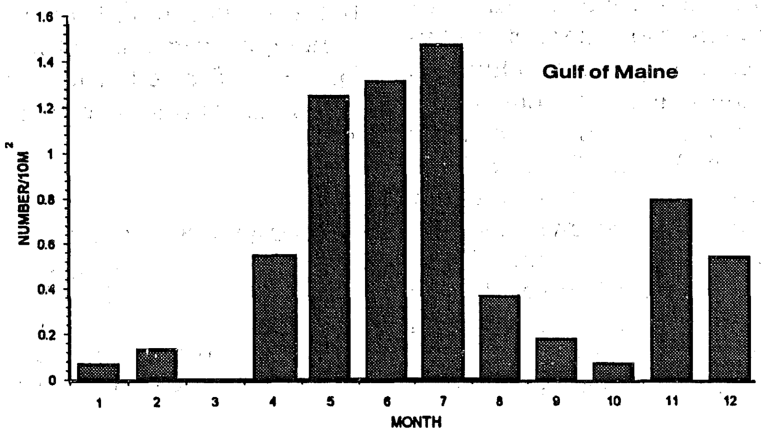


Figure 5d. Abundance of Atlantic cod larvae by month for all years in the Gulf of Maine area.

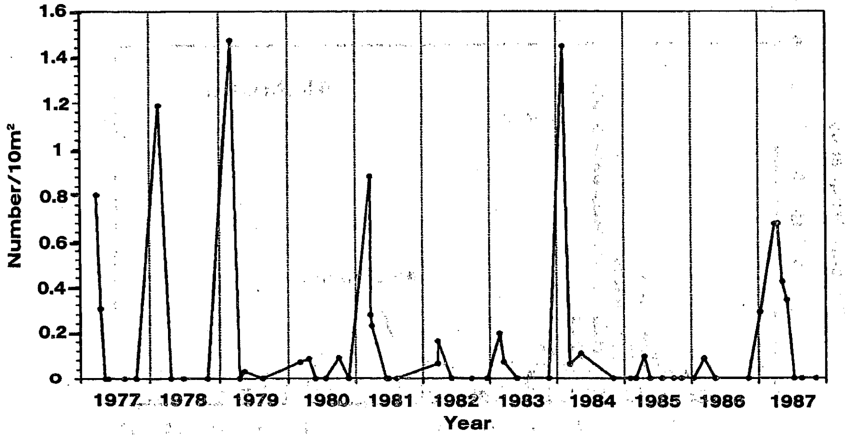


Figure 6a. Abundance of Atlantic cod larvae in the Middle Atlantic by survey for 1977-1987.

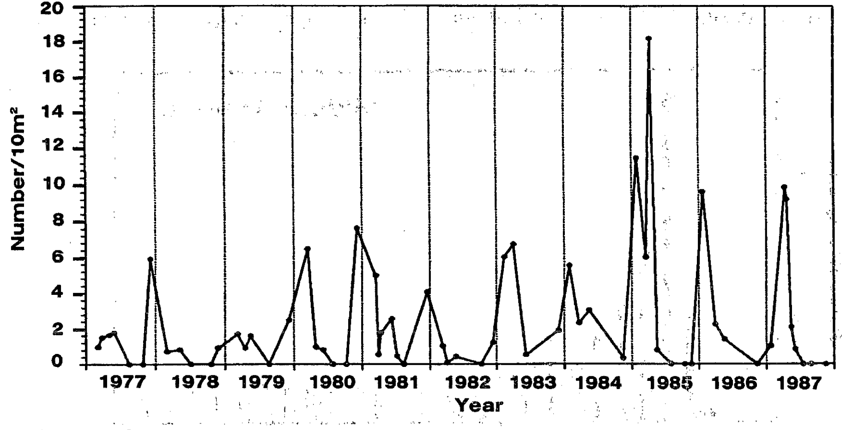


Figure 6b. Abundance of Atlantic cod larvae in Southern New England by survey for 1977-1987.

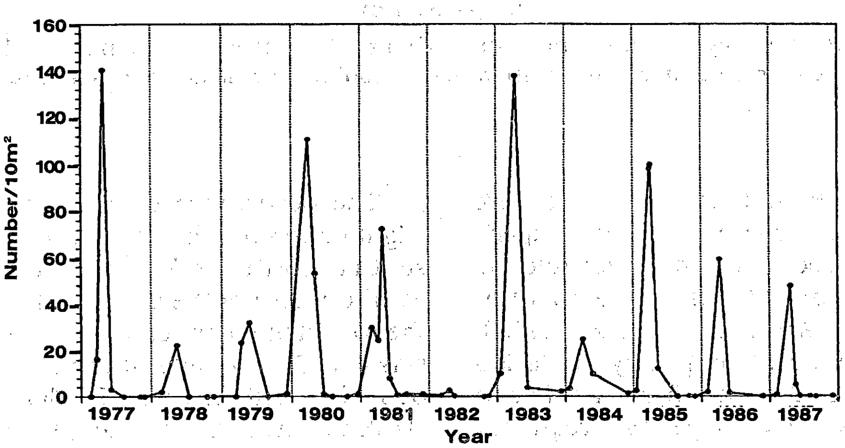


Figure 6c. Abundance of Atlantic cod larvae on Georges Bank by survey for 1977-1987.

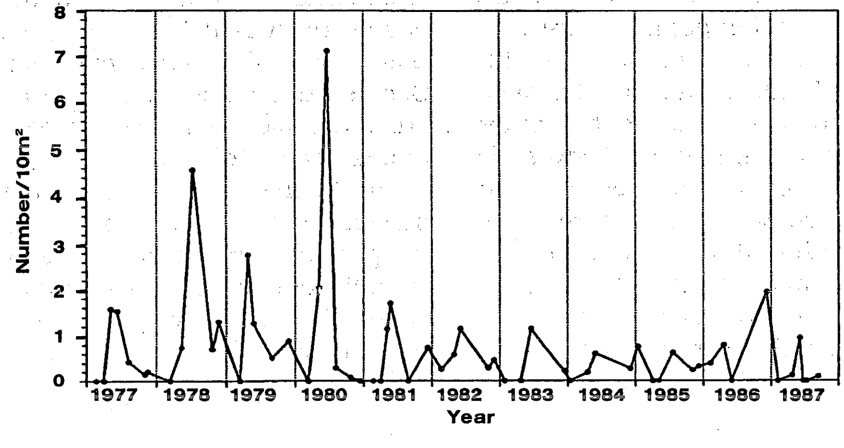


Figure 6d. Abundance of Atlantic cod larvae in the Gulf of Maine for 1977-1987.

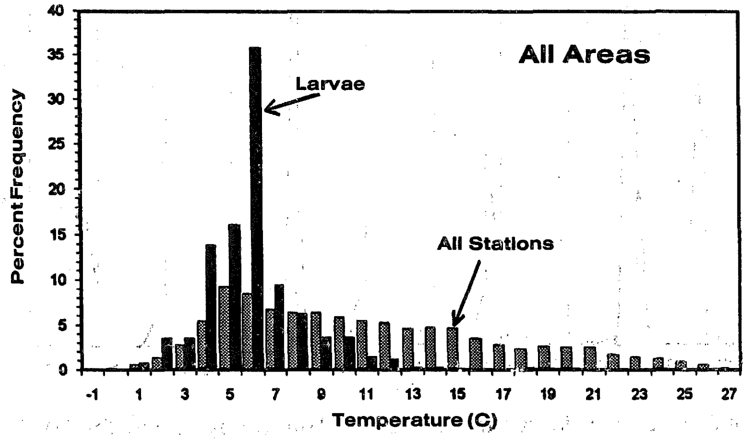


Figure 7. The percent frequency by water temperature of all stations ≤150 m deep and of Atlantic cod larvae from MARMAP surveys that contained at least three stations with cod larvae.

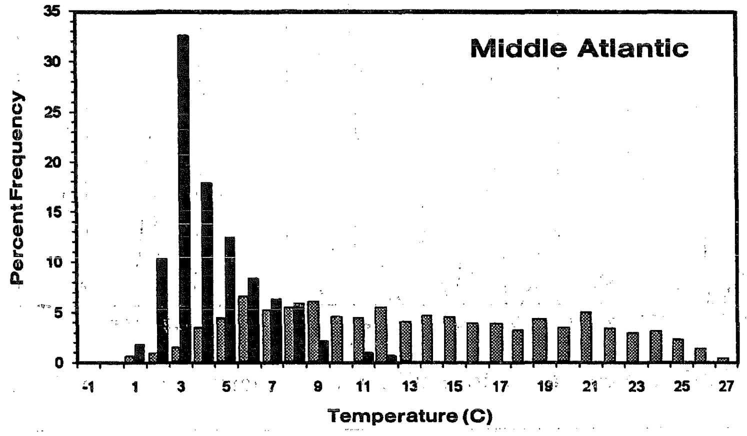


Figure 7a. The percent frequency by water temperature of all stations ≤150 m deep in the Middle Atlantic and of Atlantic cod larvae from MARMAP surveys that contained at least three stations with cod larvae.

tion in the study area indicates that they are probably eurythermal. However, rearing experiments indicate that cod larvae may not tolerate temperatures less than 4° C (Laurence 1978) or greater than 12° C (Iversen and Danielssen 1984). Simple plots of the percent frequency of station water temperatures of the top 15 m of water in depths ≤150 m compared to the percent frequency of catches of cod larvae at temperature indicate that cod larvae occur between 1° and 20° C (Figure 7). The station frequency of temperatures are from surveys that contained at least three stations with cod larvae. Georges Bank larvae are the most temperature restricted, compared to the other three areas, and occur at temperatures between 3° and 12° C (Figure 7c). The Southern New England area supports cod larvae at a temperature range from 1° to 14° C (Figure 7b), while the Gulf of Maine area shows a range between 3° and 14° C (Figure 7d). Larvae in the Middle Atlantic area are found from 1°C, the coldest temperature recorded there, to 12° C (Figure 7a).

The occurrence of cod larvae indicates a slight preference for warmer temperatures from south to north. Peak occurrence of larvae in the southern part of the study area was at 3° C and the weighted mean temperature for larvae there was 4.4° C. The highest occurrence of larvae in both the Southern New England and Georges Bank was at 6° C and the weighted mean temperatures are at 6.1 and 5.7° C, respectively. The highest abundance of larvae in the Gulf of Maine area was at 12° C and the weighted mean was at 8.0° C. Since most larvae occur on Georges Bank and in Southern New England area, the plots for these areas are the best indicators of temperature preference for cod larvae in the study area. Table 1 shows the percent of stations and of larvae that occur in temperatures from 4° to 8° C. A clear preference is indicated for Georges Bank larvae, where about 93% of all larvae occur in this temperature range.

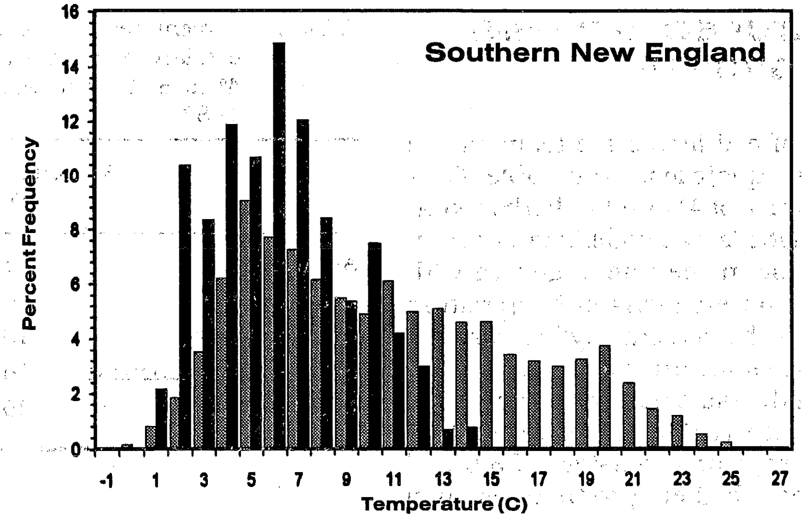


Figure 7b. The percent frequency by water temperature of all stations ≤150 m deep in Southern New England and of Atlantic cod larvae from MARMAP surveys that contained at least three stations with cod larvae.

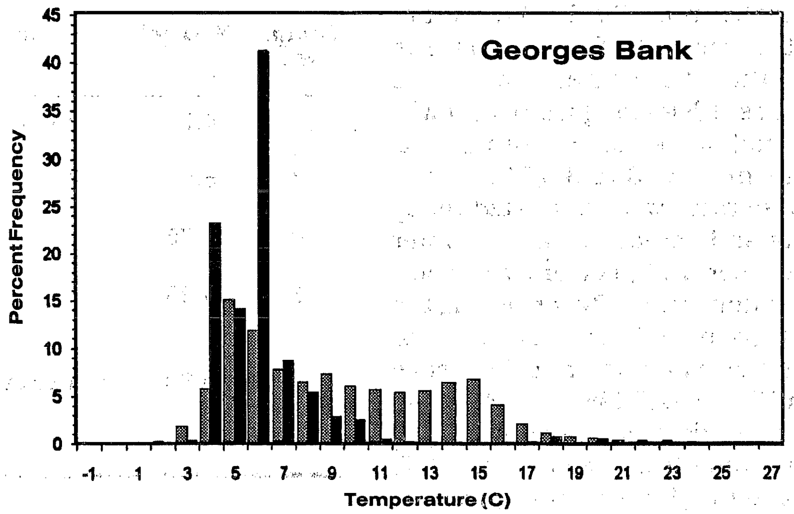


Figure 7c. The percent frequency by water temperature of all stations ≤150 m deep on Georges Bank and of Atlantic cod larvae from MARMAP surveys that contained at least three stations with cod larvae.

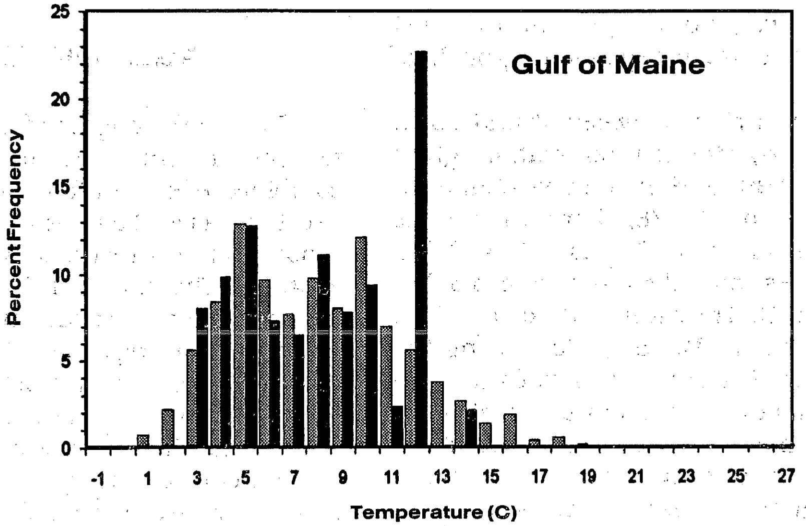


Figure 7d. The percent frequency by water temperature of all stations ≤150 m deep in the Gulf of Maine and of Atlantic cod larvae from MARMAP surveys that contained at least three stations with cod larvae.

TEMPERATURE-DEPENDENT GROWTH

Growth rates of cod larvae are temperature dependent when adequate food is available. Over the temperature range of 4° to 10° C, both laboratory and field-caught larvae combined show an exponential increase in the rate of growth with temperature. The observations of temperature and growth rate, as the percent day^{-1} increase in dry weight, for cod larvae are shown in Table 2.

It is clear from the table that the growth rates reported in Laurence (1978) are relatively low. Cod larvae grown with prey densities of 3.0 ml^{-1} showed significantly higher growth rates then larvae grown with lower prey densities (Laurence *et al.* 1981). The question is which rates are realistic for field caught larvae? The Buckley and Lough (1987) estimates from RNA-DNA ratios are from field caught larvae at 9° C. Their rate is higher by 2% day^{-1} then the 10° C estimate in the laboratory. Estimates of field-caught larval growth rates (% day^{-1} in mm) of cod larvae during their first 40 days range from 2.70 to 3.37 (Bolz and Lough 1988). These rates were estimated using otolith ring counts and without regard to water temperatures, but offer an opportunity to compare field and laboratory rates. By converting the dry weights (DW) given in Laurence (1978) to lengths (L) using the equation from Laurence (1979), where $Ln(DW) = -2.5398 + 4.081*Ln(L)$ and calculating the % day^{-1} increase in length, the range in average rates is between 1.1 and 1.7. This is approximately half of the rates given by Bolz and Lough (1988). These comparisons indicate that the growth rates reported by Laurence (1978) are too low compared to field caught larvae. The RNA-DNA rate, and the rate reported by Laurence *et al.* (1981) represent the best estimates of temperature-dependent growth of cod larvae.

Realistic growth rates between 4° and 10° C can be estimated by simple interpolation, given the rates at 7° and 9°C and the relative change in rates given in Laurence (1978). For example, the relative change from 4° to 7° C is 1.404 (6.67/4.75), so that the estimated realistic rate is 6.616 (9.29/1.404) at 4° C. The estimated rate at 10° C, using interpolation, is 12.187. Converting the rates of % day^{-1} to instantaneous rates and regressing them against temperature yields an equation to estimate the instantaneous rates (Figure 8). This method assumes that the factor(s) causing the low growth rates reported by Laurence (1978) is independent of temperature, and that the proportions are valid estimates temperature effects.

Table 1. Percent frequency of stations and of Atlantic cod larvae within the temperature range of 4° to 8° C from MARMAP surveys, 1977-1987

	Sampled Stations (%)	**Cod Larvae (%)**
All Areas	36.4	81.7
Gulf of Maine	48.4	47.6
Georges Bank	46.8	92.7
Southern New England	36.3	57.7
Middle Atlantic	25.4	51.1

Table 2. Published growth rates in dry weight (milligrams) of Atlantic cod larvae

Temp. (°C)	**% Day^{-1}**	**Source**	**Citation**
4	4.75	Laboratory	Laurence 1978
7	6.67	"	"
10	8.75	"	"
7	9.29	"	Laurence *et al.* 1981
9	10.60	RNA-DNA ratio	Buckley and Lough 1987

AGE AND GROWTH

Converting lengths of field caught fish larvae to ages presents a number of problems. The combined effects of food supply and water temperature, as well as possible genetic constraints, produced the observed length of a larva at time of capture. The model of the effects of changes in temperature on growth rates in Figure 8 is presented without regard to changes in food supply. However, if the assumption that larvae which survive to be captured by sampling nets are larvae that have experienced a constant and adequate food supply is accepted, then field-caught larvae are probably at the high end of the growth rates observed. If this assumption is

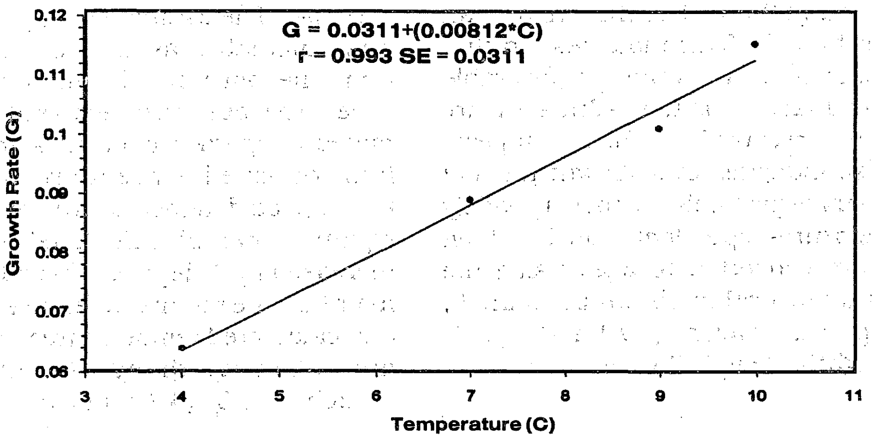


Figure 8. Interpolated instantaneous growth rates in mg day^{-1} versus water temperature for Atlantic cod larvae from published data.

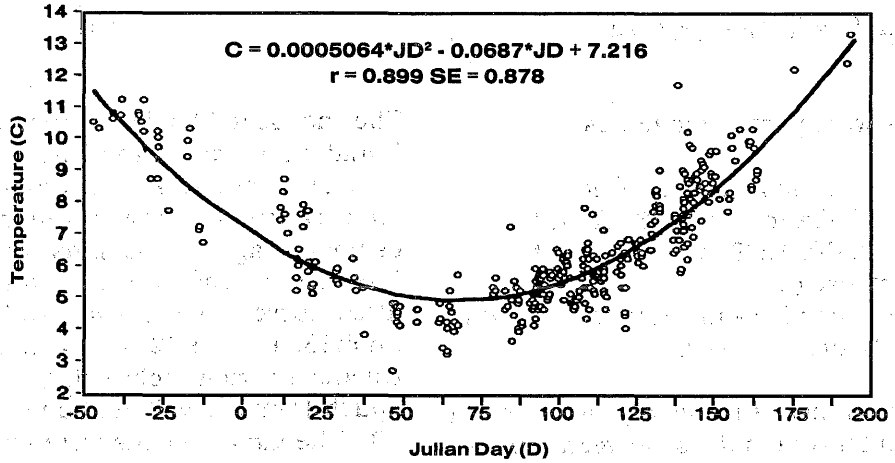


Figure 9. Water temperatures of the top 15 m for stations containing Atlantic cod larvae from MARMAP surveys on Georges Bank, 1977-1987.

wrong, then the actual rates of growth must be measured directly (*e.g.*, otolith daily ring counts) and efforts to use lengths as proxies for age will be misleading at best. The few direct measurements of larval growth rates from field-caught fish, compared to laboratory rates, do indicate that field growth is often higher then laboratory growth. It seem reasonable to assume that field-caught larvae maintain consistently high rates of growth and the equation in Figure 8 is our best estimate of average temperature-dependent growth rates of field caught cod larvae.

Water temperatures recorded during the MARMAP surveys offer an opportunity to model their changes during the winter and spring when larval cod are present. Peak occurrence of larval cod on Georges Bank is during March-May, a time of rapid warming of the water column. Since the mean age of a 20 mm cod larva is about 60 days (Bolz and Lough 1988), over this time period of 60 days a larva will experience quite different temperatures. Therefore, it is the temperature history of the water column that will determine, at least in part, the observed lengths of field caught larvae.

To model this change, the water temperatures of the top 15 m for stations on Georges Bank where cod larvae occurred were fit to a polynomial curve and are shown in Figure 9. Water temperature in the top 15 m is representative of the actual water temperatures inhabited by most cod larvae for two reasons: 1) about 90% of all cod larvae on Georges Bank occur during times when the water column is not thermally stratified (January to early May), but is isothermal; 2) cod larvae do not migrate below the thermocline, when it does exist, until they are at least 9 mm long (Lough and Potter 1993). Approximately 12% of all cod larvae analyzed were ≥ 9 mm, thus less than 2% of all cod larvae on Georges Bank were both ≥9 mm long and were likely to occur in stratified waters.

In a previous section, information was presented that showed larval cod occur in temperatures between 1° and 23° C, but that more than 80% occur at 4° to 8° C. This indicates a rather narrow range of temperatures that are favorable for survival of cod larvae (or that adults ensure their progeny are released in these temperatures). This also indicates that growth rates of most surviving larvae probably do not vary widely based on temperature-dependent growth. When larval lengths are converted to ages using the water temperature algorithm shown in Figure 9, the relationship of dry weight (DW) and age (A) and the dry weight to length (L) are:

$$\begin{aligned} Ln &= \alpha+\gamma*(A) \text{ and } Ln(DW) = \chi+\delta*Ln(L) \\ \text{so that } A &= (\chi - \alpha + \delta*\ln(L))/\gamma \text{ or} \qquad (1) \\ Ln(L) &= ((A*\gamma) - \chi + \alpha)/\delta \end{aligned}$$

The constants were parameterized as:

α = Ln(53.6μg); the mean dry weight at age = 0 (Laurence 1978, Table 2)

γ = 0.0311+0.00812*T, where T = water temperature (°C)

χ = -1.676 ; when L = 4 mm and DW = 53.6 μg

δ = 4.081 (Laurence 1979).

The water temperature history at a station was calculated for Julian days between -50 (November 11) and 200 (July 19) using the polynomial presented above. The negative Julian days were necessary to maintain time as a continuous variable. The estimated temperature on any day was calculated as the temperature estimated from the polynomial minus the difference between the observed temperature and the estimated temperature on the sampling date. Thus if the observed temperature was 1° C more than the expected temperature from the polynomial equation then all calculated temperatures were increased by 1 degree. This adjustment helps to maintain the relative difference between observed and calculated temperatures. For any length (L_o) and Julian day, the age of a larva is calculated as n such that $L_n \leq 4.1$ mm by:

$$Ln = Lo - \sum_{i=1}^{n} \Delta Li$$

The change in *L* for day i is the length at day i from Equation 1, minus the length at day i -1. The change in length is thus a function of the water temperature and growth rate relationship. The estimated age and lengths are plotted and the fitted power function are shown in Figure 10. The fitted curve is Length = 4.197+0.0178*(Age)$^{1.521}$,(n=238, r = 0.972, SE = 1.052). The curves calculated from otolith ring counts in Bolz and Lough (1983, 1988) are superimposed in Figure 10. The larval lengths were adjusted for preservation shrinkage in these original studies but are presented here as preserved lengths, *i.e.* the equation given in Bolz and Lough (1983) was

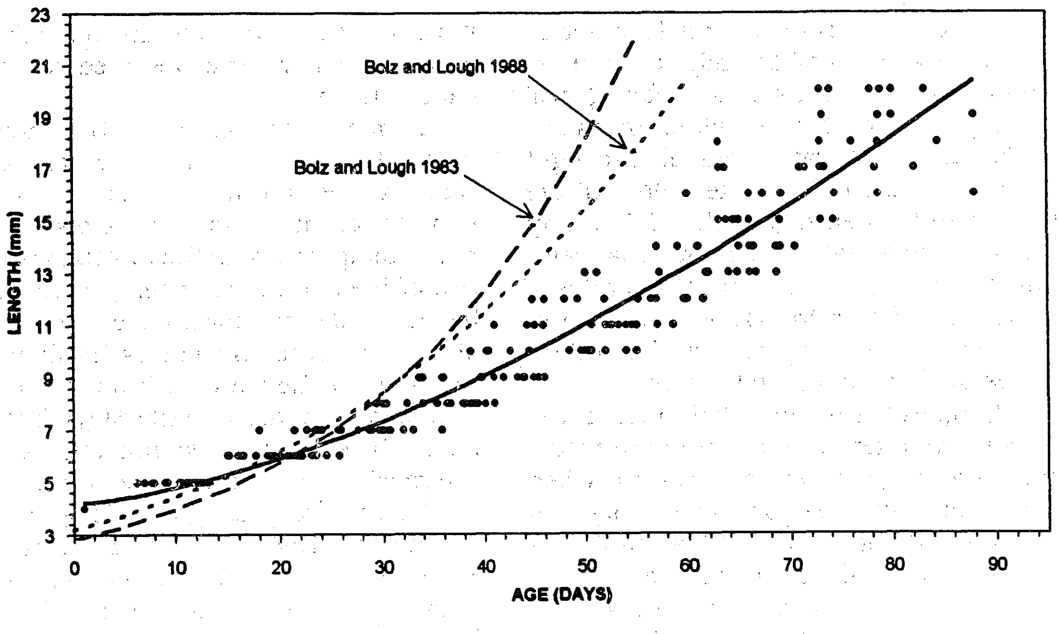


Figure 10. Estimated ages for Atlantic cod larvae on Georges Bank based on temperature-dependent growth rates and curves of published rates based on otolith ring counts.

used to convert their lengths back to preserved lengths to make comparisons possible. The growth from otolith ring counts is faster then that calculated from temperature-dependent growth. A number of factors could contribute to the differences in larval growth including: 1) underestimates of growth by Laurence (1979), due to the unique conditions of his experiments; 2) otolith rings may not be deposited daily (Dale 1984) or if they are daily, then underestimation of ring counts could be a problem (Campana and Moksness 1991); 3) field samples may represent only the fastest growing larvae. In any case, the comparison of grow based on otolith ring counts and temperature -dependent rates offers an opportunity to compare the two methods. For example, in order to make my age-length relationship approximately equal to the two otolith curves in Figure 10, the water temperature would need to be between 9.0° and 10.1° C, or the slope of the growth rate to temperature would need to be between 0.013 and 0.015. It is clear that further work is needed to resolve the effects of laboratory experiments on larval growth rates and to critically compare rates based on otolith rings and temperature-dependent growth rates of larval cod.

PRODUCTION AND MORTALITY

The ability to age larval fish by reading daily growth increments on their otoliths has made possible more accurate estimates of age based mortality. In the past, it was necessary to follow a cohort of larvae over time and estimate its decline in abundance to determine mortality. Thus mortality (Z) was then estimated using the abundance at time t and at time t+x as:

$$Nt + x = Nt^{*}e^{-Zx}$$

or

$$Z = \frac{\mathrm{Ln}(Nt) - \mathrm{Ln}(Nt+x)}{X}$$

If x is one day, then Z is the daily instantaneous rate of mortality. The problem with this method is that it is difficult, for many species, to accurately track a particular cohort through time. Variations in growth rates often make length based definitions of cohorts too crude to accurately estimate mortality. With otolith aging, a particular cohort can be identified and followed through time and, in theory, exact daily rates of mortality are possible. Both methods require two (or more) estimates of abundance separated in time, that the cohort be completely represented in both samples, and that catchability remains constant (or be accounted for through adjustments to the catches).

An alternative method of mortality estimation is the use of catch curve analysis. This involves determining the abundance of various cohorts at one time and fitting an exponential decay curve to the ages (or lengths) and the abundances at age (or length). The problem with this method is the assumption that the initial production of each age or length cohort is the same. This is rarely satisfied with larval fish because hatching intensity changes during the spawning season and produces differences in initial production. Mortality will be overestimated if samples represent times of increasing production and underestimated from samples representing times of decreasing production (Hewett and Methot 1982). Catchability remains a problem and adjustments to the catches may be necessary to assure equal catch rates throughout the age (size) range of fish included in the catch curve. The fitting of the least squares decay model to the entire catch curve yields a single, overall mortality rate that will not indicate differences in mortality with changes in age (or length). If mortality changes with age or length, it is necessary to determine mortality rates at the beginning, middle, and end of the catch curve or even at each sequential age interval along the catch curve.

A third alternative, which helps minimize the effects of non-constant larval production, is to sample numerous times during the spawning cycle and combine the catches into a single catch curve. This method combines samples from times of increasing and decreasing production to produce an unbiased mortality estimate. The estimate will be unbiased if sampling is equal during times of increasing and decreasing production. On a practical basis, it is difficult to know, *a priori*, that the times you sample in the field satisfy this requirement. This sort of sampling seems most appropriate for species with a well-known spawning and hatching season that is also reasonably constant from year to year. Disadvantages of this method are that at least two samples are necessary to make an estimate of mortality and seasonal changes in mortality are averaged.

The assumption of constant production is seldom satisfied when sampling marine fish larvae. Spawning often extends over months, beginning slowly and building to a peak, then tapering off until spawning stops. If production (y) is plotted along a time scale (x), the resulting points will often follow a bell shaped curve of the form:

$$y(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(x-\mu)^2/2\sigma^2}$$

The change in Ln(y) with respect to x is then:

$$\Delta \mathrm{Ln}(y) = \mathrm{Ln}(y(x)) - \mathrm{Ln}(y(x-\Delta x))$$

and

$$\Delta \mathrm{Ln}(y) = \frac{-(x-\mu)^2}{2\sigma^2} + \frac{(x-\Delta x-\mu)^2}{2\sigma^2}$$

and simplifying to

$$\Delta \mathrm{Ln}(y) = \frac{-\Delta x\,(x-\mu)}{\sigma^2}$$

then

$$\frac{\Delta \mathrm{Ln}(y)}{\Delta(x)} = \frac{(\mu - x)}{\sigma^2} = \frac{\mu}{\sigma^2} - \frac{x}{\sigma^2}$$

Letting y denote the derivative, then y can be expressed as a linear function of x as:

$$y = a + bx$$

where $a = m/s^2$ and $b = -1/s^2$. This equation yields a correction for the bias of estimated mortality rates for any day along the spawning curve caused by changing larval production rates. The value y is subtracted from the observed mortality to obtain the production adjusted mortality rate. Thus if the mean and standard deviation of the hatching curve are known then corrections can be made to mortality estimates.

The biases in mortality rates predicted from increasing or decreasing production rates were investigated using cod larvae from the MARMAP time series on Georges Bank. The mean catch per 10 m2 of sea surface of larvae $\leq$6 mm in length and the abundance-weighted mean Julian day of capture for each survey were fit to the following Gaussian curve by nonlinear procedures:

$$y = a * e^{-0.5\,((x-b)/c)^2}$$

The terms a, b, and c estimate the amplitude, mean and standard deviation of the fitted curve (*i.e.*, hatching curve), respectively. A plot of the mean catches and the estimated hatching curve is shown in Figure 11.

The mean hatching day corresponds to April 16 and the standard deviation is approximately 17 days. The equation for the change in abundance (*i.e.*, production) is $y = 0.3727 - 0.003492$*Julian day.

The average mortality rate for all cod larvae on Georges Bank was estimated from the slope of the exponential decay model fit to the age and the

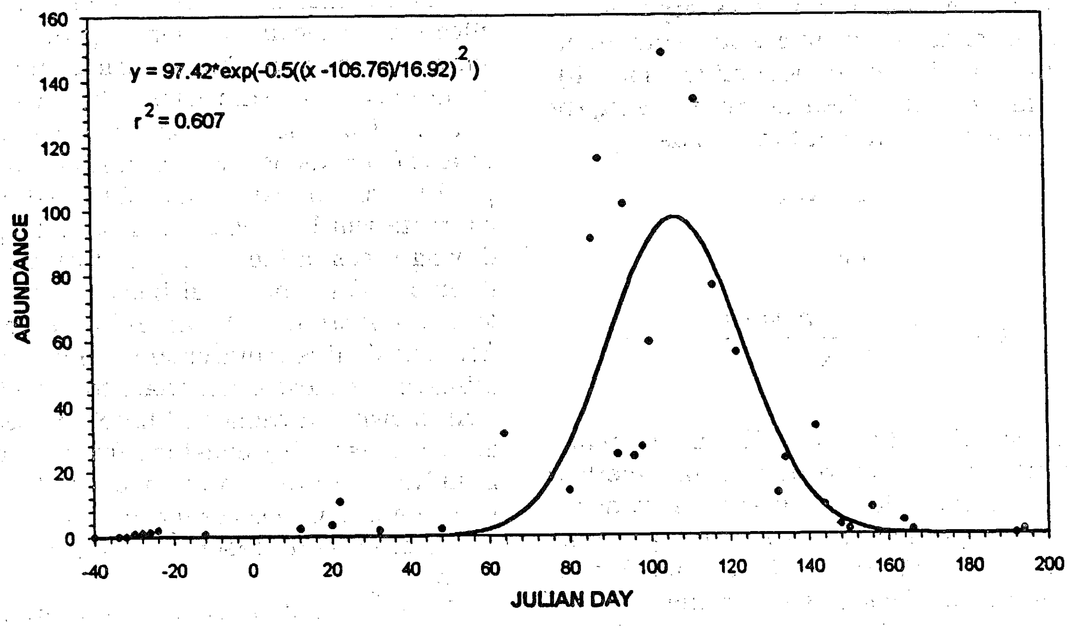


Figure 11. Survey mean abundance (number/10m^{-2}) of Atlantic cod larvae $\leq$6 mm for each survey in the MARMAP time series (1977-1987) and the fitted Gaussian curve.

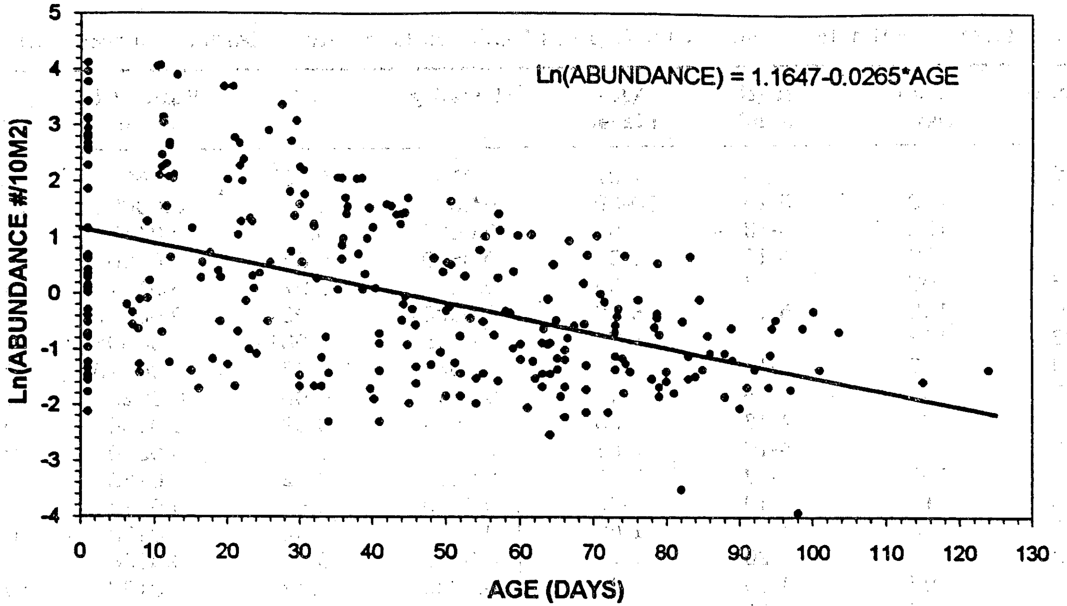


Figure 12. Plot abundance and age of Georges Bank cod larvae from MARMAP surveys, 1977-1987.

mean catch 10 m^{-2} at age in each survey (Figure 12). Mortality averaged about 2.6% day^{-1} and $r^2 = 0.240$, SE 1.387, $P<0.01$.

Age and abundance data from individual surveys on Georges Bank were used to estimate larval mortality. A preliminary summary of ages and abundances revealed that surveys within ± 3 standard deviations of the mean hatching day (*i.e.*, between February 25 and June 12) contained sufficient data to calculate mortalities. Data collected on surveys outside this time frame were often very sparse (*e.g.*, one to three stations with cod larvae) or the lengths of larvae were noncontiguous and thus suspect for mortality estimation. Of the 45 surveys that contained cod larvae, 24 were used for analysis (Table 3).

The use of the temperature-dependent growth function to estimate age from length produced nearly as many ages as lengths in the data set. Therefore, for each survey, the abundance-weighted mean age at each mm length interval and its mean catch per 10 m^2 of sea surface was fit with an exponential decay curve and the slope of least squares regression used to estimate mortality.

The effect of changing production rates over the hatching curve predicts that mortality at the beginning of the hatching season will be overestimated and underestimated at the end of the hatching season. There is no *a priori* reason to suspect that mortality at the beginning of the hatching season will be higher than later in the season. Given the multi-year data set analyzed here, it is reasonable to suspect no trend in mortality with time of year. When the mortalities listed above are plotted against Julian day and a nonlinear least squares line is calculated, the slope of the line is negative and significant (slope = -0.188, $t = 7.41$, $df = 22$, $p < 0.001$, Figure 13).

The negative slope supports the expectation of a seasonal decline in observed mortalities based on the changes in production rates of larvae. When the mortalities are adjusted for production rate changes (*i.e.* observed mortality minus y, as described earlier), the negative seasonal trend becomes positive and significant (slope = 2.44, $t = 2.09$, $df = 22$, $p < 0.05$).

The increasing trend in the adjusted mortalities with Julian day could be caused by the effects of increasing water temperature (Morse 1989). To investigate this possibility, mortality was plotted against the abundance weighted mean temperature of the top 15 m of water for stations containing cod larvae. The plot and a fitted regression line are shown in Figure 14, along with the regression line calculated from the data in Morse (1989).

The two lines indicate a positive temperature and mortality relationship and the statistics for the two lines are Mortality = -0.246 +0.188*ln(Temperature), ($R^2 = 0.71$, SE = 0.0334, $P < 0.01$), for Georges Bank cod larvae; and Mortality = 0.000562 +0.0102*Temperature, ($R^2 = 0.70$, SE = 0.00136, $P < 0.01$), for the data in Morse (1989).

Interannual trends in production-adjusted mortalities, measured as deviations greater than ±0.025 from the fitted curve of mortality versus Julian day (see Figure 14), indicate high mortality of cod larvae occurred in 1977-1979, 1983,

Table 3. Mortality estimates by survey for Georges Bank cod larvae from MARMAP surveys, 1977-1987

Survey	Julian Day	Lengths (mm)	Ages (days)	Mortality	R^2	Standard Error	P
2	78	4-6	1-21	0.210	0.90	0.0697	0.095
3	113	5-15	10-69	0.103	0.97	0.00624	<0.001
4	152	4-13	1-51	0.0054	0.03	0.0117	0.659
9	132	4-11	1-54	0.0860	0.85	0.0150	<0.001
15	97	4-7	1-33	0.125	0.97	0.0161	0.004
16	142	5-20	8-83	0.00201	0.004	0.00817	0.809
22	122	4-17	1-78	0.0445	0.087	0.00508	<0.001
23	167	4-17	1-73	0.0037	0.48	0.00275	0.016
27	63	4-08	1-41	0.164	0.06	0.0225	0.005
28	96	4-13	1-69	0.0574	0.67	0.0166	0.010
29	118	4-19	1-88	0.0381	0.74	0.0610	0.051
30	156	4-13	1-50	0.0294	0.32	0.0162	0.107
36	111	4-10	1-52	0.0513	0.66	0.0214	0.074
42	103	4-14	1-66	0.121	0.94	0.0103	<0.001
43	163	4-20	1-73	0.0072	0.67	0.0036	0.140
49	95	4-09	1-44	0.0629	0.78	0.0168	0.013
50	145	4-20	1-74	0.0106	0.14	0.0078	0.194
58	88	4-8	1-39	0.0901	0.97	0.00904	<0.001
59	94	4-14	1-69	0.0833	0.94	0.00731	<0.001
60	131	4-20	1-80	0.0154	0.27	0.00684	0.040
66	102	4-11	1-54	0.0757	0.72	0.0195	0.006
67	150	11-20	45-78	0.0174	0.36	0.0234	0.534
74	112	4-10	1-54	0.1072	0.92	0.0153	<0.001
76	139	04-20	1-80	0.0047	0.04	0.0070	0.511

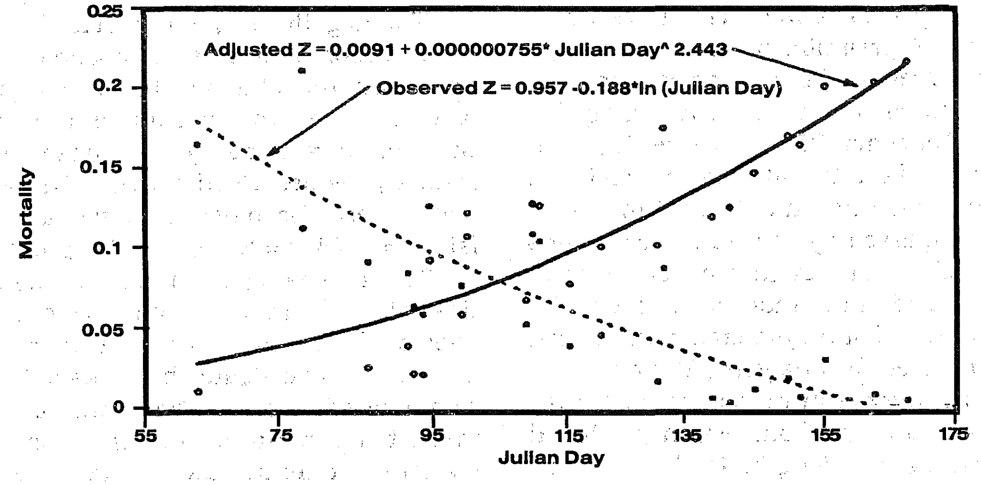


Figure 13. Estimated production-adjusted mortalities for Georges Bank cod larvae from MARMAP surveys, 1977-1987.

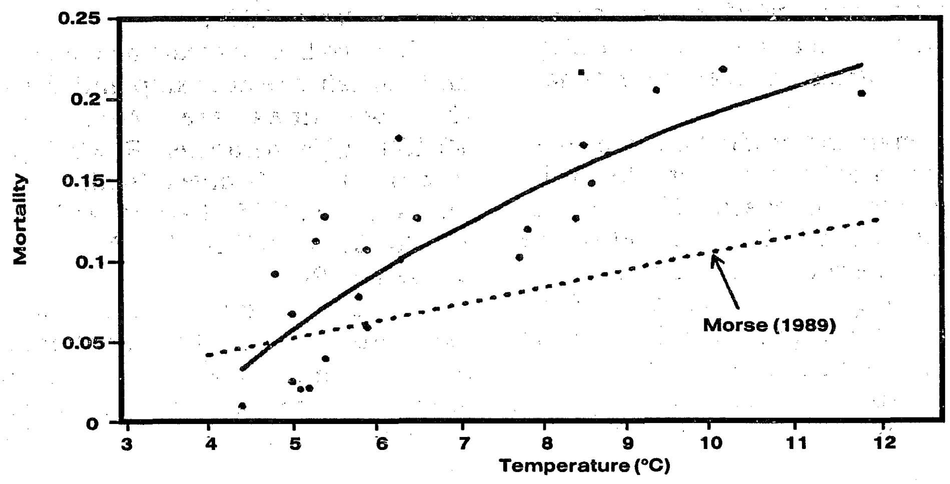


Figure 14. Relationship of water temperature and production-adjusted mortalities for Georges Bank cod larvae from MARMAP surveys, 1977-1987 and the temperature and mortality relationship from Morse (1989).

and 1987. Low mortalities were measured in 1981, 1984, and 1985. In 1984 and 1985, all survey mortality estimates were low, while consistent high mortalities were measured in surveys in 1983.

LARVAL DRIFT

Mean circulation patterns on Georges Bank are characterized by a clockwise gyre that parallels the local isobaths and varies in intensity depending upon season. Based primarily on observations >44 m deep at one station located on the southern flank of the bank in 85 m of water, the seasonal changes in flow can be characterized as follows (see Butman *et al.* 1987). In winter and early spring, along-bank flow is at its minimum (2.6-5.2 km day-*1*), although variability is high due to winter storms. Flow rates increase during late spring and early summer (5.2-6.9 km day^{-1}) and variability decreases as wind stress diminishes. By late summer flow around the gyre is at its maximum (8.6 - 11.2 km day^{-1}) and vertical shear is strong due to water-column stratification. Current speeds tend to decrease with depth during all times of the year. Cross-bank currents are very weak (<1.7 km day^{-1}) and highly variable at all depths and seasons. A distinctive hydrographic feature of Georges Bank is that the top of the bank (within the 40-60 m isobath) remains well mixed all year from tidal currents. During winter the well-mixed area extends out to about the 100 m isobath and water temperatures are at their minimum. During spring and summer a thermocline develops and intensifies due to solar warming and a decrease in storms (Flagg 1987). The times and locations where cod larvae are most abundant on the bank correspond to the times of minimum flow rates and to areas that are not yet vertically stratified (*i.e.*, the southern part of Georges Bank in April). Few current observations are available for the Northeast Peak of Georges Bank during the key months of March through May, but currents there appear to be very weak (<3 km day^{-1}) and flow towards the southwest. The larvae persist on the bank during May and June when current flows are increasing and water in depths >60 m is becoming increasingly stratified.

Given the mean current patterns on Georges Bank, passive drift of cod larvae hatched on the Northeast Peak or along the southern flank in waters 50-100 m deep should be southwest until reaching the Great South Channel. At this point, larvae would either be retained in the clockwise gyre and continue on along the northern edge or be carried into the Southern New England area. A modeling study by Werner *et al.* (1993) showed that spring-spawned eggs and larvae occurring in the surface layer (<15 m deep) would be carried off the southern edge of the bank and die.

Table 4. Abundance-weighted mean depth of cod larvae on Georges Bank from MARMAP surveys, 1977-1987

Age Group (Days)	**Mean Depth (m)**
1	71.4
2-14	71.2
15-28	71.4
29-42	67.8
43-56	67.6
57-70	67.7

To determine the possible effect of the mean residual currents on the drift of cod larvae on Georges Bank, average distribution patterns were examined using the MARMAP data set and the centroid methods of Kendall and Picquelle (1990). The centroid is the abundance weighted mean location (*i.e.*, center of mass) of cod larvae on Georges Bank. The distributions and their centroids were determined for all larvae grouped as 1 day old, followed by 2-week cohorts up to a maximum age of 70 days (Figures 15 a-f). The ellipse around the centroid shows the orientation of the abundance of larvae in space and is one standard deviation from the rotated axes. The ellipse represents the 40% confidence interval and about 40% of the observations are within the ellipse. The location of the centroid and the size and orientation of the ellipses remain essentially unchanged during the first 56 days of "drift" for cod larvae. The oldest cohort (57-70 days old) shows a pattern of dispersion across the bank and the centroid has moved northwest into shoaler waters. A portrayal of cod larval drift on Georges Bank is presented by Lough (1984) wherein the centers of abundance appeared to move along the southern edge of the bank. However, the grid of sampling stations also moved along the expected axis of drift and clearly biased the locations of the centers of abundance.

A tendency for cod larvae to move to shoaler waters as they age was noted by Lough and Bolz (1989) during three surveys of the southern flank of Georges Bank in April and May 1981 and May 1983. The MARMAP data shows a weak trend of decreasing depth with increasing age of larvae (Table 4).

Evidence for "drift" of cod larvae that is consistent from year to year and/or strong enough to be detected using average distribution patterns is clearly lacking in the MARMAP time series.

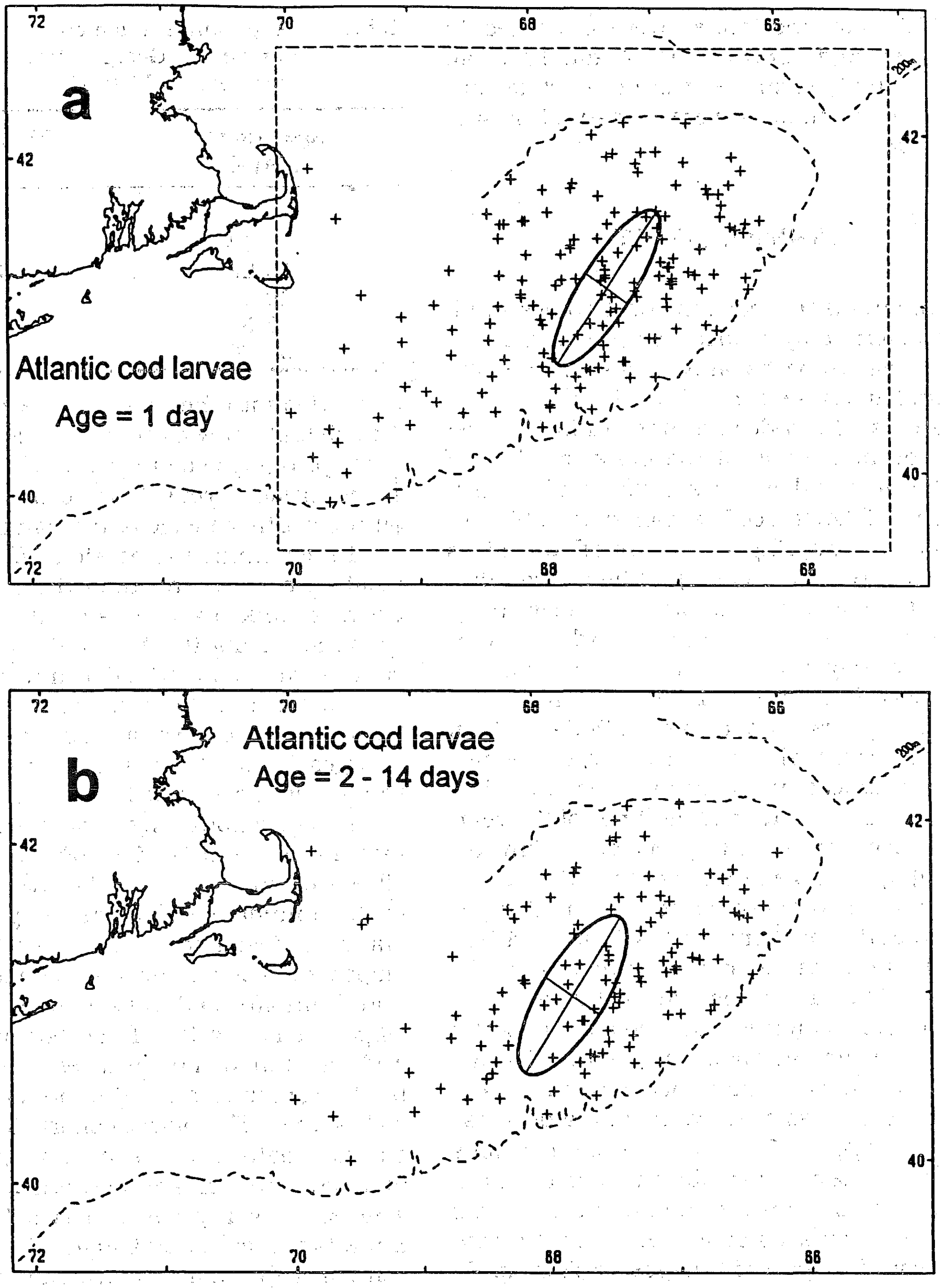
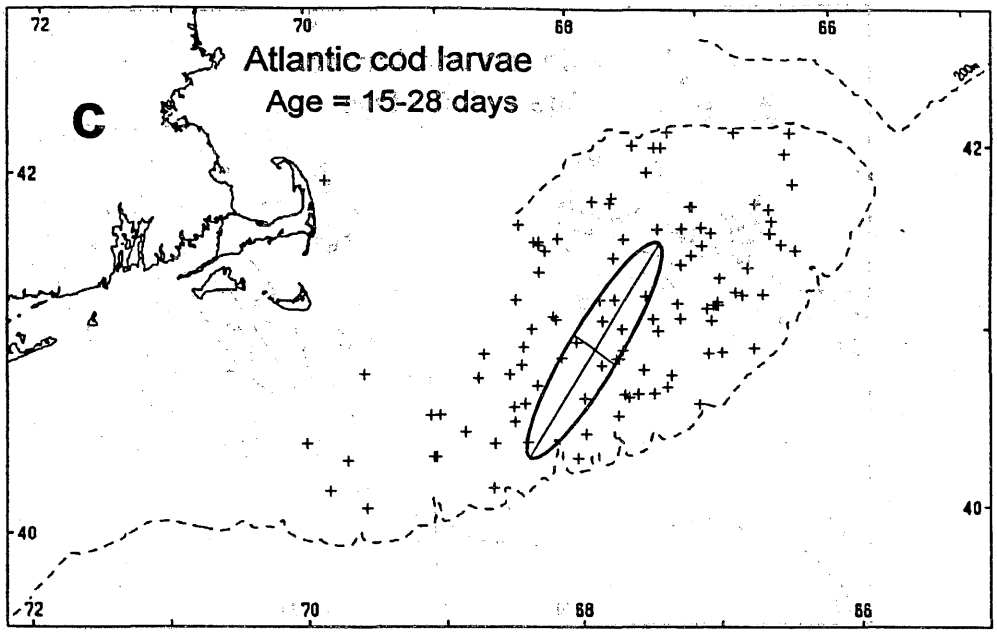


Figure 15 a-b. Centroids of Atlantic cod larvae by age group from MARMAP surveys, 1977-1987. Dashed box in Figure 15a defines limits for inclusion of stations, + = station locations where cod larvae were captured.

Annual drift trajectories, using length as a proxy for age, reveal little change in the locations of centroids, regardless of year or length (Appendix Figure 2). This lack of drift for cod larvae is in sharp contrast to drift patterns found for haddock larvae on Georges Bank (Walford 1938, Smith and Morse 1985). Using the haddock eggs and larvae from the MARMAP time series and calculating their centroids indicates that haddock, in fact, "drift" in the expected clockwise direction around Georges Bank (Figure 16).

In an analysis of larval drift, it is often difficult to separate the effects of drift from those of larval mortality and sampling bias. For example, if mortality is highest at the edges of the distribution of larvae, perhaps due to hatching in unfa-



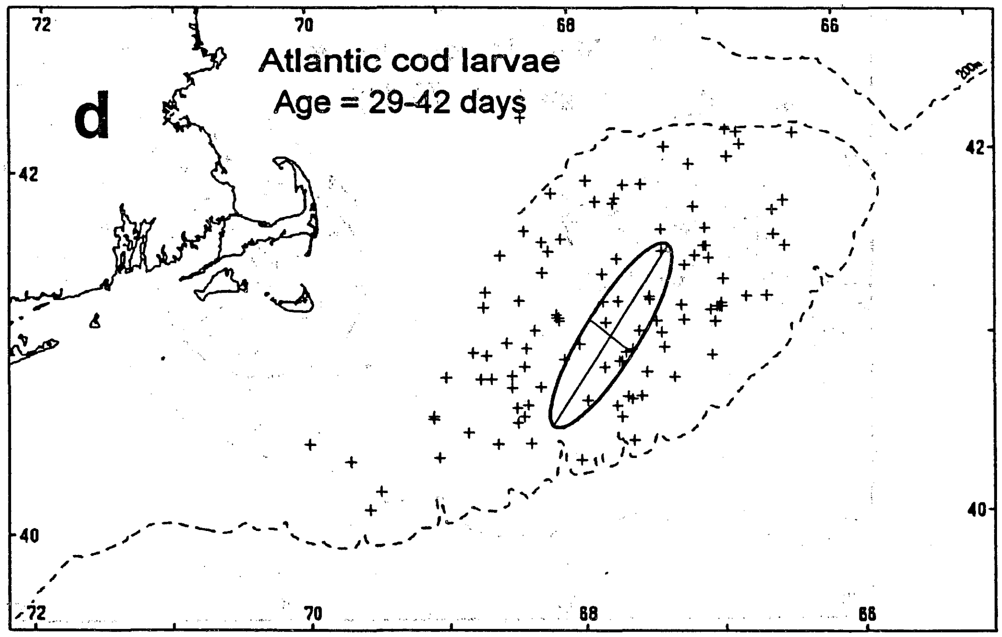
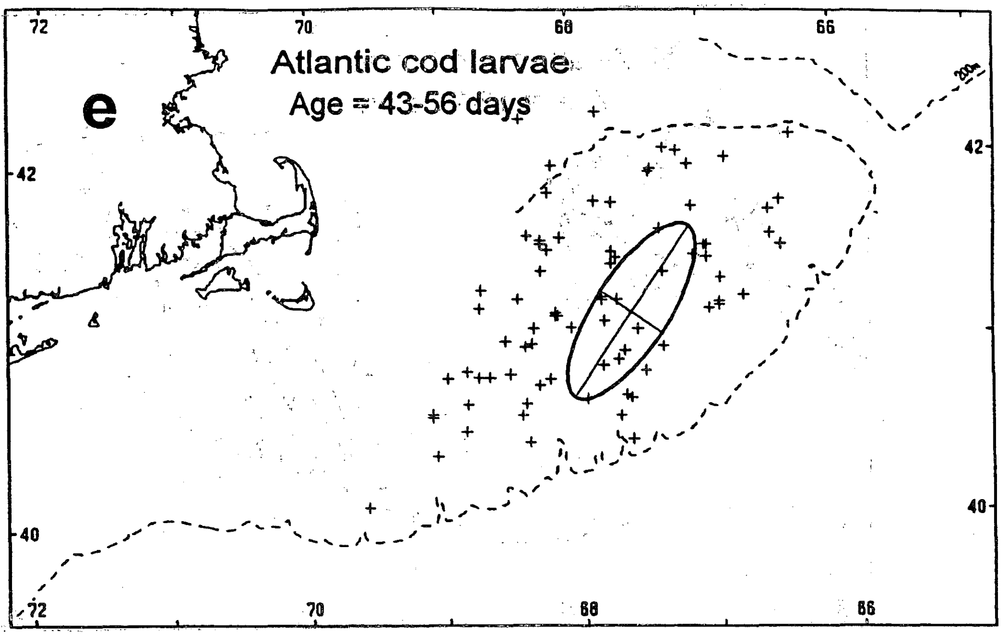


Figure 15 c-d. Centroids of Atlantic cod larvae by age group from MARMAP surveys, 1977-1987. Dashed box in Figure 15a defines limits for inclusion of stations, + = station locations where cod larvae were captured.

vorable waters, then the location of the center of distribution will appear not to move and the true drift patterns will be masked. The decline in larval abundance of older cohorts due to mortality may also be seen as a general decline in larval catches and the lack of a clear center of abundance on the bank used to track drift (*e.g.* Figure 15f). In addition, as larvae age and grow they are better able to avoid capture by bongo nets and there will be "apparent" mortality from net avoidance evident in the catch frequencies. This ability to avoid nets could vary spatially due to such factors as water clarity, subsurface currents, or net clogging, thus further obscuring any evidence of drift. It is clear that evidence of drift (or no drift) must account for those factors which affect the apparent patterns of distribution and abundance of pelagic stages of fish.



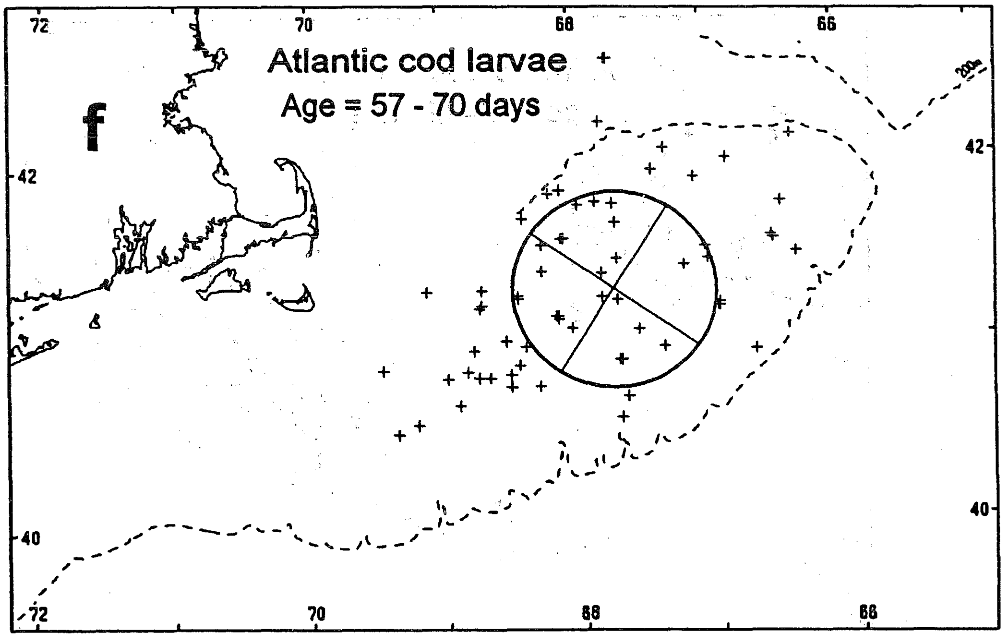


Figure 15 e-f. Centroids of Atlantic cod larvae by age group from MARMAP surveys, 1977-1987. Dashed box in Figure 15a defines limits for inclusion of stations; + = station locations where cod larvae were captured.

LARVAL ABUNDANCE AND WATER COLUMN STRATIFICATION

Some uncertainty exists about the benefits to growth and survival of cod larvae in stratified versus unstratified waters. Under certain conditions, water column stratification may concentrate both larvae and their food at the thermocline and thus increase encounter rates of larvae and their prey. This increase in prey availability was reflected in increased growth rates of cod and haddock larvae at a stratified site, compared to an unstratified site on Georges Bank (Buckley and Lough 1987). However, prey biomass was also found to be higher at a well-mixed site compared to a stratified site (Perry and Neilsen 1988). Thus, the mechanisms that tend

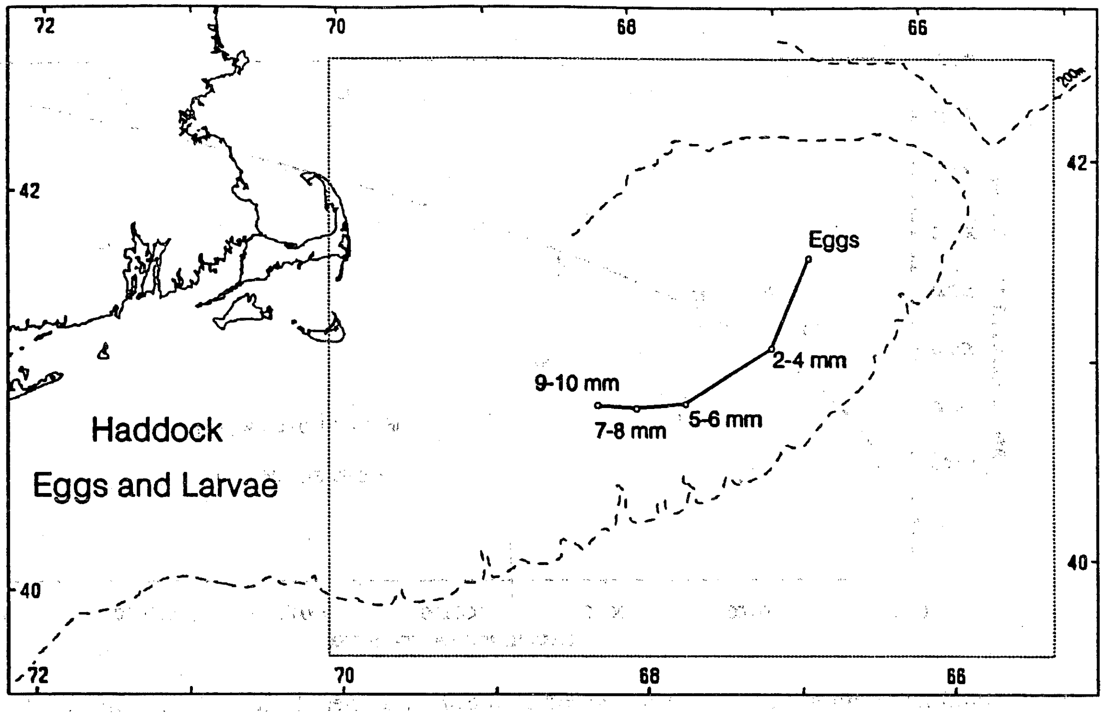


Figure 16. Larval drift trajectory for haddock larvae based on MARMAP surveys, 1977-1987.

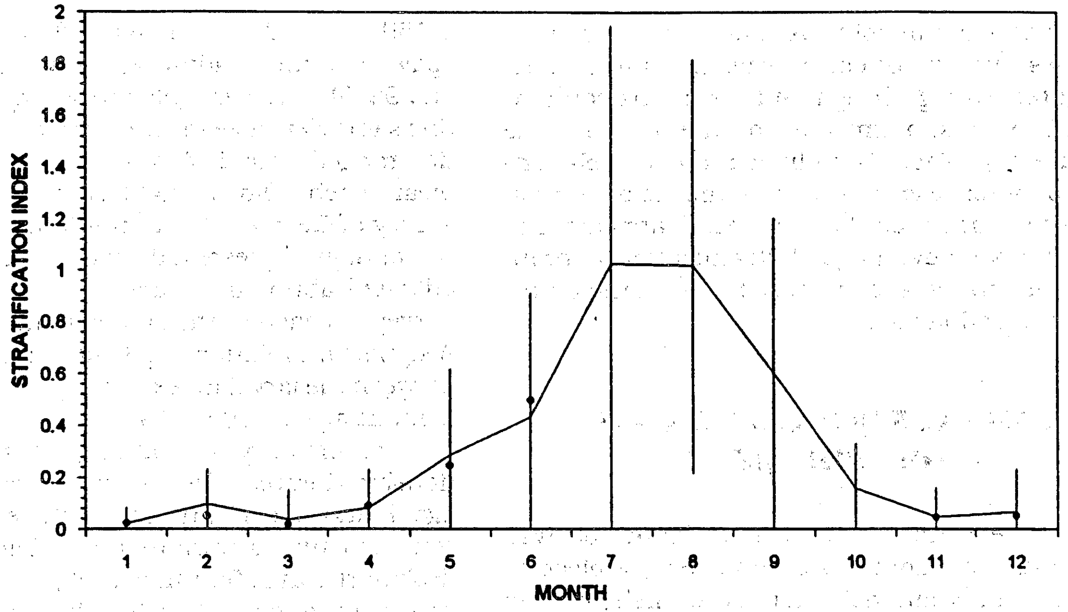


Figure 17. Annual cycle of the maximum Δ-sigma t recorded at MARMAP stations on Georges Bank, 1977-1987. Line connects the mean values for each month, vertical lines define the standard deviation and the dots are the means for stations that contained Atlantic cod larvae.

to concentrate larvae and their prey at thermoclines are likely to concentrate larval fish predators as well. The balance between increased growth and increased predator-driven mortality of larvae needs to be studied to adequately characterize larval dynamics as related to water column structure.

If stratification is a significant benefit to the survival of cod larvae, compared to unstratified waters, then on average the abundance of larvae should be highest in stratified waters. An index of water column stratification is the maximum Δ sigma-t recorded at a station. The average annual cycle of these observations on Georges Bank is shown in Figure 17. Stratification begins during late April and increases to its maximum during July and August. By November, the waters return to unstratified conditions until the following April. Cod larvae occur from November through June on Georges Bank, and peak abundance is from March - May, a period of increasing stratification.

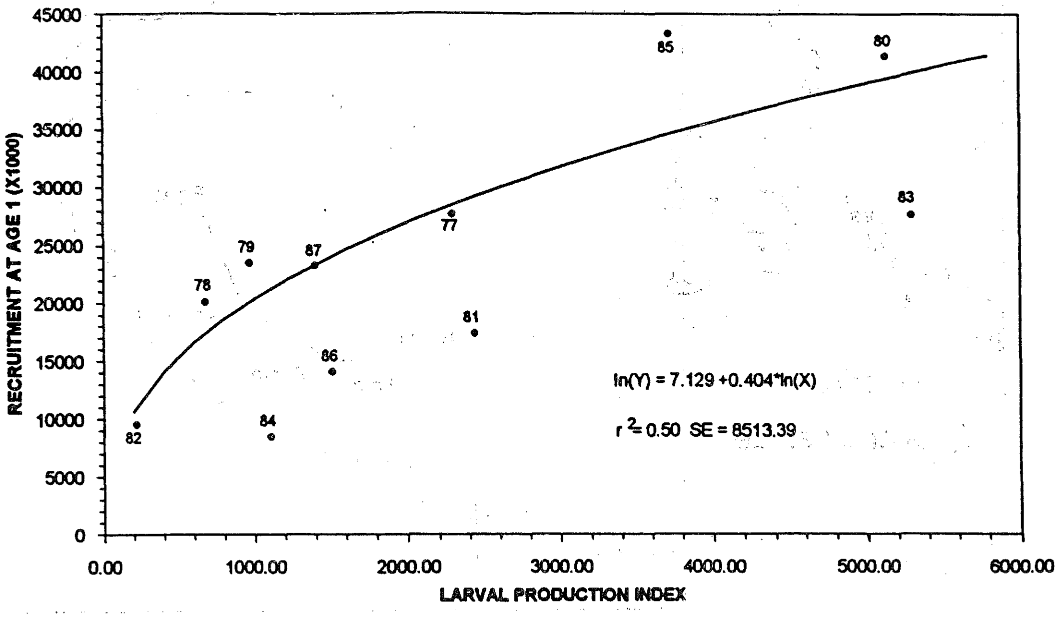


Figure 18. Production index of ≤6 mm Atlantic cod larvae and number of age 1 recruits on Georges Bank, 1977-1987. Numbers near the data points are the years of larval production (*i.e.*, spawning seasons).

To test the hypothesis that stratification increases survival of cod larvae, the abundance-weighted average D sigma-t for stations containing larvae is superimposed on the annual cycle (Figure 17). There is no indication of a relationship between average water column stratification and the abundance of cod larvae. It appears that any survival advantage of stratification is probably very subtle and is not reflected in the abundance of cod larvae.

LARVAL PRODUCTION AND RECRUITMENT

The recruitment of Georges Bank cod was found to be "more stable and less subject to extreme fluctuations" than other fish species around the world (Hennemuth *et al.* 1980). This stable recruitment pattern is not expected for a population at the extreme end of its geographic range (*i.e.*, Georges Bank), where environmental variability is expected to exert a significant effect on recruitment. When Georges Bank cod recruitment variability during 1978-1991 (Serchuk and Wigley 1992) is compared with recruitment variability in other cod stocks in the North Atlantic (Garrod and Knight 1979), Georges Bank stock is about average (SD of $\log_e$ number at age 1 = 0.51, range for North Atlantic = 0.27 - 0.95) and appears to be neither more nor less stable.

Recruitment of the 1977-1987 year classes at age 1 (March 1) on Georges Bank ranged from 8,459 to 43,298 thousand fish, which were spawned from an adult biomass between 55,479 and 92,748 mt (Serchuk and Wigley 1992). Over this same eleven years, an index of larval production ranged from 217 to 5,294. The index is the mean catch $10m^{-2}$ of cod larvae ≤6 mm on each survey of Georges Bank, multiplied by the number of days represented by each survey. These adjusted abundances are then summed across surveys in each of the eleven spawning seasons. A significant relationship ($P < 0.05$, df 1,10,) exits between the larval index and subsequent recruitment at age 1 (Figure 18).

A preliminary correlation analysis of the relationships between the residuals of recruitment at age 1 and spring and fall surface and bottom temperature anomalies on Georges Bank (Holzwarth and Mountain 1990) found no significant correlations. Lagging the anomalies by 1 year did not change the results.

SUMMARY

1. Hatching of cod larvae begins in the Gulf of Maine in October and November, spreads south during December, when two centers of abundance are located on Georges Bank and on Nantucket Shoals. Hatching has stopped in the Gulf of Maine in January and by February larvae occur from Cape Hatteras, N. C. to Georges Bank. By April, hatching has ceased in the southern most reaches of

the study area and is again centered on Georges Bank. In May and June, there is a general decline in hatching intensity throughout the area, and by August and September only a few small patches of larvae are located on Georges Bank and in the Gulf of Maine.

2. Peak abundance of larvae in the Middle Atlantic area occurs in February, although overall abundance here is very low. Peak larval abundance on Georges Bank and Southern New England areas occurs in March and April and in the Gulf of Maine in May-July. Maximum monthly mean catches per 10 m2 were only 0.9 in the Middle Atlantic, 7.5 in Southern New England, 58 on Georges Bank, and 1.5 in the Gulf of Maine. Interannual trends in abundance are evident in Southern New England and in the Gulf of Maine but not in either the Middle Atlantic or on Georges Bank. The trend in Southern New England shows a general increase in abundance during the time series with the last three years (1985-1987) having the highest peak abundances. The Gulf of Maine shows a peak in abundance during 1978-1980, then much lower and relatively constant abundances during 1981-1987. Of special note is the near absence of cod larvae on Georges Bank in the spring of 1982.

3. Simple plots of the percent frequency of station water temperatures of the top 15 m of water in depths $\leq$150 m compared with the percent frequency of catches of cod larvae at temperature, indicate that cod larvae occur between 1° and 20° C throughout the study area. Georges Bank larvae are the most temperature restricted compared to the other three areas and occur at temperatures between 3° and 12° C. The Southern New England area supports cod larvae at a temperature range from 1° to 14° C, while the Gulf of Maine area shows a range between 3° and 14° C. Larvae in the Middle Atlantic area are found from 1° C, the coldest temperature recorded there, to 12° C. A clear preference is indicated for cod larvae where more than 80% of all larvae occur in temperatures 4° to 8° C.

4. Temperature-dependent growth functions were developed for Georges Bank cod larvae based laboratory and field estimates of growth. Estimated ages from the temperature-dependent function were significantly higher then ages determined from otolith ring counts.

5. A method was developed to adjust larval mortality estimates for changes in larval production rates during the hatching season. Production adjusted instantaneous mortality rates were estimated for 24 surveys and ranged from 0.01 - 0.22. Significant and positive relationships were found between both Julian days and water temperatures and larval mortality rates.

6. Using the center of mass, *i.e.*, centroids, showed little evidence of larval drift on Georges Bank. A very weak trend for cod larvae to move to shoaler waters as they as they age was found.

7. There is no indication of a relationship between average water column stratification and the abundance of cod larvae. It appears that any survival advantage of stratification is probably very subtle and is not reflected in the abundance of cod larvae.

8. A significant relationship was found between an index of larval abundance and subsequent recruitment at age 1.

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Appendix

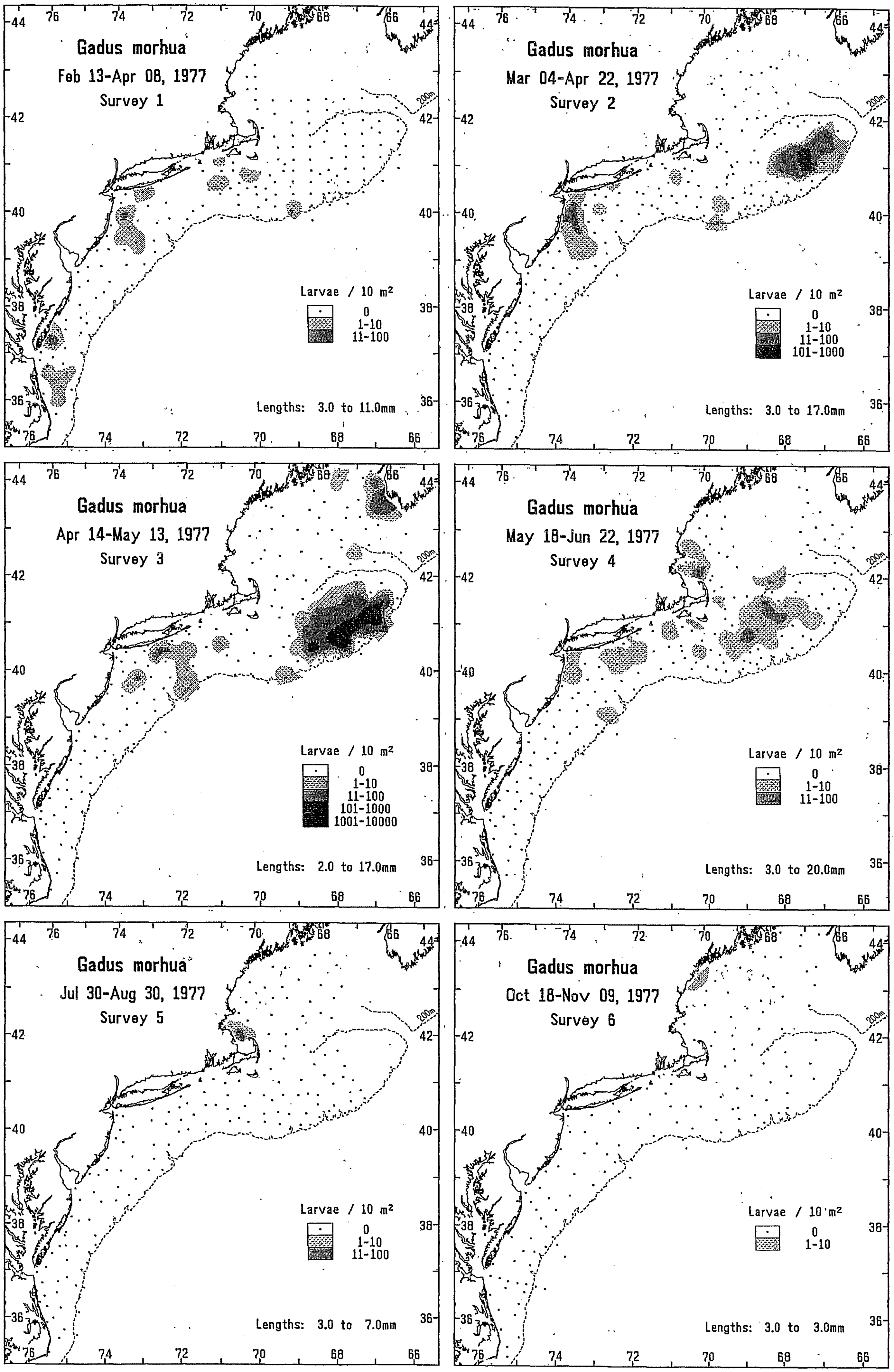


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

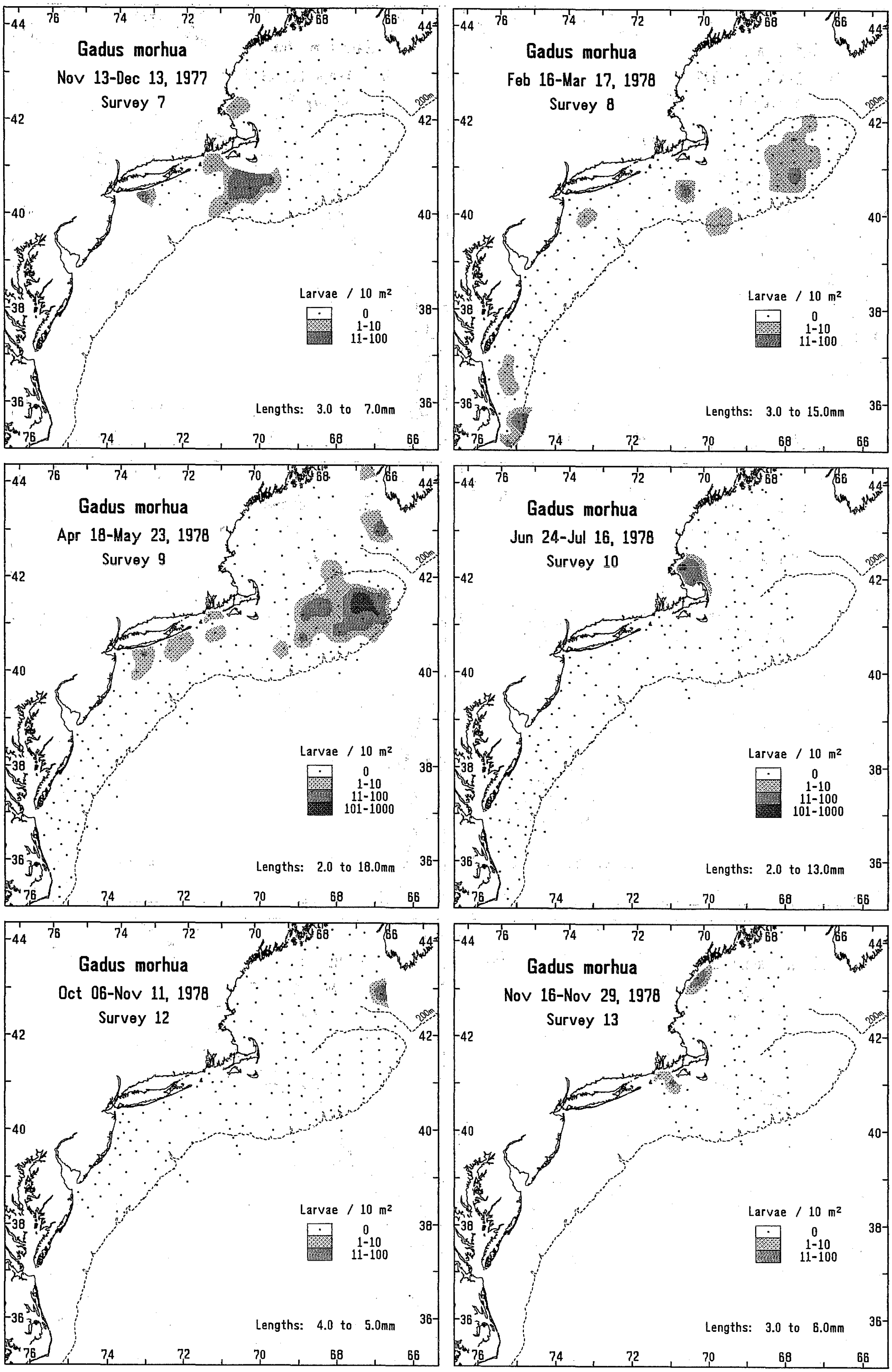


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

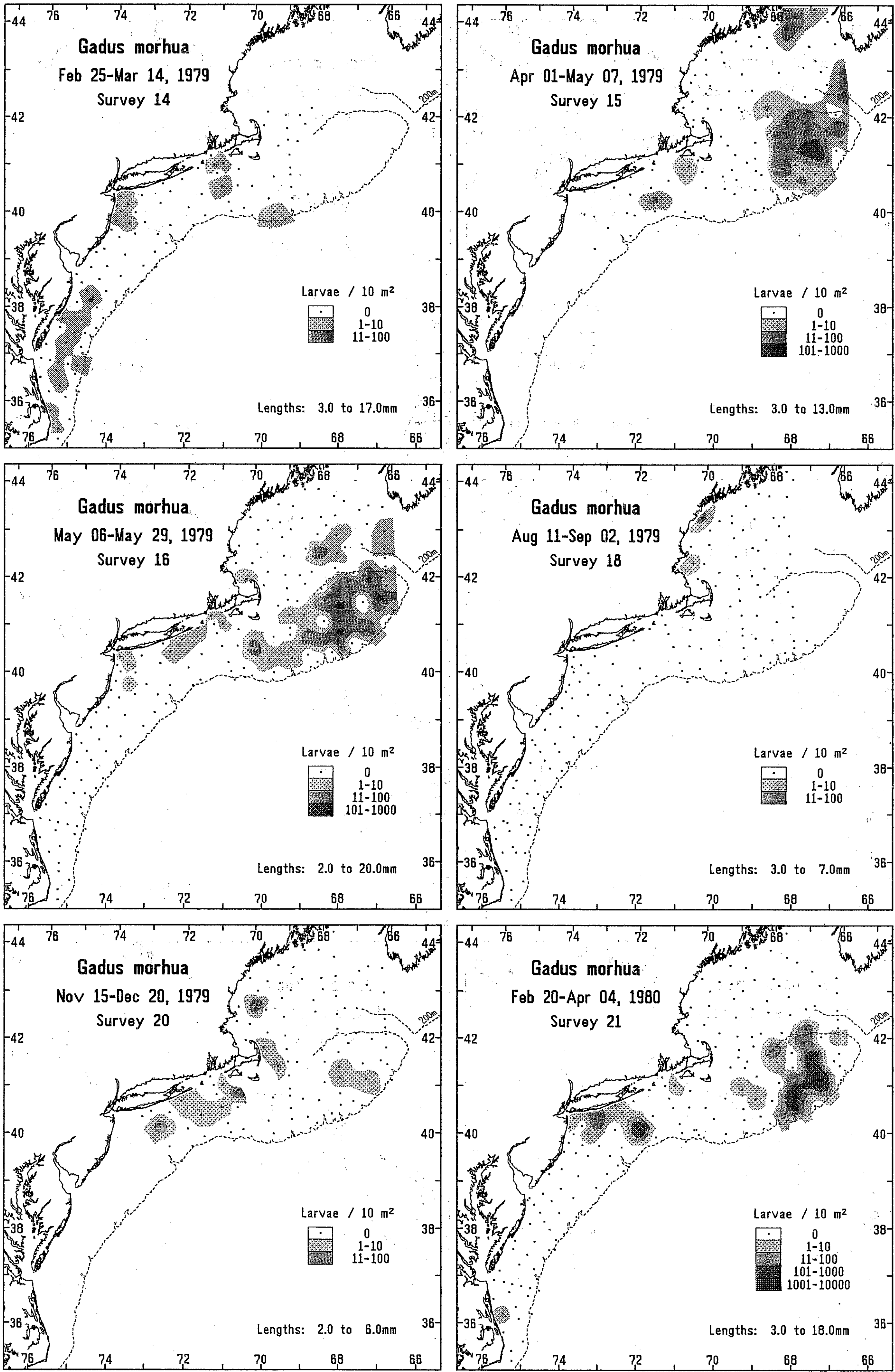
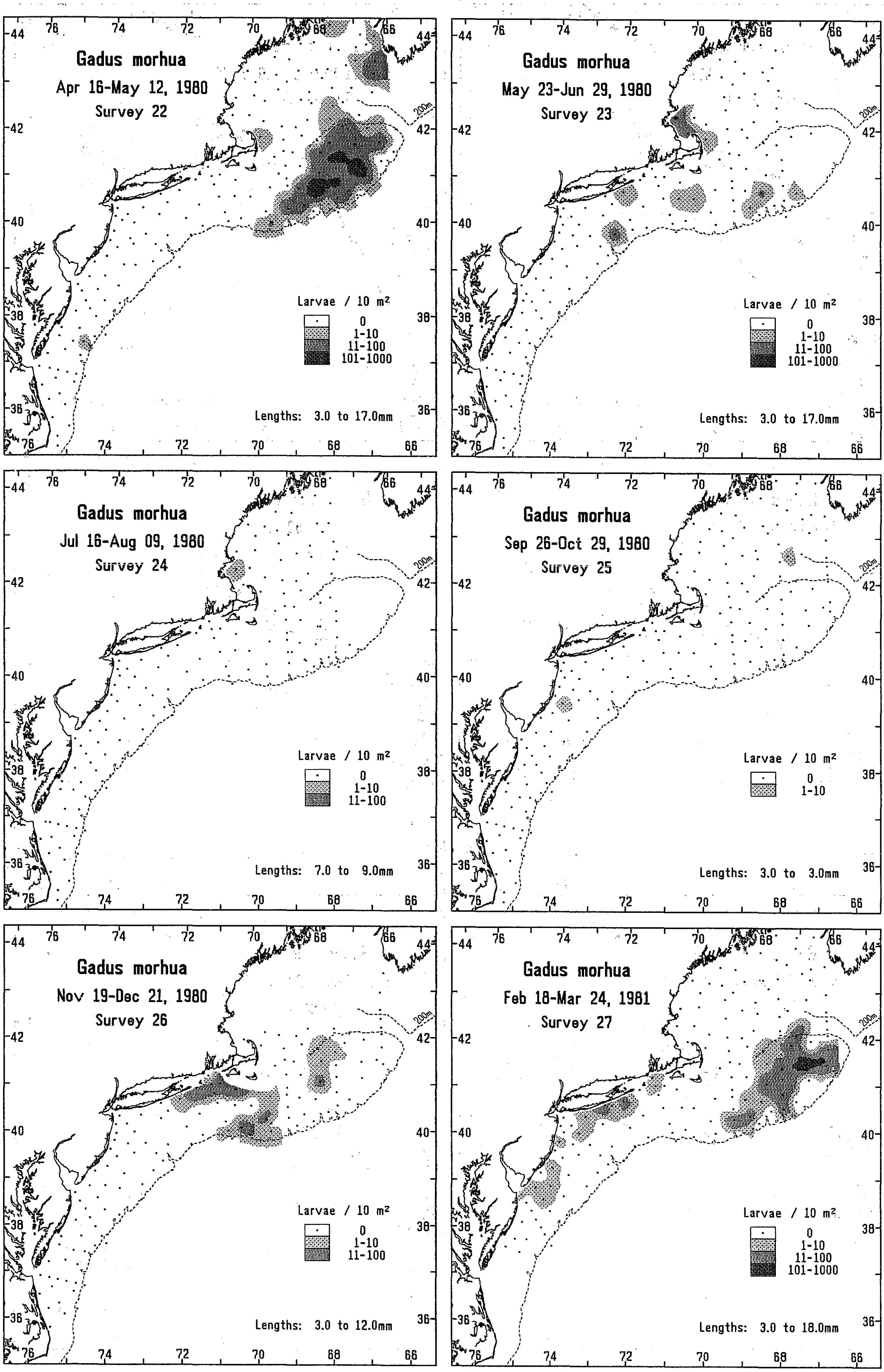


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987



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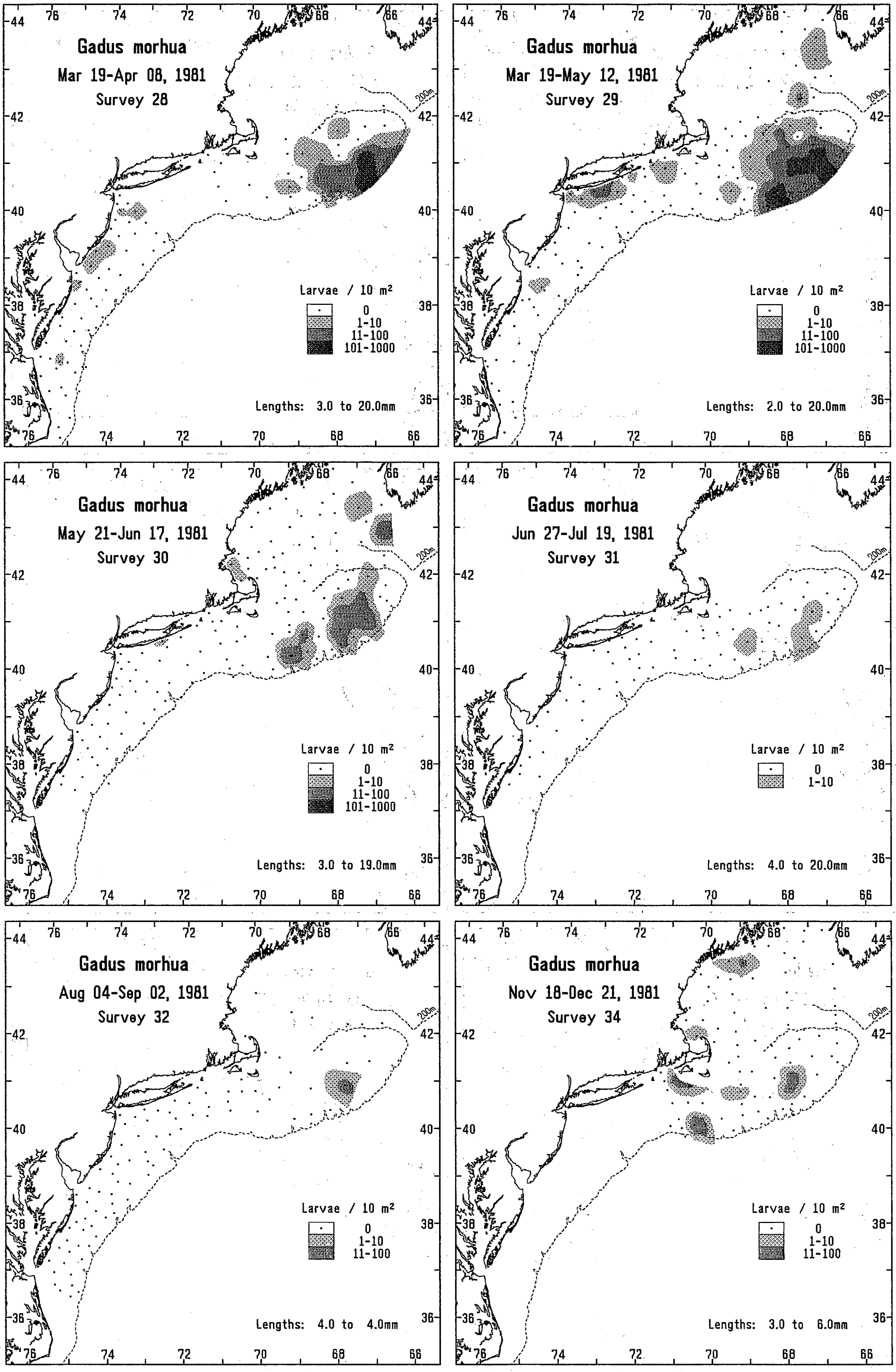


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

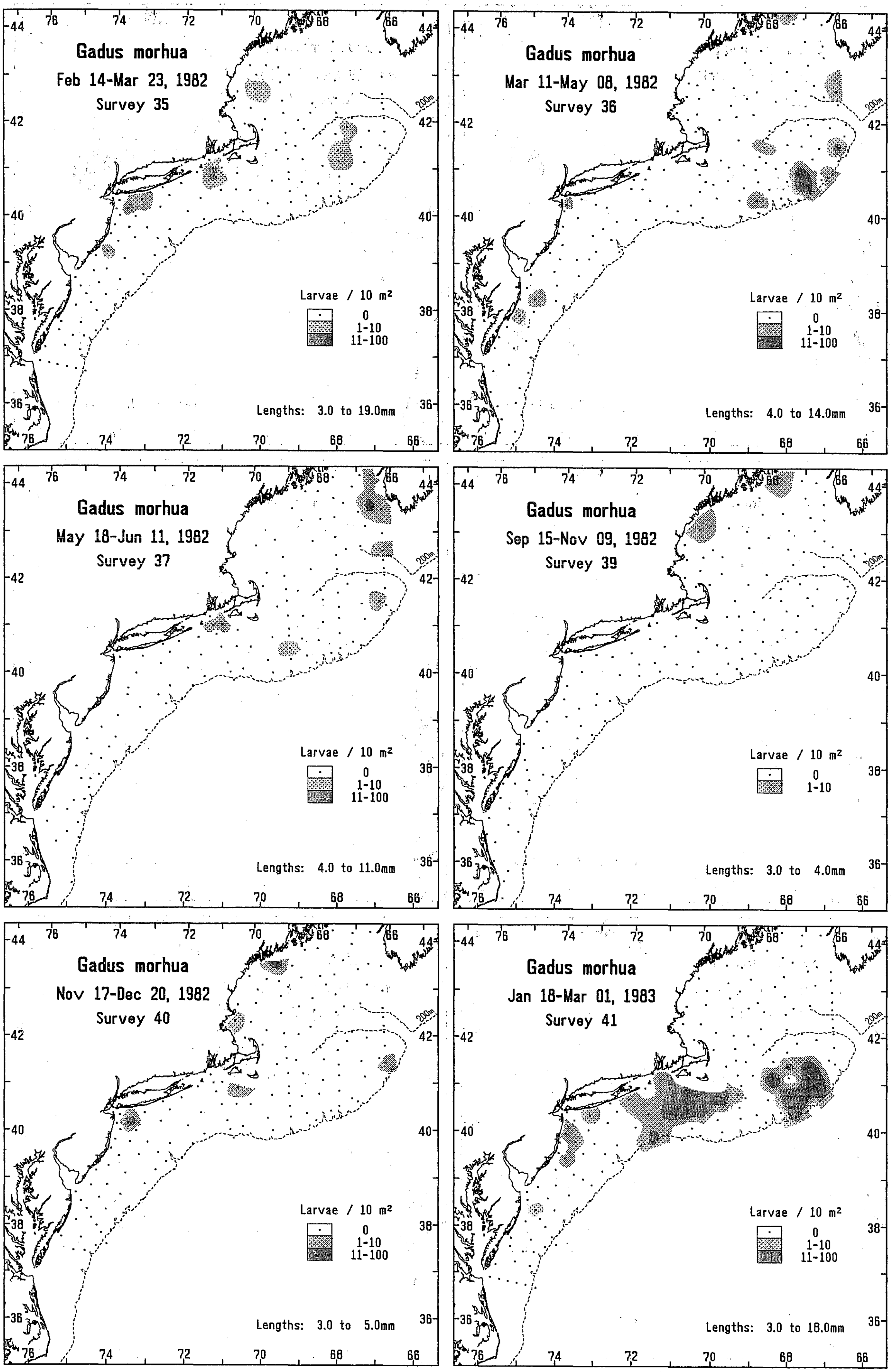
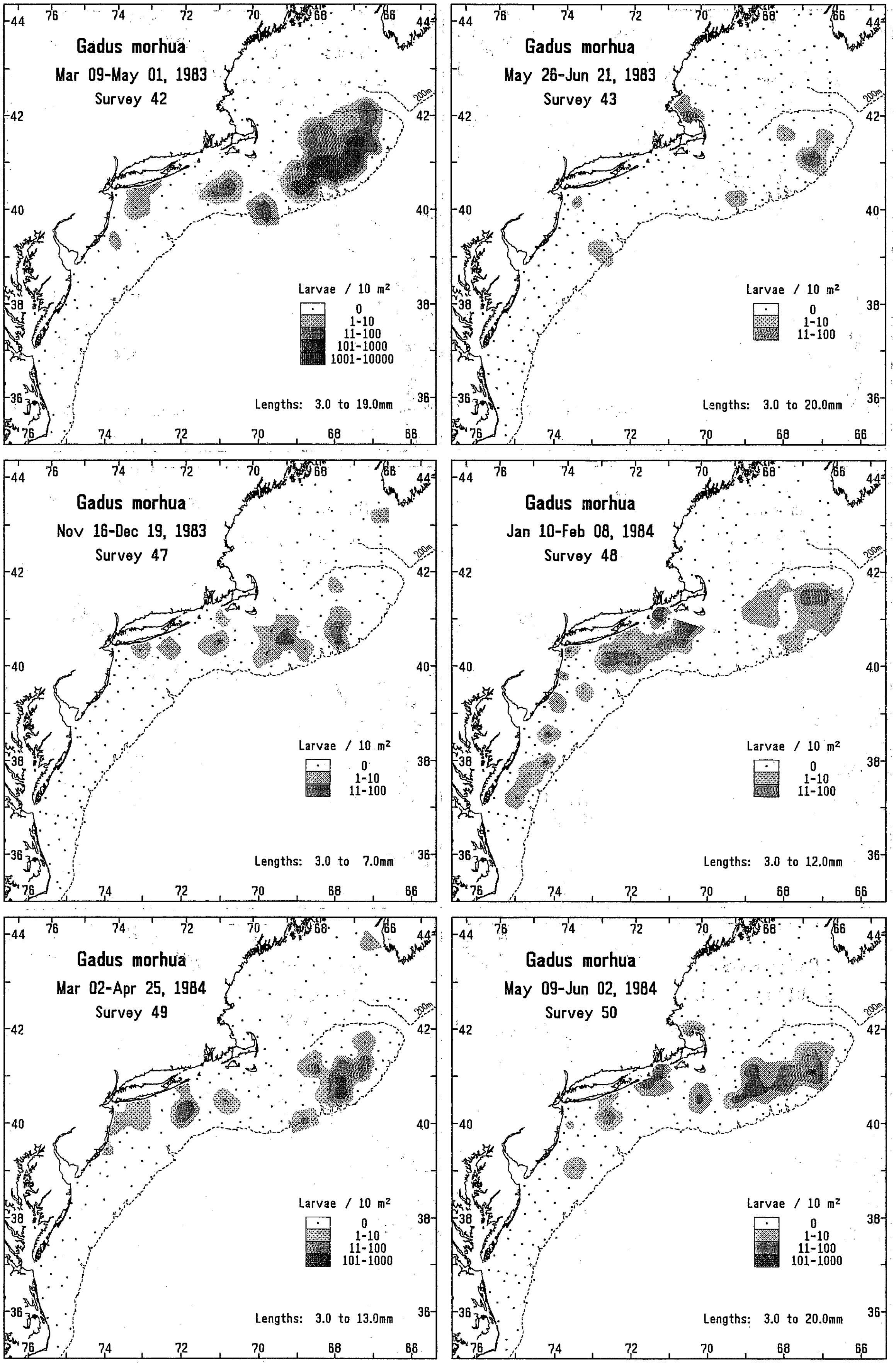


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987



Gadus morhua
Mar 09-May 01, 1983
Survey 42

Gadus morhua
May 26-Jun 21, 1983
Survey 43

Gadus morhua
Nov 16-Dec 19, 1983
Survey 47

Gadus morhua
Jan 10-Feb 08, 1984
Survey 48

Gadus morhua
Mar 02-Apr 25, 1984
Survey 49

Gadus morhua
May 09-Jun 02, 1984
Survey 50

Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

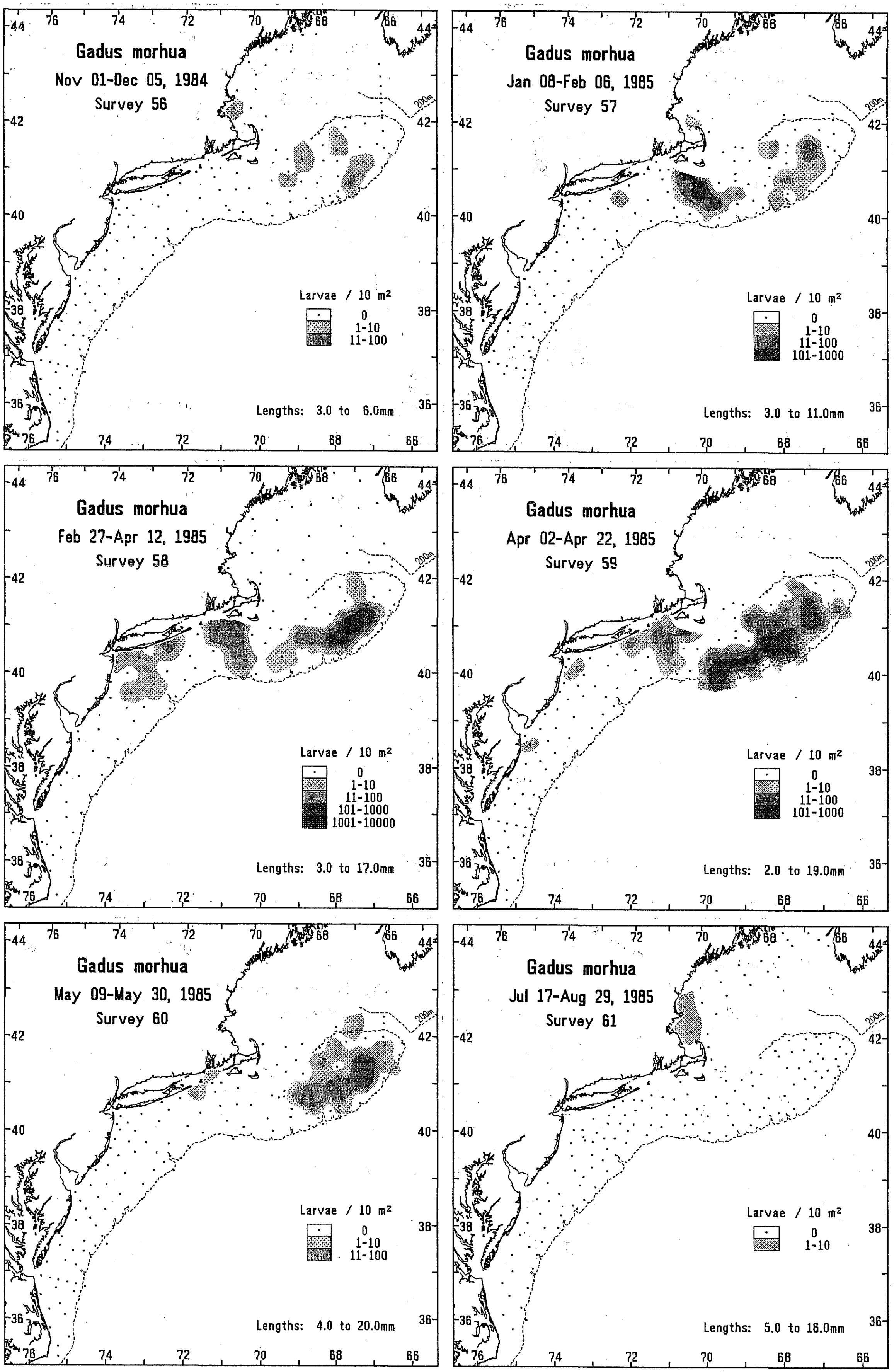


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

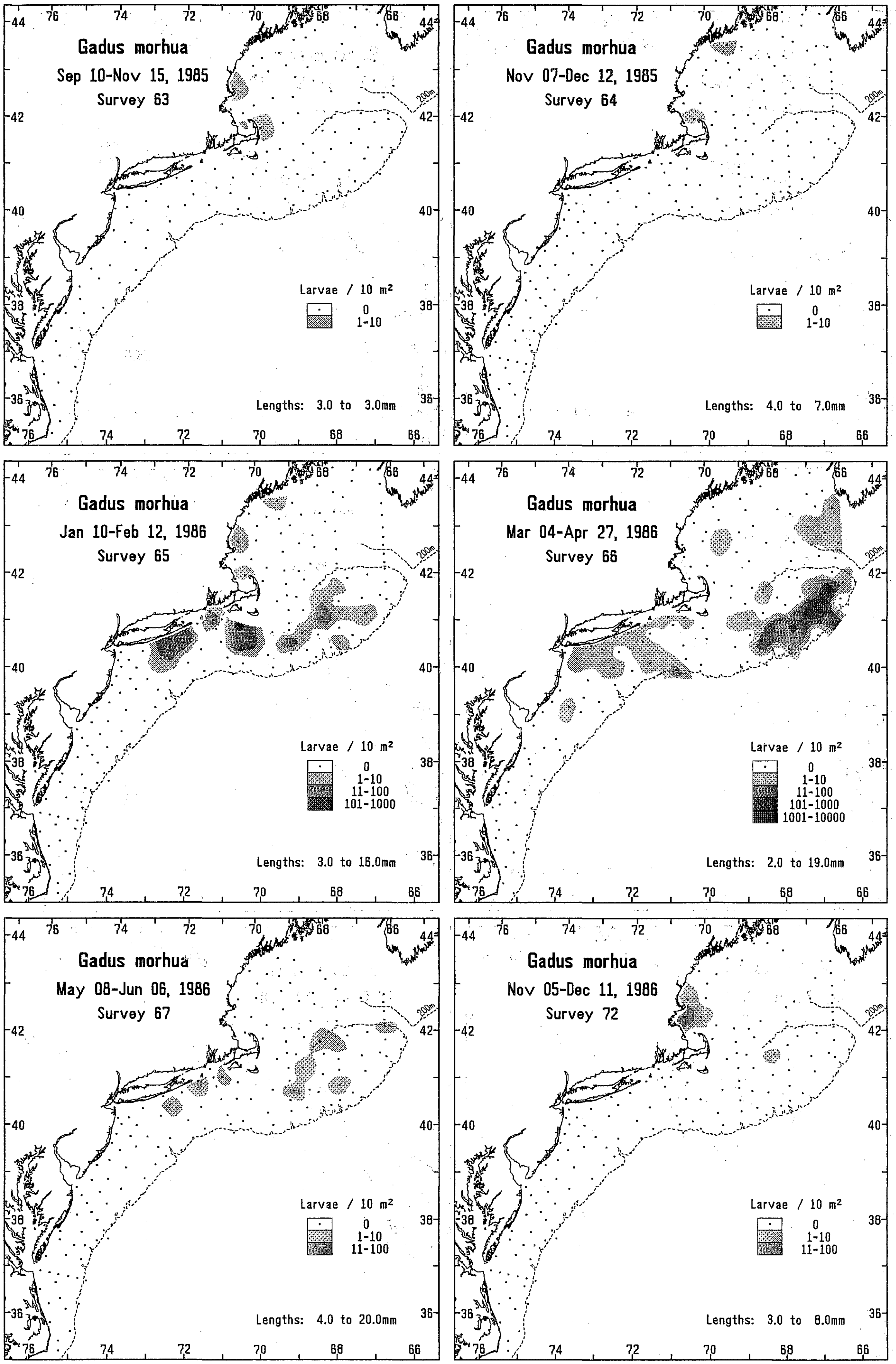


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

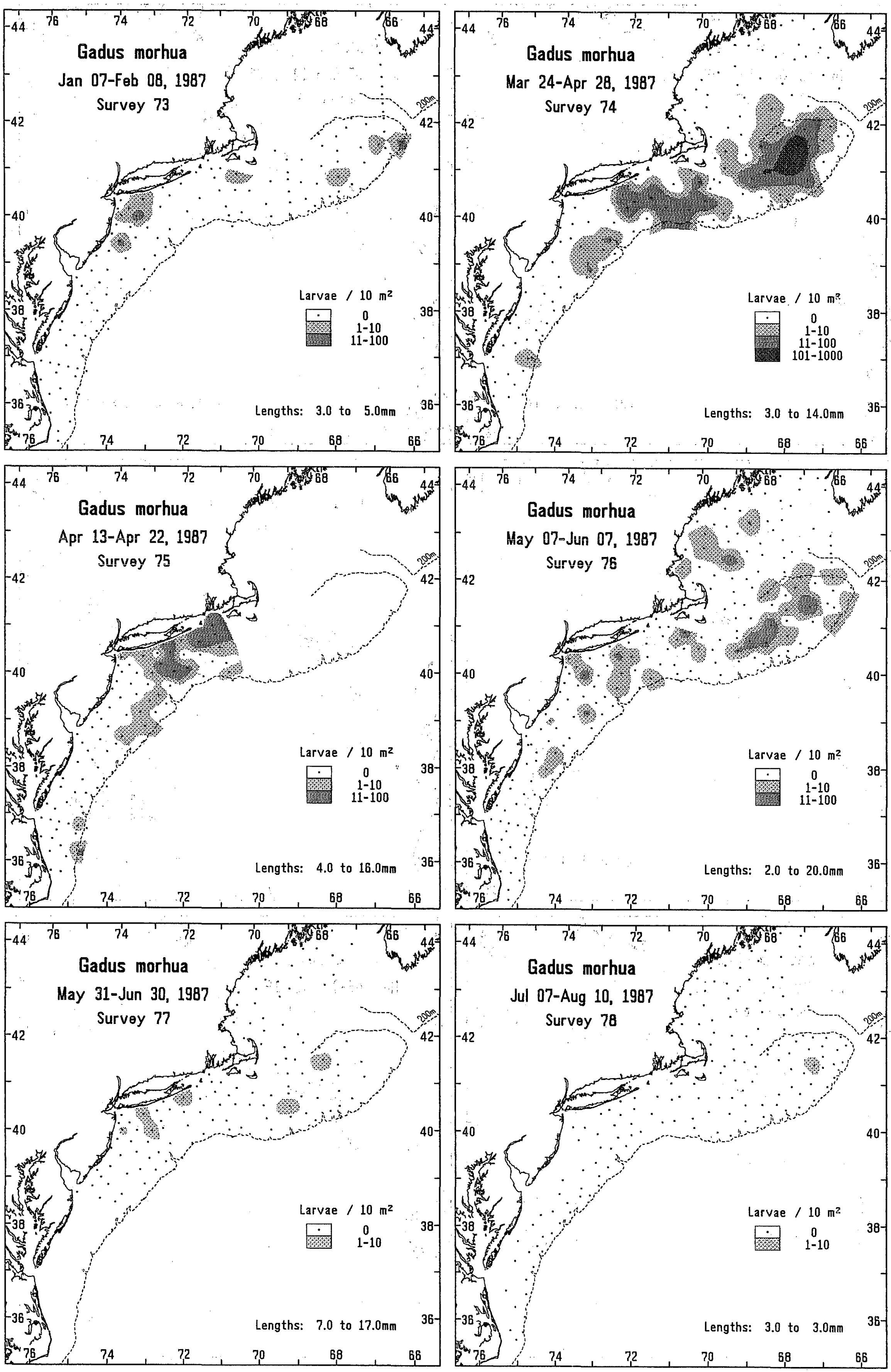


Figure A1. Distribution and abundance of Atlantic cod larvae from MARMAP surveys, 1977-1987

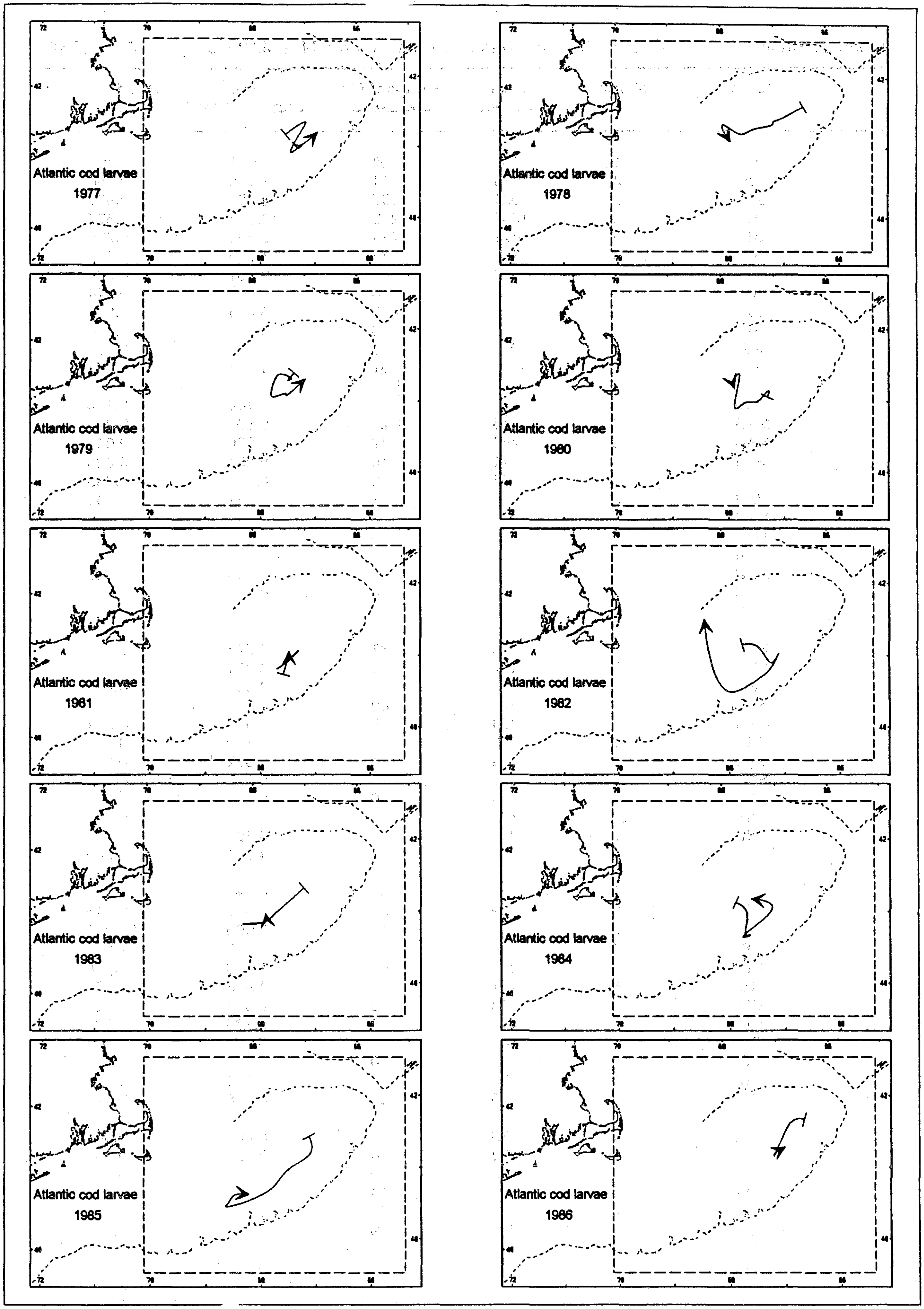


Figure A2. Drift vectors of Atlantic cod larvae (2-10 mm) from MARMAP surveys, 1977-1987.

Appendix Table 1. Catch statistics of Atlantic cod larvae from MARMAP surveys, 1977 - 1987.

Areas	Month	Total Stations	Stations With Cod Larvae	Mean Number/10 m²	Standard Error of Mean
All	1	434	62	3.627	0.725
All	2	686	74	1.106	0.186
All	3	1031	137	4.930	0.992
All	4	1281	243	12.405	1.877
All	5	1472	224	2.852	0.298
All	6	782	65	1.219	0.221
All	7	443	7	0.387	0.202
All	8	621	5	0.095	0.044
All	9	206	2	0.054	0.038
All	10	559	3	0.024	0.014
All	11	915	25	0.338	0.094
All	12	603	61	1.601	0.273
MAB	1	98	1	0.144	0.144
MAB	2	218	27	0.898	0.211
MAB	3	457	27	0.230	0.050
MAB	4	311	16	0.301	0.083
MAB	5	456	6	0.067	0.033
MAB	6	150	1	0.041	0.041
MAB	7	112	0	0	0
MAB	8	191	0	0	0
MAB	9	86	0	0	0
MAB	10	100	1	0.043	0.043
MAB	11	294	0	0	0
MAB	12	28	0	0	0
SNE	1	142	31	7.648	2.199
SNE	2	117	21	2.351	0.708
SNE	3	367	67	2.527	0.453
SNE	4	379	80	4.661	0.844
SNE	5	389	78	1.653	0.214
SNE	6	206	21	0.888	0.265
SNE	7	164	1	0.092	0.092
SNE	8	181	0	0	0
SNE	9	18	0	0	0
SNE	10	197	0	0	0
SNE	11	229	6	0.326	0.181
SNE	12	167	34	4.264	0.960
GB	1	106	29	4.842	1.231
GB	2	149	22	1.836	0.646
GB	3	144	43	53.905	21.067
GB	4	310	133	57.743	12.361
GB	5	282	103	12.616	2.028
GB	6	131	24	2.856	0.773
GB	7	62	2	0.304	0.214
GB	8	141	2	0.138	0.102
GB	9	39	0	0	0
GB	10	127	0	0	0
GB	11	203	10	0.434	0.170
GB	12	145	15	0.915	0.276
GOM	1	88	1	0.069	0.069
GOM	2	202	4	0.135	0.069
GOM	3	63	0	0	0
GOM	4	281	14	0.541	0.167
GOM	5	345	37	1.244	0.243
GOM	6	295	19	1.311	0.418
GOM	7	105	4	1.472	1.055
GOM	8	108	3	0.363	0.210
GOM	9	63	2	0.176	0.123
GOM	10	135	2	0.066	0.047
GOM	11	189	9	0.785	0.355
GOM	12	263	12	0.531	0.181

Appendix Table 2. Catch statistics of Atlantic cod larvae by area and survey from MARMAP surveys, 1977-1987; MAB = Middle Atlantic, SNE = Southern New England, GB = Georges Bank, and GOM = Gulf of Maine

Area	**Survey**	**Total Stations**	**Stations With Cod Larvae**	**Mean Number Per 10 m²**	**Standard Error of Mean**
MAB	1	51	8	0.802	0.332
MAB	2	59	4	0.303	0.154
MAB	3	57	0	0	0
MAB	4	59	0	0	0
MAB	5	52	0	0	0
MAB	6	46	0	0	0
MAB	8	51	5	1.185	0.679
MAB	9	51	0	0	0
MAB	10	50	0	0	0
MAB	12	19	0	0	0
MAB	14	48	13	1.470	0.459
MAB	15	1	0	0	0
MAB	16	49	1	0.031	0.031
MAB	18	49	0	0	0
MAB	21	50	1	0.070	0.070
MAB	22	50	1	0.084	0.084
MAB	23	50	0	0	0
MAB	24	48	0	0	0
MAB	25	49	1	0.089	0.089
MAB	26	46	0	0	0
MAB	27	27	6	0.882	0.354
MAB	28	50	5	0.275	0.126
MAB	29	43	3	0.227	0.135
MAB	30	27	0	0	0
MAB	31	16	0	0	0
MAB	32	42	0	0	0
MAB	35	38	1	0.064	0.064
MAB	36	44	2	0.160	0.114
MAB	37	29	0	0	0
MAB	39	38	0	0	0
MAB	40	28	0	0	0
MAB	41	38	2	0.194	0.136
MAB	42	39	1	0.071	0.071
MAB	43	49	0	0	0
MAB	47	50	0	0	0
MAB	48	41	7	1.445	0.615
MAB	49	40	1	0.061	0.061
MAB	50	49	1	0.106	0.106
MAB	56	49	0	0	0
MAB	57	40	0	0	0
MAB	58	34	0	0	0
MAB	59	49	1	0.094	0.094
MAB	60	49	0	0	0
MAB	61	32	0	0	0
MAB	63	37	0	0	0
MAB	64	49	0	0	0
MAB	65	49	0	0	0
MAB	66	43	1	0.084	0.084
MAB	67	48	0	0	0
MAB	72	49	0	0	0
MAB	73	49	1	0.287	0.287
MAB	74	46	3	0.673	0.434
MAB	75	53	5	0.675	0.307
MAB	76	57	4	0.419	0.244
MAB	77	18	1	0.339	0.339
MAB	78	30	0	0	0
MAB	79	49	0	0	0
MAB	81	48	0	0	0

Appendix Table 2. Continued.

Area	Survey	Total Stations	Stations With Cod Larvae	Mean Number Per 10 m^2	Standard Error of Mean
SNE	1	49	7	0.962	0.453
SNE	2	72	10	1.505	0.567
SNE	3	48	10	1.650	0.565
SNE	4	61	21	1.788	0.390
SNE	5	48	0	0	0
SNE	6	38	0	0	0
SNE	7	26	6	5.900	2.860
SNE	8	47	3	0.712	0.455
SNE	9	46	7	0.807	0.308
SNE	10	48	0	0	0
SNE	12	48	0	0	0
SNE	13	18	2	0.917	0.807
SNE	14	40	9	1.699	0.593
SNE	15	29	2	0.910	0.665
SNE	16	44	12	1.592	0.460
SNE	18	39	0	0	0
SNE	20	29	6	2.492	1.132
SNE	21	45	8	6.473	4.173
SNE	22	44	3	0.970	0.576
SNE	23	43	4	0.807	0.435
SNE	24	44	0	0	0
SNE	25	43	0	0	0
SNE	26	45	11	7.623	3.251
SNE	27	43	8	4.969	2.819
SNE	28	24	3	0.548	0.324
SNE	29	46	10	1.751	0.662
SNE	30	43	3	2.555	2.211
SNE	31	34	1	0.442	0.442
SNE	32	32	0	0	0
SNE	34	19	4	4.062	2.248
SNE	35	43	4	1.019	0.589
SNE	36	39	1	0.070	0.070
SNE	37	36	3	0.420	0.240
SNE	39	36	0	0	0
SNE	40	43	2	1.211	0.999
SNE	41	35	13	6.008	2.127
SNE	42	33	7	6.714	4.478
SNE	47	42	8	1.899	0.745
SNE	48	43	12	5.532	1.858
SNE	49	41	7	2.310	1.120
SNE	50	43	9	3.042	1.238
SNE	56	42	1	0.339	0.339
SNE	57	44	7	11.452	7.935
SNE	58	30	11	6.014	2.017
SNE	59	43	14	18.139	9.111
SNE	60	44	3	0.795	0.505
SNE	61	51	0	0	0
SNE	63	35	0	0	0
SNE	64	43	0	0	0
SNE	65	43	10	9.618	3.900
SNE	66	34	12	2.245	0.588
SNE	67	42	5	1.408	0.743
SNE	72	43	0	0	0
SNE	73	43	5	1.042	0.523
SNE	74	38	15	9.875	2.916
SNE	75	37	17	9.209	2.906
SNE	76	53	12	2.080	0.655
SNE	77	53	8	0.829	0.320
SNE	78	40	0	0	0
SNE	79	43	0	0	0
SNE	81	43	0	0	0

Appendix Table 2. Continued.

Area	Survey	Total Stations	Stations With Cod Larvae	Mean Number Per 10 m²	Standard Error of Mean
GB	1	54	0	0	0
GB	2	35	6	16.134	9.810
GB	3	33	15	140.326	86.716
GB	4	40	12	3.055	0.891
GB	5	26	0	0	0
GB	6	21	0	0	0
GB	7	27	0	0	0
GB	8	42	14	1.995	0.697
GB	9	34	14	22.240	10.388
GB	10	16	0	0	0
GB	12	36	0	0	0
GB	13	19	0	0	0
GB	14	5	0	0	0
GB	15	33	18	23.358	8.921
GB	16	30	17	31.961	11.228
GB	18	20	0	0	0
GB	20	29	4	1.196	0.645
GB	21	29	14	110.526	68.574
GB	22	30	17	53.005	18.858
GB	23	23	3	1.041	0.603
GB	24	23	0	0	0
GB	25	30	0	0	0
GB	26	30	4	1.074	0.568
GB	27	30	17	29.883	11.404
GB	28	22	11	24.339	10.899
GB	29	33	22	72.136	32.143
GB	30	29	10	7.879	3.161
GB	31	28	2	0.674	0.469
GB	32	12	1	1.062	1.062
GB	34	30	2	0.955	0.664
GB	35	30	3	0.500	0.283
GB	36	38	6	2.686	1.391
GB	37	30	1	0.224	0.224
GB	39	31	0	0	0
GB	40	30	1	0.183	0.183
GB	41	29	7	10.177	4.409
GB	42	29	15	137.770	75.268
GB	43	30	6	3.661	1.989
GB	47	30	6	2.103	1.073
GB	48	30	11	3.311	1.038
GB	49	36	8	24.828	16.278
GB	50	32	9	9.900	4.592
GB	56	33	5	1.278	0.697
GB	57	33	6	2.490	1.177
GB	58	26	5	97.926	74.866
GB	60	34	15	12.195	3.947
GB	61	44	0	0	0
GB	63	30	1	0.187	0.187
GB	64	33	0	0	0
GB	65	33	7	1.944	0.869
GB	66	27	12	59.225	34.049
GB	67	33	8	1.518	0.485
GB	72	33	1	0.089	0.089
GB	73	33	3	0.816	0.487
GB	74	27	15	47.691	24.542
GB	76	33	12	5.148	1.640
GB	77	24	1	0.193	0.193
GB	78	40	1	0.170	0.170
GB	79	33	0	0	0
GB	81	33	1	0.175	0.175

Appendix Table 2. Continued.

Area	Survey	Total Stations	Stations With Cod Larvae	Mean Number Per 10 m^2	Standard Error of Mean
GOM	1	29	0	0	0
GOM	2	23	0	0	0
GOM	3	51	4	1.575	0.988
GOM	4	45	5	1.527	0.755
GOM	5	34	1	0.424	0.424
GOM	6	37	1	0.137	0.137
GOM	7	37	1	0.200	0.200
GOM	8	26	0	0	0
GOM	9	41	3	0.737	0.428
GOM	10	34	2	4.560	3.801
GOM	12	52	1	0.701	0.701
GOM	13	37	1	1.295	1.295
GOM	14	9	0	0	0
GOM	15	43	7	2.762	1.148
GOM	16	47	6	1.262	0.536
GOM	18	38	2	0.516	0.392
GOM	20	45	2	0.882	0.740
GOM	21	47	0	0	0
GOM	22	51	10	2.044	0.825
GOM	23	32	3	7.113	5.728
GOM	24	38	1	0.287	0.287
GOM	25	52	1	0.074	0.074
GOM	26	16	0	0	0
GOM	27	52	0	0	0
GOM	28	3	0	0	0
GOM	29	22	3	1.149	0.673
GOM	30	46	6	1.694	0.772
GOM	32	10	0	0	0
GOM	34	39	3	0.742	0.421
GOM	35	34	1	0.259	0.259
GOM	36	45	3	0.588	0.342
GOM	37	37	5	1.146	0.507
GOM	39	46	2	0.288	0.204
GOM	40	51	2	0.462	0.359
GOM	41	51	0	0	0
GOM	42	38	0	0	0
GOM	43	54	2	1.148	1.044
GOM	47	29	1	0.213	0.213
GOM	48	46	0	0	0
GOM	49	39	1	0.186	0.186
GOM	50	54	1	0.608	0.608
GOM	56	20	1	0.274	0.274
GOM	57	8	1	0.755	0.755
GOM	58	30	0	0	0
GOM	59	5	0	0	0
GOM	60	7	0	0	0
GOM	61	23	2	0.624	0.431
GOM	63	38	2	0.239	0.169
GOM	64	54	2	0.319	0.224
GOM	65	48	3	0.386	0.222
GOM	66	41	5	0.797	0.343
GOM	67	38	0	0	0
GOM	72	34	3	1.950	1.489
GOM	73	8	0	0	0
GOM	74	40	1	0.124	0.124
GOM	76	50	5	0.951	0.432
GOM	77	34	0	0	0
GOM	78	45	0	0	0
GOM	79	54	1	0.1	0.1