Fløddevigen rapportser., 1, 1984. ISSN 0333-2594
The Propagation of Cod *Gadus morhua* L.

LARVAL FISH TROPHODYNAMIC STUDIES ON GEORGES BANK: SAMPLING STRATEGY AND INITIAL RESULTS

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ABSTRACT

Lough, R. G., 1984. Larval fish trophodynamic studies on Georges Bank: Sampling strategy and initial results. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Editors), The Propagation of Cod *Gadus morhua* L. Fløddevigen rapportser., 1, 1984: 395-434.

A sampling strategy is outlined to serve as a framework for determining the fine- to micro-scale vertical distribution or fish larvae and their prey on Georges Bank in a single vessel, interdisciplinary mode of operation. A major objective of this sampling program is to characterize the development and temporal-spatial variability of these distributions to evaluate growth and survival of larval populations. The operational plan, sampling gear and instrumentation, as well as special techniques employed are discussed in terms of the usefulness of the parameters measured. Initial results are presented from a two-part study conducted in April-May 1981, focused on haddock (*Melanogrammus aeglefinus* L.) and Cod (*Gadus morhua* L.) larvae.

In April, a gadid egg patch with recently-hatched larvae (c. 91% haddock) was located on the southeastern part of Georges Bank, between the tidally-well-mixed front (c. 60-m isobath) and the shelf/slope-water front (c. 100 m). The water column along the southern flank was still well-mixed in April and the larvae were broadly distributed with a weighted mean depth between 30 and 40 m. Density of their dominant copepod prey was relatively low near the surface (<3 prey/l) but increased with depth (5-10 prey/l).

When the same larval population was surveyed again in May it had moved to the southwest at a rate consistent with the residual currents. By May the water column was stratified along the southern flank. A seasonal thermocline was observed between 10 and 20 m and fish larvae and their prey (50 prey/l) were concentrated in this zone. A storm swept the region and dispersed the larvae and prey (5-10 prey/l) throughout the water column. On the crest of the bank in the well-mixed waters (<60 m), larvae and their prey (10-25 prey/l) were broadly distributed vertically, but the mean depth of the larvae coincided with the highest density of prey at middepth. The implication of these observations to haddock and cod survival are discussed.

INTRODUCTION

Other than catastrophic losses, trophic (feeding) interrelationships involving both growth and predation are considered to be the basic factors controlling larval mortality. The mortality process at the individual level is thought to be a function of chance encounters by larvae with their predators and zooplankton prey which (like the larvae themselves) are distributed contagiously or in patches (Lasker, 1975; Vlymen, 1977; Beyer, 1980). It is believed that the degree to which larvae are able to grow rapidly through a succession of decreasing predatory fields, thereby reducing mortality, determines their potential population size. However, this process is a complex function of the density distribution (patchiness) of the larvae, their prey and predators, and possible competitors or other forms which may be alternative prey of larval predators. Since prey abundance below some level will be a critical factor influencing larval survival, it is necessary to know how feeding of larvae in the field is affected by the fine-scale (patchy) distribution of plankton communities and to understand the biological and physical processes which lead to the formation and dissipation of such patches.

At the Northeast Fisheries Center (NEFC), the Marine Ecosystems Division is conducting a broad-based research program (MARMAP) on the Continental Shelf, involving both monitoring and process-oriented studies, directed towards a better understanding of the recruitment process (Grosslein et al., 1979; Sherman, 1980). In the last decade, process-oriented studies have been carried out by the NEFC in the Georges Bank area addressing the recruitment problem. The first major study is represented by the autumn 1978 Larval Herring Patch Study which was conducted as an international, multi-ship, multi-disciplinary experiment (Lough, 1979). The primary objective was to define and follow a patch (homologous cohort) of herring larvae as a dissipative feature to gain a better understanding of the physical processes affecting its dispersal. The sampling strategy was designed to provide short-term estimates of larval growth and mortality in relation to the prey-predator field as the patch advected. More recent studies have been conducted on haddock and cod larvae since spring 1980 in a single vessel, inter-disciplinary mode of operation. Most of the sampling effort in this mode is to determine the fine- to micro-scale vertical distribution of larvae and their prey (copepods) in well-mixed and stratified waters. A major objective in this case is to characterize the development and temporal variability of these distributions for use in simulation models. These studies require different sampling strategies within the constraints of available resources to meet the desired objectives.

Each sampling strategy must be uniquely designed for the specific objectives and hypotheses investigated, taking into account the peculiarities of the target species and its biological and physical environment. However, as an investigation of larval fish growth and mortality is inherently complex, involving the intimate interaction of three trophic levels simultaneously (Shepherd and Cushing, 1980; Laurence, 1981), a multi-faceted sampling strategy is required to

resolve patterns and interactions occurring on the overlapping time-space scales (Haury et al., 1978). In this paper our sampling strategy is presented on the haddock-cod study which has evolved in part from the results of the Larval Herring Patch Study. The experimental objectives, sampling gear and instrumentation employed are discussed in terms of the usefulness of the parameters measured and highlighted with data analyzed to-date.

Target Species

Haddock (*Melanogrammus aeglefinus* L.) was chosen as the main target species, followed by cod (*Gadus morhua* L.), because of its commercial and ecological importance and the best overall base of life history data. This data base includes extensive laboratory experimental data, an index of year-class strength at the '0-group' stage, and fecundity and spawning population biomass data. The northeastern part of Georges Bank is a principal spawning ground for haddock and cod and their early life histories are similar in many respects. Their spawning seasons overlap, but for cod it is considerably longer and also its spawning distribution appears to extend further south than the haddock's (Colton et al., 1979). Cod spawn from late autumn into April-May, whereas haddock spawn from February to June. Peak spawning for both cod and haddock occurs in the spring with cod spawning about a month earlier than haddock. The onset and duration of haddock spawning appears to be associated with increasing water temperature (Marak and Livingstone, 1970).

Fertilized cod and haddock eggs hatch in about 2-3 weeks at average spring temperatures (Marak and Colton, 1961; Laurence and Rogers, 1976), and the larvae are planktonic for several months thereafter. The larvae hatch at c. 4 mm SL (Colton and Marak, 1969) and yolksac resorption is

completed 6-7 days post-hatch at 7°C (Laurence, 1974). Lab-reared larvae were considered metamorphosed (c. 10 mm, 1000 µg dry wt) in 30 days at 9°C and 40-50 days at 7°C. Fig. 1 depicts the principal haddock spawning time and area on Georges Bank, the generalized egg and larval drift, and areas where demersal 0-group fish are most abundant 6-8 months later (Grosslein and Hennemuth, 1973). The distribution of late stage eggs and recently-hatched larvae indicate that dispersion from the spawning center on northeast Georges follows the general pattern of drift, predominantly to the southwest at 1-4 miles/d (2-7 km/d) (Walford, 1938; Marak and Colton, 1961; Colton, 1965; Smith et al., 1979). During April-May, high concentrations of larvae (>0.1/m^3) can be found along the southern flank of Georges between the 60 and 100 m isobaths. Some

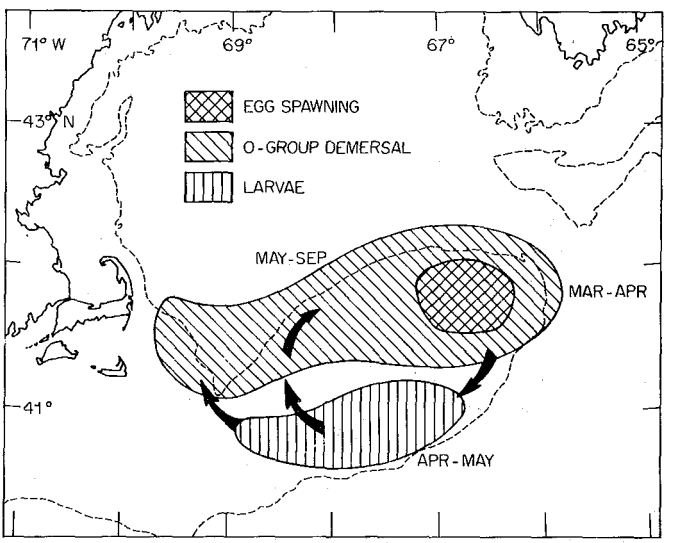

Fig. 1. Principal haddock spawning area on Georges Bank and generalized larval drift (indicated by arrows) and areas where demersal 0-group haddock are most abundant 6-8 months later.

portion of the larvae apparently are transported north on the western side of Georges Bank, but little is known about possible losses of larvae off the bank. The 0-group fish tend to be concentrated on the northern part of the bank indicating a favorable environment for their survival.

Hydrography of Georges Bank

The residual drift of Georges Bank is described as a semi-enclosed clockwise circulation with a mean speed of approximately 10 cm/s or 5 km/d (Fig. 2). A counter-clockwise circulation develops in the Gulf of Maine and both gyres intensify in the summer (Bumpus and Lauzier, 1965). In winter the

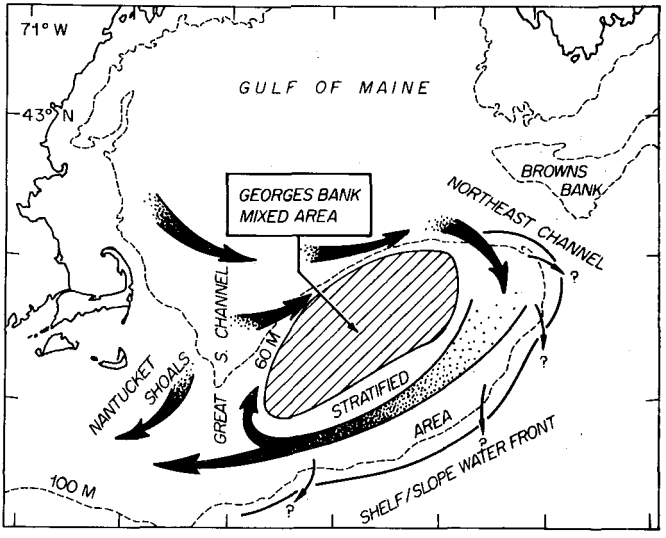

Fig. 2. Schematic representation of the well-mixed and stratified waters on Georges Bank and mean circulation flow (arrows) during spring and summer.

near surface flow is generally driven by the winds; the mean transport is offshore. Recent studies summarized by Butman et al. (1982) concluded that the observed mean flow at 10 m has a permanent clockwise circulation around Georges Bank with a mean circuit time of c. 2 months for a parcel moving along the 60 m isobath. Despite the considerable variability that could occur in the trajectory of such a parcel, they inferred that the clockwise circulation around the crest of the bank may provide a mechanism for partial retention of plankton.

The water on Georges Bank shoaler than 60 m is vertically well-mixed throughout the year by the semi-diurnal, rotary tidal currents that have speeds up to >2 knots (103 cm/s) (Bumpus, 1976). Progressive vector diagrams of the tidal elipses are oriented NW-SE on the crest with their long axes ranging 4-8 miles (7-15 km) in length. Summing the hourly speeds over a 12 h period, an approximation of the distance travelled by a parcel of water ranged 10-20 miles (19-37 km) over the shoals and 5-6 miles (9-11 km) over the deeper parts.

Besides the dominant tidal energy on the shelf, storms at 4-5 d intervals have an important role in shelf water dynamics (Beardsley et al., 1976).

In winter the well-mixed water is separated from adjacent water masses by two fronts. On the southern flank, the shelf/slope-water front intersects the bottom at about 80 m and separates the cooler, fresher shelf water from the warmer, more saline slope water. On the northern side, a subsurface front separates the Georges Bank water from the Gulf of Maine water. In late spring-summer a seasonal thermocline (20-30 m) develops in waters greater than 60 m. A subsurface band of cool winter water is found along the southern flank between the 60 and 100 m isobaths.

Gulf Stream warm-core eddies moving near the southern edge of the bank may play an important role in the movement of shelf/slope-water, both on and off the shelf, and the entrainment of organisms residing there (Lough, 1982; Joyce and Wiebe, 1983).

Objectives and Sampling Strategy

The main focus of the haddock-cod study to-date is to describe the spatial-temporal variability of larvae and their prey (copepods) during their first month of life on Georges Bank. Observations also are made to better understand factors governing their production and to survey post-larvae and potential predators of larval fish by sampling the macro-plankton and micro-nekton components on the same cruise. Our sampling program is presently designed to investigate the following hypotheses which we feel are important in order to understand the feeding dynamics and survival of larvae retained on Georges Bank:

1. Growth of larvae is related to the density of micro-zooplankton prey.
2. Micro-zooplankton are concentrated in areas of relatively high phytoplankton biomass.
3. Micro-zooplankton are contagiously distributed (clumped).
4. Stratification of the water column along the southern flank of Georges Bank in late spring serves to concentrate zooplankton and fish larvae vertically.
5. Feeding success is a stochastic process of random encounters with 'patchy' prey.

Supportive evidence for the first four hypotheses can be made by field observations; the fifth hypothesis must be investigated through probabilistic food encounter models or quasi-realistic laboratory experiments. The thermocline is potentially important because biological productivity appears concentrated near this layer and larval and juvenile haddock appear to be uniquely associated with it (Miller et al., 1963; Colton, 1965, 1972; Houghton and Marra, 1983). During spring when recently-hatched larvae are present, the seasonal thermocline is beginning to form, vertically stratifying the water column (>60 m bottom depth). The presence of a discontinuity layer resulting in a greater degree of structure and patchiness of the plankton may be critical to the survival of larvae in this region. There is a need to measure prey availability prior to, during, and after thermocline formation in order to evaluate the importance of this phenomenon.

A field program addressing these hypotheses requires sampling on spatial scales ranging from centimeters to kilometers and temporal scales from minutes to weeks. Considerable emphasis is given to the smaller scales of pattern as individual larvae encounter their prey on the micro-scale level (1 cm to 1 m); however, a larva's swimming capabilities soon develop to where it can migrate vertically 10's of meters in a matter of hours. Sampling larvae at the population level requires discrete samples at the fine-scale level (1 m to 1 km), for example, to resolve vertical migration patterns. To define a coherent patch of larvae, or to sample post-larvae or larger predators, requires sampling on a coarse scale (1 to 100 km). Synoptic, three-dimensional sampling of the variable fields is needed, but our present technology and sampling techniques usually only permit quasi-synoptic sampling of the parameters or organisms of interest (Kelley, 1976). The sampling gear used should be directed towards collecting discrete samples of the target organism

as synoptically as possible at the population level. However, since populations of larvae, their prey and predators usually occur at different scales, an array of sampling gear is required which tends to negate simultaneous sampling, unless more than one research vessel is used. Nevertheless, we can approach near synopticity for some elements of the sampling program utilizing just one vessel.

The rotary tides (12.4 h period) are the dominant forcing function on the bank so that experiments should be nested within its space-time domain. According to the Nyquist theorem, which states that a function can be detected if its period is at least twice the sampling frequency, station sampling on a grid would have to be taken at least once every 6 h at a sampling distance between 5 and 20 miles (9 and 37 km) depending on bottom depth. And in order to encompass a before and after storm event, observations should be repeated every 2 d over at least an 8-10 d period. Sameoto (1975, 1978) found that zooplankton variability was similar over a broad area of the Scotian Shelf so that an accurate and efficient estimate of population means could be made by taking 2 net samples 6 h apart at a fixed station.

Our basic field strategy is to locate and characterize a population of larvae and their prey, and then to compare and contrast their fine- to micro-scale distribution within stratified and well-mixed waters on Georges Bank. Previous experience from the 1978 Larval Herring Patch Study indicated that relatively coherent and stable patches of larvae and zooplankton could be defined with conventional sampling techniques (bongo-net samples) and followed for a number of days to weeks at a spatial scale somewhat greater than the tidal excursion (>5 miles or >10 km). It was assumed for sampling purposes that variability within the tidal regime was similar as mixing processes dominate on this scale. Also, by following a drogue for station time-series observations, one assumed the same parcel of water was being sampled with the

same larvae-prey population. Thus, by reducing horizontal variability, aliasing of observations vertically would be reduced in order to conduct time-series observations over a minimum of two tidal cycles. The limitations of time-series analyses in marine ecosystems are discussed by Denman and Platt (1978).

The deployment of moored current meter arrays can provide a truly synoptic three-dimensional picture of the horizontal current field within the study area. Coarse to meso-scale MARMAP plankton-hydrography surveys conducted on Georges Bank and contiguous waters during the same time provide a broader background in which to compare our more intensive fine-scale studies. Remote sensing offers the potential of regional synopticity for a number of near-surface parameters such as ocean temperature and color (Chamberlin, 1982; Gower, 1982).

METHODS

Gear, Instrumentation, and Special Techniques

Bongo-net sampler

Standard MARMAP bongo-type samplers are used to make integrated water-column hauls from 5 m above the bottom to the surface to collect zooplankton (Posgay and Marak, 1980). A 61-cm bongo sampler (505 and 333 μm mesh nets) and 20 cm bongo sampler (253 and 165 μm nets) array are towed obliquely at 1 1/2 knots (78 cm/s) and lowered at a wire speed of 50 m/min and retrieved at 20 m/min. Water filtered through each net is measured by a flowmeter and the tow depth profile is measured with a time-depth recorder.

MOCNESS

A Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976; 1982) with three separate underwater sampling units (1/4 m, 1 m, 10 m) provides us with wide spectrum capabilities of sampling discrete vertical strata encompassing three trophic levels from micro-plankton, fish larvae-zooplankton, to micro-nektonic organisms. MOCNESS is a rectangular sampler whose nine serially linked nets can be opened and closed sequentially by commands through a conducting cable from the surface vessel, thus permitting sampling of up to nine discrete depth levels or horizontal series in a single haul. The three underwater samplers are designed to be hauled at 1 1/2 knots (78 cm/s), 45^{o} net angle, for an effective mouth area of 1/4 m^2, 1 m^2, and 10 m^2. Standard net mesh size for the underwater units are 64 μm, 333 μm, and 3 mm, respectively. On-deck, real-time monitoring includes depth (pressure), net angle, number of the net presently filtering water, volume of water filtered, temperature and chlorophyll fluorescence (Aiken, 1981). Parameter data are stored on an HP-85 computer system for real-time X-Y plots of temperature and fluorescence vs. depth, which are useful in selecting sampling depths (see Fig. 3). A Northstar Loran C unit with plotter also is integrated with the MOCNESS for recording the position at each net release. Other sensors such as salinity, light, and oxygen will be integrated with MOCNESS.

Plankton pump

In 1981 a 1-hp submersible well pump was used to sample micro-zooplankton at depth. The pump is typically deployed attached to 1/4" (6.4 mm) wire with a 45 kg lead ball. Delivery of water from depth to a deck manifold fitted with fine-mesh nets (20 and 53 μm mesh) is by a 7.5 cm diameter PVC discharge hose. Water is typically pumped from five

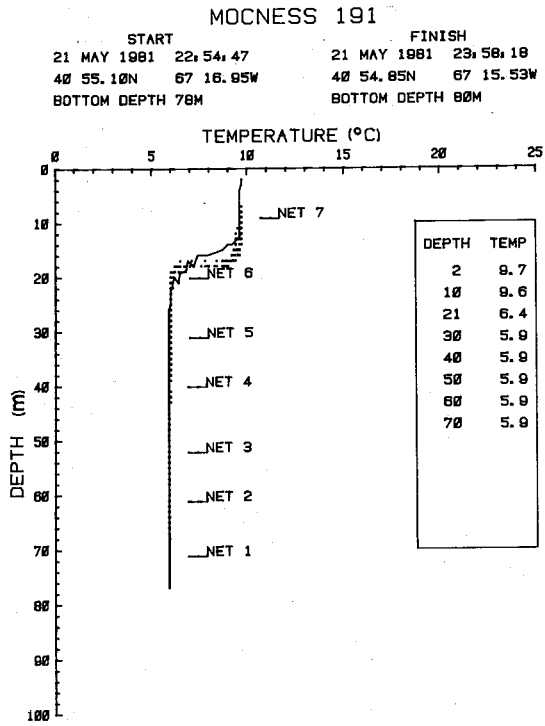

Fig. 3. Real-time temperature-depth plot of 1 m MOCNESS haul 191. A solid temperature line is drawn as net is set to maximum depth and dotted after first net is opened and sampling sequence begins.

depth levels in the upper 50 m of water for 10 min each depth to filter 1 m^3 of water. Since the 1982 season, a larger submersible pump has been used to filter 1 m^3 of water in 1 min.

CTD-fluorometer

A Neil Brown CTD micro-profiling system with a General Oceanics Niskin bottle rosette is used for rapid continuous profiling of temperature and salinity with depth. The water

bottle collections also are used to make discrete observations of micro-zooplankton, nutrients, and phytoplankton biomass measures by conventional methods. Continuous *in-situ* fluorescence is measured at the same time by deploying an ENDECO submersible fluorometer (Turner Designs Model) with on-deck recording of depth, fluorescence, and temperature via conducting cable. A recently acquired Variosens *in-situ* fluorometer will be interfaced with the CTD.

Real-time zooplankton processing

In process-oriented studies there is need for real-time results so that decisions can be made to optimize the experimental operations. A method we employ at sea to make routine, quantitative analyses of plankton-net samples using silhouette photography techniques coupled with a microfiche reader, an electronic digitizer, and a small personal computer is described by Lough and Potter (1983). More than 90% of the organisms can be identified to species level and life stage, and a subsample enumerated within 20 min after collecting by this method.

A HIAC Criterion PC320 12-channel particle counting and sizing system (Pugh, 1978; Tungate and Reynolds, 1980) has been acquired for development as a real-time tool for the quantification of marine plankton. Three sensors (CMH-150, CMH-600, E-2500) are used to count particles in the range of 5-2500 μm. However, at present we process Niskin bottle water samples only in a batch mode. The HIAC unit has been interfaced with a Canberra Multi-Channel Analyzer and an HP-85 computer system to control all settings and functions. The instrument is being modified for *in-situ* particle profiling along the lines reported by Tilseth and Ellertsen (1984).

Larval condition and growth indices

Special collections of larvae, preserved throughout the cruise, are analyzed in the laboratory for biochemical content, histological and morphological assessment, and otolith increment deposition. Laboratory studies by Buckley (1979, 1981) have demonstrated relations between food availability and larval RNA/DNA ratios and growth rate. A regression model has been developed recently (Buckley, 1982) between temperature, RNA-DNA ratio, and mean daily protein growth rate which accounts for short-term growth over the previous 2-4 days. This sensitive technique is now being used to study the relations between environmental conditions and larval growth and survival in the field. From the same samples larvae are being analyzed histologically (O'Connell, 1976) and morphometrically (Theilacker, 1981) to evaluate their condition and develop criteria for detecting starved and weakened larvae. Population mean age and long-term average growth of larvae can be estimated by relating otolith growth increments to larval size (Bolz and Lough, 1983). An individual larva's past environmental growth history also may be revealed with proper laboratory verification of their otoliths (Radtke, 1984).

Prey selection

Larvae from selected MOCNESS hauls are processed for gut contents by the methods described in Cohen and Lough (1983) and Kane (in press).

Field Operational Plan

A concentration of larvae (or eggs) on Georges Bank is located from a previous MARMAP broad-scale survey, or at the time of the cruise by exploratory transects using standard bongo-net gear in likely areas. Then a grid of

40-50 stations, 5 miles apart, is occupied within a 2 d period to characterize the larval fish, plankton, and temperature-salinity field in an area sufficiently large (c. 30 x 50 miles [56 x 93 km]) to encompass the anticipated dispersal of plankton having a residual drift of 4 miles/d (7 km/d) in which the fine-scale station studies will be carried out over 4-6 d. The survey grid usually is situated so that stations overlap the shoal front of the well-mixed waters (<60 m) and the southern shelf/slope-water front (c. 100 m) bounding the stratified waters on the bank. A bongo haul and XBT drop are made on each grid station, and surface temperature, salinity and fluorescence are monitored continuously.

Based upon real-time sample analyses made during the grid survey, a station is selected for the fine-scale time-series observations and a drogue is deployed at the depth corresponding, ideally, to the weighted center of gravity of the larval population. On one occasion, a drogue was deployed with an array of vector-averaging current meters (VACM) positioned to measure current velocity and temperature at selected depths to determine shear in the water column. On station, the sampling scheme used is a combination of fine- to micro-scale observations in order to sample fish larvae and their prey, and other environmental parameters. This scheme allows 2-4 observations of each kind during a tidal period (12.4 h). On each drogue-follower station, time-series observations are made for a minimum of 30 h and sometimes as long as 50 h encompassing 2-4 tidal periods. A complete series of observations is made every 6 h in the following sequence: CTD-fluorometer cast, MOCNESS 1 m haul, plankton pump cast, CTD-fluorometer cast, and MOCNESS 1/4 m haul.

CTD-fluorometer cast

The objective of this operation is to obtain a vertical profile (and variability) of temperature, salinity, and chlorophyll *a* fluorescence on a micro-scale level. Casts may be repeated for short-term variability. Niskin water bottle samples are collected at selected depths for calibration purposes and particle size analysis using the HIAC PC320 system. Ancillary observations include a light-meter cast to define the light extinction curve, and a bottom-trip Niskin bottle cast to collect a phytoplankton sample within a meter of bottom.

MOCNESS 1 m haul

The objective of this haul is to determine the vertical distribution and abundance of fish larvae and larger zooplankton from near bottom (<5 m) to surface with 10 or 5 m resolution. An adequate sample of larvae (30-100 individuals) is usually obtained by filtering 250 m^3 of water which takes about 5 min for each net. During this 5 min the net travels a horizontal distance of c. 235 m.

Plankton pump cast

Micro-zooplankton samples are collected at 4-6 discrete depth levels based upon the vertical distribution of the fish larvae and environmental conditions. At each depth level, 1 m^3 of water is pumped on deck and filtered through 20 and 53 µm mesh nets. Sampling resolution is 1-2 m vertically and 10's of meters horizontally, depending on the rate of pumping and ship's drift.

MOCNESS 1/4 m haul

The objective of this haul is to determine the vertical distribution and abundance of micro-zooplankton retained by 64-μm mesh nets over the vertical distribution range of fish larvae. About 20-36 m^3 of water is filtered by each net (1-3 min) within an integrated strata of 10, 5, or 2-m resolution (94-170 m horizontal distance traveled).

Following the fine-scale station observations, the grid of stations may be resurveyed and new transects added in the direction of the residual current, or MOCNESS 10-m hauls may be made on a transect of stations in the study area. The 10 m MOCNESS is used to determine the vertical distribution and abundance of potential micro-nektonic predators and post-larvae with 15 or 25 m resolution, each net filtering 7000-14000 m^3 of water in 15-30 min (705-1410 horizontal distance traveled). A 1 m MOCNESS haul usually is made immediately before or after to collect larval fish or other food prey.

RESULTS AND DISCUSSION

Some of the initial results are presented here from a two-part study conducted aboard R/V ALBATROSS IV, 15-30 April 1981 and 18-30 May 1981. On the April cruise a well-defined concentration of gadid eggs was located on the southeast part of Georges Bank between the 60 and 100 m isobaths by the bongo sampling grid of stations (Figs. 4-8). Recently-hatched haddock and cod larvae (3-5 mm SL) were found most abundantly towards the southeastern part of the grid and a ratio of their abundance indicated that about 91% of the gadid eggs were haddock, the other 9% cod. The majority of eggs were at a late stage of development (Colton and Marak, 1962) and were estimated to have been spawned 8-10 d previously in the 6°C water. Early stage eggs were more abundant to the northeast near the

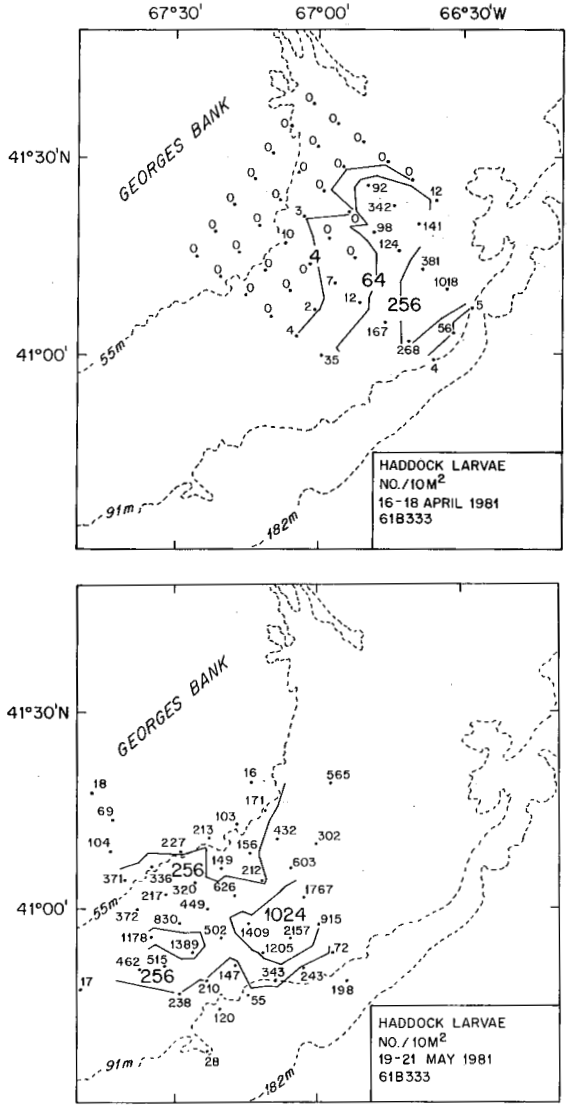

Fig. 4. Haddock larval distributions from April and May 1981 grid surveys. Densities contoured by factor level of 4.

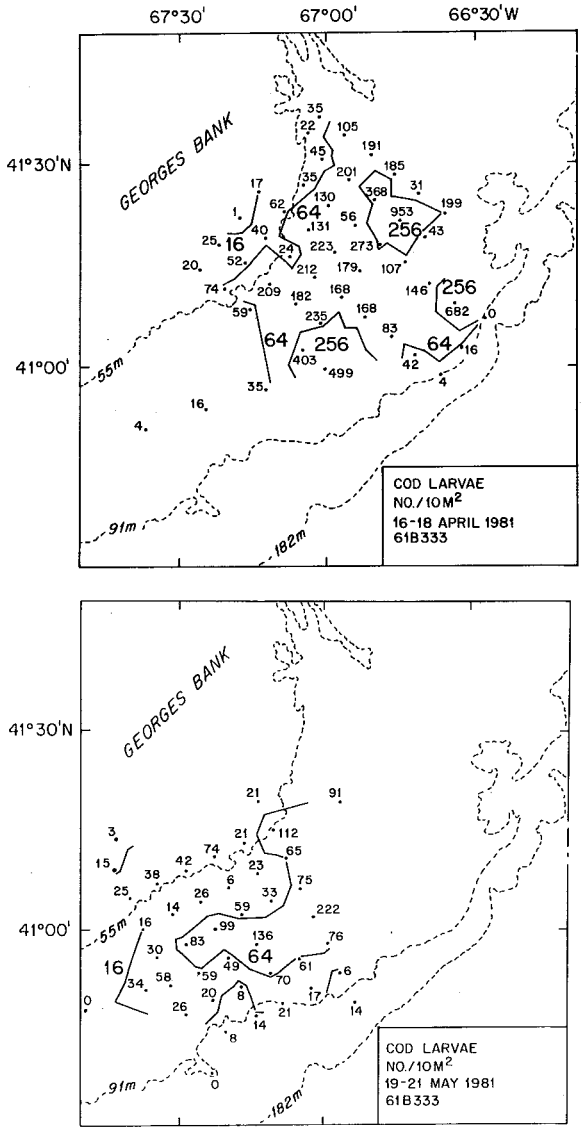

Fig. 5. Cod larval distributions from April and May 1981 grid surveys. Densities contoured by factor level of 4.

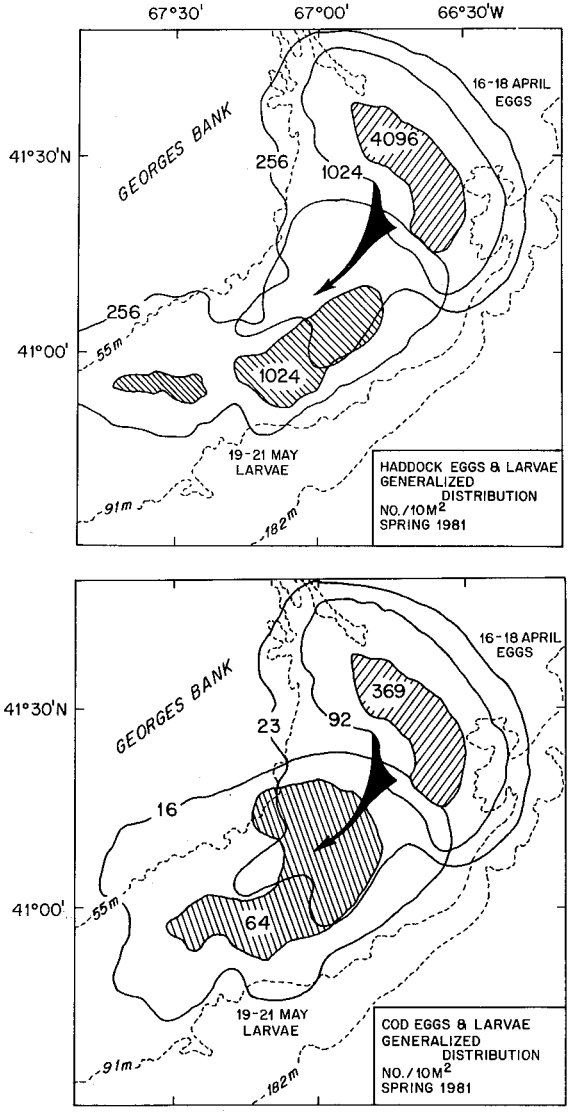

Fig. 6. Haddock and cod egg and larval distributions generalized from the April and May 1981 grid surveys.

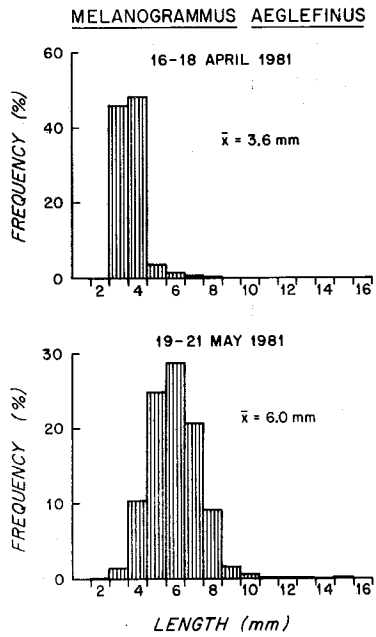

Fig. 7. Length-frequency distributions of haddock larvae collected on the April and May 1981 grid surveys.

historical spawning grounds. Cod larvae were more widespread than haddock and their greater size range was indicative of their earlier spawning in February-March.

By May, a concentration of larval haddock and cod was located along the southern flank of Georges to the southwest of the April distribution, situated between the shoal tidal front and the deeper shelf/slope-water front. The mean length of both larval populations sampled on the grid was 6 mm and is consistent with laboratory growth rates over the period of time between hatching in April and the May survey (Laurence, 1978; Bolz and Lough, 1983). Also, an estimated transport of 1-2 miles/d, which is consistent with the long-term residual currents reported for this area, would account

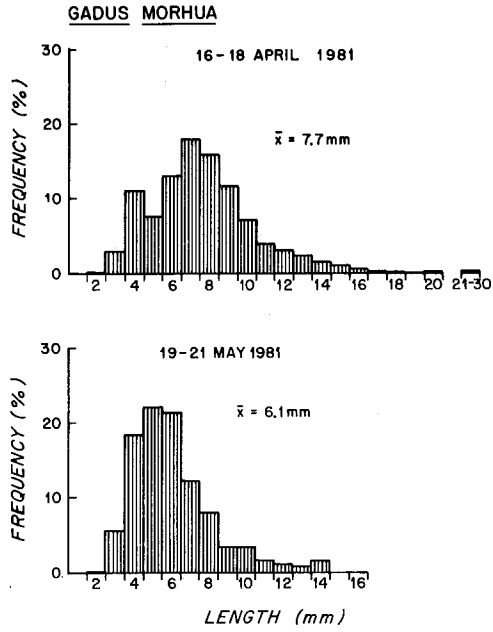

Fig. 8. Length-frequency distributions of cod larvae collected on the April and May 1981 grid surveys.

for the displacement between the highest concentration of eggs in April and larvae in May. Coupled with the fact that no other egg or larval concentrations were found in the area, these observations support the view that the egg and larval concentrations defined belonged to the same spawning population.

An important feature of these egg and larval concentrations is their coherence and stability which provide continuity in the sampling program. The grid station densities have been contoured by a factor of 4 as the coefficient of variation of a single plankton haul typically is in the range of 22-44% (Cassie, 1963). Note the internal consistency of the station values within the contoured areas. Resampling a grid transect once on the April survey and again in May 4-7 d later

produced egg and larval concentrations nearly identical to the previous station values (within a factor of 4). Using all available information, the haddock and cod egg and larval concentrations have been generalized in Fig. 6 to show their size, shape, and dispersal between surveys. The highest concentrations of eggs and larvae contoured were elliptical in shape with major and minor axes of about 30 x 15 miles (56 x 28 km). The smallest patch resolved is about 10 x 5 miles (19 x 9 km), which is on the scale of the tidal excursions and the sampled grid of stations. The lowest concentration of larvae defined and contoured as a patch was about 60 miles (111 km) long between the shelf/slope-water front and the tidal front. If one assumes that the patch dimensions are reasonably accurate, an estimate of mortality can be made between the eggs in April and the larvae in May. Using methods similar to those described in Lough et al. (1980), mortality of haddock and cod from their hatching midpoint through the 6-mm size class (18-24 d post-hatch) was estimated to be 6-8%/d. These loss rates are consistent with the range of rates (5-15%/d) reported by Saville (1956) for Faroe haddock larvae.

It also is of interest to note that the largest and presumably oldest larvae collected on the grid survey were found to the extreme southwest and on the shoals (<60 m). This past May 1983, using the 10 m MOCNESS, relatively high densities (70-450/10 000 m^3) of cod post-larvae (15-50 mm) and sand eel, *Ammodytes* sp. (45-80 mm), were collected throughout the shoaler parts of western Georges Bank, both of which have been observed to prey upon young fish larvae.

In April, winter conditions still prevailed; the water column was well-mixed throughout the study area, isothermal (6°C) from surface to bottom. Only during the final days of the cruise was a slight warming of surface waters observed, indicating the onset of spring thermal stratification on the flank of the bank. Net-phytoplankton (>20 μm) biomass increased with depth from 1-2 mg chl *a*/m^3 near the surface to 5-

10 mg chl a/m^3 near the bottom, apparently due to sinking of larger diatoms and dinoflagellates (Busch and Mountain, 1982). Nanno-phytoplankton (<20 µm) biomass was evenly distributed throughout the water column at 1-2 mg chl a/m^3. The vertical distribution of gadid eggs was low at the surface and also generally increased in density with depth to a maximum at the bottom (Fig. 9). The cod larvae were separated into two size groups for analysis (3-8 mm and >8 mm)

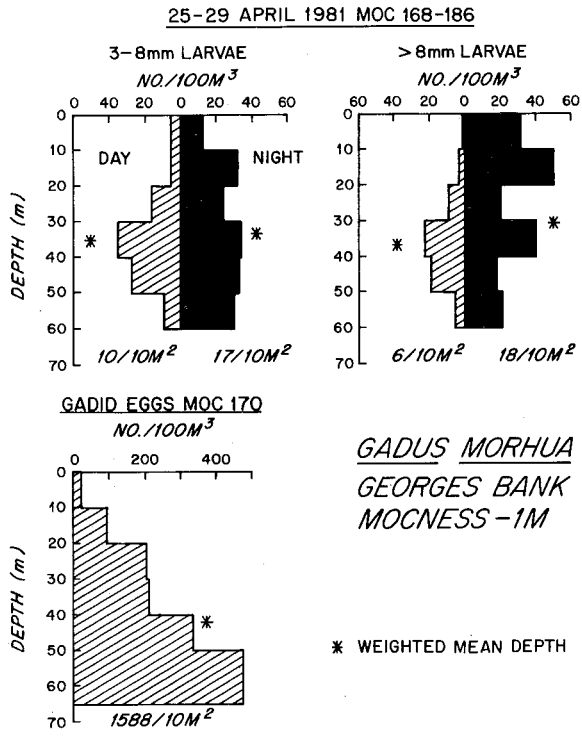

Fig. 9. Vertical distribution of cod larvae and gadid eggs collected by 1 m MOCNESS (333 µm mesh) on the southeast part of Georges Bank (41°20'N 66°53'W), 25-29 April 1981.

because of reported differences in behavior of the larger larvae (Wiborg, 1960; Miller et al., 1963). Their mean day and night abundances within 10 m sampling strata over a 54 h period are shown in Fig. 9. The size range of larvae collected by the 1 m MOCNESS are essentially the same as that collected by the 61 cm bongo net shown in Figs. 7 and 8. Both size groups of cod larvae are broadly distributed throughout the water column with weighted mean population depths between 30 and 40 m in water 66-70 m bottom depth. More cod larvae are usually caught by night than day, especially in the upper 20 m. A significant vertical displacement between day and night is shown by the larger size group. Night mean abundance of these larvae in the upper 20 m of the water column (mean length of 11 mm) was greater by a factor of 14-26 than that of the mean day abundance.

By mid-May, the water column was well-stratified at bottom depths greater than 60 m. At the first time-series station (80 m), 21 May, the surface temperature approached 10°C, a strong thermal gradient (0.75°C/m) was evident between 15 and 20 m, and below the thermocline the water was 5.9°C to bottom (refer Fig. 3). Both net- and nanno-phytoplankton biomass were reduced to <1 mg chl a/m^3, but showed a slight increase in the nanno-phytoplankton biomass above 20 m. Both haddock and cod larvae were almost exclusively confined to the upper 20 m of the water column with maximum abundance within the thermocline (Figs. 10 and 11A, MOC 191). An intense storm swept the area with high northeasterly winds, 35-40 knots (18-21 m/s), and upon resuming operations at the same site several days later on 24 May, it was evident that the water column was well-mixed, c. 7°C isothermal. Phytoplankton biomass was uniformly dispersed from top to bottom. Haddock and cod larvae now were broadly distributed throughout the water column with a weighted mean depth between 30 and 42 m, although there was a suggestion of an upper shift in the vertical distribution of larvae during the night (Figs. 10 and 11A, MOC 193-207). On 28 May, a single MOCNESS haul

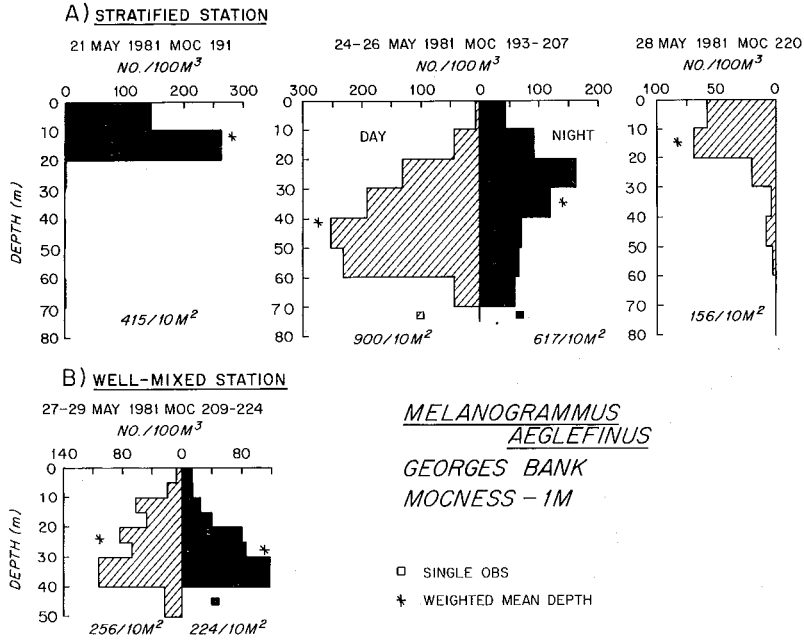

Fig. 10. Vertical distribution of haddock larvae on (A) stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station (41°07'N 67°35'W), 27-29 May 1981.

(220) showed that a shallow thermocline had formed and the larvae were reaggregating in the upper 20 m associated with the restratification. By plotting water column density (sigma-t) values during this period in Fig. 12, one can see the process of restratification between the time the storm abated sufficiently to resume sampling on 24 May (MOC 193) and the last haul on 28 May (MOC 220). At this rate it would take a total of about 7-10 d for the water column and fish larvae to restructure to the same degree observed prior to the storm. Miller et al. (1963), in a mid-May 1958 vertical distribution study of larval haddock around the flank

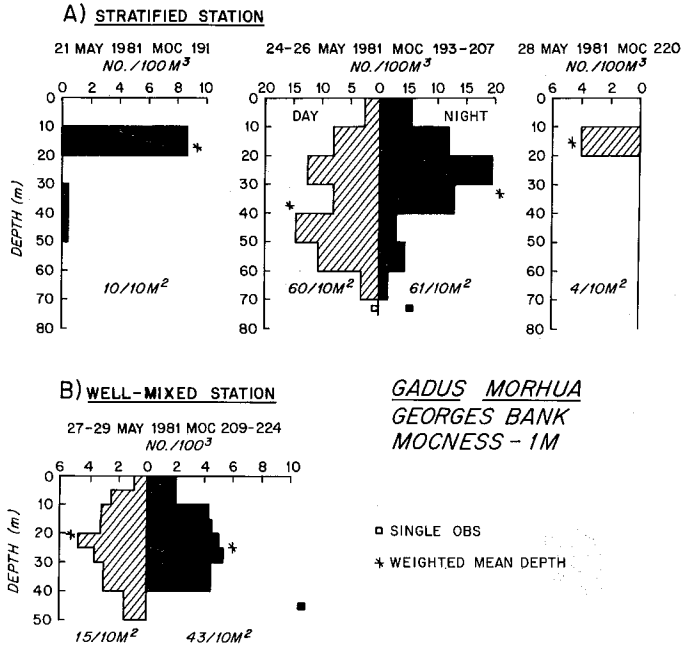

Fig. 11. Vertical distribution of cod larvae on (A) stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station (41°07'N 67°35'W), 27-29 May 1981.

of Georges Bank, found that 84% of the larval population occurred within the discontinuity layer, the confines of a thermocline, which occupied about 25% of the water column.

A shoal-water station (50 m bottom depth) was occupied for 25 h, 27-29 May, where the water column was well-mixed, 8-9°C. Haddock and cod larvae were broadly distributed through the water column with weighted mean depths between 20 and 30 m (Figs. 10 and 11B). There was no significant difference between their day and night vertical distribution.

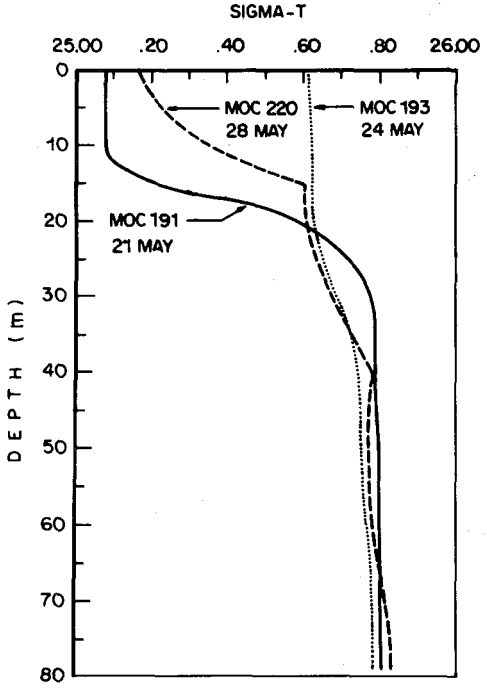

Fig. 12. Water-column density (sigma-t) profiles on stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981. Corresponding MOCNESS haul numbers shown.

Phytoplankton biomass was uniformly low throughout the water column with a noticeable increase in the bottom few meters, but slightly higher (1-2 mg chl a/m^3) than the deeper station (80 m).

The dominant copepods on Georges Bank in late-winter and spring are *Pseudocalanus* sp., *Calanus finmarchicus*, and *Oithona similis*. *Pseudocalanus* tends to be more abundant on the shoal area of Georges while *Calanus* develops high abundance in the near-surface waters of the stratified zone along the southern flank. *Oithona*, a small copepod, is widespread in its distribution. Prey selection studies of larval

haddock and cod show that the naupliar and copepodite stages of *Pseudocalanus* and *Calanus* are their most important prey (Sherman et al., 1981; Kane, in press). Eggs of these two species can sometimes comprise a significant number of prey items for the smallest larvae (<6 mm), especially for the more passively feeding haddock larvae. The preferred prey size of four length groups of larvae is depicted in Fig. 13. Note that cod feed upon larger prey at a smaller size than haddock. Both species of larvae (<10 mm) select 50-80% of their prey in the 0.10-0.19 mm width class. Recently-hatched larvae, 3.5-5.9 mm, are particularly dependent on this size class of prey which encompasses the nauplius III through copepodite II stages of *Pseudocalanus* and the nauplius II-V stages of *Calanus*.

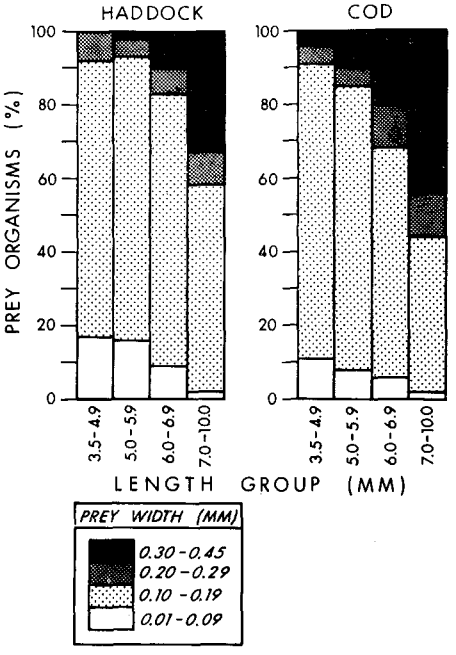

Fig. 13. Preferred prey size of larval haddock and cod length groups from May 1980 Georges Bank study (Kane, in press).

A conservative estimate of prey density in the field has been made by summing the appropriate life stages of *Pseudocalanus* and *Calanus* in the same prey size classes used above in Fig. 13 from the 1/4 m MOCNESS hauls made during the April and May station time-series. A comparison of various sampling gear and net mesh sizes indicated that the naupliar and copepodite stages of these two species were quantitatively sampled by the 1/4 m MOCNESS. In well-mixed waters, a coefficient of variation of 26% was estimated for the total copepod nauplii count from net samples within a selected stratum. In Figs. 14 and 15 the mean number of prey per liter within each depth stratum is plotted by width class. In April (Fig. 14), the vertical distribution of prey was low near the surface and increased with depth. The dominant and most important size class of prey, <0.19 mm, had <3 prey/l above 20 m depth and 5-10 prey/l at greater depths. The weighted mean depth of the small cod larvae in this same series of hauls was between 30 and 40 m. In May (Fig. 15A), the single 1/4 m MOCNESS haul

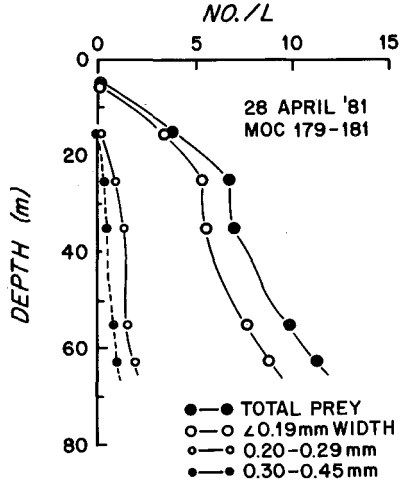

Fig. 14. Vertical distribution of larval prey field collected by 1/4 m MOCNESS (64 μm mesh) on the southeast part of Georges Bank, 28 April 1981.

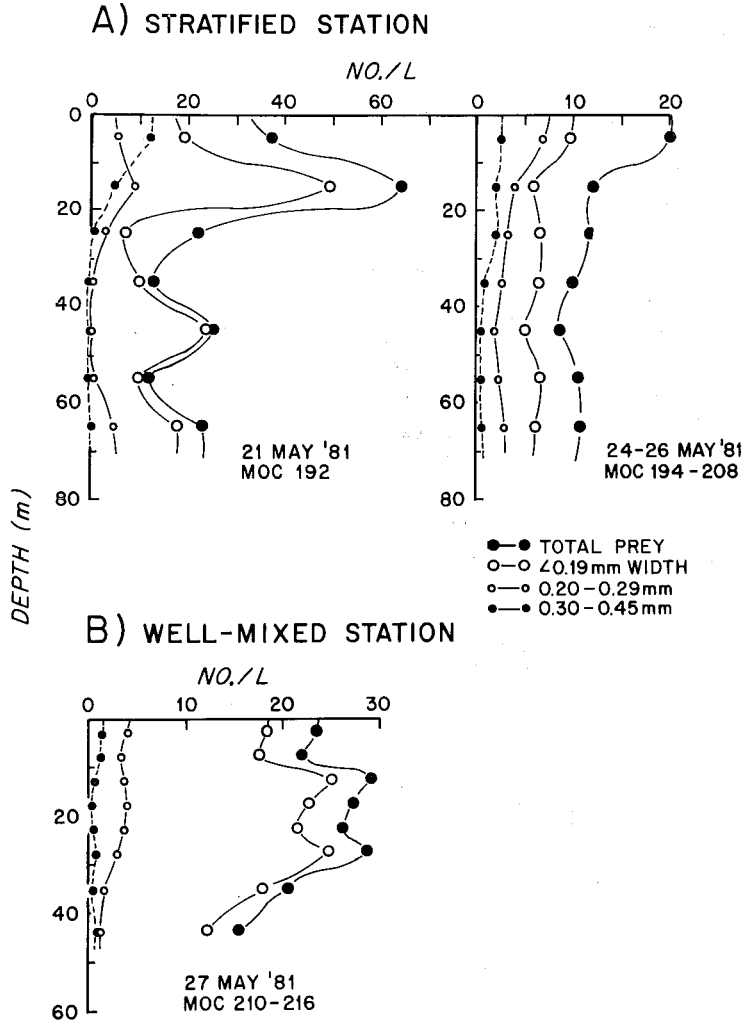

Fig. 15. Vertical distribution of larval prey field on (A) stratified station before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station, 27 May 1981.

(192), 21 May, made in the well-stratified waters showed a peak concentration of c. 50 prey/l for the <0.19 mm prey size class at 10-20 m depth where the thermocline layer resided, as well as the peak concentration of both haddock and cod larvae. A range of 5-25 prey/l was observed at other strata sampled. During 22-24 May, the storm which mixed the water column, also throughly redistributed the zooplankton. The important size class of prey now were uniformly distributed from top to bottom with a range of 5-10 prey/l. On the shoal, well-mixed station, 27 May (Fig. 15B), the <0.19 mm size class of prey ranged from 12-25 prey/l with peak densities between 15 and 30 m depth. The weighted mean depth of larvae at this station was between 20 and 30 m.

Probabilistic larval prey encounter models, similar to that developed by Beyer and Laurence (1980, 1981), are being used to assess the degree of food limitation on Georges Bank. The most recent empirical results from laboratory experiments and field studies have been incorporated into the model and preliminary simulation runs provide some interesting contrasts in the survival capabilities of larval haddock and cod. One model run (Laurence, 1983) shows that haddock larvae need 20 prey/l for minimal survival, and about 50 prey/l for 50% survival through 42 days. On the other hand, cod larvae only require about 5 prey/l for minimal survival, and 20 prey/l for 50% survival. These kinds of relatively high prey densities for larval survival have been observed in the Georges Bank area for the first time. Our field methods and modeling techniques now appear sufficiently sophisticated to produce an accurate picture of the environment in which the larvae grow and survive. Although haddock larvae hatch at a somewhat larger size than cod and remain larger, cod are more efficient behaviorally and metabolically and consequently, require lower prey densities for the same percentage survival. Cod larvae appear to be more adapted as a winter species when prey densities are generally lower. Haddock larvae, more

adapted to spring conditions, require higher prey densities which appear to be concentrated by spring stratification. Prey densities tend to be uniformly higher in the shoal, well-mixed waters, but stratification along the southern flank of Georges offers a greater potential for higher than average prey densities on which an opportunistic species like haddock can capitalize. The recruitment pattern of haddock also tends to be a 'boom or bust' type with 3-4 good years out of 20, whereas cod recruitment tends to be relatively low but with less variation (Hennemuth et al., 1980).

Further evaluation of population growth and survival in the sea may best be made through a comparison of biochemical condition indices derived from larvae reared in laboratory experiments. The RNA/DNA ratios of haddock and cod larvae collected in spring 1981 are plotted against size in Fig. 16. A minimum laboratory-determined RNA/DNA ratio of 3.2 has been established for cod, below which starvation and death occur (Buckley, 1979). However, very few (<2%) of the larvae analyzed from the field had ratios <4, indicating recent high population growth rates. Nevertheless, differences in station mean ratios occur which may be related to short-term variations in prey density, and may in turn be related to predation of the slower growing individuals. Perhaps in future simulation studies, population growth rates can be associated with discrete predation proabilities.

In conclusion, our sampling scheme is similar in many aspects to other multidisciplinary studies of larval growth and survival (Report of the Working Group on Larval Fish Ecology, 1982), but specifically designed to be carried out within the spawning season of haddock-cod and the physical regime of the Georges Bank region. Our sampling strategy is unique for a single vessel operation in its attempt to allocate a suitable balance of sampling effort among the various spatial and temporal scales needed to estimate the abundance and distribution of fish larvae, their prey, and predators in order to achieve the proper integration of

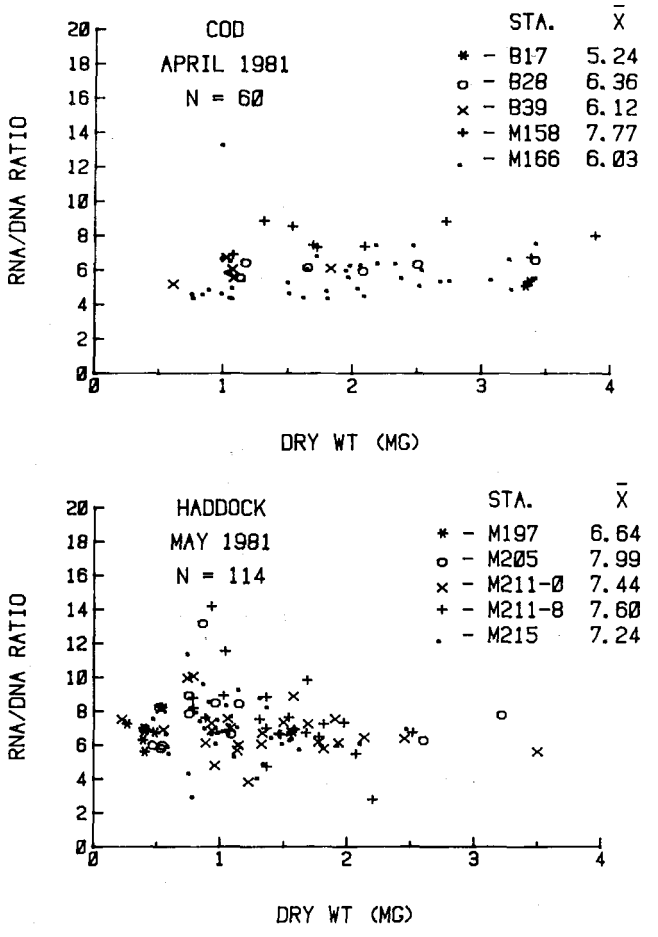

Fig. 16. RNA/DNA ratio values versus size of individual cod and haddock larvae (denoted by station) collected during April-May 1981 on Georges Bank.

observations for evaluating the causes of mortality. Special effort is made to make our program truly interdisciplinary by linking laboratory studies and model simulations with field observations.

ACKNOWLEDGEMENTS

The core of our research program described in this report is based on staff biologists and oceanographers from various investigations within the Marine Ecosystem Division of the Northeast Fisheries Center. Other individuals intimately involved in the planning, execution, or data analysis are: Geoffrey C. Laurence, John R. Green, Laurence J. Buckley, Donna S. Busch, David G. Mountain, Ronald J. Schlitz, David C. Potter, George R. Bolz, Rosalind E. Cohen, Joseph Kane, Philip R. LeBlanc, Peter J. Auditore, Bruce Burns, Jacquelyn Anderson, and Harold G. Merry. This report is MARMAP Contribution MED/NEFC 83-31. Reference to trade names does not imply endorsement by NMFS, NOAA. Special thanks to Cheryl D. Windsor for typing the manuscript.

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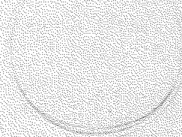

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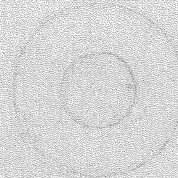

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A Det modne Æg, seet fra Siden, saaledes som det viser sig efter ½ Times Tid at have flydt i Vandet. (Begyndende Adskillelse mellem Dannelses- og Næringsblommen.)

B Samme Æg efter 2 Timers Forløb, flydende i Vandet; Kimskiven eller Dannelsesblommen fuldstændigt afsat.