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STUDIES ON THE EFFECT OF THE FRONTAL ZONE ON THE NORTHERN FACE OF GEORGES BANK, GULF OF MAINE, ON LARVAL LOBSTER AND PLANKTON DISTRIBUTION

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ABSTRACT

Our geographic coverage of the Canadian sector of the Gulf of Maine indicates that larval lobsters are hatched and released on the offshore banks. At Georges Bank the first and second moult stages occur primarily over the Bank. Moult Stages III and IV lobster were collected both on and off Georges Bank, and at times Stage IVs appear more abundant off the Bank. The higher lipid index, triacylglycerol/sterol ratio, measured in Stages III and IV collected off the Bank, on two separate years, is interpreted to indicate better growing conditions for the later planktonic stages of the lobster in the Gulf of Maine proper.

An attempt was made to track larval lobsters located both on and off the northern edge of Georges Bank using Loran C drifters drogued at 10-m depth. Lobster larvae were sampled with a Tucker trawl at least three times over a two-day period while following three drifters off and three drifters on the Bank. The lobster stage composition and abundance did not change significantly around the three off-Bank drifters. This was not the case for the larval lobster population tracked on the Bank, which was dominated by the first two development stages. It is believed that the more pronounced vertical migration of Stages I and II lobsters undertaken each day in the upper 30 m results in

their separation from the drifter due to exposure to different current shears. The Stages III and IV lobster are more surface-living throughout the day and would be expected to stay in the vicinity of a surface-drogued drifter.

Examination of plankton transects taken across the tidal front indicate that species inhabiting the surface waters are relatively unaffected by the hydrography and are distributed throughout. This is believed to explain how some lobster larvae escape the gyre on Georges Bank to complete their development and settle at various locations in the Gulf of Maine. Planktonic larvae of various groundfish are thought to retain their position on the Bank by not entering the surface waters.

INTRODUCTION

Rogers et al. (1968) were the first to suggest that the offshore release of lobster larvae may be related to coastal recruitment in inshore regions with an onshore flow. This hypothesis was based on observations off Rhode Island where the first-stage larvae were more abundant toward the edge of the continental shelf, whereas the converse was true for the final planktonic or fourth stage. Inshore was defined as within Rhode Island Sound in water generally less than 30-m depth. Lund and Stewart (1970) did not find any supportive evidence for this hypothesis from their offshore larval lobster surveys off southern New England, although they did record unusually high concentrations of stage IV larvae in Long Island Sound, MA.

Lobster larvae were considered initially to be sparse in Canadian offshore waters (see Stasko 1977). Aggregations of larvae were located over or near German and Browns Bank, with a scattering of local concentrations along the continental shelf as far west as Emerald Bank and Western Gully from a Scotian Shelf icthyoplankton survey. Stasko speculated that larvae originating on Georges Bank could settle on Browns Bank, based on known surface currents and a drift duration of approximately 1 mo at local temperatures, and larvae from Browns Bank in turn could settle as far inshore as southwestern Nova Scotia. Stasko (1978) expanded this hypothesis to include a return movement of mature lobsters to the deeper waters off Browns, Georges, and German Banks and east of Grand Manan Island, which would complete the life cycle. Special surveys conducted inshore and offshore off southwestern Nova Scotia in 1977 and 1978, with largely neustonic gear, confirmed the widespread presence of lobster larvae, with the first stage appearing in the plankton in early July, increasing in August, and declining rapidly in abundance in September (Stasko and Gordon 1983). Their inshore stations conformed roughly to the 20-m depth contour which included the Trinity Ledge area (Harding and Trites 1989). Stasko and Gordon (1983) failed to find their predicted temporal gradient of developmental stages from the offshore Banks (Browns and German Banks) to the coast of southwestern Nova Scotia. This was due to their collections, inexplicably at the time, being overwhelmed with Stage IV (66%) lobster. Stage I lobster made up the remainder of the catch (29%) and Stages II and III were almost absent. Subsequently, Harding et al. (1987) showed that these observations could be explained by the extensive diurnal vertical migration of Stage I, and possibly lesser migrations of Stages II and III larvae, with a small proportion of the population present at any one time in the upper metre at night. Earlier experimental work suggested that immediately after moulting Stage I larvae are attracted to the light (surface), but this is reversed by the second day (Hadley 1905; 1908). This would explain why there are always some early-stage larvae near the surface during daylight. Likewise, the predominance of Stage IV larvae in previous surveys over offshore Banks can be explained by their continuous presence in the upper metre both day and night (Harding et al. 1987). Even so, Stasko and Gordon (1983) found that there was a significant movement of Stage IVs out of the upper 0.15 m to the 0.3- to 1.3-m depths in daylight. Stasko and Gordon (1983) did find an increase in the relative abundance of Stage IVs over time toward the coast, but this could reflect the differences in spawning time and development rates of the two areas due to the seasonal temperature cycles of the two areas. Approximately 2.5 times as many larvae were caught per tow offshore as inshore in both years. Campbell and Pezzack (1986), on the other hand, estimated that 23 to 53% of the larvae produced off southwestern Nova Scotia would come from inshore sources based on berried females, but they included deep-water migrants from the Gulf of Maine on German Bank to Lurcher Shoal and Grand Manan in their calculations. Watson and Miller (1991) examined collections from the 1978 to 1981 Scotian Shelf ichthyoplankton surveys and confirmed earlier observations that most of the offshore lobster larvae were located near Browns and Georges Banks. It was particularly interesting that the distribution of Stage IVs formed a plume with diminishing abundance from Browns Bank toward the northeast. The authors conclude that this distributional pattern could be explained by larval dispersion with residual currents and/or surface forcing by summer winds.

Harding et al. (1983) estimated that in general there was not enough time available at local temperatures off southwestern Nova Scotia for larval development to reach the settling stage. It was concluded that successful inshore recruitment should be largely confined to small bays where higher surface temperatures prevail for longer periods of time. They calculated that recruitment in southwestern Nova Scotia based on laboratory-determined development rates, local sea-surface temperatures, residual current speeds, and directions could be derived primarily from offshore lobsters releasing larvae on the northern face of Georges Bank. In addition, Lawrence and Trites (1983) predicted from models based on residual currents and wind vectors that surface oil from the Georges-Browns Bank region in summer would frequently impact the coastline of southwestern Nova Scotia and the Bay of Fundy with a drift time of more than 20 d. Harding et al. (1983) concluded from larval drift considerations that all regions neighbouring on the Gulf of Maine gyre are probably within one lobster recruitment system, and pointed out that this conclusion was supported further by the similarity of the commercial lobster landing patterns around the Gulf.

Harding and Trites (1988) reinterpreted the larval surveys of Stasko and Gordon (1983), together with the unpublished drift bottle results of the 1977 surveys, to project larval dispersion from Browns Bank at first hatch (early July) and maximum Stage I abundance (early August). It was concluded that offshore larvae could make an important contribution to recruitment not only to southwestern Nova Scotia but the entire eastern sector of the Gulf of Maine to Casco Bay. Off southwestern Nova Scotia it was calculated that 3.6 x 10^6 Stage IV larvae were produced inshore compared to 1.8 X 10^{-8} offshore; and, if dispersion predictions are correct, a large part of this inshore production could have been derived from females on Browns and German Banks (Harding and Trites 1989).

In the present study we introduce subsequent work designed to first identify major spawning sites in Canadian offshore waters of the Gulf of Maine and secondly to better understand the issue of larval transport and dispersion through the frontal region on Georges Bank.

METHODS

The first survey was undertaken in 1983 with a rectangular 1- x 1.2-m neuston net divided vertically into three equal 40-cm compartments to sample the subsurface waters with 1028-μm mesh nets. The grid was specifically designed to locate larval lobster hatching areas "upstream" from southwestern Nova Scotia (Fig. 1). The first station was sampled on July 12 off Yarmouth, Station 15 on Browns Bank on July 14, Station 29 on the eastern tip of Georges Bank on July 16. After Station 35, in the Gulf of Maine, we steamed to Station 65 (July 17) at the upper end of the grid on Georges Bank because few lobster larvae were being caught in the east, then worked our way back to Station 47 by July 19 and finally performed day and night tows concentrated on Browns Bank between July 20 and 21. In 1987 horizontal time-depth sampling was done with the Vass-Tucker trawl (Harding et al. 1987) at 5-m depth intervals down to 30 m then at 10-m intervals down to the bottom over Browns Bank (July 14 to 20) and Georges Bank (July 20 to 30). In 1988 transects were run across the northern frontal zone on Georges Bank during late June to early July and August cruises as part of a joint physical-biological study (see Perry et al. 1993). Samples were taken at standard depths at each station with a CTD-rosette, multiple opening-closing net (Sameoto et al. 1979; 0.25 m^2 mouth size, 333-μm mesh) sampling seven discrete depths and A Vass-Tucker trawl (Vass 1988; $\sim$2.5-m^2 effective mouth size, 1.6-mm mesh) sampling an integrated water column above and below the thermocline.

Drift measurements were obtained in 1988 from undrogued surface buoys using satellite (ARGOS) tracking (Drinkwater et al. 1992). In 1989 transects were again run across the northern section of the Bank; and internally recording Loran-C drifters, drogued at 10-m depth, were successfully deployed at six locations across the front on two separate occasions: July 24 to 26 and July 27 to 29. The position of the drifters was obtained every 30 min. with an absolute accuracy of 250 m and a repeatability of 25 to 50 m (Crawford 1988). A detailed description of the Loran-C buoys can be obtained from Woodward et al. (1991). Three Loran-C drifters were followed consecutively on each occasion for macroplankton-nekton sampling with a stepped, oblique integrated Vass-Tucker trawl, of 30 min.' duration, from close to the bottom or 50-m depth to the surface. Three integrated Vass-Tucker trawls of the upper 50 m of the water column and one surface trawl were done in the vicinity of each drifter before steaming to the next. At the end of the 1989 cruise one of our transect lines was continued out into the Gulf of Maine proper in search of later development stages of the lobster.

In 1988 and 1989 lobster larvae were identified to intramoult stage at sea (Aiken 1973; Sasaki 1984) and immediately frozen in dry ice for later analysis of lipid types and content on shore (Fraser 1989). Phytoplankton, zooplankton, and nekton were identified later in the laboratory from paraformaldehyde+glutaraldehyde (50:50, 5%) and formalin (5% buffered) preserved samples, respectively.

Planktonic species associations were examined by means of multivariate classification and ordination methods. The analysis of the net (zooplankton) and water samples (phytoplankton) each consisted of four steps: 1) identification of groupings for each transect (Bray-Curtis index used for zooplankton, the Czekanowski index for phytoplankton), 2) variable transformation (square root for zooplankton and Ln+1 for phytoplankton) and reduction, 3) determination of a discriminant function (DCA) using the classification of Step 1 and principal component analysis (PCA), and the classification of the other transect samples, and testing for group differences with ANOVA.

RESULTS AND DISCUSSION

The 1983 neuston survey reaffirmed earlier work that the larval lobster planktonic cycle begins over Browns and German Banks between the second and third week of July (Stasko and Gordon 1983) and confirmed predictions that the northern face of Georges Bank could be a prolific source of larvae downstream (Stasko 1977; Harding et al. 1983). All developmental stages were prevalent between July 17 to 19 over Georges Bank in surface waters of 14 to 21°C (Fig. 1). However, the presence of Stage IVs over Browns Bank and Northeast Channel at temperatures of less than 11°C strongly suggests that they were advected into the area from areas "upstream" with more degree days such as the shelf break east of Northeast Channel or Georges Bank (Fig. 1). No lobster larvae were captured at the mouth of Northeast Channel which seems to negate this possible source for the larvae. Another pertinent piece of information is the apparent absence of lobster larvae in the Gulf of Maine proper during daylight but the consistent presence of Stage IVs if towing was continued after dusk. This suggests that even the Stage IVs which are reported to reside day and night in the upper metre over Browns Bank (Harding et al. 1987) are descending below the upper metre in daylight in the clear waters of the Gulf. No such phenomenon was observed at a Georges Bank station with Stages III and IVs being equally common in day and night samples. Stage IVs were taken in both day and night sampling over Browns Bank, although Stage Is were taken only at night consistent with the vertical migration observations of Harding et al. (1987).

The 1987 survey of lobster larvae on Browns and Georges Banks does not have the above limitations of previous offshore studies which may have missed substantial portions of the population beneath the surface metre (Harding et al. 1987). It can be seen that Stages I and II lobsters were observed over or near Browns Bank (at locations <100-m depth) and over Georges Bank (<50-m depth) in mid to late July (Fig. 2). Very few Stage II and no Stages III and IV lobster were present over Browns Bank in these collections, which is consistent with previous accounts of the timing of the seasonal cycle there (Stasko and Gordon 1983). Stages III and IV lobster were present over Georges Bank at expected higher abundances considering the more advanced hatching time to the south. The distribution of Stage IVs, however, was centred along the northern slope of Georges Bank with some individuals present in the Gulf of Maine proper collections. The 1989 survey over Georges Bank support these results in that Stages I and II lobster were caught almost entirely on the Bank whereas Stage III was located on and near the periphery of the Bank and Stage IVs were located mainly off the Bank (Fig. 3). Either the fourth and truly pelagic stage swims actively through the northern tidal front or the concentration of Stage IVs we are observing along the edge of the Bank are advected from the Cape Cod area where the seasonal cycle would be yet more advanced again. Tidal rectification (barotropic) and a seasonal baroclinic density structure contribute to an eastward, along-Bank current or "jet" of up to 50 cm sec^{-1} in the summer months (Loder et al. 1993).

Stage IV larvae are truly pelagic and could possibly swim off the Bank (Ennis 1986; Cobb et al. 1989). Abiotic mechanisms may also help transport larvae off the Bank. For example, satellite imagery shows plumes of water escaping off the northern edge of Georges Bank into the Gulf of Maine (J.W. Loder, pers. comm.). Winds can transport water and larvae off the Bank as evident from surface ARGOS buoy data (Drinkwater et al. 1992). On August 23, 1988, four buoys were deployed on the northern edge of the Bank. They were tracked for 3 d during which winds blew from the east at speeds of up to 12 ms^{-1}. Three of the four moved northward off the Bank as well as upwind in the direction of the residual current. The northward motion is consistent with wind-driven Ekman response. While eddies and winds may transport lobster larvae northward it must be remembered that these processes are not continual but only occur occasionally. For example, surface drifters were not observed to leave the Bank in July and August of 1988 during five other deployments of two to four buoys each, tracked for from 1 to 3 d (Drinkwater et al. 1992). Between July 14 and 29, 1989, 28 Loran-C, drifters drogued at 10 m, and 14 surface ARGOS drifters were found to maintain their position either on or off the Bank or occasionally to move from near the northern edge onto the Bank (Drinkwater et al. 1992). During two buoy deployments the abundance of lobster larvae from the immediate vicinity of six Loran-C drifters was analyzed for change over the three to four sampling intervals (Fig. 4 and 5). A significant alteration of the larval lobster population occurred during the drift time of the three on-Bank drifters whereas no difference was observed in the immediate vicinity of the three drifters located in the Gulf of Maine (ANOVA, Wilkinson et al. 1989). The latter population was dominated by the more advanced stages whereas the on-Bank population consisted mainly of Stages I and IIs. One most plausible reason why the off-Bank drifters tracked the larval population better is that the latter stages do not undergo such a marked daily vertical migration and therefore their drift was approximated by the 10-m drogue. Stage I lobster, however, are known to reside chiefly between 15- and 30-m depth during daylight and above 10-m depth during the night, but always above the thermocline, on nearby Browns Bank (Harding et al. 1987). It is less likely that their movement would be expected to approximate that of the 10-m drogued drifters.

The plankton assemblages that exist across the frontal zone are illustrated here with the third of four transects run in August of 1988 (Fig. 6). In the upper panel the strong summer stratification in the Gulf of Maine, portrayed by the sharp temperature gradient in the upper 30 to 50 m, gradually dissipates over the Bank through tidally induced turbulence in the frontal zone on Georges Bank. The front was located close to Station 4 during this transect. The distribution of the phytoplankton and zooplankton associations present at this time of the year was similar, indicating that the greater vertical mobility of the larger organisms was not altering substantially the species distribution, at least not with the present broad statistical approach used. A Bank association existed (designated Pattern A), which can be subdivided into a near-surface (A1) and deeper-water component (A2) in the case of the zooplankton, that extends from the tidally well-mixed area to near the edge of the Bank along the bottom but out over the edge of the Bank in the more surface waters. The Gulf of Maine association can likewise be divided into a shallow- (B1) and deep-water component (B2). This Bank plankton pattern (A) corresponds to our observations of the distribution of Stages I and II larval lobsters, but not the more plentiful presence of Stages IIIs and IVs in the B1 area off the Bank. In conclusion, these more advanced stages most likely originated upstream either from Georges Bank, being transported off the Bank by eddies or by wind events, or from further upstream in more coastal waters off Cape Cod. The predominance of later stages off the Bank in the Canadian sector in July and August could partly be explained, then, by the more advanced seasonal cycle in the south. However, it could also be explained by directed swimming of Stage IV larvae off the Bank.

The lipid content of our lobster larvae was identified and quantified to assess the health and presumed viability of individuals caught over and in the proximity of Georges Bank in 1988 and 1989. Triacylglycerols (TAGs) are the predominant storage lipid in lobster embryos and larvae, and their levels subsequently reflect the feeding history of the organism as they are utilized under starvation conditions(Sasaki 1984; Sasaki et al. 1986). Sterols, conversely, are largely structural lipids which have been found to remain essentially unchanged in larvae after 5 to 6 d starvation (Sasaki 1984). The ratio of the triacylglycerols to the structural sterols or dry weight of the individual has been used successfully as a condition index for larval lobsters to avoid the dependency of triacylglycerol content on organism size (see Fraser 1989). In the present study TAG/STEROL and TAG/DRY WEIGHT ratios of larvae residing on Georges Bank were compared to those collected either on the periphery of the Bank or in the Gulf of Maine (Fig. 7). Stages III and IV lobster larvae residing off the Bank in both 1988 and 1989 had significantly higher TAG/STEROL and TAG/DRY WEIGHT ratios (t-test on log-transformed variables and Mann-Whitney U-test, $p<0.005$) than their counterparts on Georges Bank. Stages I and II larvae were not found off the Bank in 1988, but the few larvae collected on the periphery of the Bank in 1989 had significantly higher ($p<0.001$) TAG/STEROL and TAG/DRY WEIGHT ratios than the vast majority of the population collected over the Bank. This suggests that either the larval feeding conditions were better off the Bank or that predator avoidance behaviour used more energy on the Bank. The latter appears more plausible at this time of year because the Bank is swarming with *Gammarus annulatus*, *Sagitta elegans*, etc., and planktivorous feeding fishes such as billfish (*Scomberesox saurus*), sandlance (*Ammodytes americanus*), etc., whereas production has slowed considerably in the lower trophic levels following the establishment of a strong summer stratification of the surface waters in the central Gulf of Maine (Sissenwine et al. 1984).

CONCLUSIONS

1. Offshore larval lobster hatching in the Gulf of Maine is largely restricted to the shoal areas such as Georges, Browns, and German Banks.

2. Stage IV lobster larvae are present in the Browns Bank area earlier than would be expected from their known hatching time. The most likely source at this time of the year would be "upstream" from the northern face of Georges Bank.

3. The predominance of later-stage larvae in the Gulf of Maine near Georges Bank in July similarly could be explained by Stage IV larvae swimming through the front or an upstream source, either from southwestern Georges Bank or the coastal area off Cape Cod.

4. Wind events are shown to displace near-surface waters, and satellite imagery has documented eddies carrying plumes of water and presumably lobster larvae off of Georges Bank.

5. Larval lobster populations were successfully followed off the northern face of Georges Bank for up to 66 h with an overall displacement of $\sim$30 nm. This demonstrates that rapid transport occurs along the northern periphery of Georges Bank and carries lobster larvae from either Georges or further upstream toward Northeast Channel.

6. Phytoplankton and zooplankton distributions demonstrate that the summer Bank community is not bounded by the tidal front on the northern side of Georges Bank but extends off the Bank, depending on the tidal cycle, into the Gulf of Maine through the frontal zone. This distribution makes it more likely that surface-living plankters, such as lobster larvae, could be displaced off of the Bank with wind events or hydrographic features such as periodic eddy formation.

7. The lobster larvae caught off Georges Bank appear to be in better health, judging from their lipid reserves, than their counterparts over the Bank. Considering the bountiful presence of prey on the Bank, the poorer condition of larvae over the Bank must be related to their energy consumption during predator avoidance. The

prolific amphipod *Gammarus annulatus* would be the major cause for avoidance behaviour by lobsters during July and August.

8. The relative importance of settling Stage IV lobsters over Georges Bank, compared to the off-Bank population, in the recruitment of the Gulf of Maine system needs more study.

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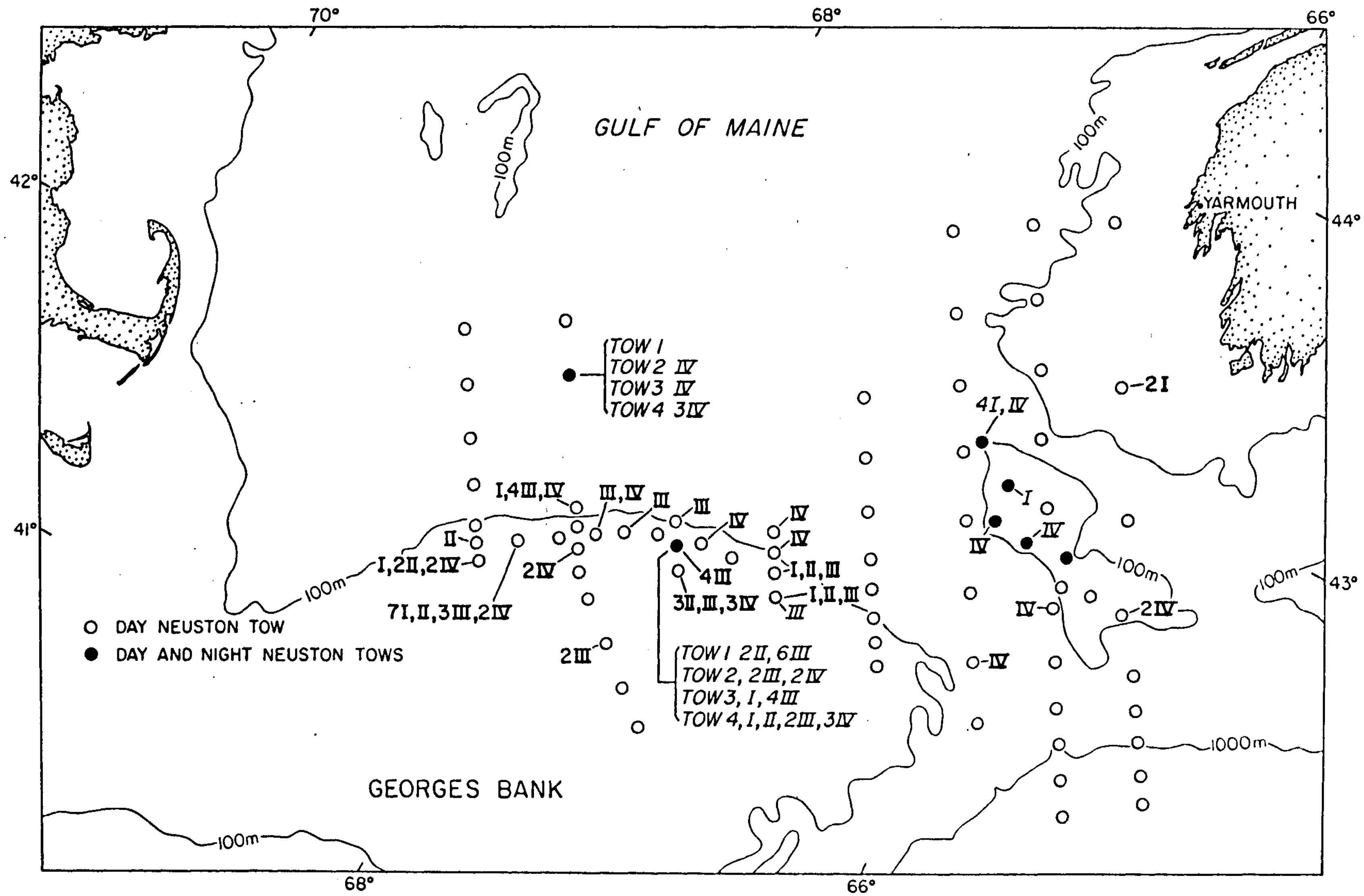

Figure 1. Distribution of larval lobster abundance (individuals per 30-min. tow) by stage in a July 12 to 21, 1983, survey of the upper 1 m surface layer of the German, Browns, and Georges Bank region of the Gulf of Maine.

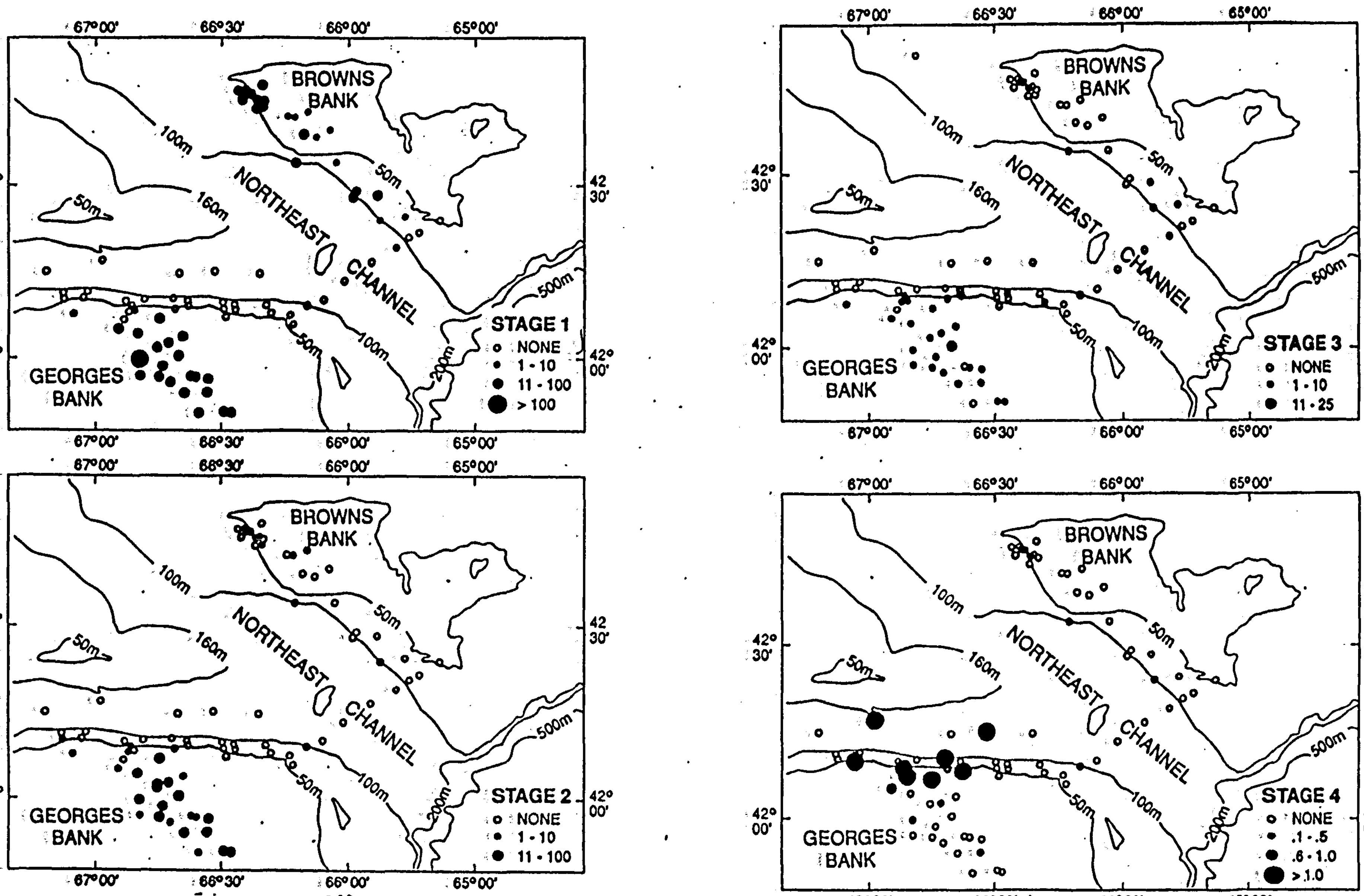

Figure 2. Distribution of larval lobster abundance by stage (individuals • 1000 m^{-2}) in the July 14 to 28, 1997, study with amalgamated horizontal Vass-Tucker trawls from 50 m maximum depth or the bottom to the surface (5 m depth intervals sampled in the upper 30 m and 10-m depth intervals below this).

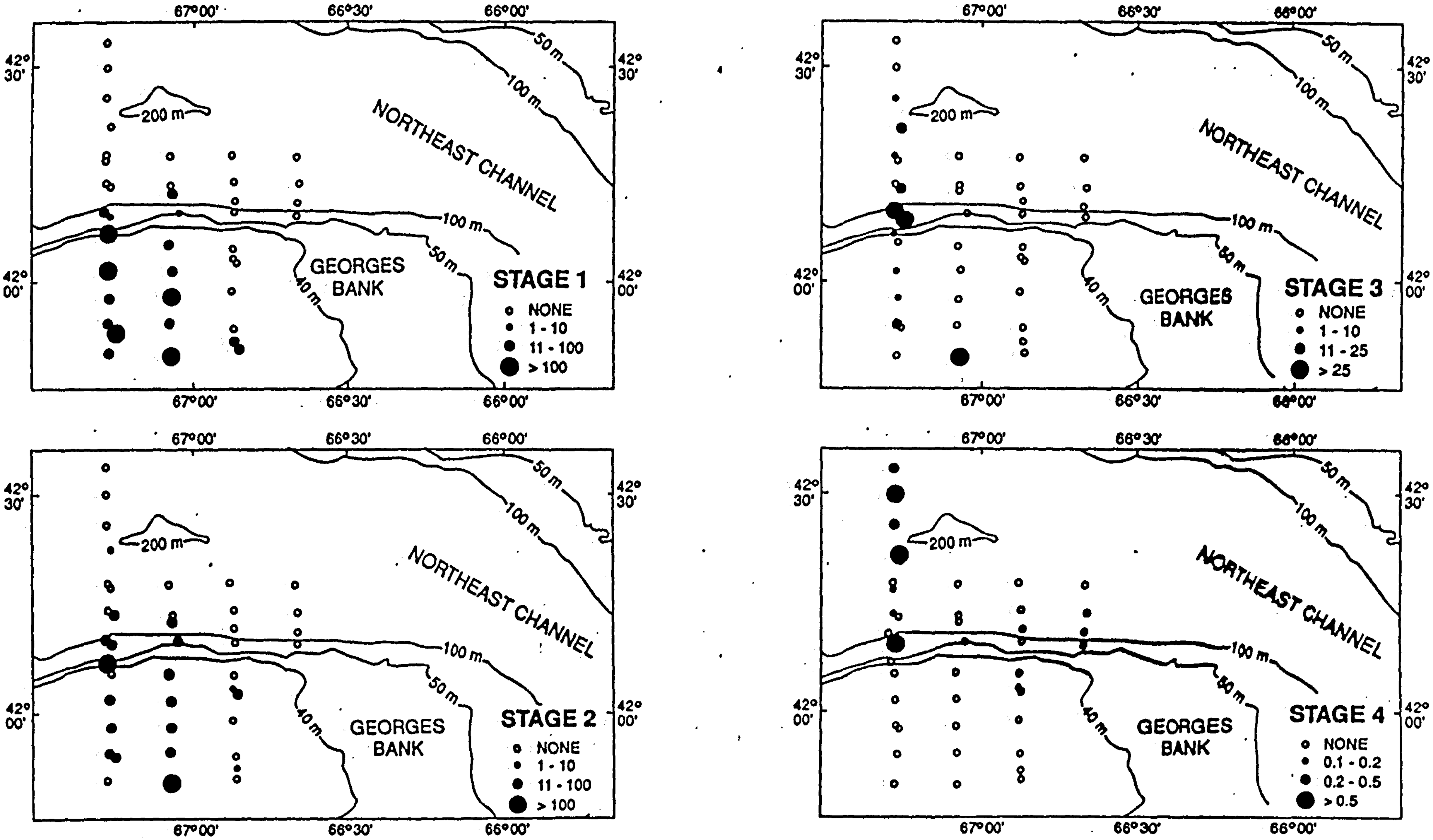

Figure 3. Distribution of lobster larvae abundance by stage (individuals $\cdot$ 1000 m^{-2}) in the July 14 to 17 and 30, 1989, survey with stepped oblique Vass-Tucker trawls from 50 m on the bottom to the surface.

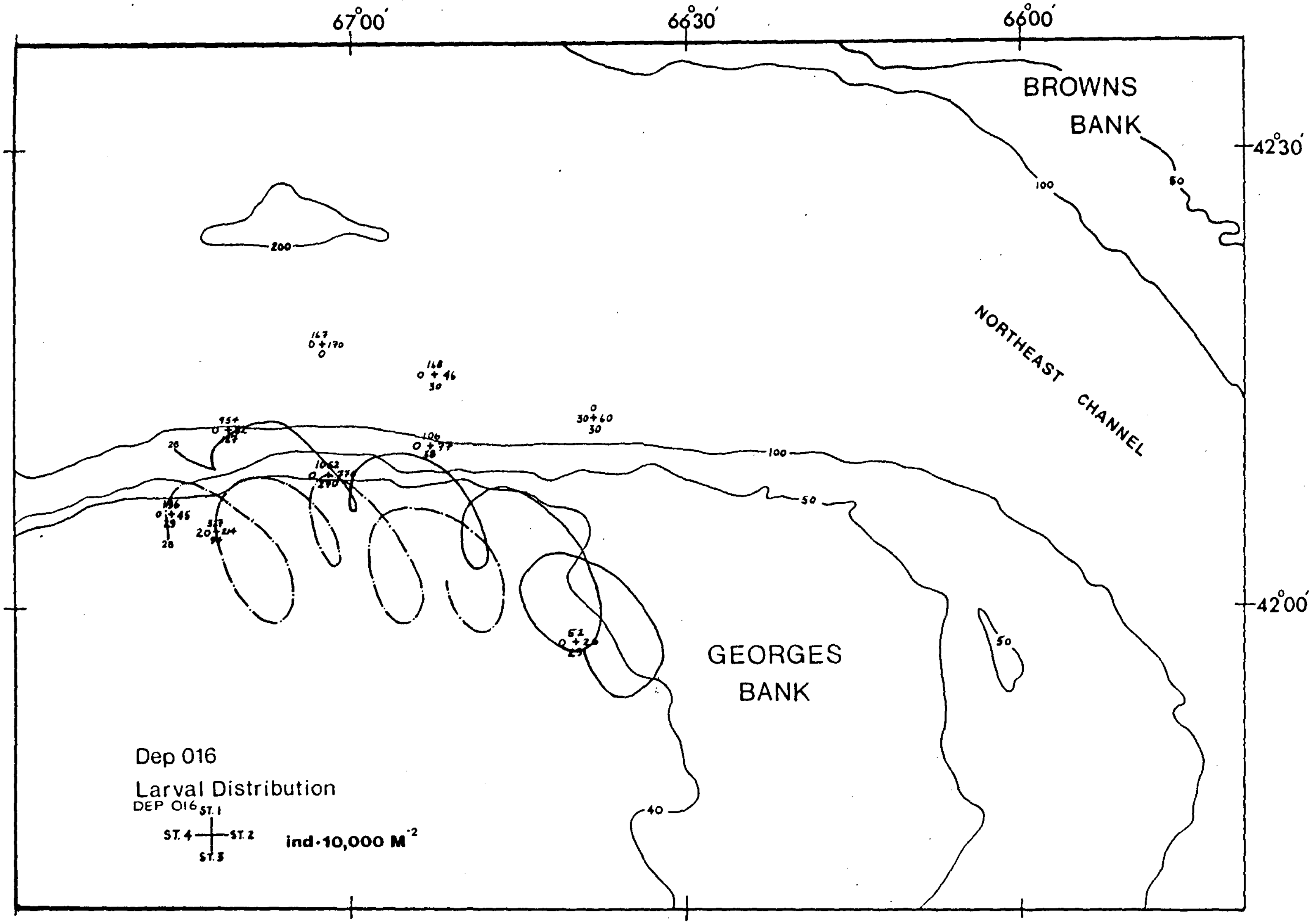

Figure 4. Movement of Loran-C drifters drogued at 10-m depth and the average larval lobster abundance by development stage from three replicate trawls at various locations along their drift track, July 24 to 26, 1989.

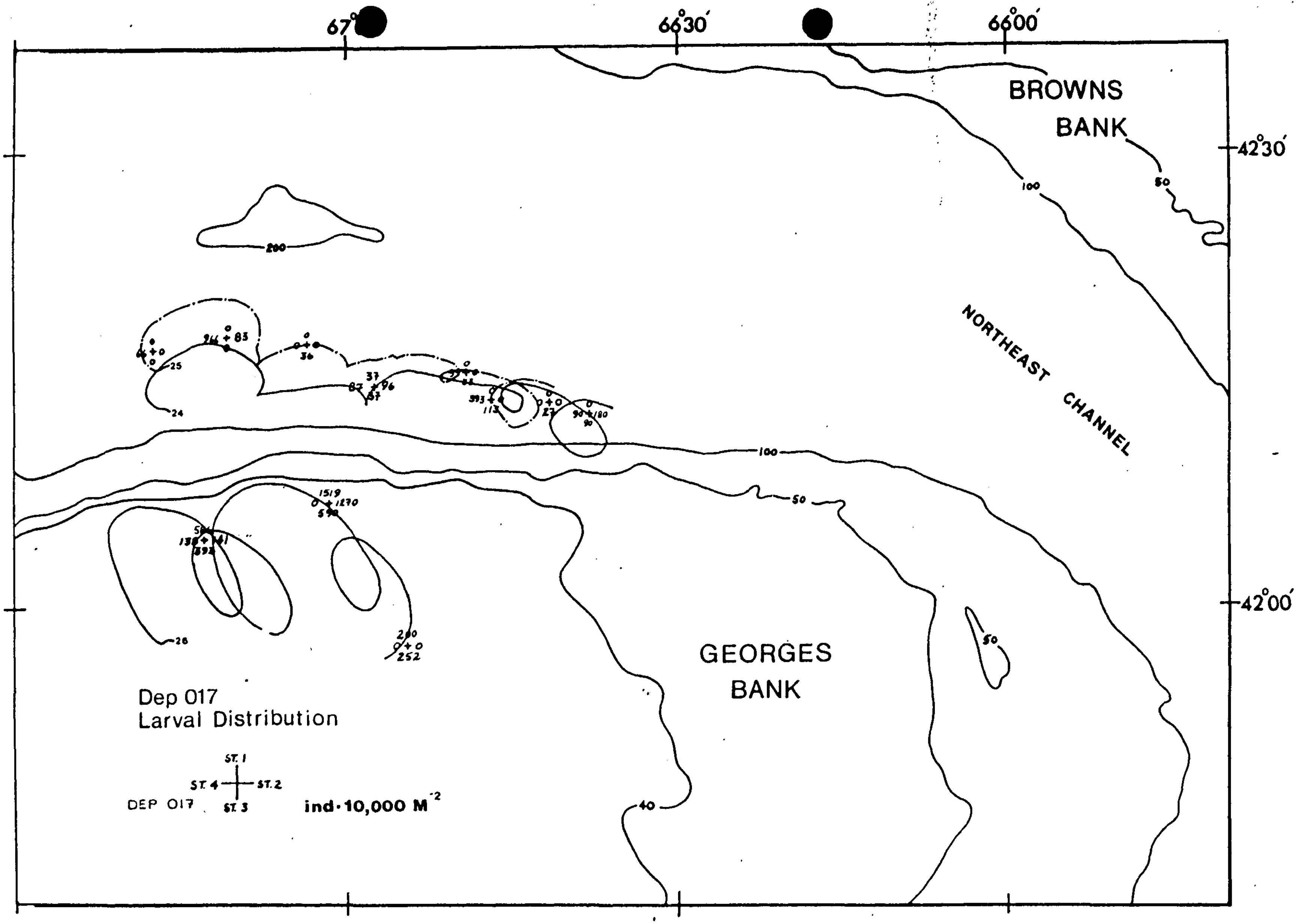

Figure 5. Movement of Loran -C drifters drogued at 10-m depth and the average larval lobster abundance by development stage from three replicate trawls at various locations along their drift track, July 27 to 29, 1989.

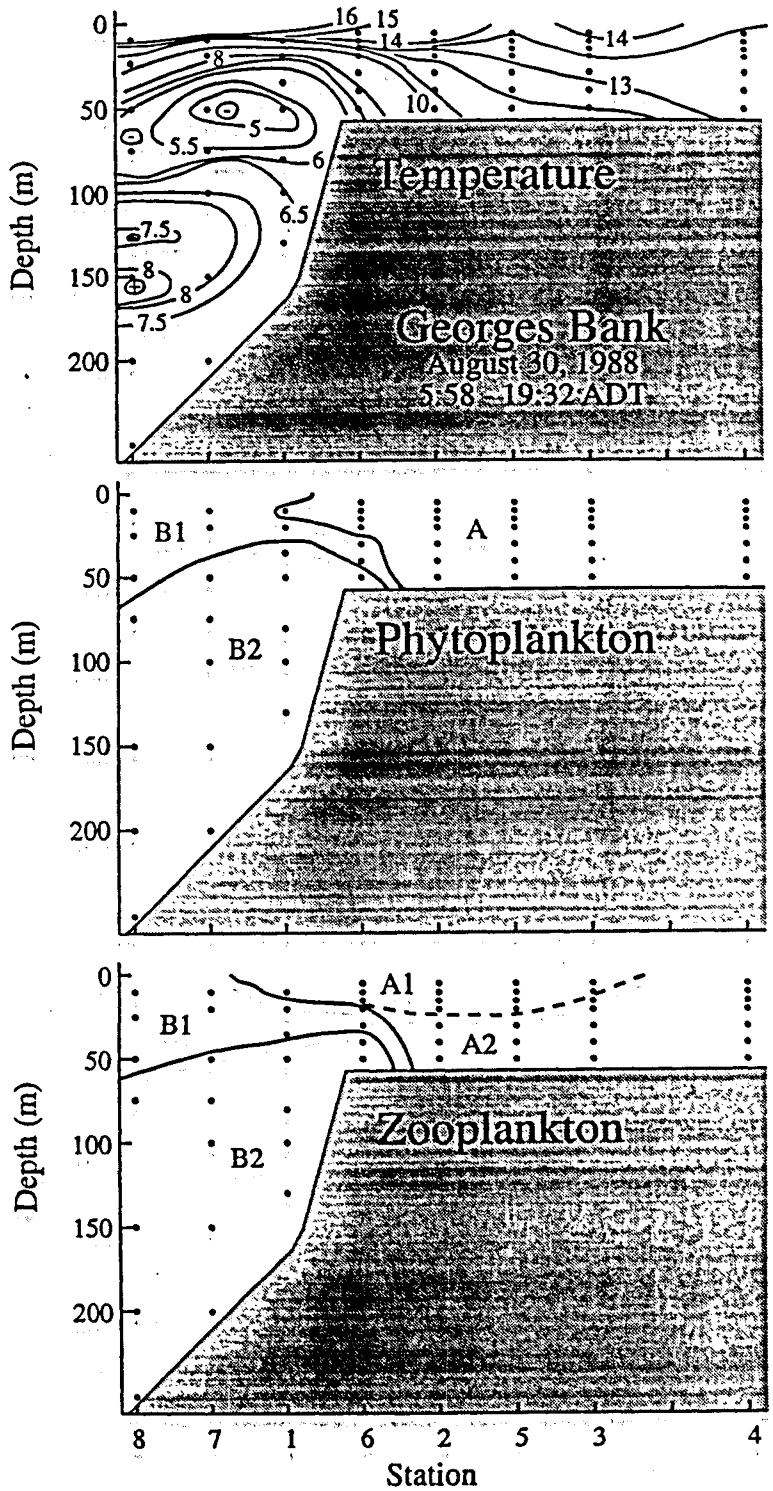

Figure 6. The distribution of temperature, phytoplankton, and zooplankton associations across the northern edge of Georges Bank, August 30, 1988.

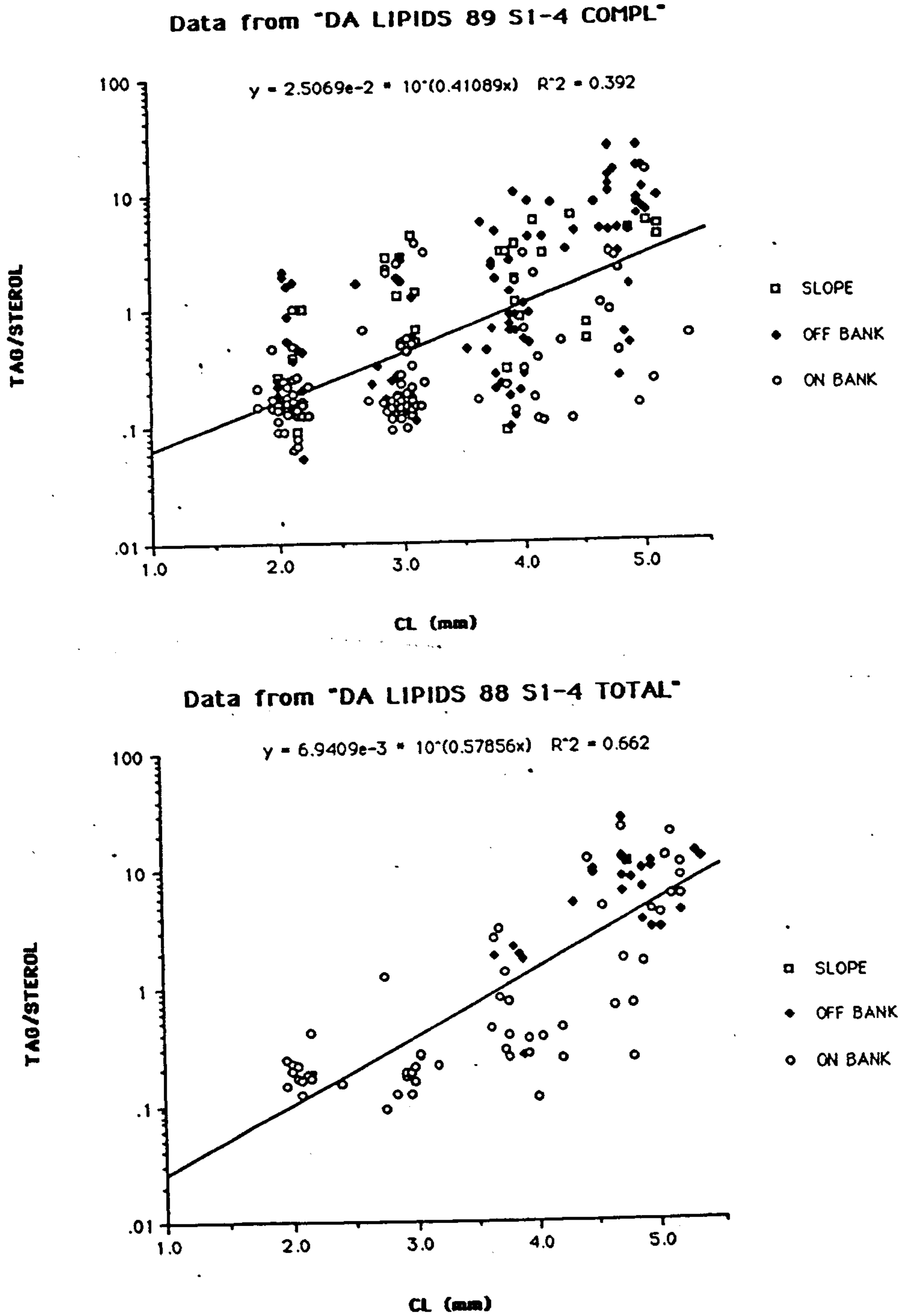

Figure 7. The triacylglycerol (TAG) sterol weight ratios of larval lobsters collected on, over the edge, and off the northern face of Georges Bank in July 1989 (upper panel) and August 1988 (lower panel) plotted against carapace length (CL). The best least-square fitted equation is shown.