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Chaetognaths and Oceanography on Georges Bank

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SPECIAL SESSION ON RECRUITMENT

A. INTRODUCTION

1. Background for Study

In autumn, 1978, an international project designed to learn more about larval herring patches on Georges Bank, including the role played by the physical environment, was carried out (Wright and Lough, 1979; Lough, 1979). Biologists and oceanographers from five countries (Canada, Federal Republic of Germany, Poland, United States, and the Soviet Union) and eight vessels (Albatross IV, Anton Dohrn, Atlantis II, Belogorsk, Canso Condor, Dawson, Lady Hammond, and Wieczno) participated in the coordinated study which took place principally from early October through mid-November (Wright and Lough, 1979). The experiment was the culmination of more than two years of planning following a 1975 proposal by the Environmental Subcommittee of the International Commission for the Northwest Atlantic Fisheries (ICNAF).

Initially, field measurements and sampling were focussed on the northeast part of Georges Bank where, from earlier studies (see Lough et al., 1985) herring spawning was known to occur (Figure 1). Although repeated bongo tows taken during the period 17-30 October, 1978, at a grid of more than 49 stations spaced at 5 minutes of latitude and 10 minutes of longitude, failed to capture significant numbers of herring larvae, an extensive concentration of chaetognaths (Sagitta elegans) was found and mapped. Shipboard estimates of unsorted chaetognath volumes suggested that a high concentration "patch" remained in about the same geographical position for a fortnight, despite a residual current in the upper layers ranging from about 6 to 11 km/day in an easterly direction. Based on the preliminary data available at the time of the survey, it was speculated that the diel vertical movements of chaetognaths, in combination with the tidal current regime may be of paramount importance in keeping them in a relatively small geographic area.

Subsequent sorting of chaetognaths from the bongo samples by stage of development, and analyses of MOCNESS data on their diel vertical movements, as well as processing of current meter data from moorings sited within the area, have enabled us to further explore the importance of currents combined with vertical movements in maintaining adult chaetognaths within a given area of Georges Bank. The specific objective of this paper is to determine what effect the tidal and non-tidal currents have on the spatial variability on the vertically migrating versus non-migrating parts of the Sagitta elegans population on northeastern Georges Bank. Only selective parts of the oceanographic and biological data are included in this paper to support the objective. A more comprehensive paper on the biology of S. elegans is to be written in the future.

2. General distribution and life history of Sagitta elegans

Sagitta elegans is a coldwater, epiplanktonic species found only in the northern hemisphere (Grant, 1963). Along the east coast of North America S. elegans ranges from the Grand Banks to as far south as Chesapeake Bay (Bigelow and Sears, 1939; Tiselius and Peterson, 1986). In the Gulf of Maine (Redfield and Beale, 1940) and on Georges Bank (Clarke et al., 1943) dense populations occur within the 100-m isobath. Georges Bank is considered the most southern extent of the endemic populations (Alvariño, 1965) where bottom temperatures do not exceed 13°-14°C, the upper limit for breeding (Russel, 1932; McLaren, 1969; Tiselius and Peterson, 1986). The dense populations of S. elegans that accumulate on Georges Bank were believed by Redfield and Beale (1940) and Clarke et al. (1943) to be a consequence of the relatively stable clockwise circulation and the favorable well-mixed waters atop the bank (inset, Figure 1).

The Georges Bank S. elegans population was reported by Clarke et al. (1943) to have a major breeding period in the spring (April-May) and another period in the late summer-autumn (September-October), over-wintering as immature stages. The results of the present study clearly indicate an autumn breeding period (Lough and Michaels, 1981). Chaetognaths are protandric hermaphrodites; the testes and ovaries mature at different rates (Alvarino, 1965; Reeve and Cosper, 1975). The eggs are shed individually and are immediately suspended in the sea water (Kotori, 1975). The larva hatches within a week depending on temperature at a length of about 1.3 mm (Huntsman and Reid, 1921; Kotori, 1975). Growth and maturity of S. elegans is temperature dependent which greatly determines its size and life span. Clarke et al. (1943) found S. elegans to mature at a modal length of 16 mm in September, but at 23 mm in March. Their life span was estimated to range 1-3 months. Sameoto (1971) predicts that larger chaetognaths are produced at the lower range of temperatures and estimates that at least 738 degree days are required for maturity. Given the mean temperature range on Georges Bank during the autumn breeding period to be 9°-13°C, S. elegans would be expected to mature in 2-3 months.

Besides chaetognaths being an important invertebrate predator of plankton communities (Davis, 1984b), their extensive vertical migration has often been studied. The vertical distribution and migration of S. elegans varies with stage of maturity and/or size and with season (Russel, 1933; Clarke et al., 1943; Pearre, 1973; King, 1979; Lough and Cohen, 1982; and others). Larvae and immature stages generally are dispersed throughout the water column and show little evidence of diel migration. However, the larger, mature adults exhibit the typical migration pattern of ascending towards the near surface waters around sunset, and after midnight scattering downward through the water column. By sunrise or before noon the population has reached its maximum depth. The adults have been observed or sampled in high concentrations within 1-2 m of the bottom (Jakobsen, 1971; Sameoto, 1975; Hesthagen and Gjermundsen, 1979). Light is believed to play a primary role in the control of diel migrations, but other factors such as hunger satiation influences their depth control (Pearre, 1973).

3. General Oceanographic Features

(i) Tidal Currents

As a result of the near-resonance of the lunar semidiurnal tide (M_2 period 12.4 hours) in the Bay of Fundy-Gulf of Maine system, the tidal currents are particularly strong (Moody et al., 1984). During each tidal period, this component of current swings in a clockwise sense through an ellipse whose major axis lies in a northwest-southeast direction (Figure 2). The length of the major axis over the northeast part of the Bank is typically 12-15 km. The maximum M_2 tidal current increases with decreasing water depth, varying from about 20 cms^{-1} to the north of the bank to over 100 cms^{-1} over the shallower parts of the Bank.

(ii) Circulation

The means of fixed-point current measurements indicate that the seasonal and annual-mean circulations are primarily along-isobath and in a clockwise direction around Georges Bank and diminish with depth (Butman et al., 1982). Highest speeds occur near the edge of the Bank, particularly on the northern slope, where a narrow jet-like flow occurs. In winter when the intensity and vertical structure are minimal, the clockwise currents are about 5 km d^{-1} except along the northern side where speeds of 15-20 km d^{-1} occur. This current pattern is primarily associated with tidal rectification (Loder, 1980; Greenberg, 1983). During spring and summer, associated with the development of stratification and tidal fronts around the Bank, the clockwise circulation approximately doubles in intensity and extends around the entire Bank (Butman et al., 1986; Loder and Wright, 1985). The mean speeds, which reach maximum intensity in the late summer/early autumn, are about 10-15 km d^{-1} in the upper portion of the water column, except on the northern edge where maximum values in the range 30-50 km d^{-1} occur.

Although the mean currents are primarily along-isobaths, the degree to which individual water parcels recirculate around the Bank also depends on the horizontal dispersion rates associated with higher-frequency processes as well as with the influence of wind events and Gulf Stream rings. Available Lagrangian data indicate that recirculation of the same water parcel can occur, particularly in summer, but not on a routine basis (Butman et al., 1982; Flagg et al., 1982). When recirculation occurs, a complete circuit of the Bank should take about 40 days in summer and about 90 days in winter.

(iii) Mixing and Dispersion

The strong tidal currents generate vertical mixing, sufficiently intense to maintain a well-mixed water column year-round within the 50 m isobath. Within this area an initial concentration of any passive scalar introduced at any point in the water column can be expected to be mixed over the entire water column within a day.

In winter, owing to the combination of tidally-generated turbulence, convective cooling, and more intense winds, the vertically well-mixed region extends in area to about the 100 m isobath.

Residence times for water and water mass properties depend on the region of the Bank under consideration, the location of any initial distribution, and the season. Existing estimates (Loder et al., 1982) indicate that for an initial distribution of a passive scalar at the centre of the Bank, only one-third of the initial amount will remain over the shoals after a period of 32 days. Existing estimates (Loder and Platt, 1985) for exchange across the summertime tidal fronts (i.e., exchange between the mixed and stratified waters) suggest that all of the water in the vertically well-mixed region is replaced on a time scale of 50-100 days. In winter the time scale may be shorter by a factor of about two. This suggests that in winter the time scale for off-bank exchange is less than that for recirculation so that water parcels generally do not make complete circuits.

B. METHODS

1. Field Program

(i) Oceanography

To provide physical oceanographic measurements relevant to the multi-ship larval herring patch experiment, moorings were established at six sites in the area, and fitted with several current meters at each site (Figure 1). At sites 1, 2, and 3, Aanderaa current meters, measuring current speed and direction, temperature, and salinity, were deployed, while at sites 4, 5, and 6, VACM meters were installed to measure current speed and direction, and temperature. A Guildline STD was used to acquire more than 500 salinity and temperature profiles both inside and beyond the area of intensive biological sampling. A time series of temperature, salinity, and current profiles were measured over a 24-hour period at a site near the tidal front along the northern edge of the Bank. Additional observations on currents were obtained by tracking drogued high flyers for periods generally of 1-2 days. Both dye and a drogue cluster release were made in order to estimate lateral diffusion rates.

(ii) Biology

A survey grid of 49 standard plankton stations was established across the frontal region on the northern edge of Georges Bank from 41°45' to 42° 15'N latitude and from 66°35' to 67°35'W longitude (Figure 1). Station spacing was 4-7 n miles (7.4-13.0 km), designed to be within the scale of the tidal ellipses. These stations were to be sampled every three to four days with the option of extending the grid coverage as time permitted over a broader area of northeastern Georges Bank (Table 1). On each station a double-oblique bongo-net tow was made at 3.5 knots (6.5 km/h) to sample the zooplankton. The bongo array (Posgay and Marak, 1980) consisted of a 61-cm frame fitted with 0.333- and 0.505-mm mesh nets, as well as a smaller bongo (20-cm diameter) with finer mesh nets (0.165- and 0.253-mm). The gear was deployed at 50 m/min to within 5 m of the bottom, or to a maximum tow depth of 100 m, and continuous retrieval at 10 m/min. In addition to sampling zooplankton on the surveys, vertical profiles of chlorophyll and particle size distributions were obtained on each station (see O'Boyle et al., 1979).

Over the course of the study more fine-scale vertical distribution sampling was conducted on various sites within the survey grid by the participating vessels. Discrete depth samples of zooplankton were collected using the MOCNESS (Wiebe et al., 1976; 1985), BIONESS (Sameoto and Lewis, 1980a, b), and plankton pump (Dagg and Turner, 1982). The vertical distribution of chaetognaths reported in this paper were collected by the 1-m MOCNESS, an electronically-controlled multiple opening/closing net and environmental sampling system. MOCNESS has an effective mouth opening of 1 m^2 when towed at a 45° angle near 2 knots (3.7 km/h). The nine nets (0.202-mm mesh) open and close sequentially on command. Temperature data is obtained with other sampling parameters. Once a site was selected, the sampling strategy was to make a tow every 3 h over a 1-2 day period. Discrete depths were sampled at 10m intervals to within 5 m of the bottom, each net filtering about 250 m^3 of water while integrating the 10-m stratum over a 5 min period. Ancilliary observations included photometer and secchi disc readings for daylight vertical profiles.

All zooplankton samples were preserved in 4% formaldehyde seawater solution.

2. Laboratory processing of samples

Zooplankton from the 61-cm bongo 0.333-mm mesh samples was sorted, identified, and enumerated by the Plankton Sorting Center, Szczecin, Poland, using standard protocols (Sherman et al., 1976a, b). The chaetognath S. elegans was classified to life stage as larva, immature, and adult based on ovary development. The Polish sorted and archived subsamples were sent to the Norhteast Fisheries Center, Woods Hole, Massachusetts, where body length measurements (excluding tail fin) are presently being made to the nearest 0.5 mm. Processing of these subsamples is incomplete at this time. A new maturity staging system is being used to classify the survey specimens comparable to the MOCNESS specimens processed in Woods Hole. The new staging system is a modification of King's (1979) five categories for S. elegans in Puget Sound, Washington, and is based on the development of both ovaries and testes (Table 2). Four stages are used for the Georges Bank study. Stage I is considered recently hatched with no gonadal development. In Stage II the immature ovaries and testes are slightly visible and it is this stage that overwinters on Georges Bank. The testes mature (Stage III) somewhat before the ovaries (Stage IV) which in some cases can lead to a subjective classification, but usually the criteria described in Table 2 was readily observed and resulted in repeatable classifications among the sorters.

3. Data processing and analyses

S. elegans enumerated from each net sample were grouped by maturity stage and initially standardized to number of individuals per m^3. For the survey bongo tows, the station abundance, number per m^2 sea surface, was estimated by multiplying the average density (no./m^3) times the maximum depth of tow. All station abundances are plotted but only the standard 49 station grid surveys were used for further statistical analyses. The standard grid was divided into three hydrographic regimes: Area A, the eastern weakly stratified water of 67 m average depth; Area B, the western well-mixed water of 48 m average depth; and Area C, the northern Gulf of Maine well-stratified water of 158 m average depth (Figure 1). Each station tow within the grid surveys also was classified as night, day, or twilight based on time of sunset and sunrise. Variability of the abundance estimates for each maturity stage by time and area was determined for the surveys by an unbalanced ANOVA program (STATGRAPHICS, PLUS*WARE Products, ST SC, INC.) on $\log_e$ (X+0.1) transformed data. Test of area or time differences between geometric means of maturity stages was determined by a two-sample T-statistic.

The MOCNESS vertical distribution tows were plotted as a time series showing the density of S. elegans at each depth level sampled. The weighted-mean depth of each tow profile also was calculated for the four maturity stages and plotted to show the median depth of the population in relation to the light and tidal cycle. Variability in the vertical distribution time series was explored using the same unbalanced ANOVA program above on $\log_e$ (X+0.1) transformed data. Samples were classified to depth level and time of day or night.

C. RESULTS

1. Horizontal distribution of Sagitta elegans

The grid of stations on northeastern Georges Bank was surveyed four times during the period 17-30 October 1978 (Table 1). Some station observations are missing because of sample breakage. The contoured station abundances (no./m^2) of the adults and larvae are drawn in Figures 3 and 4, respectively. The immature stage chaetognaths are not shown as their distribution is essentially the same as the larvae. A high concentration of adults was clearly delineated in all four surveys located on the eastern part of the study area in the weakly-stratified water shoaler than the 100-m isobath. Few S. elegans of any stage were found north of the Bank in the well-stratified Gulf of Maine water. The high concentration "patch" of adults as defined by stations having numbers greater than 5,000/m^2, was generally eliptical in shape with a northwest-southeast major axis of about 30 n miles (56 km), the same orientation as the tidal ellipses. Within the adult patch the highest abundance observed was during the 27-30 October 1978 survey of $54{,}000/m^2$. The eastern boundary of the adult patch was not always defined by the surveys, and during the fourth survey, 27-30 October 1978, it appears that another patch of adults was located due east near the 100-m isobath. The larvae (and immatures), in contrast to the adults, appear to be more evenly spread across the well-mixed and weakly stratified waters and in much lower abundance (less than $2{,}000/m^2$). Besides the normal patchiness of planktonic populations, some of the variability in the contoured distributions may have been induced by the tidal ellipses which have a spatial scale comparable to the station grid spacing. Some of the variability may be due to escapement of the net, i.e., below the maximum sampling depth. The smallest larvae (less than 5 mm) may be extruded through the net mesh as an individual of 4.6 mm length has a maximum body width of 0.33 mm on average.

For purposes of statistical analysis, the standard 49 station grids were partitioned into three hydrographic areas in order to have comparable sampling units over the four surveys. An initial unbalanced ANOVA (Table 3) showed the mean abundance of the three stages of S. elegans to be significantly different ($P < 0.001$ level) as well as the mean abundance among the three areas. There was a less significant ($P < 0.05$) area x stage interaction effect for survey grids I and III. No significant time effect was determined averaged across all three stages. Furthermore, even though on average more adults were caught in night tows than by day ($\bar{x} = 1.13$ night/day ratio), no significant difference was found by a T-test statistic within any area. The $\log_e$ mean abundance for each stage from the eastern area A and the western area B is provided in Table 4 and the significance level noted between the two areas. The mean abundance of adults was consistently higher for the eastern area A than the western area B. These means are statistically different ($P < 0.05$) for survey grids I, III, and IV and marginally significantly ($P < 0.11$) for grid II. In contrast for the immature and larval stages, there was no significant difference in mean abundance between the eastern and western areas. Also, note that the mean abundance for any stage-area was comparable through the four grid surveys.

The length-frequency distributions between the eastern (A) and western (B) areas further highlights the population differences (Figure 5). The Gulf of Maine area C had too few indiviuals to make a meaningful comparison. From the first grid survey, 17-19 October 1978, for eastern area A the modal size of S. elegans was 14-15 mm, corresponding to the mean length and range of the adults (10-18 mm, see Table 2). Relatively few chaetognaths less than 10 mm were found in area A. On western area B there was a broad distribution of lengths, 2-17 mm, with a modal length of 9 mm, corresponding to the mean size and range of the immature population. The larvae, 1-6 mm, comprise a relatively greater part of the total population in area B than in area A. An estimate of their age from hatching through the mean lengths of the four maturity stages is shown in Figure 6. The length at age estimates are based on Sameoto's (1971) requirement of 738 degree-days to reach adult maturity and the average seawater temperature on northeastern Georges Bank (upper 50 m) during September and October 1978. The estimated total time from hatching of the larva to an adult stage IV with mature ova is 84 days. In terms of length the increase from 1- to 15-mm would account for a growth rate of 0.17 mm/day (5 mm/month) on average. The period of time between the immature stage II and the adult stage III is about 28 days, or from their respective mean lengths of 9.1- and 14.1-mm this would again account for a growth rate of 0.18 mm/day (5.5 mm/month). The difference in population modal size between the eastern area A and the western area B was greater (5-6 mm) than the small increase in population mean size (2-3 mm) during the 13 days between the first and fourth grid surveys.

At this point there appears to be sufficient supporting evidence to indicate that the adult chaetognaths are retained in the eastern, weakly-stratified area over the two weeks of the study. The larval and immature chaetognaths were more or less distributed equally across the two areas, resulting from a combination of west to east transport and in situ production in both areas. The question to be addressed now is what aspects of their life history-behavior in conjunction with the local oceanography were responsible for maintaining the observed distributional patterns on northeastern Georges Bank.

2. Vertical distribution of Sagitta elegans

At the end of the fourth grid survey a vertical distribution study site was selected in the eastern area A (41°59'N, 66°39'W) near current meter site 5, the center of the most recently mapped chaetognath patch. Eleven MOCNESS hauls were made at this site every three hours over a 30-hour period, 31 October - 1

November 1978. Bottom depth over the course of the study ranged 71-88 m. Approximately 1°C temperature difference existed between surface (11.6°C) and bottom (10.6°C).

The average abundance of adults (7,118/m^2), immatures (1,202/m^2), and larvae (844/m^2) integrated over depth at this site were within the range of abundance estimates mapped on the fourth grid survey near the boarder of the high concentration patch. The densities of four stages of S. elegans for each haul profile in the time series are detailed in Figure 7. The stage I larvae and the stage II immatures were broadly distributed through the water column centered around a median depth of 30-35 m both day and night. The somewhat deeper depth distribution of the immatures in the morning (0800-1100 hours) suggests that part of the population may already be responding to day light. The mature adults (stages III and IV) clearly were found concentrated in the lower half of the water column by day and in the upper half by night, with the populations ascending and descending through the water column prior to sunset and sunrise, respectively. Note that at 1100 hours (M71) virtually none of the adults were caught in the midday haul. The dotted densities of stage III and IV adults in Figure 7 at 1100 and 1400 hours are averaged estimates of the population expected near the sea bottom, assuming they are below the maximum sampling depth of the haul. These data, as well as previously published studies, strongly suggest this to be the case, rather than avoidance of the net. Also, it is uncertain whether the bimodal depth distribution of the stage III and IV adults at 1400 hours reflects a different response by two parts of the population since there was no replicate haul at this time of day.

The unbalanced ANOVA of the vertical distribution data supports the diel migration pattern as it develops by the adult stage (Table 5). There was no significant difference between time of night or day mean densities for the stage I larvae and stage II immatures, but highly significant differences ($P < 0.001$) for both adult stages. The significant depth x time interaction for the stage II immatures reflects the deeper depths of the early day population where some part is initiating a migration response, which becomes fully developed as stage III adults as indicated by the more significant ($P < 0.01$) depth x time interaction effect. Interpretation of the stage IV adult ANOVA results is misleading; i.e., no significant depth and depth x time interaction effects, because a large percentage of the population probably was not sampled during midday. While there is considerable variability in the vertical profiles, the time series of moving averages show a coherent trend in population diel movement through the water column as adults.

The time series of weighted-mean depths of the four maturity stages are plotted in Figure 8 for ease of viewing in relation to light intensity and tidal current regime. The adults exhibited a pronounced vertical migration related to the light-dark cycle but no indication of cueing on the 12.4-hour tidal cycle. The larger stage IV adults appear to have a greater range of depth migration than the stage III adults, being closer to the bottom by late morning and nearer the surface a few hours after sunset. On the clear, sunny day of the study (31 October 1978) it would appear that more of the population moved to deeper depths than on the cloudy day (1 November 1978) when light penetration is shoaler. Also one can speculate that the stimulus for migration may be related to the change in light intensity rather than the absolute light level, although there are other factors needed to explain the night-time descent. 'The adults appear to begin their migration to depth at least by midnight which may increase prior to sunrise, and around midday they begin their ascent towards the surface, again perhaps increasing at sunset. Based on the mean population depths, the adults transverse a 50 m water column in around six hours. In contrast, the larval and immature stages remained at mid-depth. The stage II immatures showed some light-induced response like the adults only their range may be limited to 10-20 m. The mean depth of the stage I larvae fluctuated by 5-10 m from haul-to-haul, but remained within the 25-40 m depth zone throughout the 30 hour sampling period.

3. Oceanographic conditions during grid survey

A plot of bottom temperatures just prior to the commencment of the four occupations of the grid, identifies the location of the thermal front near the northern edge of the Bank separating the highly stratified water in the Gulf of Maine from the vertically well-mixed or weakly stratified water on the Bank (Figure 9). The transition zone (band of water in the 8-11°C range) identifies the approximate location of the eastward flowing jet. The area of vertically well-mixed water lies to the southwest of the 13.5°C isotherm.

Currents, temperature, and salinity were measured over a 25-hour period (13-14 Oct 1978) at a site located near the northern edge of the Bank (Figure 1). Owing to the rotary tidal currents, the water column at this location alternates between mixed and stratified as the front is advected northward and southward (Figure 10).

During the 17-30 Oct 1978 period, moored current meters were operating at six sites in the area. Four of these were located on the bank in depths less than 100 m (Figure 1). Although the strongest component of mean flow was eastward at all stations, appreciable horizontal and vertical variation in speeds were evident (Figure 11). At sites 2 (15 m depth) and 5 (19 m depth) mean currents over the 13-day period were 11.3 km d^{-1} at 103° T and 10.5 km d^{-1} at 104° T respectively, while at sites 3 (15 m) and 6 (11 m) currents were 5.7 km d^{-1} at 087° T and 6.2 km d^{-1} at 072° T respectively. The vertical variation in mean speed was particularly marked at site 6 with speed diminishing to 3.1 and 1.5 km d^{-1} at depths of 26 and 36 m respectively.

Although the mean flow displayed appreciable vertical shear, and was distributed relatively uniformly over the water column, tidal current shear is mainly confined to a layer near bottom (Moody et al., 1984). The bulk of the shear occurs within 10 m of the bottom and even at 1 m off bottom values are still nearly 50% of those at 30 m off bottom.

D. POSSIBLE RETENTION MECHANISM

The net movement over a 13-day period of a passively drifting organism will depend both on its geographic location on the Bank and its vertical position in the water column. For example, an organism drifting at 15 m depth at site 2 would, if the velocity field were horizontally uniform, have moved completely out of the sampling area during the 13 day period. Even at site 6, a velocity of 6.2 km d^{-1} would have carried animals out of the region relatively quickly. Adult chaetognaths, however, complete a vertical migration cycle over a 24-hour period. From the MOCNESS data, acoustic records (Sameoto and Lewis, 1980), and recent submersible observations (Lough, R.G., personal observation, see Footnote 1) there is good evidence that during daylight hours, the bulk of the adults are concentrated very near to the bottom on Georges Bank. In this zone both the tidal and non-tidal motions are markedly reduced.

Based on the MOCNESS data, it was assumed that the adult chaetognaths remained on or very near bottom from 0840 to 1540 hrs (EST) daily and for the remaining 17 hours that they were well up into the water column. Using the current meter records for site 2, 3, 5, and 6, and assuming that chaetognaths were passive drifters, progressive vector plots of their expected movement were constructed for the 17-30 October 1978 period by assuming that for the period 0840-1540 (EST) the drift rate was zero, and during the period 1540-0850 (EST) that their drift rate was equal to that indicated by a particular current meter.

A progressive vector plot using the hourly current meter record for 15 m depth at site 3 is shown in Figure 12, covering the period 12 Oct - 3 Nov 1978. The mean velocity over the 13 day period, 17-30 Oct 1978, using the unmodified (Figure 12) and modified (Figure 13) record is 5.7 km d^{-1} at 087°T and 4.1 km d^{-1} at 079°T respectively. Thus the principal effect of the diel movement over this 13 day period was simply a reduction in speed by about 30% with little change in direction. However, over shorter periods the results are strikingly different. For example, for the 13-18 Oct 1978 period, a net movement of about 50 km to the northwest is indicated, while the period 14-24 Oct 1978 shows almost no net movement (Figure 13).

Footnote 1

During the JOHNSON-SEA-LINK I (with support ship R.V. EDWIN LINK) submersible dive no. 1854, 0804-1103 E.D.T., 13 August 1986, on northeastern Georges Bank (41° 50.79'N, 66° 26.02'W, bottom depth 79m, temperature 10.6°C), adult <u>Sagitta elegans</u> were observed at high density (>500/m^3) within 3m of the bottom adrift with the strong tidal current throughout the morning. At the beginning of the dive, the tidal current was 46 cm s^{-1} from 330°T measured at 2.4m off bottom, and by the end of the dive the current had tapered to 15 cm s^{-1} from 060°T. When the submersible drifted with the current, swarms of chaetognaths gathered at the strong underwater lights. Upon turning into the current and maintaining position with the motors, all the chaetognaths were swept away. A subsample of the chaetognaths collected near the lights with a suction device confirmed them to be <u>Sagitta elegans</u>, mostly stage IV adults ($\bar{x}$ length = 16.8mm, 1 S.D. = 1.4mm, range = 14.4 - 19.5mm, n = 26). A small percentage of stage III adults also were present ($\bar{x}$ length = 17.1mm, range = 16.0 - 18.5mm, n = 4).

Progressive vector plots of daily resultant movement at site 6 is shown in Figure 14 for 11 and 36 m depths for the period 16 September - 13 November, 1978. The mean current over the 17-30 October period is 6.2 km d^{-1} at 072° T at 11 m and 1.5 km d^{-1} at 082° T at 36 m. Simulation of Sagitta elegans expected displacement for the period 17-30 October, under the assumption that no drift occurred during the time period 0840-1540 EST, was 4.6 km d^{-1} (Figure 15) and 1.4 km d^{-1} (Figure 16) for animals whose night-time depth was 11 and 36 m respectively.

The MOCNESS data shows that the mean weighted depth for stage IV adults is about 42 m. Even during the period from 1540 to 0840 hours the weighted mean depth is approximately 35 m. Thus, the net movement over the 13 day period during which the four surveys took place, would have likely not exceeded about 20 km for the bulk of adults in the vicinity of current meter mooring site 6.

E. DISCUSSION

The chaetognath, Sagitta elegans, observed at high abundance on northeastern Georges Bank in October, 1978 was found to have a life history and diel vertical migration pattern similar to previously reported studies on Georges Bank and other regions of the boreal northern hemisphere (see Introduction for references). The relatively permanent clockwise circulation on Georges Bank is largely responsible for the retention and maintenance of a number of endemic plankton populations that investigators have been able to account for their spatial pattern of demographics at the meso-scale (100 - 1,000 km) (Clarke et al., 1943; Davis, 1984a). In fact, Clarke et al., (1943) noted in May, 1940 on Georges Bank that only large S. elegans were collected on the eastern stations whereas smaller sizes dominated the western stations. They inferred (p. 216) that "the remnants of the older animals persisted chiefly in central and eastern eddies, while the production of younger individuals was beginning most actively in the western part of the Bank". On a coarse scale of 50 - 100 km, Davis (1984a) was able to simulate the population structure of the copepod Pseudocalanus sp. in February, 1975 on Georges Bank from the interaction of its population dynamics and the mean circulation around the Bank. On a somewhat finer scale of less than 50 km, modelling studies have shown that biological interactions such as herbivore feeding -predation coupled with vertical migration and shear dispersion can generate smaller scale patterns under certain conditions (Riley, 1976; Wroblewski, 1982; Davis, 1984a). It is at this smaller scale (less than 50 km) that the chaetognath patch was observed to reside on the northeast part of Georges Bank for at least two weeks.

Over a period of a week, the combination of vertical movements of chaetognaths tied to the solar diurnal cycle together with vertical shear in the tidal currents can produce a resultant displacement of many tens of kilometers. Because the principal tidal constituent on Georges Bank is the lunar semi-diurnal (M_2) with a period of 12.42 hours, the phase of the current shifts daily by approximately 50 minutes. Thus, after a period of about 15 days the resultant translation arising from diel vertical movements of chaetognaths is approximately zero. The diel movement in the presence of vertical shear in the mean currents will, of course, produce a different net displacement than will occur in the absence of vertical movements. For the 17-30 October 1978 period, the horizontal displacement arising under the conditions of diel vertical movements, compared to no diel movements, was in a similar direction, but reduced in magnitude by approximately 30%. If animals are to utilize the shear in tidal currents to move, over a period of a fortnight or longer, in a direction that differs from that of the residual current, their vertical movements would have to be tied to the lunar cycle, not the solar one. However, the evidence presented for S. elegans supports vertical movements in response to the solar cycle. Although the movement of adult chaetognaths to greater depths during daylight hours results in a longer residence time within a given area of the Bank than for the larval and immature stages, the shear in the tidal currents appears to play only a secondary role in altering their retention time on the northeastern part of the Bank. More importantly perhaps, variations in the tidal regime can be viewed as an important mechanism for generating variability in the smaller scale (less than 50 km, less than two weeks).

Diffusion as well as advection will produce changes in the distribution of passive drifters. Many point-source dye diffusion experiments in the surface layer of coastal waters have indicated that patch size, as expressed by the mean square distance from the centre of mass (variance), can be related to the diffusing time. For radially symmetric diffusion, Okubo (1971) found that the equation:

$$\sigma^2 = 0.0108t^{2.34}$$

where σ^2 is the variance in cm^2 and t the diffusion time in seconds, represents fairly well the spread of dye from a point source over a time varying from 2 hours to nearly a month. On the assumption that the distribution is Gaussian, approximately 95% of the diffusing material remains within a radius of 2σ. A 13-hour drogue-cluster release experiment on

31 October, 1978, sited within area A yielded a variance close to that predicted from the above equation. Using this equation indicates that over a 13-day period a point source release would have a 2σ value of 25 km. Thus in the area of site 6 and at depths below about 30 m, lateral diffusion would appear to be as important as advection in altering the distribution of passive drifters. For shallower depths (e.g., 15 m) however, advection at all current meter sites dominates over diffusion in altering the distribution of a passive scalar.

F. ACKNOWLEDGEMENTS

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Table I Summary listing of the four bongo-net grid surveys on the northeastern part of Georges Bank, October, 1978.

NE Georges Bank Grid Survey	Survey Dates (E.S.T.)	Research Vessel	No. Stations Sampled
I	17-19 October 1978	Lady Hammond	49
II	19-23 October 1978	Lady Hammond	80
III	24-27 October 1978	Lady Hammond	51
IV	27-30 October 1978	Anton Dohrn	64

Table 2. Stages of maturity for Sagitta elegans on Georges Bank. The mean lengths and 95% confidence limits for each stage were derived from the MOCNESS vertical series.

Stage	Identifying characters	Length (mm)	
		$\bar{x}$	95% CL
Larva I	Newly hatched; no visible testes or ovaries	3.3	1.1 - 6.3
Immature II	Immature testes and ovaries, slightly visible	9.1	3.1 - 15.1
Adult III	Testes mature with seminal vesicle development. Ovaries immature all similar size.	14.1	10.5 - 17.7
Adult IV	Both testes and ovaries mature. One or more enlarged, ripening ova, diameter greater than 1/4 body length	15.1	12.9 - 17.3

Table 3 Summary of unbalanced designs analysis of variance for Sagitta elegans northeast Georges Bank bongo-net survey grids. The number per m^2 for each haul was transformed by $\log_e (X + 0.1)$. F-ratio values are denoted by their level of significance.

F-values

Factor	17-19 Oct 78 Grid I	19-23 Oct 78 Grid II	24-27 Oct 78 Grid III	27-30 Oct 78 Grid IV
Area (3)	29.70***	48.76***	63.19***	62.07***
Stage (3)	7.47***	4.67*	11.77***	11.19***
Time (3)	1.71	1.46	0.014	0.08
Area x Stage	3.07*	1.03	2.93*	1.57
Area x Time	1.09	1.46	0.80	4.41*
Stage x Time	1.00	0.25	0.26	0.54

*** $P < 0.001$

** $P < 0.01$

* $P < 0.05$

Table 4 Mean abundance ($\log_e(X+0.1)$ transformed number per m^2) of three stages of Sagitta elegans within the eastern (A) and western (B) subareas of the Georges Bank grid surveys. Differences between the two subareas for a stage were tested by a two-sample T statistic and their level of significance is denoted.

Stage	Area	17-19 Oct 78 Grid I	19-23 Ocxt 78 Grid II	24-27 Oct 78 Grid III	27-30 Oct 78 Grid IV
Adult	A (Eastern)	7.10**	6.12[a]	6.45**	7.01*
	B (Western)	3.23	4.07	3.43	3.95
Immature	A	4.80	5.44	5.69	6.95
	B	4.61	5.28	6.71	5.34
Larva	A	2.83	2.96	2.75	3.23
	B	1.80	3.79	2.49	1.28

** $P < 0.01$ significance level

* $P < 0.05$

a $P < 0.11$

Table 5 Summary of unbalanced designs analysis of variance for Sagitta elegans MOCNESS vertical distribution data. The number per cubic meter at each depth level was transformed by $\log_e(X+0.1)$. F-ratio values are denoted by their level of significance.

F-values

Factor	Maturity Stage I	II	III	IV
Depth (7)	4.15**	2.55*	3.67**	0.76
Time (2)	0.05	0.001	18.12***	28.81***
Depth x Time	0.19	3.02*	4.36**	1.39

*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

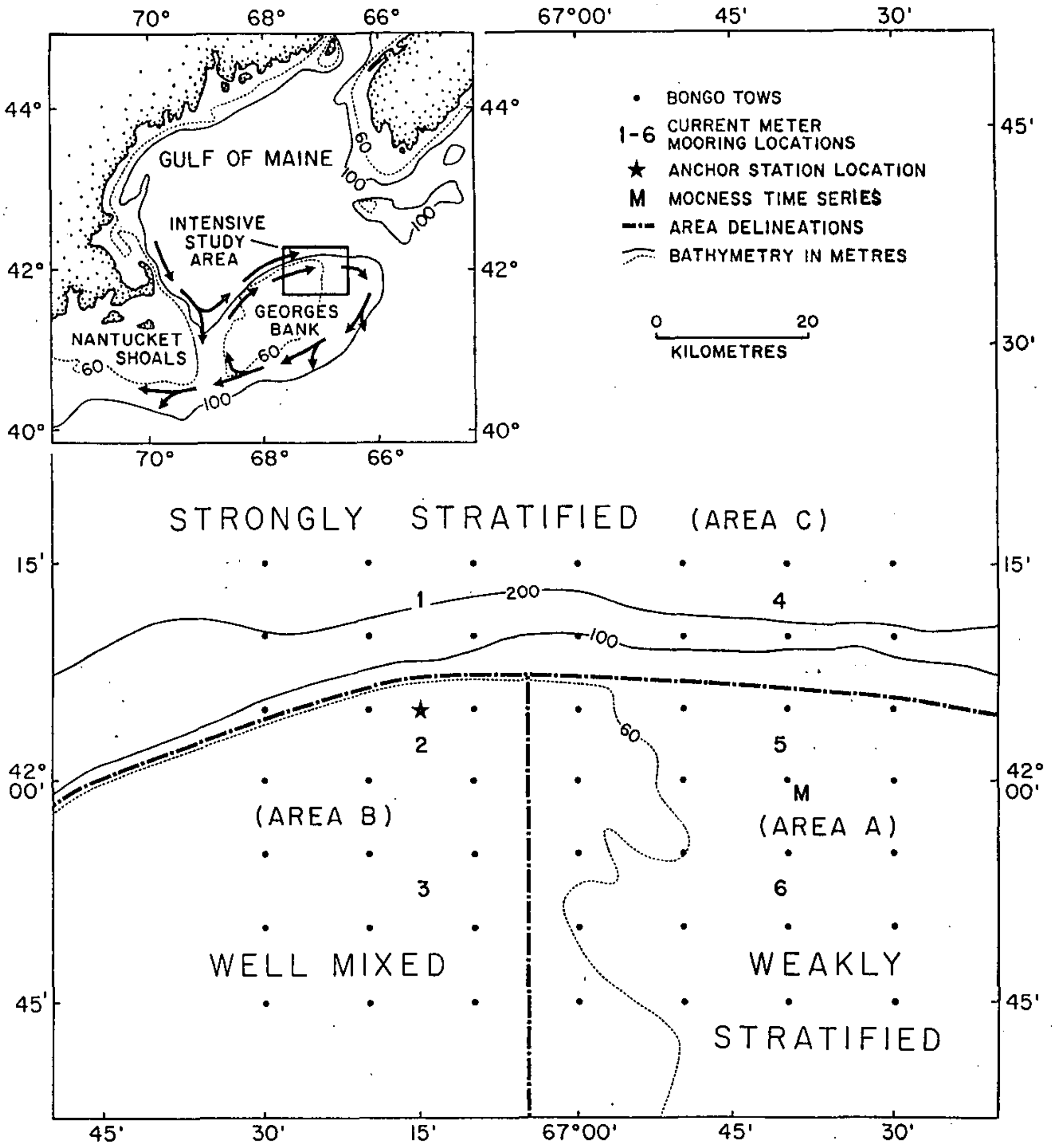


Figure 1 Map of Georges Bank study area showing general circulation pattern and location of standard bongo-grid stations, MOCNESS vertical time series, moored current meters, and temperature, salinity, and current profile anchor station.

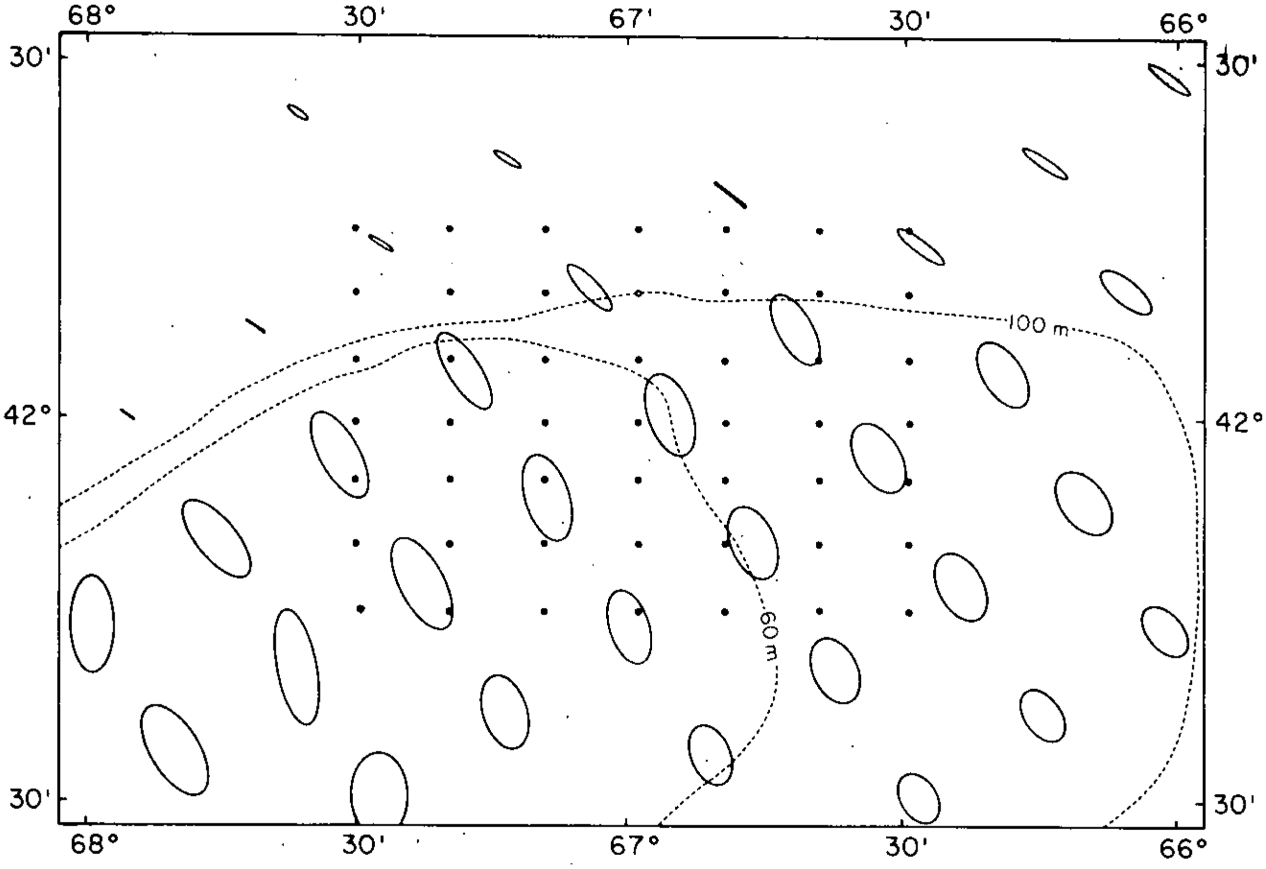


Figure 2 Georges Bank M_2 tidal ellipses in the area of bongo-grid sampling stations.

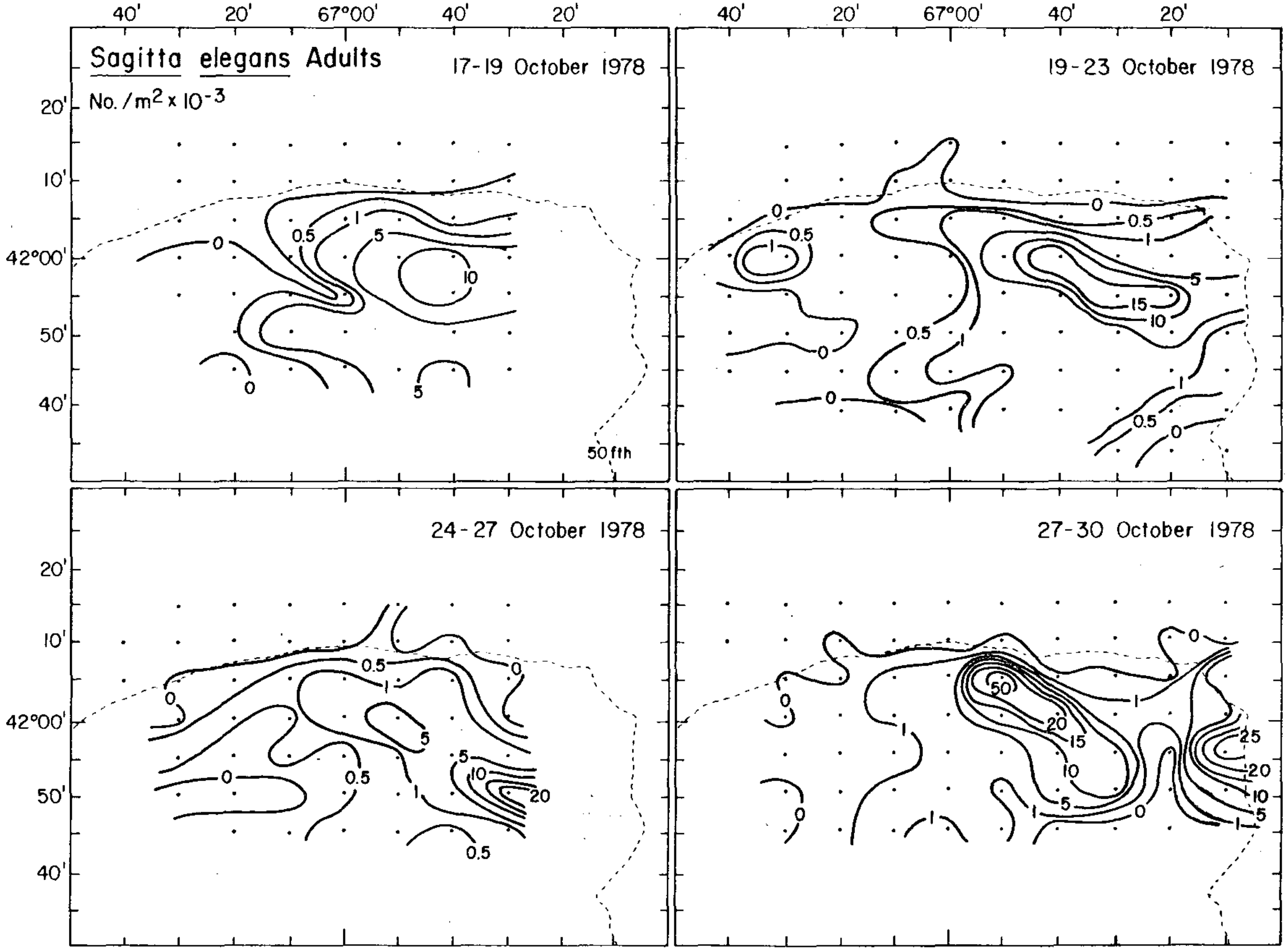


Figure 3 Distribution of adult Sagitta elegans on four grid surveys during the period 17-30 October 1978.

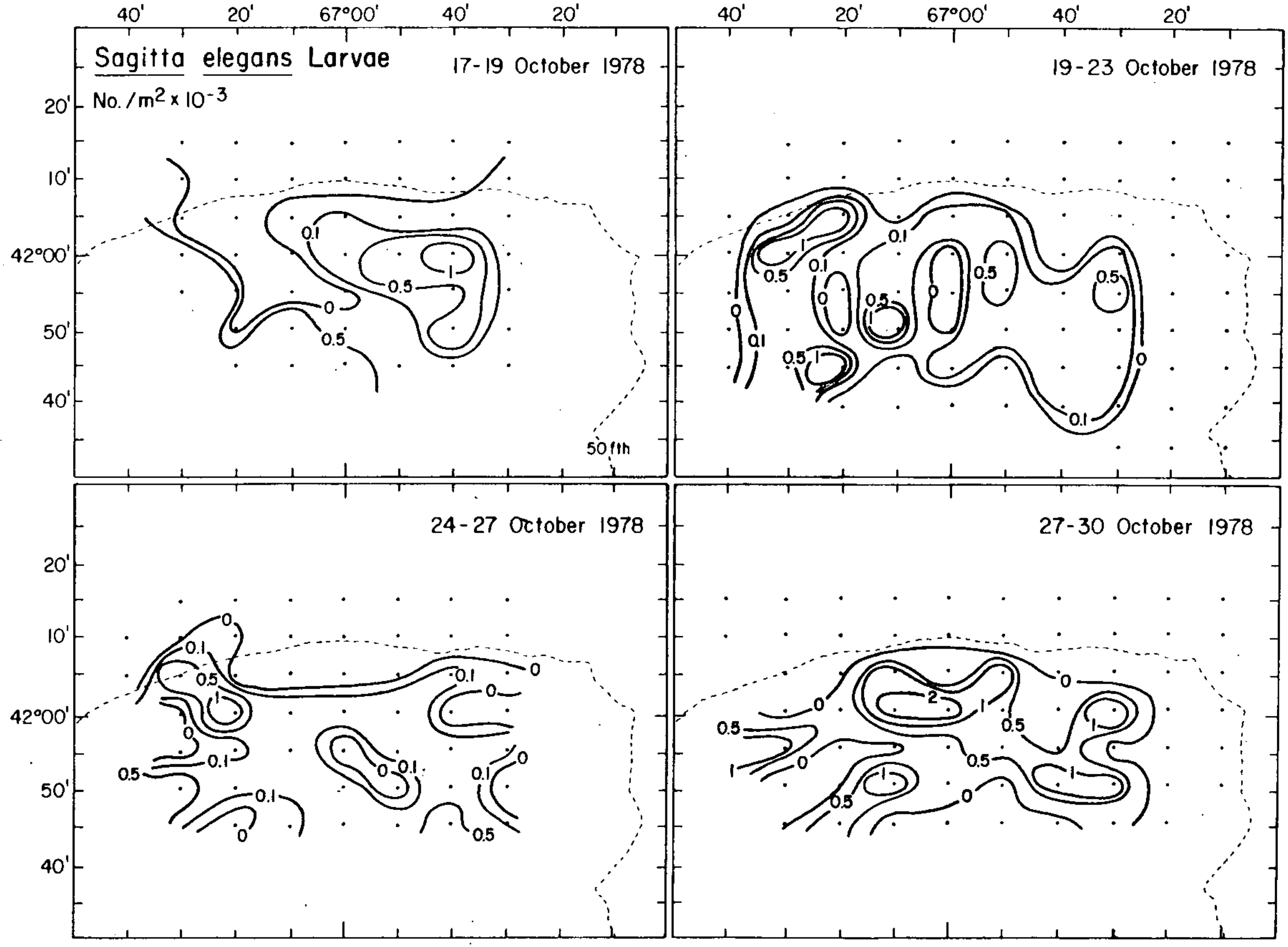


Figure 4 Distribution of larval Sagitta elegans on four grid surveys during the period 17-30 October 1978.

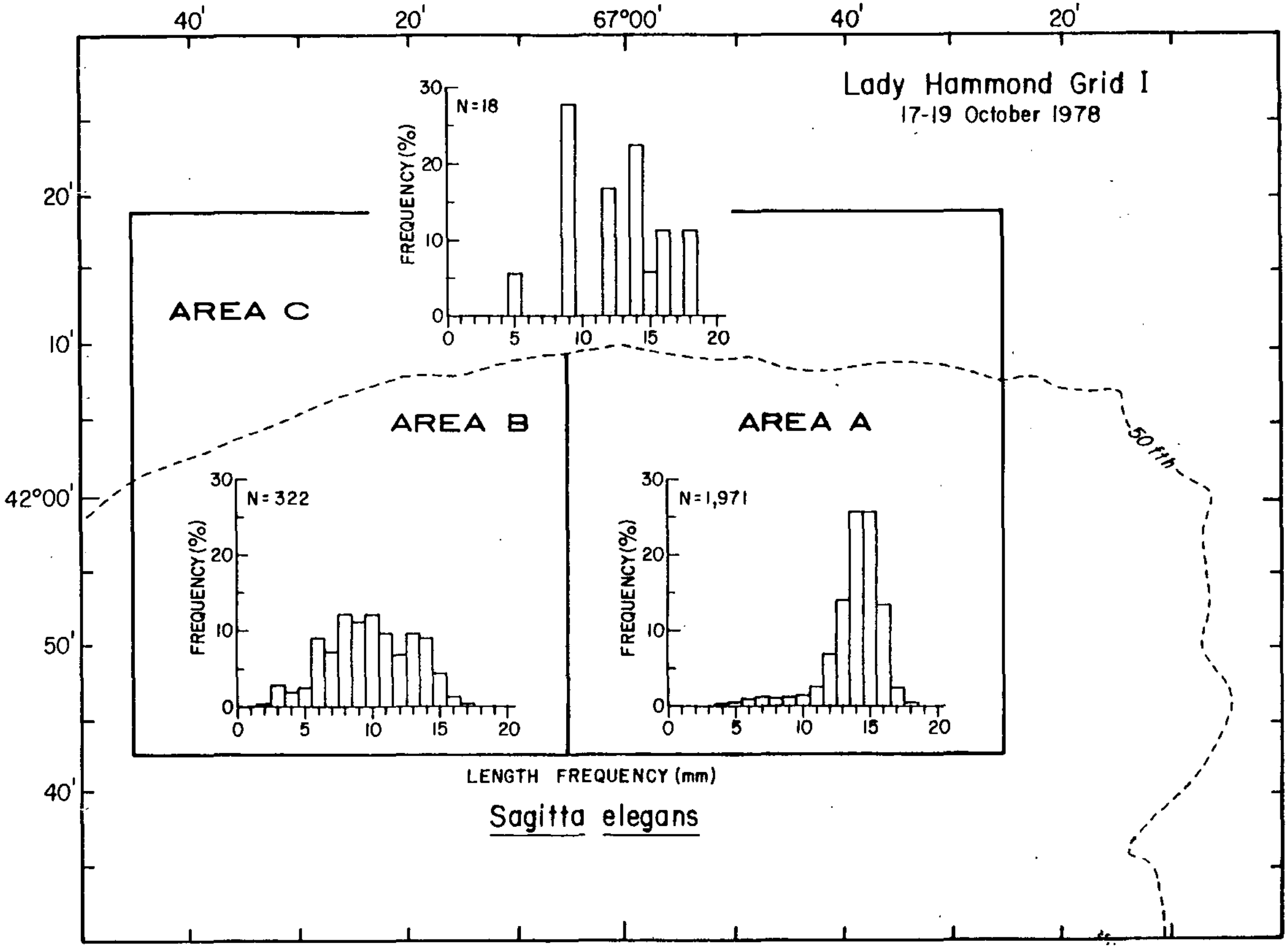


Figure 5 Combined length-frequency distributions of Sagitta elegans for the three hydrographic areas during the first grid survey, 17-19 October 1978.

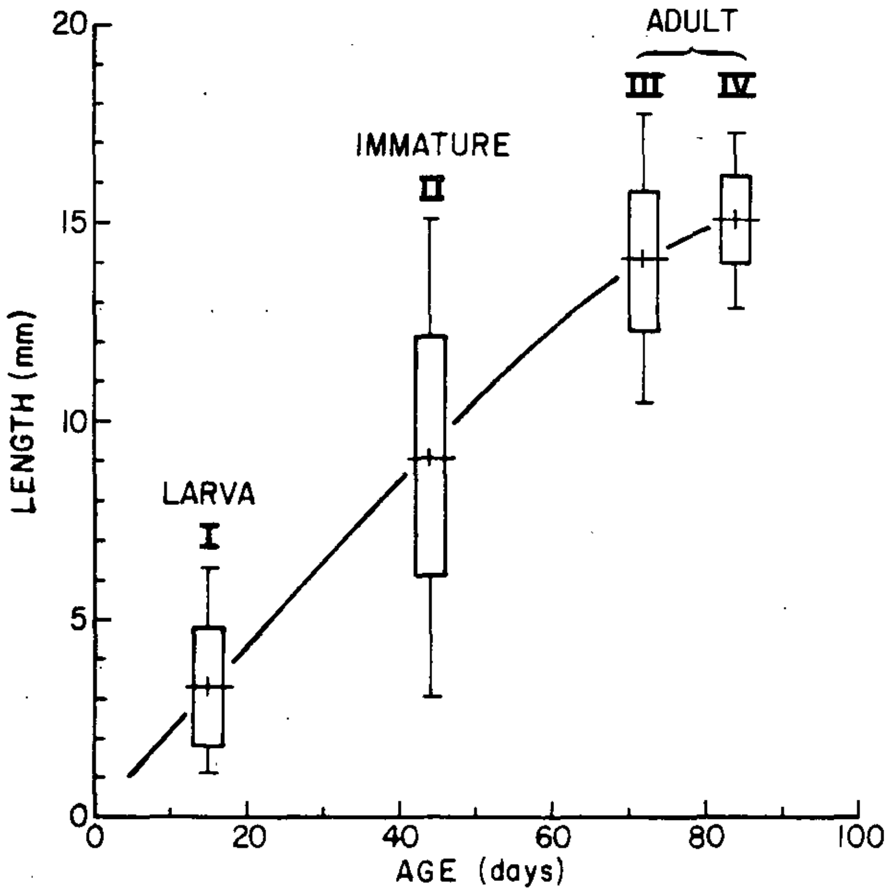


Figure 6 Estimated age-length plot of Sagitta elegans based on four maturity stages. The bars represent ± 1 standard deviation and the extended lines represent the 95% confidence limits of mean length for each stage.

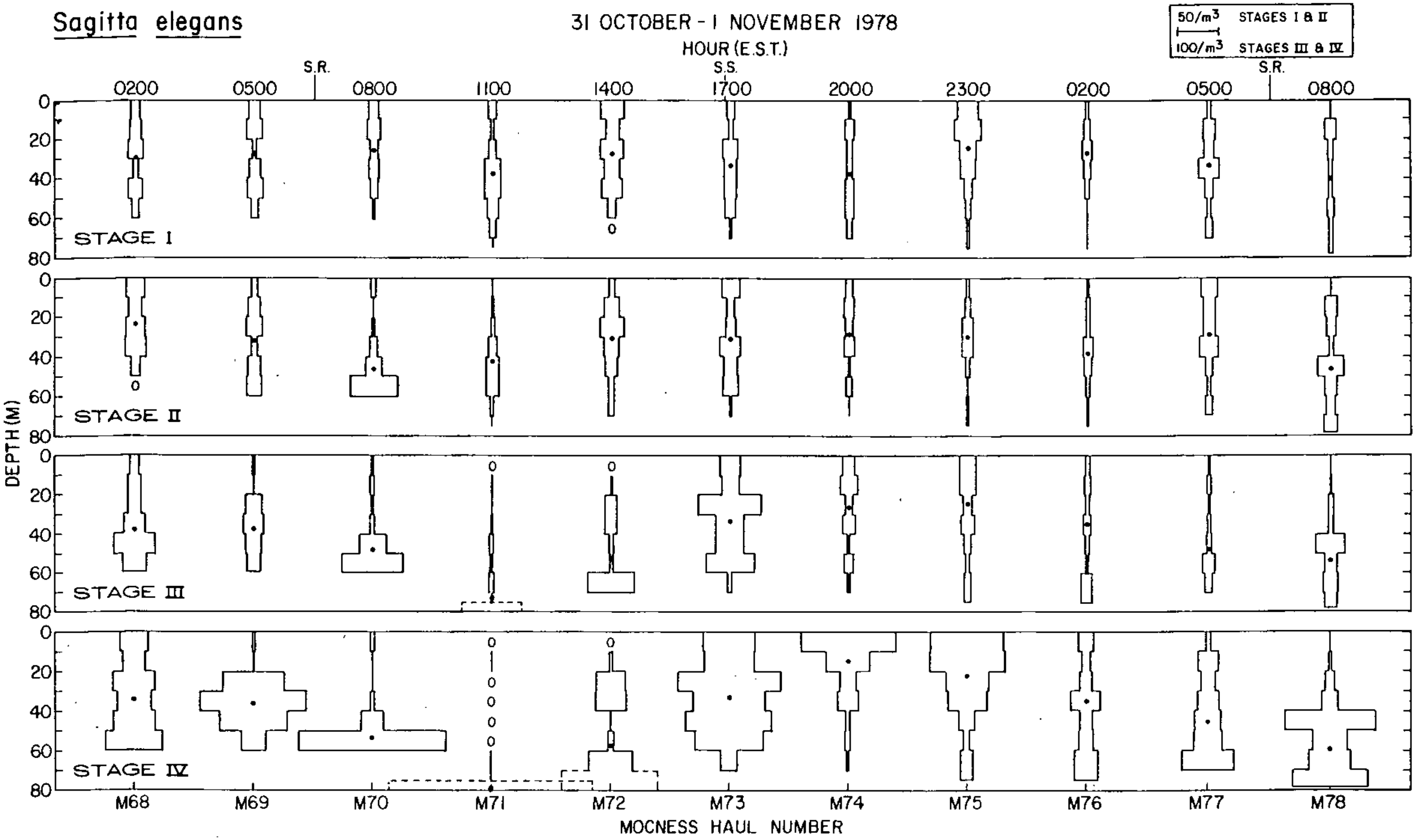
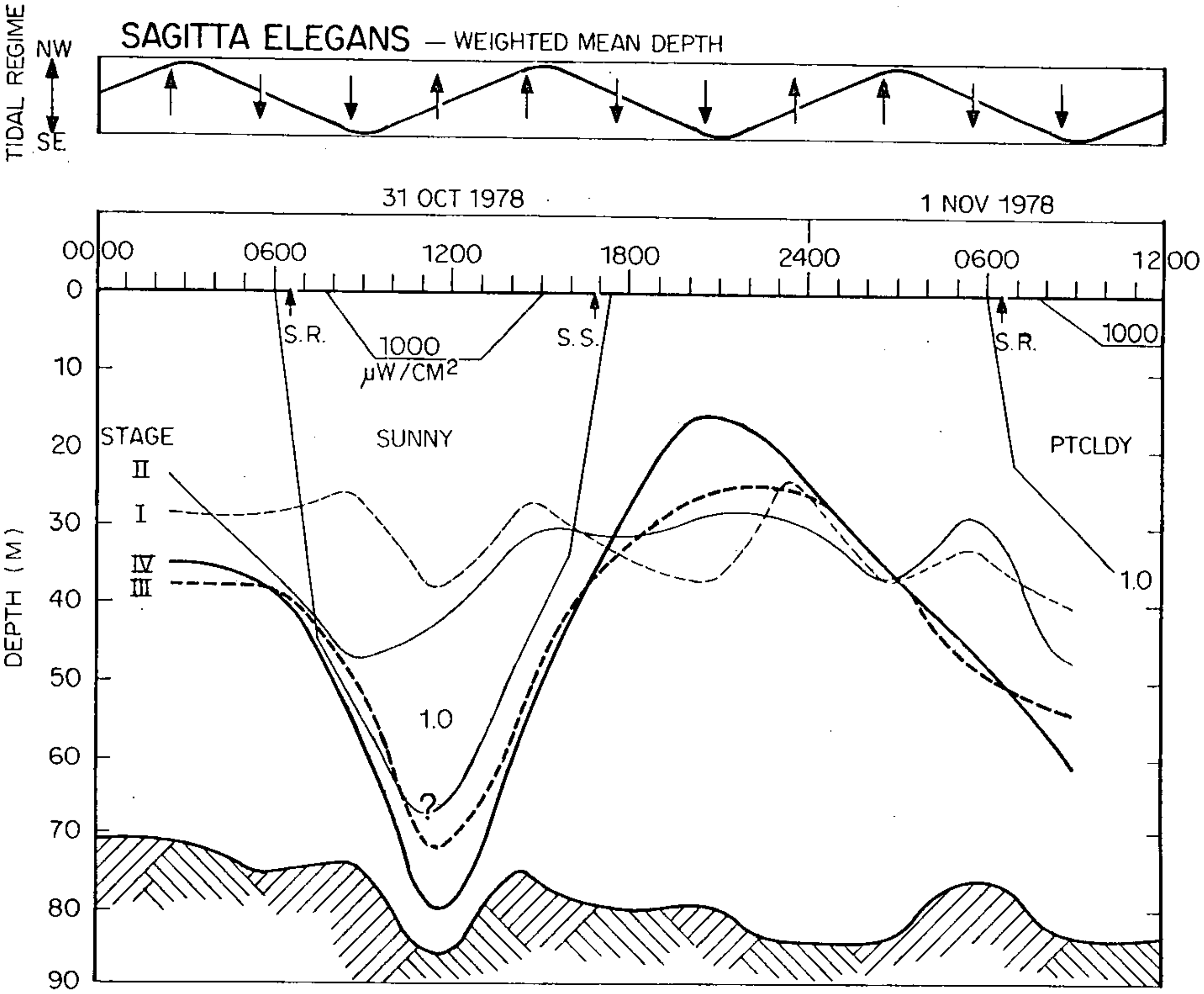


Figure 7 Vertical distribution of the four maturity stages of Sagitta elegans from the time series of 11 1-m MOCNESS hauls, 31 October - 1 November 1978. Note the different density scale used for the maturity stages. The dotted strata densities are estimates expected from the average population abundance. S.R. = sunrise, S.S. = sunset. The dot located within each haul profile represents the weighted-mean depth for that distribution.



S.R. = (SUN RISE) 0631 E.S.T. S.S. = (SUN SET) 1656

Figure 8 Plot of the weighted mean depths for the four maturity stages of Sagitta elegans from the MOCNESS time series, 31 October - 1 November 1978, in relation to the light level and phase of the tidal cycle.

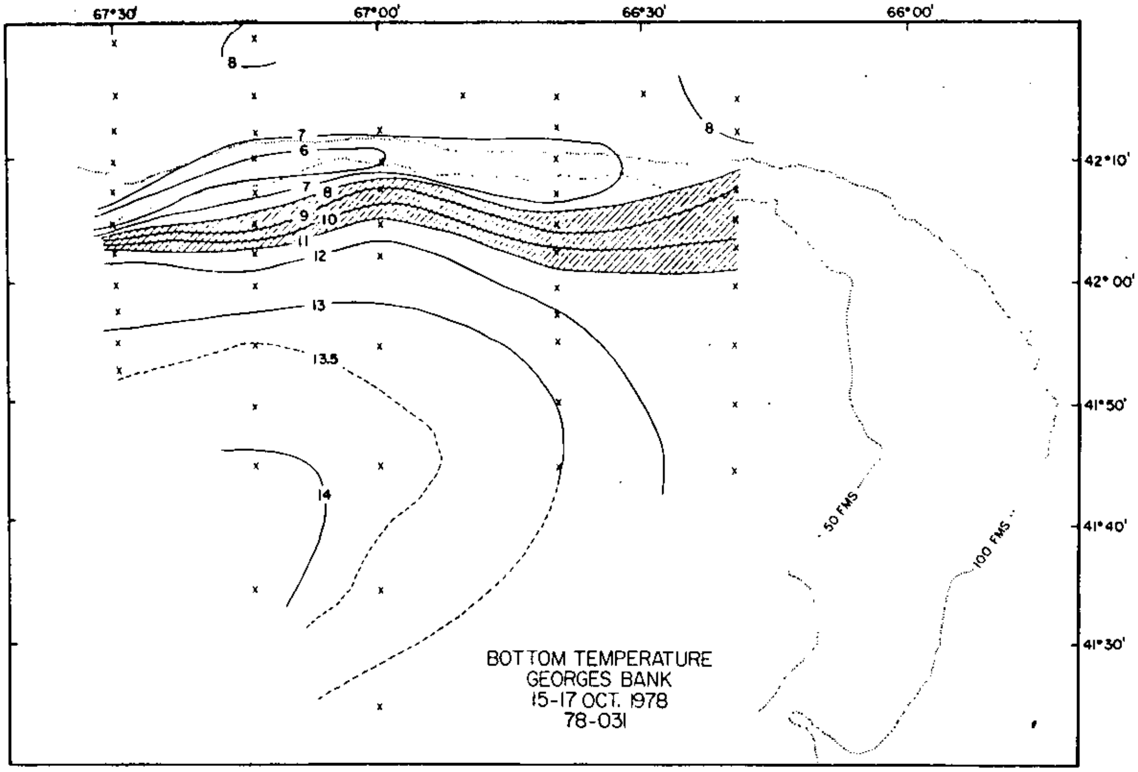


Figure 9 Bottom temperature contours in the Georges Bank study area during the period 15-17 October 1978.

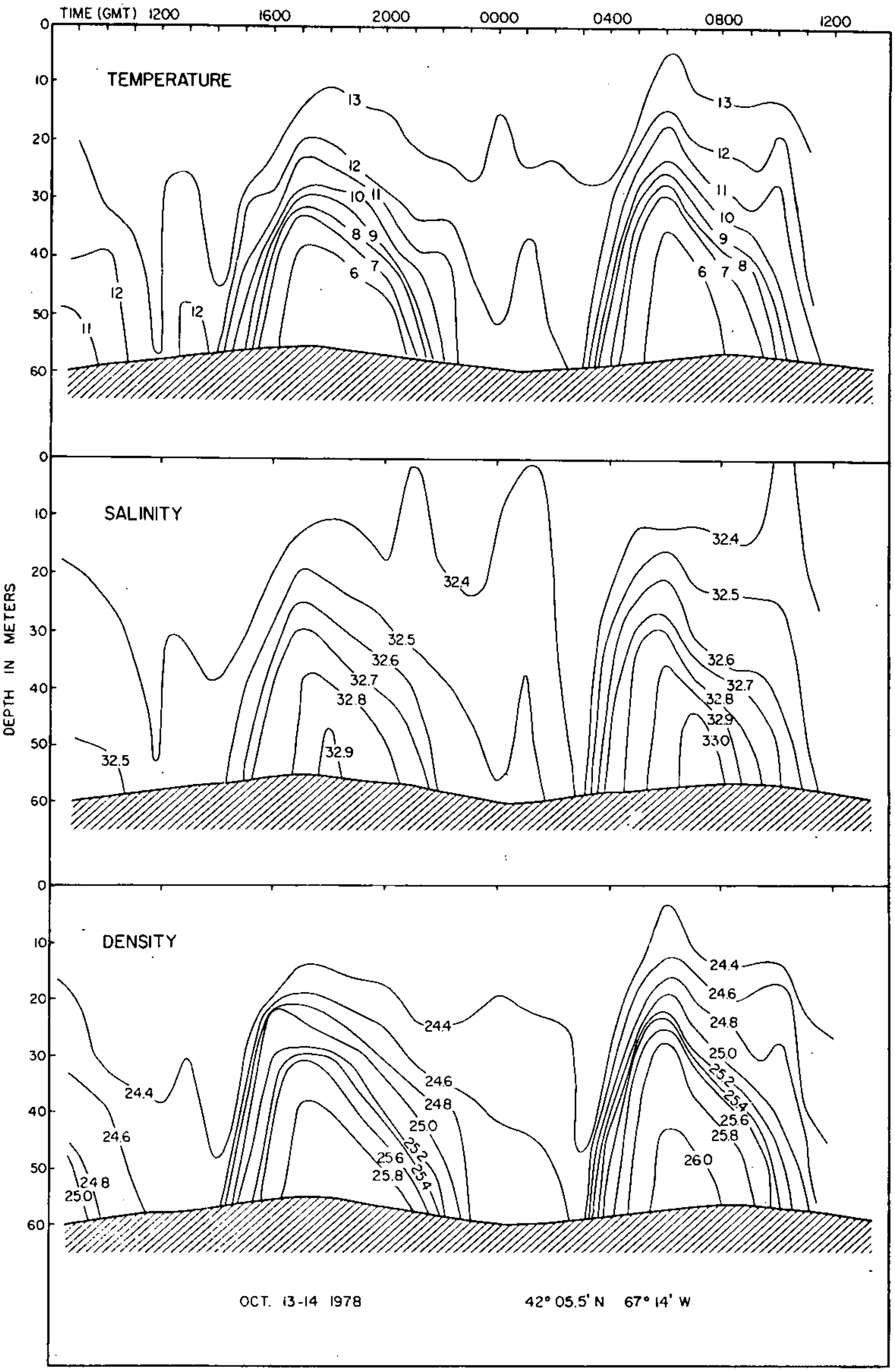


Figure 10 Time-depth plot of temperature, salinity, and density distribution as observed at 25-hour anchor station, 42°5.5'N, 67°14.0'W, 13-14 October 1978.

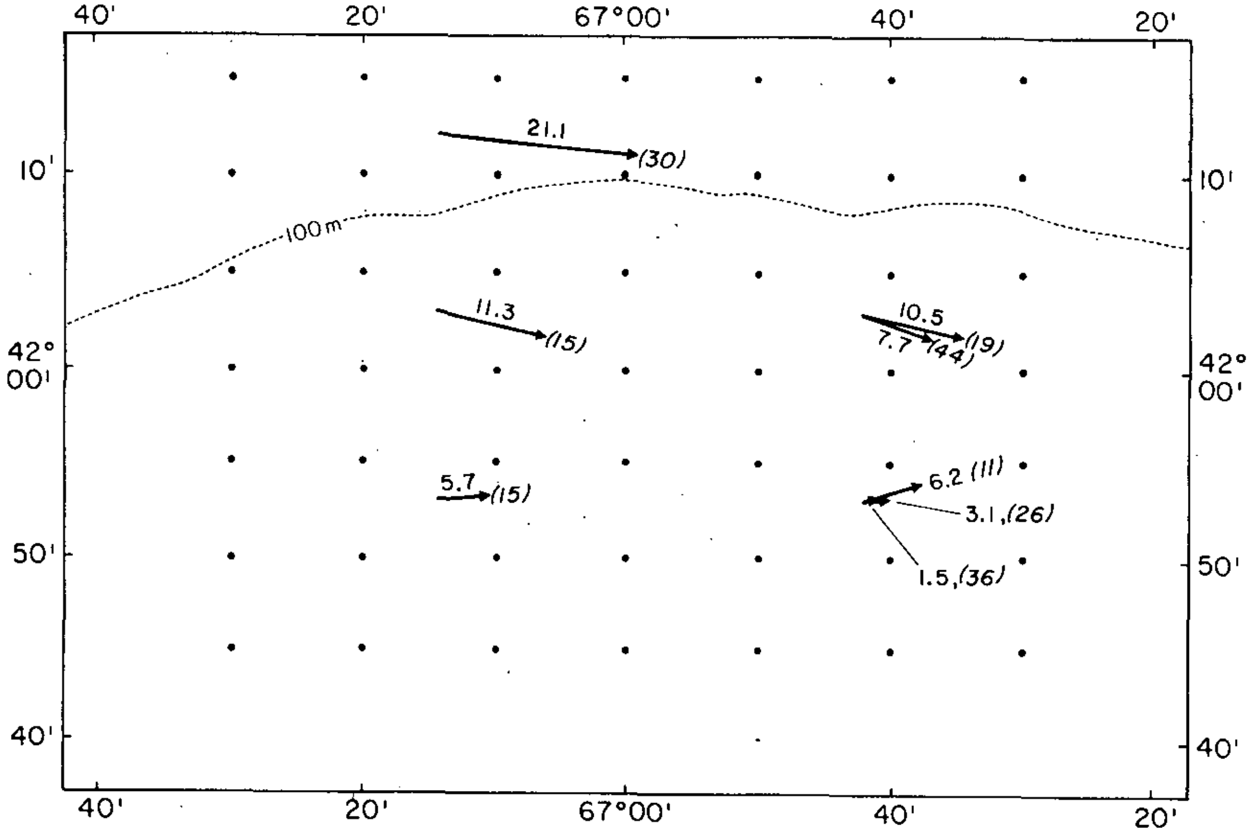


Figure 11 Mean current speed and direction determined from moored current meters during the period 17-30 October 1978. Speed of the current is given in km/day; the number in brackets is the depth of the measurement in metres.

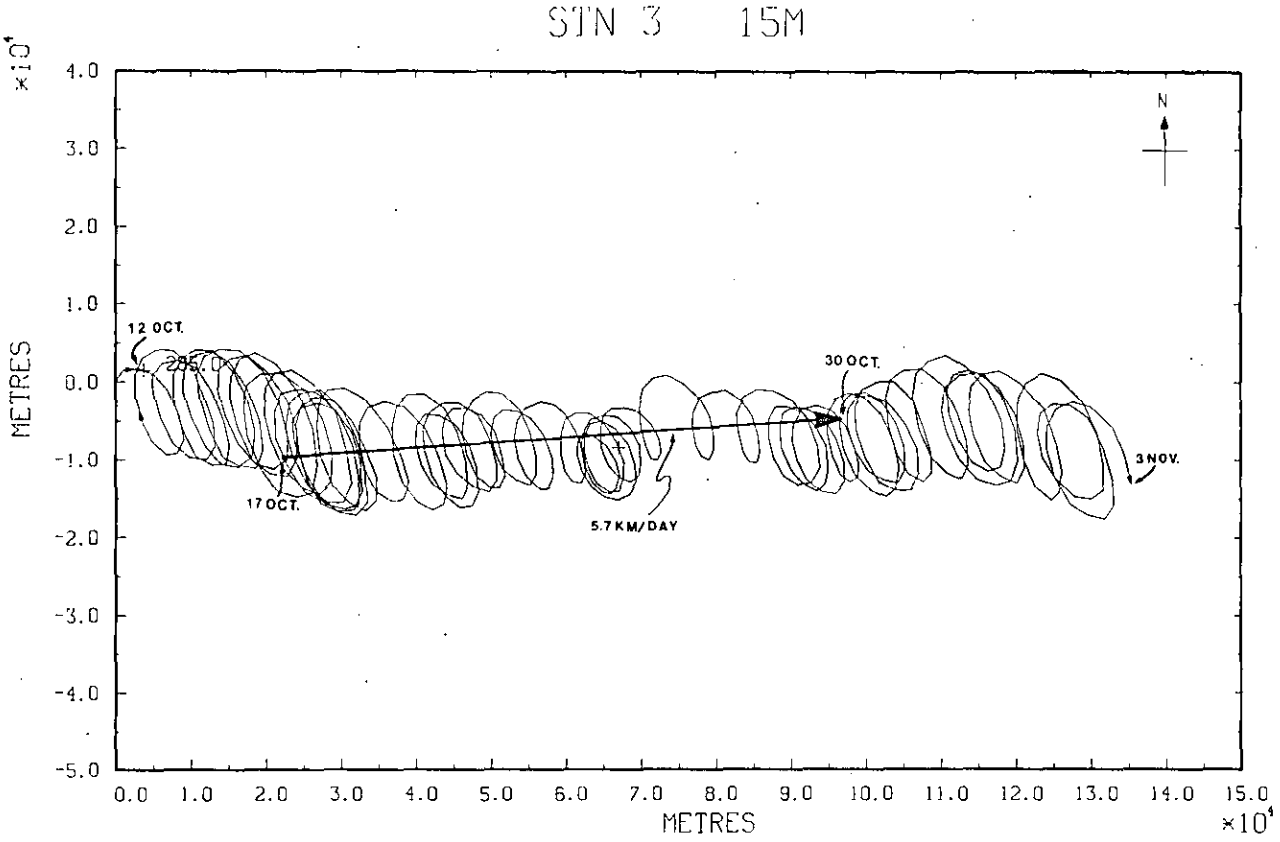


Figure 12 Progressive vector plot of the hourly currents measured at 15-m depth, site 3, during the period 12 October - 3 November 1978. The mean velocity over the 13-day period, 17-30 October 1978 is shown.

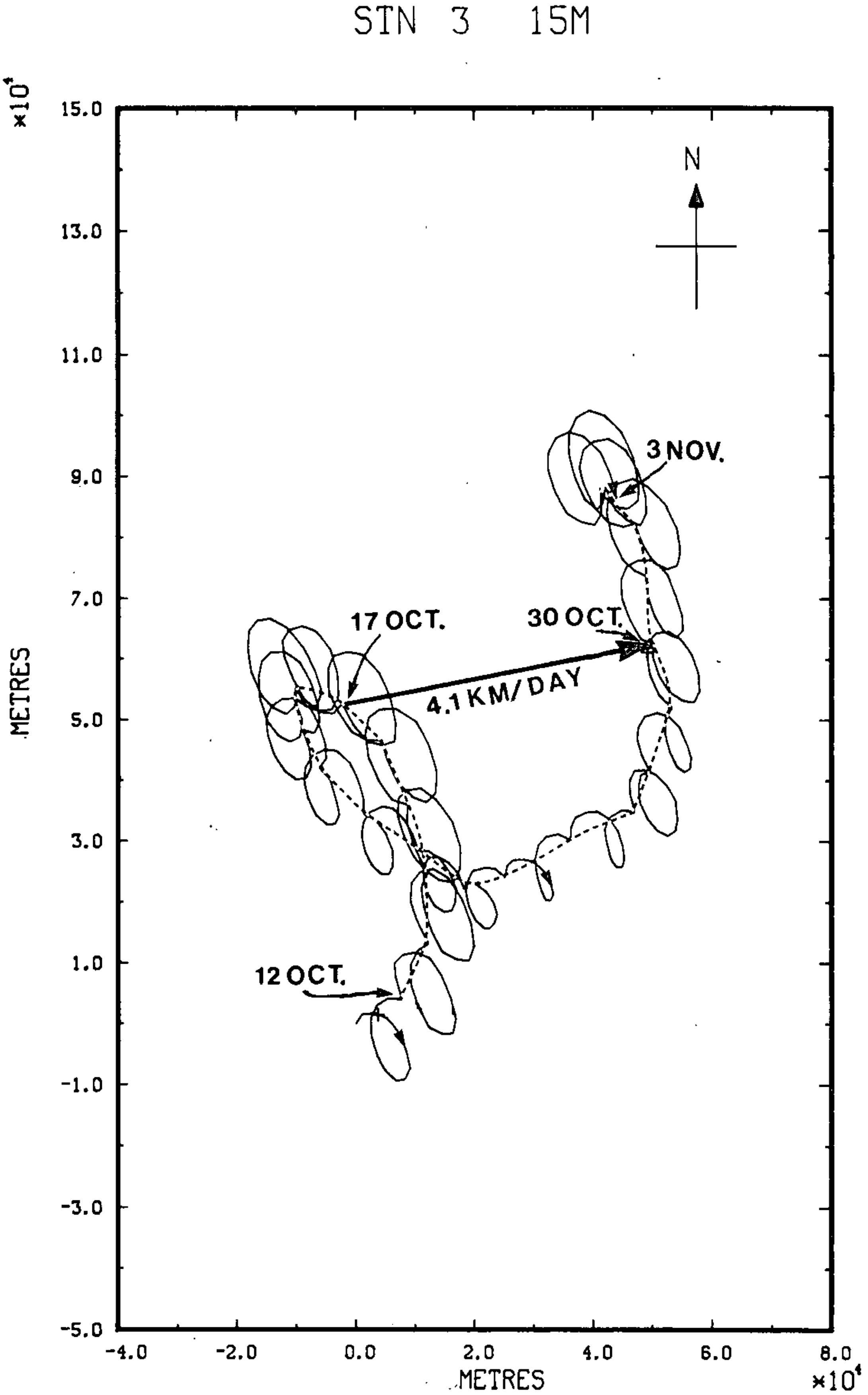


Figure 13 Simulation of Sagitta elegans expected displacement with a diel vertical migration pattern that assumes they were drifting freely with the currents at 15 m during the period 1540-0840 hours (EST) and they were at or near the bottom during the period 0840-1540 hours (EST) where the current was assumed to be zero.

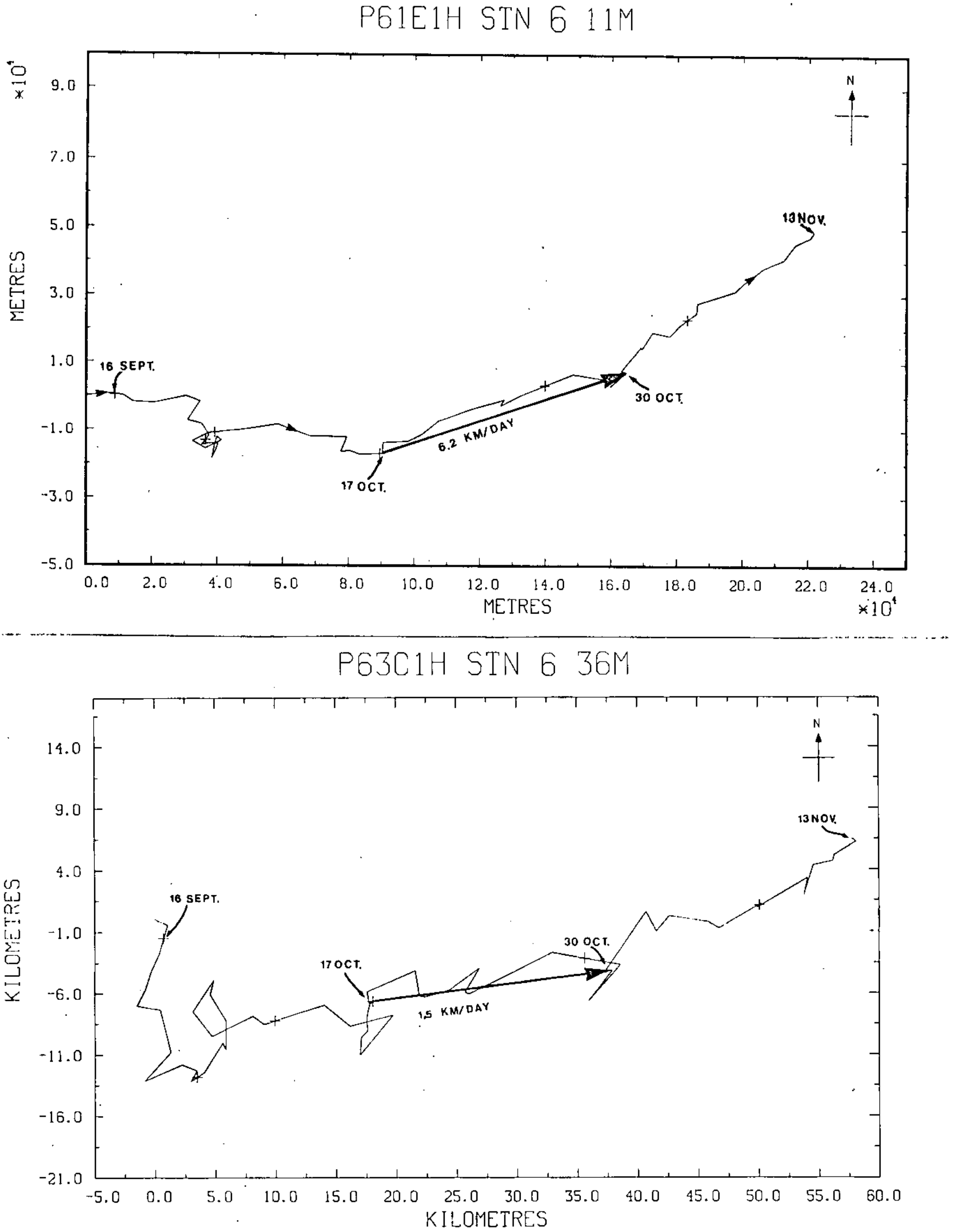


Figure 14 Progressive vector plots of the daily resultant displacement measured at 11 and 36 m depth, mooring #6, during the period 16 September - 13 November 1978. The mean velocity over the 13-day period, 17-30 October 1978 is shown.

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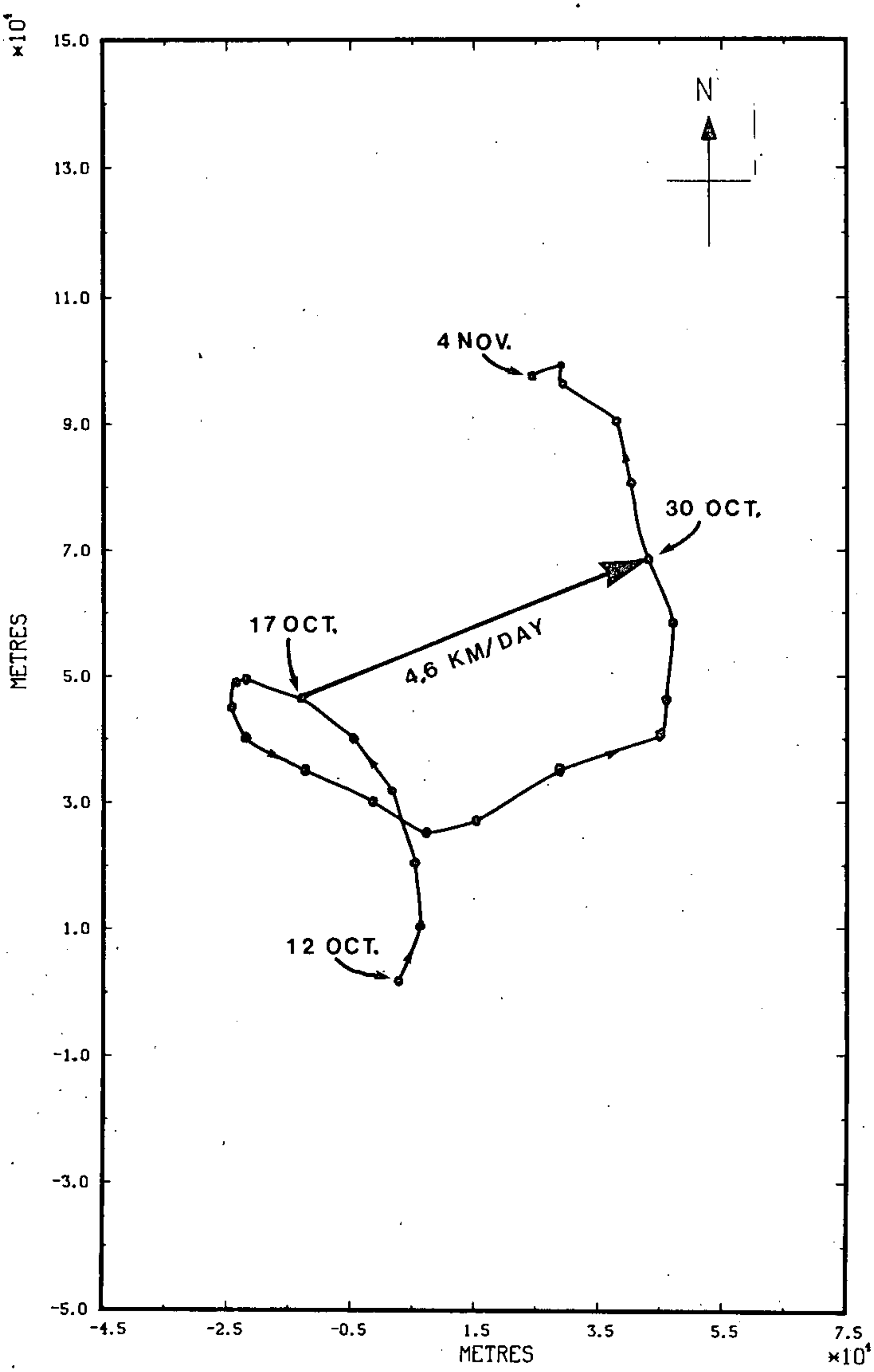

Figure 15 Simulation of Sagitta elegans expected displacement with a diel vertical migration pattern that assumes they were drifting freely with the currents at 11 m during the period 1540-0840 hours (EST) and they were at or near the bottom during the period 0840-1540 hours (EST) where the current was assumed to be zero.

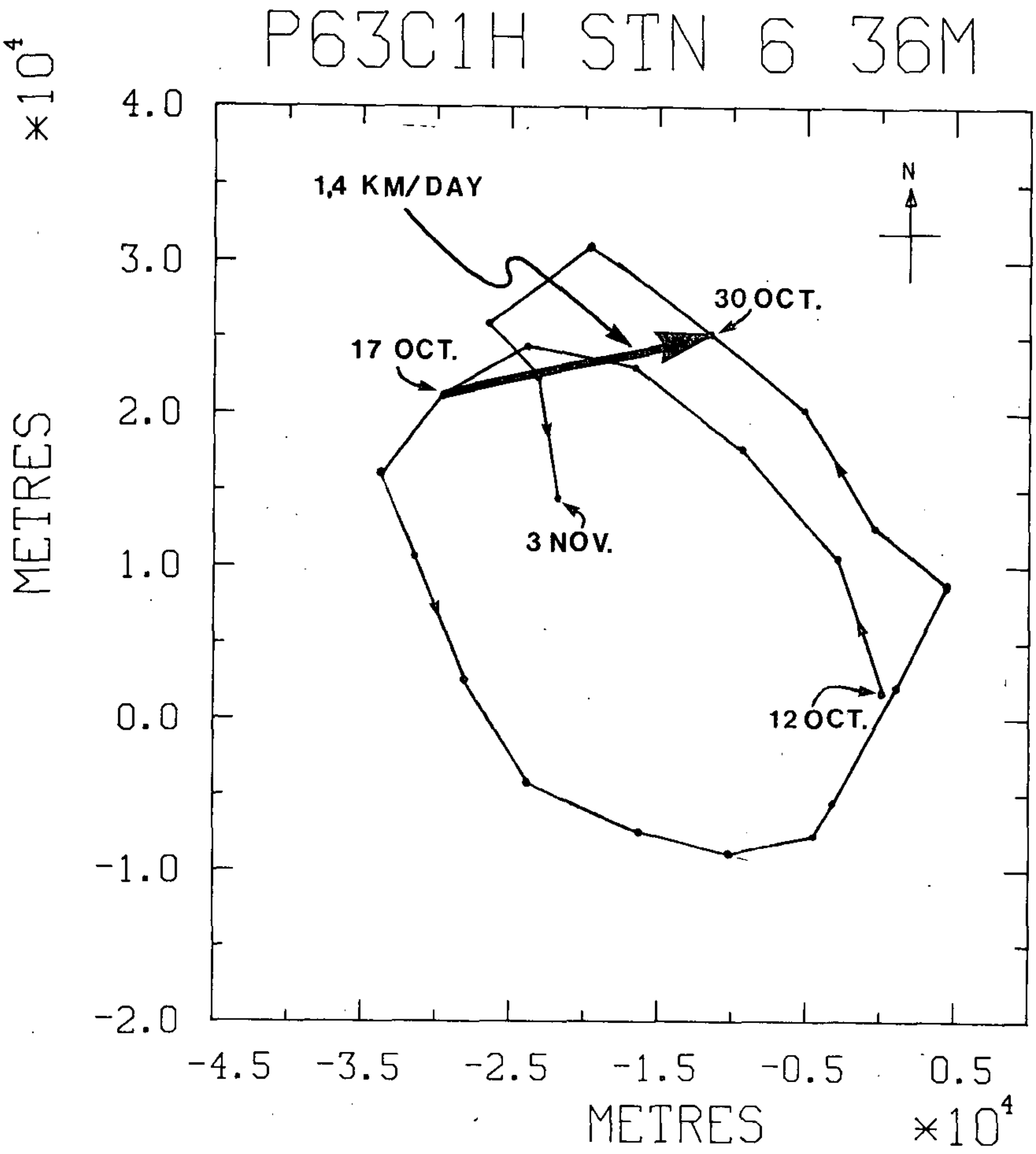

Figure 16 Simulation of Sagitta elegans expected displacement with a diel vertical migration pattern that assumes they were drifting freely with the currents at 36 m during the period 1540-0840 hours (EST) and they were at or near the bottom during the period 0840-1540 hours (EST) where the current was assumed to be zero.