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Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992

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Abstract—In late May 1992, cod and haddock eggs and larvae were sampled at discrete depths using MOCNESS on the southern flank of Georges Bank when seasonal stratification of the water column was developing. A deeper, stratified site (80-m bottom) was sampled over 7 days in relation to the temporal evolution of vertical structure and compared to a nearby shoal, mixed site (50 m). Sampling also was conducted to the west along two transects in the Great South Channel. Larval biochemical composition was measured and nutritional condition inferred from RNA:DNA ratios.

During the period 22–24 May 1992, surface warming resulted in a temperature gradient from 6 to 10°C (0.6 σ_t units) in the upper 20 m at the stratified site. Gadid eggs (93% haddock) were most abundant (6–14 per 100 m^3, on average) in the surface 20 m, with maximum density just above the base of the thermocline at 20–10 m. The few recently-hatched larvae (5–6 mm) caught were broadly distributed in the water column, with maximum average densities (1–3 per 100 m^3) deeper at 10–40 m. The naupliar and copepodite stages of *Pseudocalanus* spp. were principal prey of these larvae, and also were more abundant (3–7 prey l^{-1}) in the surface 20 m, with a maximum density at 20–10 m. A moderate storm on 25 May mixed the upper part of the water column to 5–6°C. The day after the storm, gadid eggs and copepods had highest densities in the surface 10 m.

At the shoal (mixed site) egg densities were low (1–3 per 100 m^3) and distributed evenly through the water column. Cod and haddock larvae were larger (7–8 mm modal length) and more abundant than at the stratified site. At night, they were evenly distributed at 4–6 per 100 m^3 on average, but by day, maximum density increased to 6–16 per 100 m^3 in the deepest strata sampled (40–30 m). The larger larvae at this site preyed predominantly on copepodite stages of *Pseudocalanus* spp., which were uniformly distributed in the water column.

Of all the larvae sampled for biochemical analysis, 10% of haddock and 1.5% of cod had ratios below 4.1. Based on laboratory studies, fish larvae with RNA:DNA ratios below 4.1 are considered to have been in poor condition. There were no larvae in poor condition at the Great South Channel Transect, where their mean size was greatest; no larvae were collected at the stratified site for comparison. At the mixed site, cod larvae sampled before and after the storm had identical ratios, while haddock larvae had significantly higher ratios after the storm. Larvae from different sampling depths had significantly different ratios, inferring that they remained together long enough to acquire a unique signature.

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INTRODUCTION

Cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) spawn on northeastern Georges Bank in late-winter through early spring and generally are advected southwest in the clockwise gyral circulation (Lough and Bolz, 1989). By May, when seasonal stratification of the deeper water begins, the eggs and larvae can be found along the southern perimeter of the Bank. The decreasing wind mixing and increased solar insolation in the spring cause the water column to become stratified in temperature and density (Flagg, 1987). However, in the shallow, central part of the Bank, the water column remains well-mixed due to strong tidal stirring. A tidal front develops near the 60-m isobath separating the well-mixed water from the stratified water to the south.

The development of stratification on the southern flank of Georges Bank is associated with increased concentrations of zooplankton and larval fish within and above the pycnocline (Lough, 1984). Development of stratification in deeper waters on the southern flank may be an important factor in the growth and survival of larval fish. In May 1983, Buckley and Lough (1987) found recent growth (dry weight) of haddock larvae was higher (8–13% day^{-1}) at two stratified sites than at a shoal, well-mixed site (7% day^{-1}). Based on RNA:DNA ratio analysis, larvae were in good condition at the stratified site, but up to 50% of the haddock were considered starved by laboratory criterion at the well-mixed site.

In May 1992, another study was conducted on Georges Bank to examine further the relationship between water column structure, prey abundance, and condition of larvae. The hypotheses investigated were: (i) larval growth is significantly different with depth of capture in stratified waters, but not in well-mixed waters, (ii) larval growth is directly related to prey density, and (iii) prey (copepod) densities are highest in the vicinity of a thermocline. Measured biochemical parameters included RNA, DNA, and protein concentration, and RNA:DNA ratio. The RNA:DNA ratio has proven to be a reliable index of nutritional condition of larval fish (Buckley, (1979,1980,1981, 1984); Clemmesen, (1987, 1988); Canino, 1994; Canino *et al.*, 1991), higher ratios indicating better condition and faster growth at a given temperature.

METHODS

Field sampling

An initial survey was conducted on 19–21 May 1992 to locate cod and haddock larvae on the southern flank of Georges Bank using a 61-cm Bongo-net equipped with 333- and 505-m mesh nets and Seabird CTD profiler. Tow profiles were double oblique to within 5 m of the bottom. The Bongo-net was lowered at 50 m min^{-1} and retrieved at 20 m min^{-1} while the vessel was underway at 1–2 knots.

A deep, Stratified Site (SS) was selected at 80-m depth (40°42.5′N, 67°52.3′W) and an oceanographic mooring was deployed (Fig. 1). A near-by shoal, Mixed Site (MS) at 50-m depth (40°59.0′N, 68°2.0′W) also was selected. Loran-C buoys tethered with drogues at 15-m depth were deployed and followed for sampling operations at the SS. During the period 21–27 May 1992, vertical profiles for fish larvae and zooplankton were made at these two sites using MOCNESS (Lough and Potter, 1993). A 1 m^2 MOCNESS equipped with nine 333 μm mesh nets was used to sample larval fish, and a 1/4 m^2 MOCNESS with nine 64 μm mesh nets was used for zooplankton. Discrete depths were sampled at 10-m intervals from

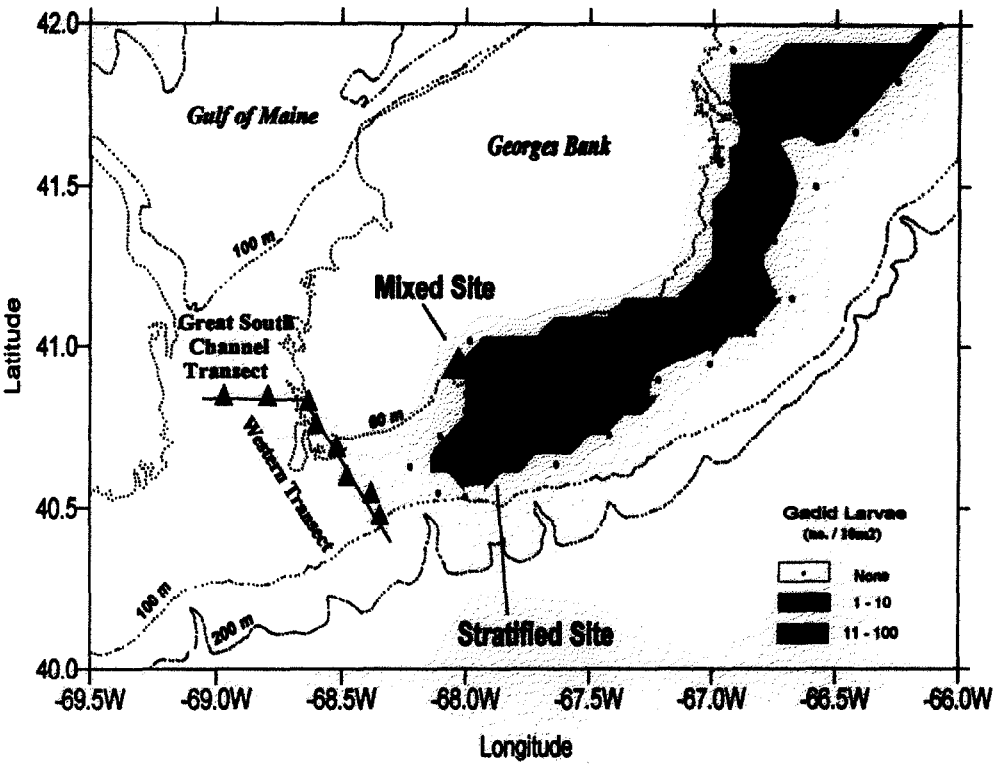

Fig. 1. Map of the May 1992 Georges Bank Stratification Study region showing the stratified and mixed sites, and Western and Great South Channel Transects where MOCNESS tows were made (▲). Distribution and abundance estimates of cod and haddock larvae are derived from bongo-net tows (•). Total gadid larval abundance shadings (no. per 10 m^2) are by order of magnitude.

5 m above the bottom to surface. Each net of the 1 m^2 MOCNESS filtered about 250 m^3 of water, and the 1/4 m^2 MOCNESS filtered about 25 m^3 of water. At the end of the cruise (27–28 May 1992), a Western Transect and Great South Channel Transect were made using the 1 m^2 MOCNESS. Net samples were preserved in 4% formaldehyde–seawater solution except for the fish larvae used for biochemical analysis. These fish were removed from the samples as soon as possible after capture, placed on petri dishes and stored at −20°C in the ship's freezer. The samples were later stored at −80°C in the lab until they were analyzed.

Temperature–salinity profiles were obtained by the MOCNESS Seabird CTD sensor and averaged over the 10 m stratum. Temperature, salinity, and current measurements also were obtained from the oceanographic mooring and reported by Manning *et al.* (1995). Wind speed was reported by hourly averages from the vessel sensor logs. A complete set of hydrographic transect data can be found in Manning *et al.* (1995).

Laboratory processing and analysis

All fish eggs and larvae were removed from the formaldehyde-preserved samples, larval standard lengths were measured to the nearest 0.1 mm, and preserved length corrected for

shrinkage to live length by the method described in Bolz and Lough (1988), adapted from Theilacker (1980). The fish were initially grouped by length into 1 mm size classes, and net totals were standardized to number per 100 m^3 and number per 10 m^2. The day and night tow profiles were averaged by depth strata and a standard error calculated.

Fish eggs were identified and separated into three developmental stages: Stage I: spawned to before blastopore closure; Stage II: blastopore closure to before tail bud lifts free from yolk surface; and Stage III: tail bud free to before hatching (Berrien and Sibunka, 1996). Visually, only Stage III eggs can be separated by species. Incubation rates for cod and haddock are similar ranging from 10–20 days on Georges Bank (Page and Frank, 1989). The duration of the cod egg stage is about 19 days at 5°C (Thompson and Riley, 1981), with Stages I and II accounting for 60% of the incubation time. Depth profile stratum means and standard errors were calculated for the eggs.

Gut contents of larval cod and haddock were analyzed from the SS and MS MOCNESS samples. Soft-bodied organisms such as protozoa were already digested or to the point where they could not be identified. Prey remains were identified to the lowest level possible and tallied for two size classes of larvae: 3–5 and 5–8 mm SL.

The RNA and DNA content of each frozen fish was determined following the FIA procedure outlined in Caldarone and Buckley (1991). The fluorochrome working reagent of Hoechst was modified by reducing the Hoechst dye concentration to 25 ng ml^{-1}, the NaCl concentration to 0.1 N and the pH to 7.0. Calf liver RNA (Type 1V, Sigma) and an 18s, 28s rRNA molecular weight marker (United States Biochemical Corp.) were used as RNA standards. All RNA values were converted to the rRNA standard. High molecular weight calf thymus DNA (Boehringer-Mannheim Corp,) was used as a DNA standard. Protein content of each larva was determined using a bicinchoninic acid colorimetric method outlined in Smith *et al.* (1985). Lengths were measured from a video image of individual frozen larva using OPTIMAS image analysis software and converted to live length by the method used in Bolz and Lough (1988). Indices that were measured to determine the condition of larvae were RNA, DNA, and protein content and RNA:DNA ratio. The effect of site, time of day, depth at capture, and date sampled was determined for each of the parameters. RNA, DNA, and protein content were analyzed using one-way ANOVA for unbalanced designs with the natural log of length (ln length) as a covariate. Means were computed as least-square means. RNA:DNA ratios were analyzed using one-way ANOVA for unbalanced designs. Differences among main effect means were tested for significance using Fisher's LSD test (SAS Institute software).

Zooplankton from the 1/4 m^2 MOCNESS were subsampled, identified and enumerated. Copepod nauplii were not routinely identified to species. Zooplankton data were standardized to number per m^3 or l and a few select profiles have been plotted. Some of the smallest nauplii of copepods such as *Oithona* spp. and *Centropages* spp. may be extruded through the 64 μm mesh based on their widths, but most of the larval cod and haddock prey items are greater than 70 μm (Kane, 1984).

RESULTS

From the Bongo-net survey (Fig. 1), larval cod and haddock were distributed broadly from the shoal, mixed region of the Bank across the flank to about the 90-m isobath. A high concentration was found on the southern flank where the study sites were located.

Oceanographic conditions during the study

Temperature and salinity in the mixed region was 6.4°C, 32.3 psu, typical for this area and time of year. At the deeper stratified site (Fig. 2), 4–5°C water was observed from about 10 m to bottom. Over the period 22–24 May, surface warming resulted in a 4°C temperature gradient in the upper 20 m, with 9–10°C water at the surface. This represented a difference of 0.6 σ_t units. A moderate storm of strong northeasterly winds (15–25 knots) on 25 May mixed the upper 20 m of the water column to 5–6°C. The storm also contributed to the unusually fast (15 cm s^{-1}) westward drift of the Loran-C Buoy (Manning *et al.*, 1995).

Vertical distribution of eggs and larvae

Gadid eggs were more abundant at the SS than the MS (Fig. 3). Eggs were distributed throughout the water column, increasing towards the surface, especially at the SS. Mean egg density in the upper 30 m at the SS ranged from 6 to 14 per 100 m^3, but at deeper depths were < 5 per 100 m^3. Egg densities at the MS were low at 1–3 per 100 m^3. The vertical distribution of eggs by three stages of development at the SS (Fig. 4) shows Stage I eggs were most abundant (64%), compared to Stage II (20%) and Stage III (16%), with highest densities in the upper 30 m of the water column. Whereas Stage I eggs had the highest mean density in the surface 10 m, the highest mean density of Stage II and III eggs appeared deeper in the 20–10-m stratum. This may reflect the greater specific gravity of late stage eggs. Based on the species separation of Stage III eggs, 92.7% were identified as haddock and 7.3% cod.

Cod and haddock larvae were more abundant at the MS than the SS. Larval haddock was more abundant than cod on both sites; however, primarily small haddock and cod (< 8 mm) were found at the SS, associated with the higher abundance of eggs (Figs 5 and 6). Both small and large (> 8 mm) cod and haddock larvae were caught at the MS compared to the SS. The mean length of cod and haddock at the SS was 6.9 and 5.1 mm, respectively, and at the MS, 7.3 and 6.6 mm.

At the SS, cod and haddock larvae were broadly distributed through the water column based on their mean night and day vertical distributions (Fig. 7). Larvae were more abundant in day than night tows. Only five larval cod were caught in night tows. The larval cod population was centered at 30–20 m depth, whereas haddock larvae extended over a broader range; the highest day mean densities were at 30–10 m depth. Haddock night mean densities increased somewhat in the surface 20 m.

At the MS, where larger larvae were found, larvae were divided into two size classes since vertical migrations become detectable and established by 9 mm (Lough and Potter, 1993). Smaller cod larvae (< 8 mm) were distributed more or less evenly from surface to bottom at night, but by day they were nearly absent from the surface 10–0 m stratum and increased to maximum density near the bottom, 40–30 m (Fig. 8). More larvae were caught by night (17.8/10 m^2) than by day tows (10.5 per 10 m^2). The larger cod larvae (> 8 mm) were distributed throughout the water column day and night with no apparent trend. Equal numbers of larvae were caught by night (5.0 per 10 m^2) and day (4.9 per 10 m^2).

Small haddock larvae (< 8 mm) at the MS (Fig. 9) had a vertical distribution similar to cod. The small larvae were evenly distributed throughout the water column by night, but by day were absent from the surface and increased to maximum density near bottom. These larvae were more abundant in day tows (31.0 per 10 m^2) than night ones (22.1 per 10 m^2). The larger haddock (> 8 mm) had vertical night and day profiles similar to the small

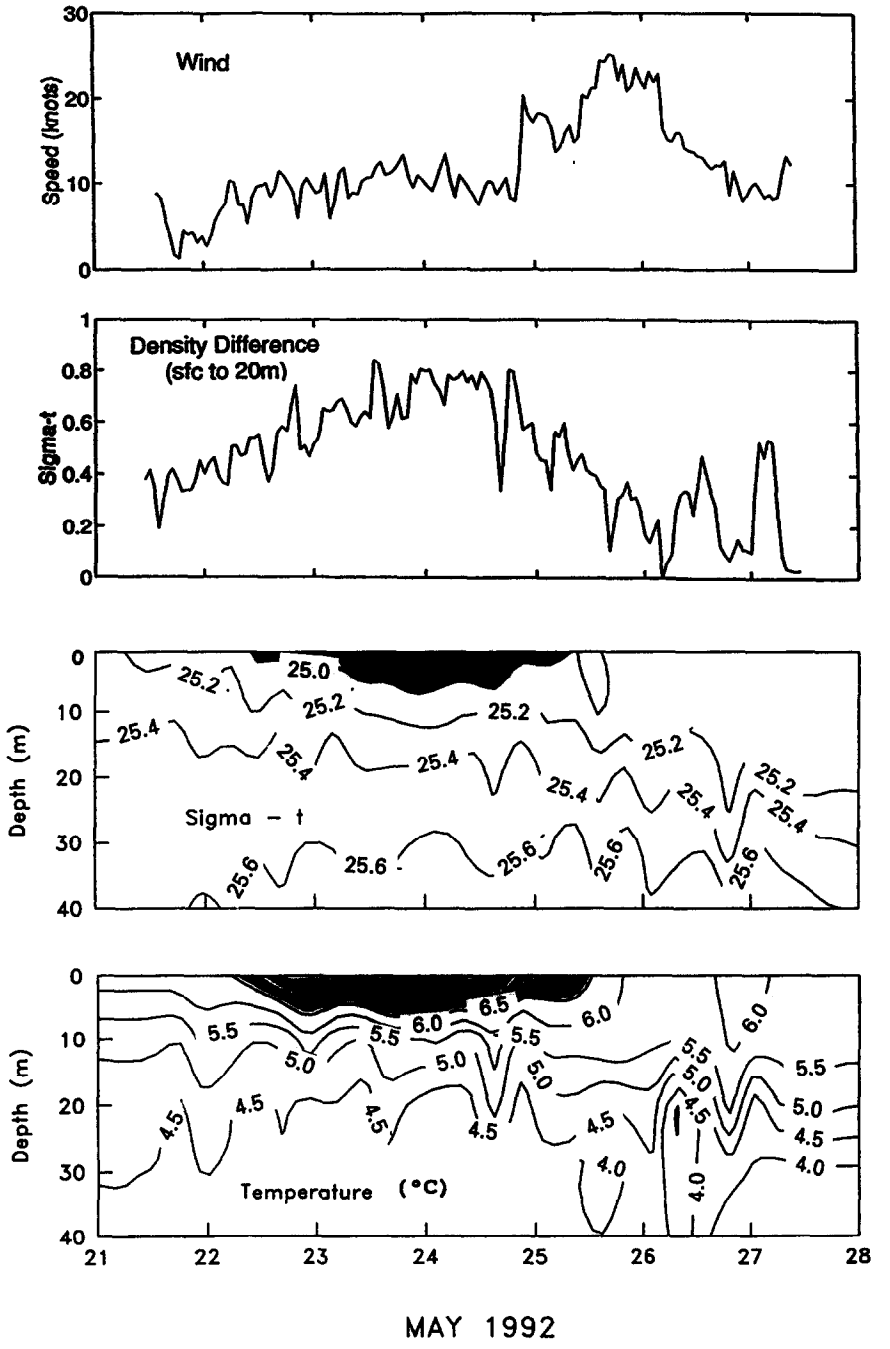

Fig. 2. Wind speed and water-column temperature and density (σ_t) from the stratified site mooring over the period of study, 21–28 May 1992. Surface shading of temperature and σ_t values show formation of a shallow thermocline.

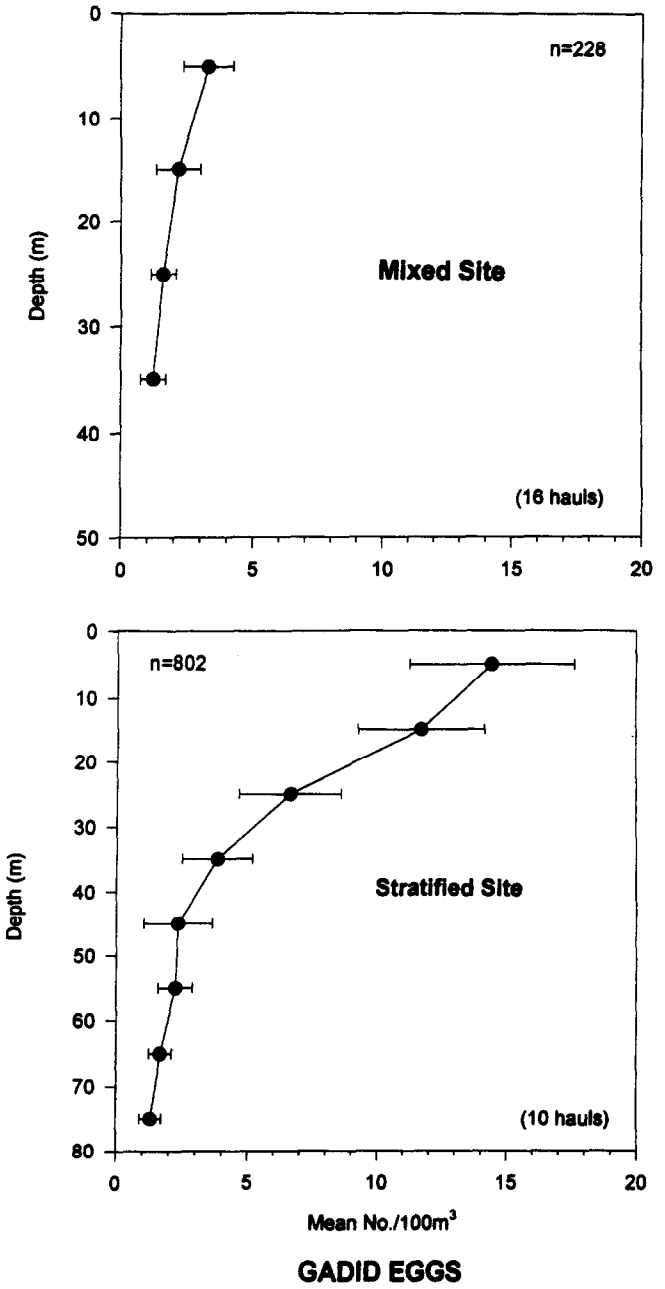

Fig. 3. Vertical distribution mean (no. per 100 m^3) and standard error (horizontal bar) of gadid (cod and haddock) eggs from 1-m^2 MOCNESS tows at the mixed and stratified sites. *n* is the total number of eggs from all tows.

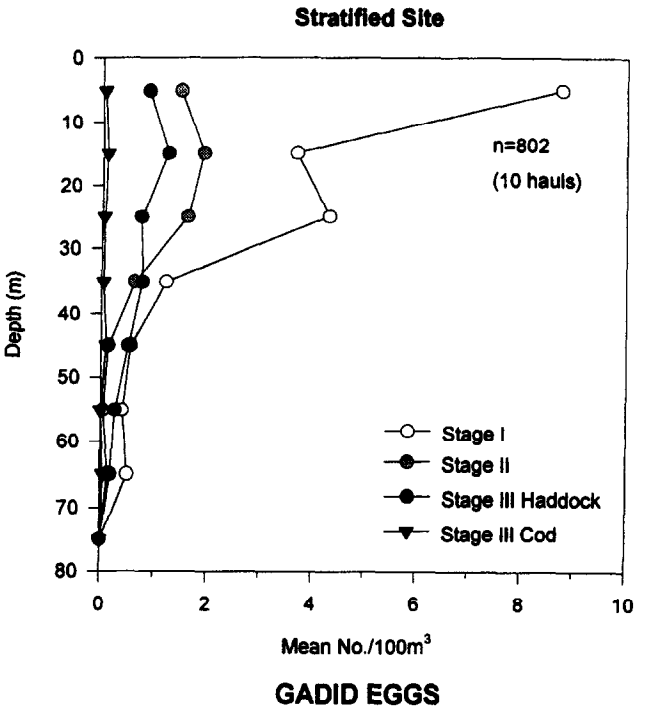

Fig. 4. Vertical distribution (mean no. per 100 m^3) of gadid eggs by three stages of development from 1-m^2 MOCNESS tows at the stratified site. Only Stage III eggs could be identified as cod or haddock. *n* is the total number of eggs from all tows.

haddock larvae. Larger haddock larvae also were caught more abundantly by day (5.2 per 10 m^2) than night (2.9 per 10 m^2).

Selected vertical profiles of eggs and larvae at the SS are shown in Figs 10–12 during the development of surface stratification (MOCNESS tows 977 and 990) and after the wind event on 25 May 1992 (MOCNESS tow 995). The temperature profiles in the bottom panels are stratum averages from the MOCNESS tows. During the onset of warming on 22 May (MOC977), gadid eggs were found mostly in the upper 40 m of the water column (Fig. 10). The maximum density for all egg stages combined was at 20–10 m depth. On 24 May (MOC990), with increased stratification of the surface water, maximum density of the eggs was still near the base of the thermocline (pycnocline) at 20–10 m. While Stage I eggs were most abundant in the surface 10–0 m, the Stage II and III eggs were deeper, mostly at 20–10 m. On 26 May (MOC995), following the storm, most of the eggs were still located in the surface 20 m, the highest densities of all egg stages were now at the surface 10–0 m, perhaps due to wind mixing. However, it is possible that another population was sampled.

Since few cod larvae were collected in this series of MOCNESS tows (Fig. 11), their pattern of vertical distribution is less discernable. A few larger larvae were caught on 22 May (MOC977) near 20 m depth. Smaller larvae were caught on 24 May (MOC990) in the upper 40 m of the water column, the highest density at 40–30 m depth. Following the storm, on 26 May (MOC995) only a few scattered larvae were caught.

Haddock were more abundant than cod at the SS, and on 22 May (MOC977) small haddock larvae were distributed mostly within the upper 40 m of the water column;

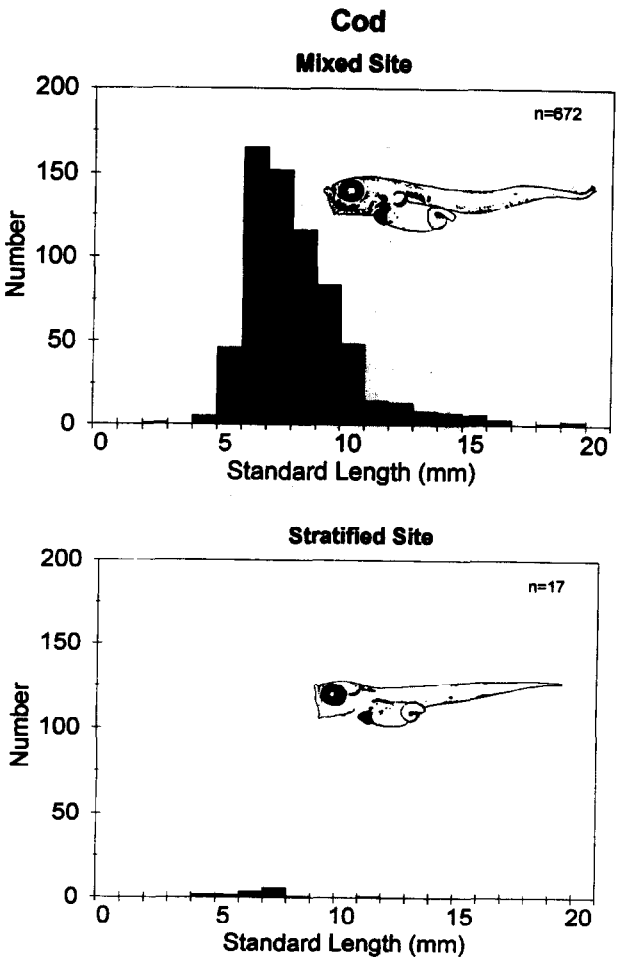

Fig. 5. Length frequency of cod larvae on the mixed and stratified sites from all 1-m^2 MOCNESS tows. *n* is the total number of fish.

maximum density was at 30–20 m depth (Fig. 12). On 24 May (MOC990), surprisingly, most of the recently-hatched larvae were located below the thermocline at 20 m; the maximum density was at 60–50 m depth. Following the storm, only a few haddock larvae were caught on 26 May (MOC995) between 40–10 m.

Vertical profiles of eggs and larvae at the Western and Great South Channel Transects have been presented by Manning *et al.* (1995). On the Western Transect, gadid eggs were found throughout the water column in tows between 75 and 100 m bottom depth, with highest densities in the upper 20 m. Cod and haddock larvae were caught primarily in shoaler water, 75–57-m bottom depth, but also tended to be concentrated in the surface 20 m. On the Great South Channel Transect (59–84-m bottom depth), a few gadid eggs were observed in the surface 20 m; cod and haddock larvae were broadly distributed between 10 and 50 m depth. Mean lengths of cod and haddock at the Western Transect were both 7.5 mm (Figs 13 and 14). Larger larvae were caught at the Great South Channel Transect; the mean length of cod was 9.2 mm and of haddock was 9.0 mm.

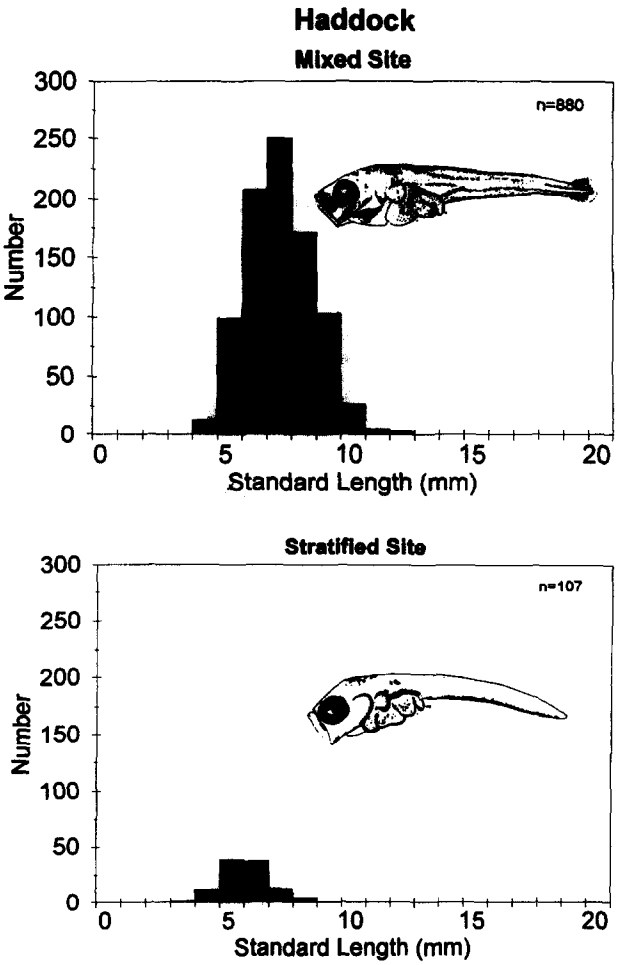

Fig. 6. Length frequency of haddock larvae on the mixed and stratified sites from all 1-m^2 MOCNESS tows. *n* is the total number of fish.

Larval gut contents

A small number of larvae were processed to determine gut contents from the SS (MOC977, 984, 991) and MS (MOC985, 994). There was a relatively large percentage (37–54%) of empty guts for the first-feeding larvae, 3–5 mm, (Fig. 15), which may reflect the fact that they were newly hatched. Thirty-nine per cent of the haddock first-feeding larvae preyed on copepod nauplii and little else. Cod yolk-sac larvae preyed on copepodite stages of *Pseudocalanus* spp. (47%). The larger cod and haddock larvae, 5–8 mm, preyed predominantly on copepodite stages of *Pseudocalanus* spp. Feeding differences between sites appeared to be related to larval size, that is the smaller recently-hatched larvae at the SS fed mostly on copepod nauplii (26%), where as the larger larvae on the MS preyed predominately on *Pseudocalanus* spp. copepodites (79%). However, there were not enough larvae to draw definite conclusions. At the MS, there were enough specimens to examine trends in feeding intensity at the different depths. For haddock larvae, 5–8 mm SL ($n = 27$),

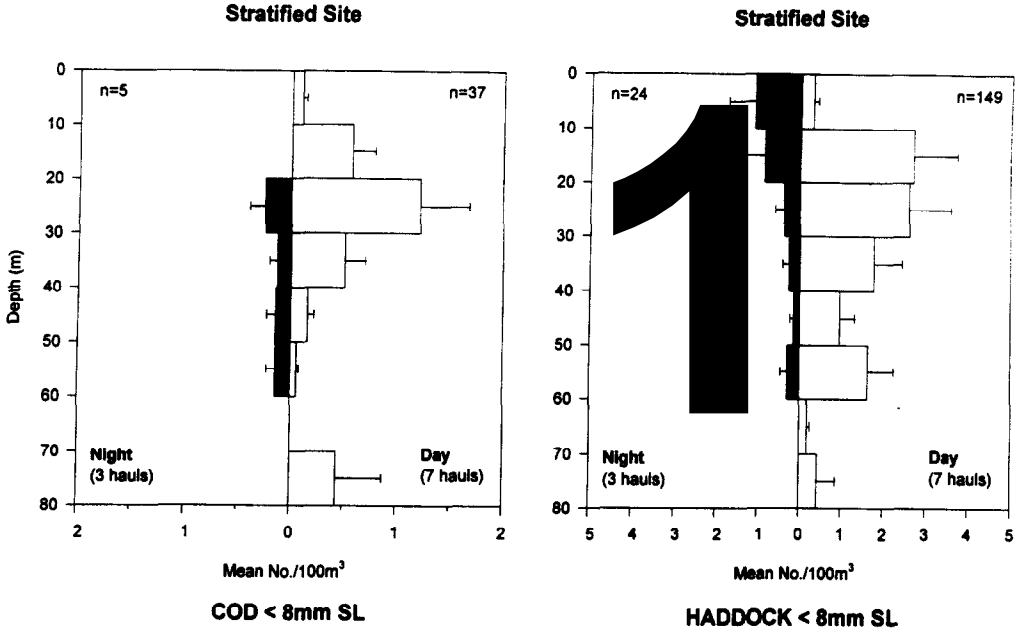

Fig. 7. Mean day and night vertical distribution (no. per 100 m^3) of cod and haddock larvae <8 mm SL collected by the 1-m^2 MOCNESS on the stratified site. Horizontal bar represents standard error of stratum mean. *n* is the total number of fish from all tows.

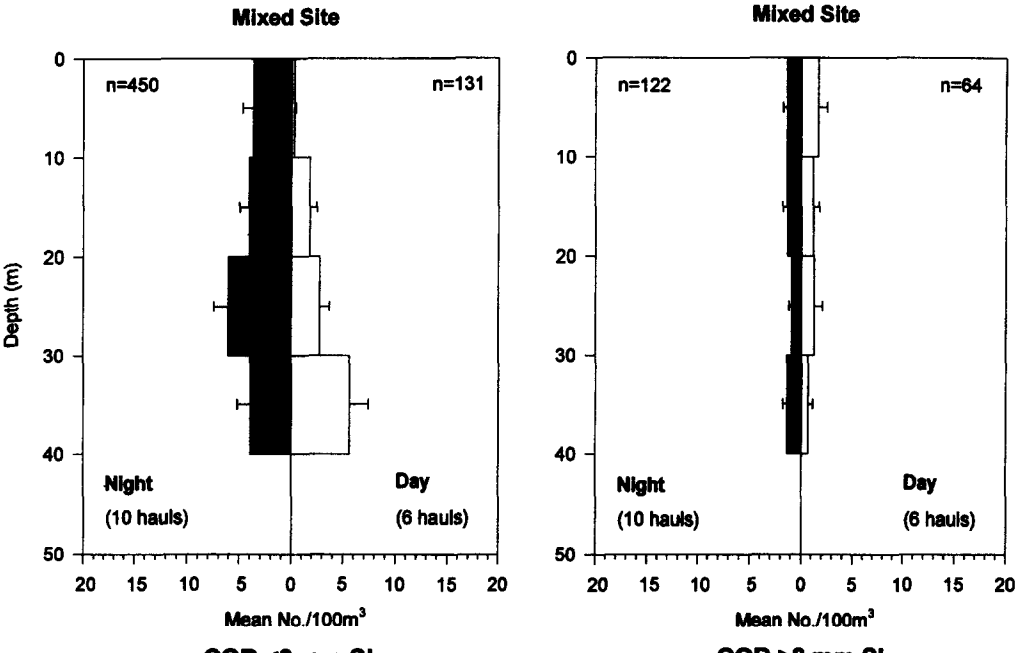

Fig. 8. Mean day and night vertical distribution (no. per 100 m^3) of cod larvae, <8 mm and >8 mm SL collected by the 1-m^2 MOCNESS on the mixed site. Horizontal bar represents standard error of stratum mean. *n* is the total number of fish from all tows.

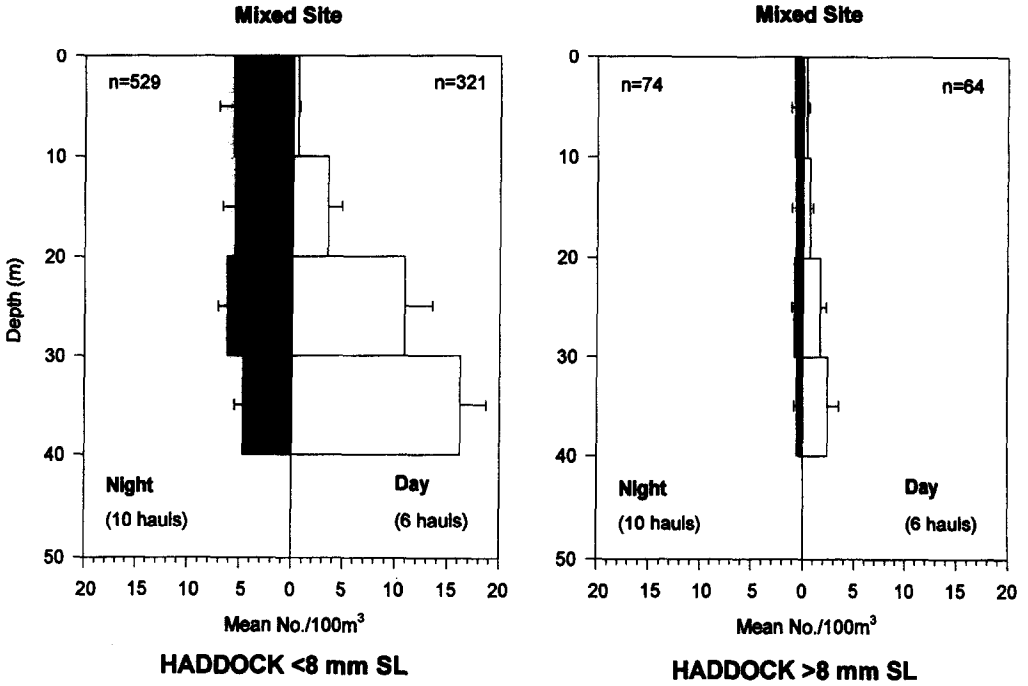

Fig. 9. Mean day and night vertical distribution (no. per 100 m^3) of haddock larvae < 8 mm and > 8 mm SL collected by the 1-m^2 MOCNESS on the mixed site. Horizontal bar represents standard error of stratum mean. *n* is the total number of fish from all tows.

the mean number of prey per larva was uniformly 1.2–1.8 through the water column to 40 m depth; however, for cod larvae of the same size, the mean number of prey per larva was higher from the surface 10–0 m stratum (2.7 prey $larva^{-1}$, $n = 6$) than at deeper depths (1.5–1.6 prey $larva^{-1}$, $n = 7$).

Vertical distribution of copepod prey

Vertical profiles of the dominant copepods, *Calanus*, *Pseudocalanus*, *Oithona*, and copepod nauplii at the SS were different before and after the storm on 25 May (Fig. 16). Most of the copepod nauplii were *Pseudocalanus* spp. On 23 May (MOC983) these copepods were most abundant in the upper 20 m of the water column with a peak density at 20–10 m, the base of the wind-mixed region. Copepod nauplii densities above 20 m were in the range of 3000–7000 m^{-3}; adults and copepodites of the three species were about 1000–2000 m^{-3} in the upper 20 m and less abundant at deeper depths. After the storm, on 26 May (MOC996) maximum copepod densities were near surface, 10–0 m, perhaps due to the increased wind mixing or sampling of a different population due to advection. At the MS on 22 May (MOC976), copepod densities (1000 m^{-3} or less) were uniformly distributed throughout the water column (Fig. 16). Copepod nauplii were somewhat more dense (1600–2200 m^{-3}) at the surface (10–0 m) and near bottom (40–30 m).

Since *Pseudocalanus* spp. was the primary prey of cod and haddock larvae, vertical profiles of its naupliar and copepodite stages are shown for the same three tows (Fig. 17). Densities of the copepodite stages were similar ($< 1\ l^{-1}$) for the SS and MS; only the

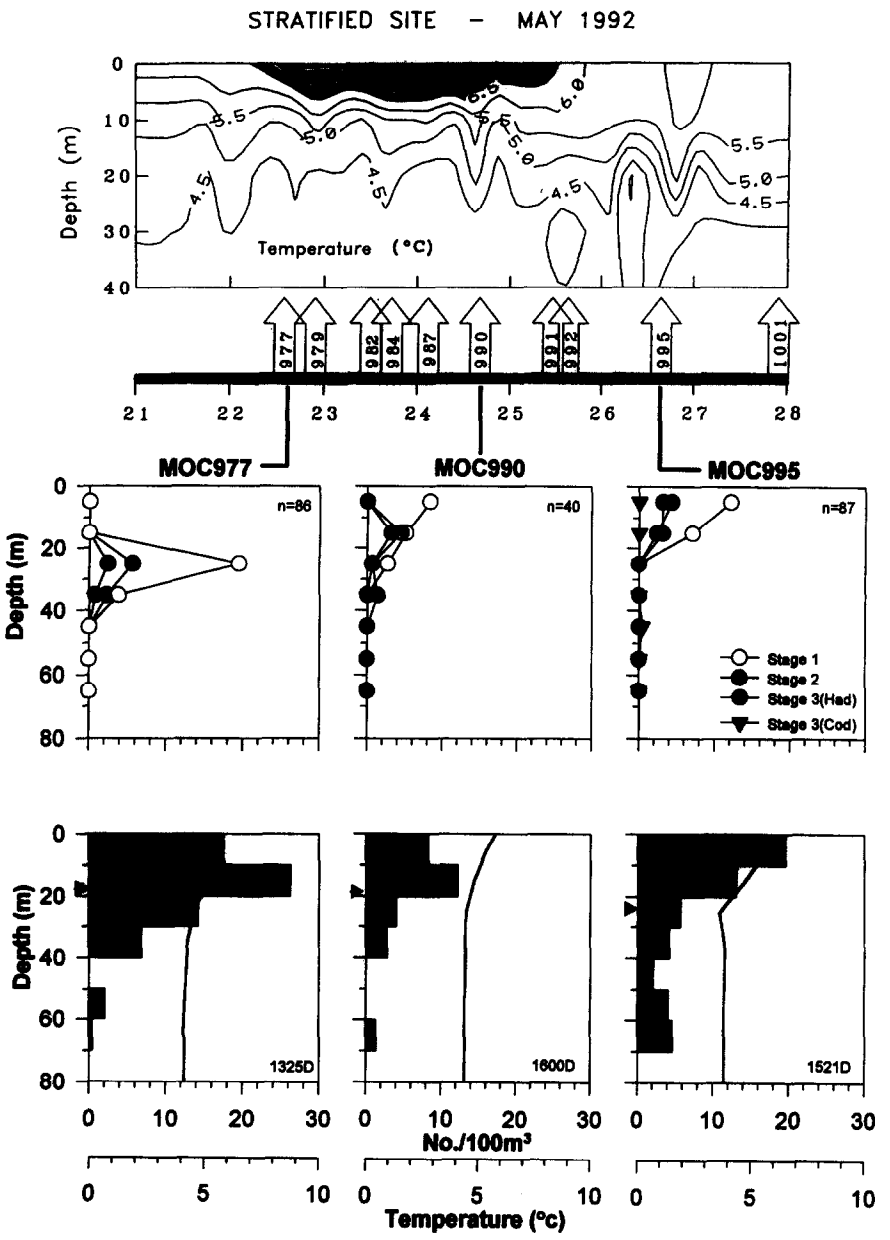

Fig. 10. Vertical profiles of total gadid eggs (lower panels) (no. per 100 m^3) and stage composition (middle panels) during the onset of surface stratification (MOCNESS tows 977 and 990) and after the storm on 25 May 1992 (MOCNESS tow 995). Top panel shows sequence of MOCNESS tows in relation to water-column temperature from Fig. 2. Note that for the middle panel showing the egg stage profile, eggs sorted from the surface two net samples, 20–10 m and 10–0 m, were lost before staging could be done. Arrow-head on lower panels represents weighted-mean depth of population. A temperature profile is shown for each of the tows in the bottom panels. Start time (D.S.T.) of each tow is shown in the lower right-hand corner. *n* is the total number of eggs from all tows.

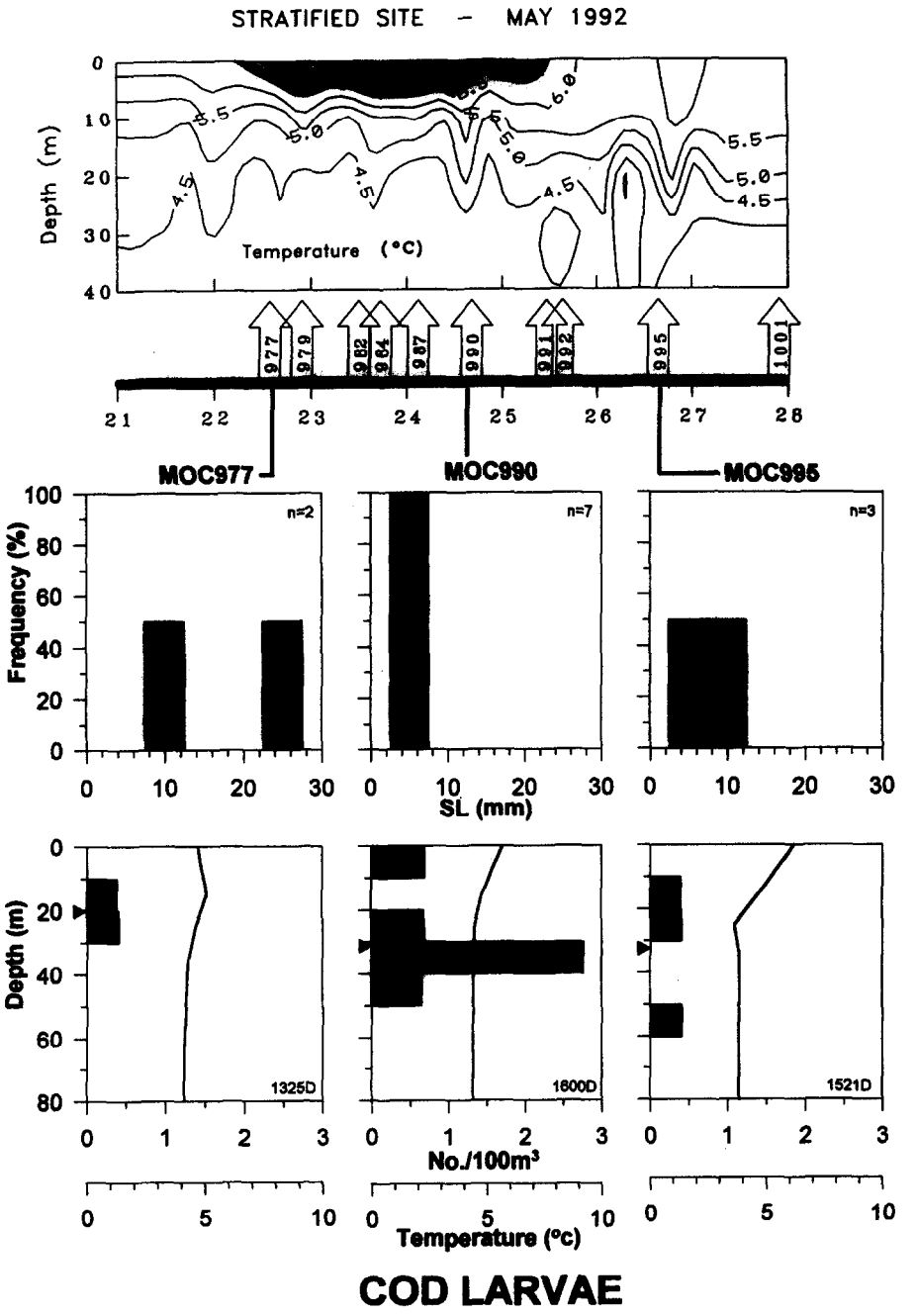

Fig. 11. Vertical profiles of cod larvae (lower panels (no. per 100 m^3)) and length frequency (middle panels) during the onset of surface stratification (MOCNESS tows 977 and 990) and after the storm on 25 May 1992 (MOCNESS tow 995). Top panel shows sequence of MOCNESS tows in relation to water-column temperature from Fig. 2. Arrow-head on lower panels represents weighted-mean depth of population. A temperature profile is shown for each of the tows in the bottom panels. Start time (D.S.T.) of each tow is shown in the lower right-hand corner. *n* is the total number of larvae from all tows.

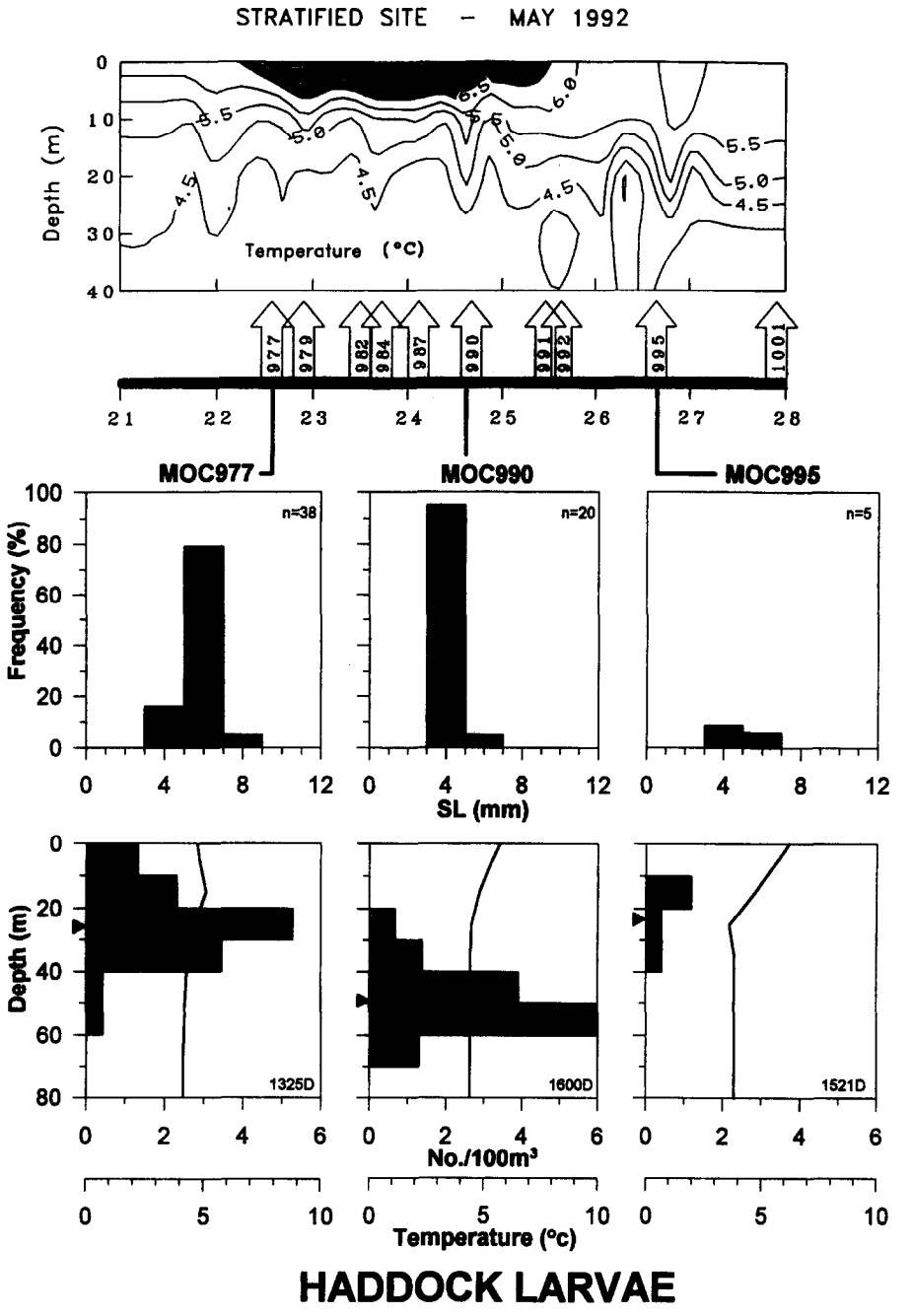

Fig. 12. Vertical profiles of haddock larvae (lower panels) (no. per 100 m^3) and length frequency (middle panels) during the onset of surface stratification (MOCNESS tows 977 and 990) and after the storm on 25 May 1992 (MOCNESS tow 995). Top panel shows sequence of MOCNESS tows in relation to water-column temperature from Fig. 2. Arrow-head on lower panels represents weighted-mean depth of population. A temperature profile is shown for each of the tows in the bottom panels. Start time (D.S.T.) of each tow is shown in the lower right-hand corner. *n* is the total number of larvae from all tows.

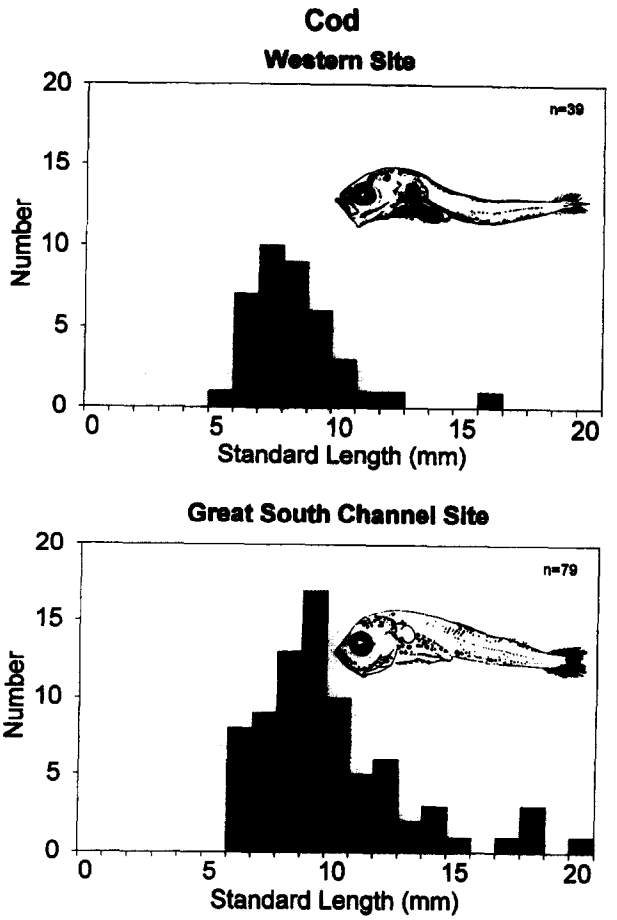

Fig. 13. Length–frequency of cod larvae on the Western and Great South Channel Transects from all 1-m^2 MOCNESS tows. *n* is the total number of fish.

naupliar stage had markedly higher densities (3–7 l^{-1}) at the SS within the upper 20 m of the water column. In terms of water-column abundance, the percentage composition of the stages at the SS was: 72% Nauplii, 11% CI–II, 11% CIII–IV, 6% CV–VI; and at the MS: 53% Nauplii, 18% CI–II, 11% CIII–IV, 18% CV–VI. Nauplii were 2.3 × more abundant at the SS than at the MS. Stages CV–VI were 1.7 × more abundant at the MS.

Condition of larvae

A total of 193 haddock and 130 cod larvae were collected for biochemical analysis. Larvae were sampled from both integrated and discrete depth nets from a total of eight tows, representing both day and night hauls, mixed and transect sites (Table 1). Insufficient numbers of larvae (two cod, six haddock) were collected for biochemical analysis at the SS for comparison with the MS and Transects.

Natural log transformed larval length was positively correlated with RNA, DNA, and protein content in cod ($r^2 = 0.72, 0.73, 0.79$, respectively) and haddock ($r^2 = 0.61, 0.61, 0.60$,

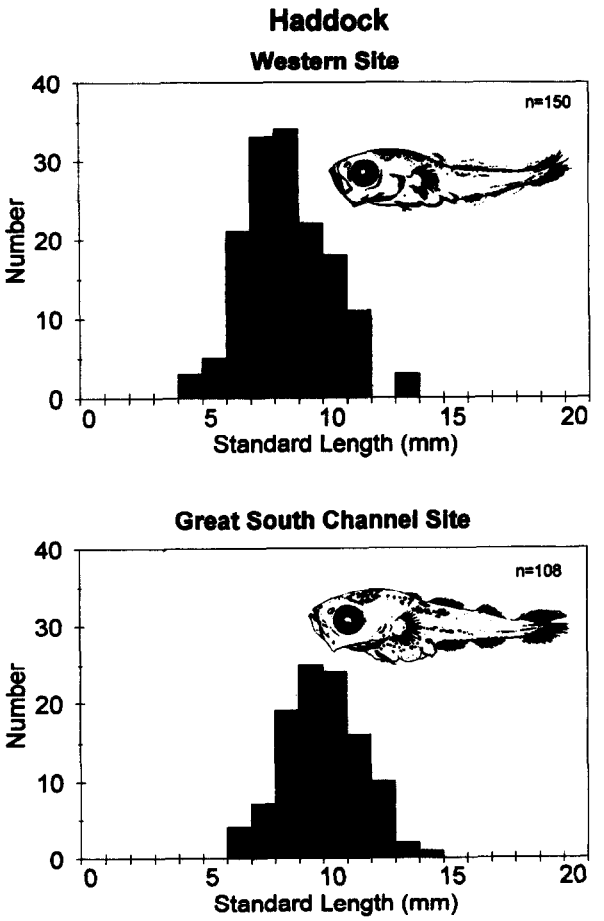

Fig. 14. Length–frequency of haddock larvae on the Western and Great South Channel Transects from all 1-m^2 MOCNESS tows. n is the total number of fish.

respectively) and was used as a covariate in all of the statistical analyses involving these parameters. Ln length was poorly correlated with RNA/DNA ratio values in both cod and haddock ($r^2 = 0.21$ and 0.09, respectively) and was not used as a covariate.

Within the MS, initial comparisons showed no significant differences between time of day or date of capture with length and RNA:DNA ratio of cod; thus pooled means were used for all further analyses. Significant differences were observed in RNA:DNA ratio and length of cod sampled from the three sites (Table 2). Mean RNA:DNA ratio of cod larvae at the MS were lower than on the Western and Great South Channel Transects; the transects were not significantly different from each other. Mean lengths of cod larvae collected from the MS and Western Transect were not significantly different from each other but were smaller than fish caught at the Great South Channel Transect. (Table 2). RNA content showed similar patterns to RNA:DNA ratio.

For haddock, date of capture but not time of day appeared to have a significant effect on RNA:DNA ratio. Within the MS, haddock collected on 26 May had significantly higher mean RNA:DNA ratios than those collected on 23 May (Table 2). Mean RNA:DNA ratios

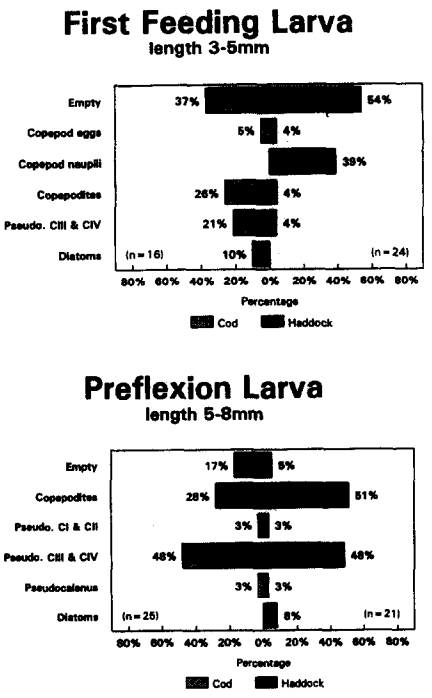

Fig. 15. Prey selection of cod and haddock for two stages: first-feeding/yolk-sac larvae (3–5 mm), and preflexion larvae (5–8 mm). The number (n) represents the total fish stomachs examined for the stage size range combined from both stratified and mixed sites.

of haddock sampled from the three sites were significantly different (Table 2). Ratios were the lowest on 23 May at the MS, intermediate at the 26 May MS and Western Transect, and highest in the Great South Channel Transect. Haddock mean length did not vary with time of day or date of capture. Mean lengths of haddock larvae increased significantly from the MS to the Western Transect to the Great South Channel Transect. RNA content showed similar patterns to RNA:DNA ratio.

Mean RNA:DNA ratios of haddock at the MS on 23 May and the Western Transect were lower than that of cod collected at the same time (Table 2). RNA:DNA ratios of cod and haddock larvae sampled on 26 May at the MS and in the Great South Channel Transect were not significantly different from each other. Cod sampled at the MS were larger than the haddock, while cod and haddock larvae collected from the two transect sites were not significantly different in length from each other (Table 2).

At the MS, in one tow, sufficient numbers of cod and haddock larvae ($n \geq 5$) were collected at discrete depths to examine larval condition vertically in the water column (Table 3). Cod in the upper 20 m had significantly higher RNA:DNA ratios than fish sampled at 40–20 m. The smallest cod were collected at 40–30 m (6.99 mm), and the largest in the top 10–0 m (10.30 mm). The mean RNA:DNA ratio of haddock larvae taken in this tow were not significantly different throughout the water column. The RNA:DNA ratio of haddock differed with depth of capture at the Western Transect (Table 3). Haddock collected in the top 30 m were in much better condition than those sampled at 40–30 m. Mean lengths of haddock larvae were similar throughout the water column at each of the sites sampled.

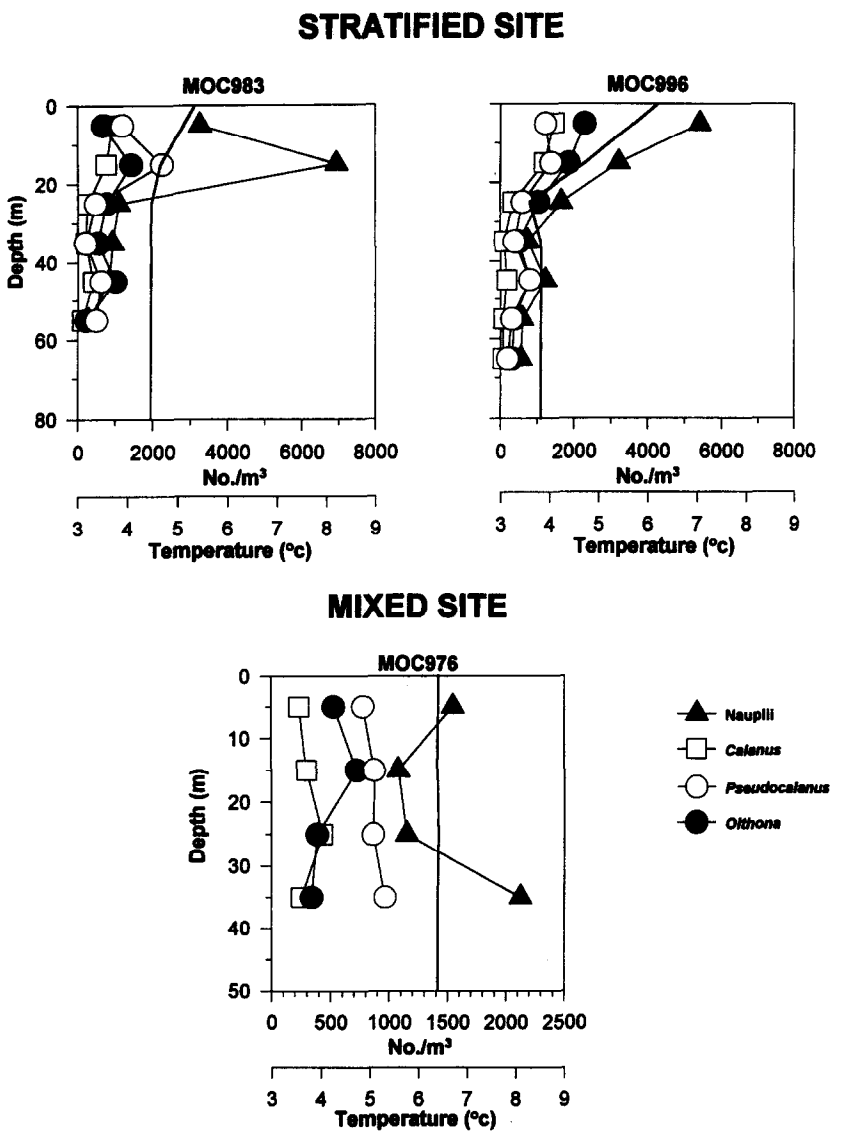

Fig. 16. Vertical profiles of dominant copepods (no. per m^3) collected by the 1/4-m^2 MOCNESS at the stratified site before (tow 983, 23 May 1982) and after (tow 996, 26 May 1992) the storm on 25 May 1992. The lower panel is a single profile (tow 976, 22 May 1992) at the mixed site. A temperature profile is shown for each of the tows.

Preliminary laboratory studies have shown 4.1–4.5 to be the minimum RNA:DNA ratio of fed cod larvae reared at 7°C. Larvae aged 8 days or older, starved in the laboratory 2 days or longer, had values less than 4.1 (unpublished data). Ten per cent of the total haddock larvae sampled (19 fish out of 193) had RNA/DNA ratios below 4.1 (Fig. 18). The highest percentage of poor condition haddock were caught at the MS. Overall, cod were in good condition with only 1.5% of the fish sampled having ratios below 4.1 (2 fish out of 130) (Fig. 18).

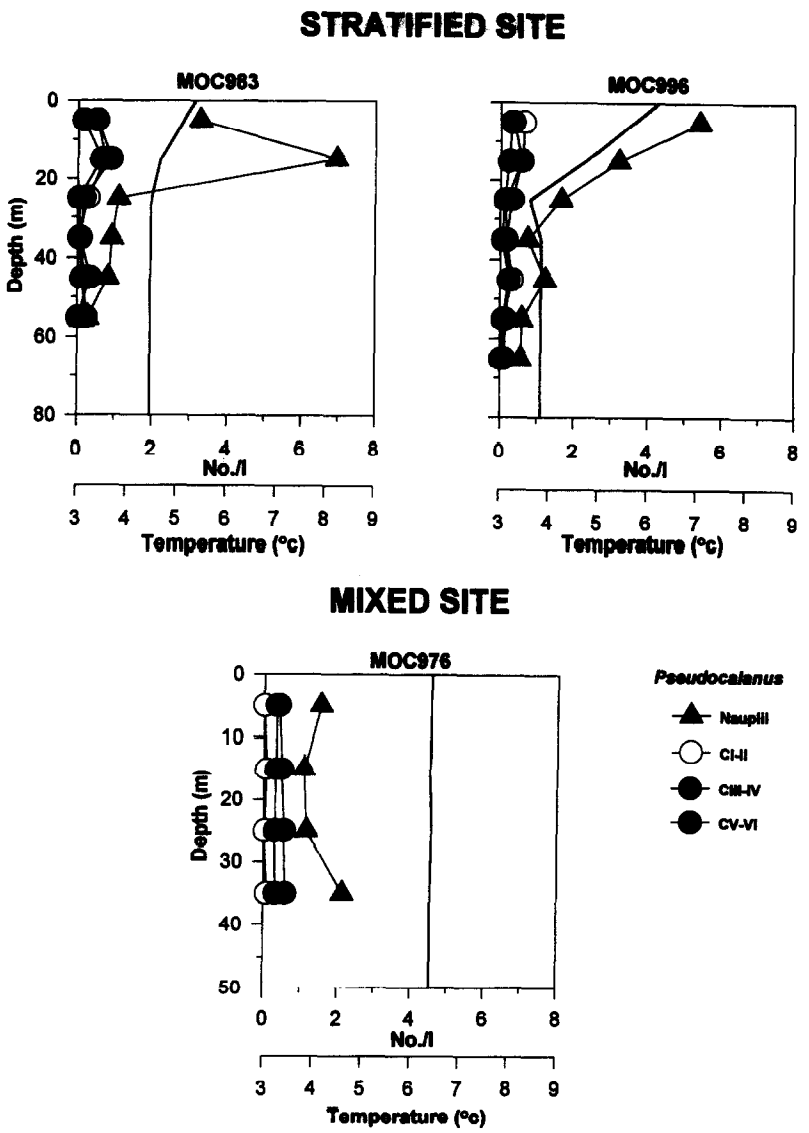

Fig. 17. Vertical profiles of *Pseudocalanus* spp. nauplii and copepodite stages (no. per l) collected by the 1/4-m^2 MOCNESS at the stratified site before (tow 983, 23 May 1992) and after (tow 996, 26 May 1992) the storm on 25 May 1992. The lower panel is a single profile (tow 976, 22 May 1992) at the mixed site. A temperature profile is shown for each of the tows.

DISCUSSION

Vertical distribution of eggs and larvae

Along the southern flank of Georges Bank there is a transition from mixed waters < 60 m to seasonally stratified waters in the deeper regions. Bisagni (1992) defined two separate but contiguous zones within this region: (i) 60–80 m bottom depth, where the depth of the pycnocline is strongly constrained to about 20 m, and (ii) at 80–100 m, where the pycnocline deepens from 20 m in June to 60 m in December. Studies by Frank *et al.* (1989) on haddock

Table 1. *Total number of cod and haddock larvae used in biochemical analyses, listed by date, time of day and tow number*

Location	Date	Time of Day	Tow no.	Cod (*n*)	Haddock (*n*)
Mixed Site	May 23	night	980	26	17
	May 23	day	981	49	60
	May 23	night	985	3	5
	May 26	day	993	9	23
	May 26	night	997	20	18
Western Transect	May 28	day	1004	13	53
Great South Channel	May 28	day	1005	7	12
		day	1008	3	5

Table 2. *Mean and standard deviation of RNA:DNA ratios and length of cod and haddock larvae sampled from three sites. Means in the same column without a letter in common, or in the same row without a number in common, are significantly different (Fishers LSD;* $P \leq 0.05$*)*

	Location	Date	Cod	*n*	Haddock	*n*
RNA:DNA Ratios	Mixed Site	May 23	5.23 ± 0.65^{a1}	78	4.74 ± 0.70^{a2}	82
		May 26	5.23 ± 0.52^{a1}	29	5.15 ± 0.53^{b1}	41
	Western Transect		5.83 ± 0.67^{b1}	13	5.12 ± 0.70^{b2}	53
	Great South Channel		5.96 ± 0.32^{b1}	10	5.87 ± 0.64^{c1}	17
Length (mm)	Mixed Site	May 23	8.15 ± 1.69^{a1}	73	7.53 ± 1.26^{a2}	72
		May 26	9.07 ± 2.11^{a1}	29	7.81 ± 1.30^{a2}	39
	Western Transect		9.43 ± 2.04^{a1}	13	9.11 ± 1.44^{b1}	53
	Great South Channel		11.87 ± 4.08^{b1}	11	10.78 ± 1.37^{c1}	18

Table 3. *Mean and standard deviation of RNA:DNA of cod and haddock larvae sampled at discrete depth intervals. Means in the same column without a letter in common are significantly different (Fishers LSD;* $P \leq 0.05$*)*

		Depth (m)	Cod	*n*	Haddock	*n*
Mixed Site	Tow 981	10–0	5.73 ± 0.33^{a}	5		<5
		20–10	5.67 ± 0.47^{a}	11	5.01 ± 0.64^{a}	8
		30–20	5.04 ± 0.56^{b}	13	4.46 ± 0.47^{a}	20
		40–30	4.97 ± 0.68^{b}	11	4.85 ± 0.84^{a}	27
Western Transect	Tow 1004	10–0			5.47 ± 0.69^{a}	14
		20–10			5.31 ± 0.40^{a}	17
		30–20			5.17 ± 0.80^{a}	10
		40–30			4.35 ± 0.45^{b}	11

eggs and larvae on the Scotian Shelf, and by Lough and Potter (1993) on cod and haddock larvae on Georges Bank, have shown that late-stage eggs and early larvae are aggregated within the pycnocline in relation to the intensity of surface stratification that develops in May. The stronger the stratification, the more they are confined to this depth zone. The vertical distribution of eggs depends on their specific gravity or buoyancy in relation to water-column density surfaces and vertical mixing. Early stage eggs of haddock are typically found near the surface, whereas late stage eggs have a subsurface maximum due to their

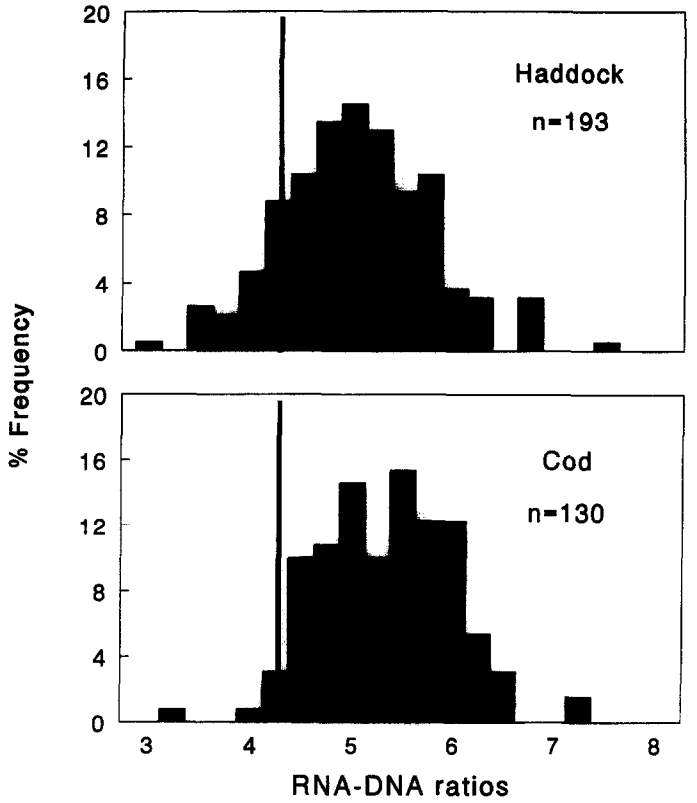

Fig. 18. Per cent frequency distribution of the RNA:DNA ratios from cod and haddock larvae collected at all three sites combined. Larvae with ratios below 4.1 are considered to be in poor condition.

increased specific gravity (Frank *et al.*, 1989; Page and Frank, 1989). In this study at the SS, most of the gadid eggs (93% haddock) were located within the wind-mixed layer above the pycnocline (25.5 σ_t value near 20 m). The maximum density for Stage I eggs was in the 10–0 m stratum, whereas for the Stage II and III eggs maximum density was at 20–10 m during the development of stratification, 22–24 May. After the storm event on 25 May, Stage II and III eggs were more or less evenly distributed in the upper 20 m wind-mixed layer.

The mean depth of recently-hatched larvae is usually near the mean depth of the late stage eggs (Frank *et al.*, 1989). In this study at the SS on 24 May, most of the recently-hatched larvae were found below the 20-m pycnocline with a maximum density at 60–50 m depth for haddock and 40–30 m for cod. The egg profile from this same tow (MOC990) showed maximum density to be at 20–10 m depth (Fig. 10). It is possible that the recently-hatched larvae could have settled in the water column from the more surface distribution of eggs as a result of the decreased wind mixing and increased stratification. Another explanation is that the larvae were hatched from eggs located at the deeper depths. An earlier tow (MOC987) on 24 May showed a secondary density peak of Stage I eggs at 60–50 m depth. Also, a later tow (MOC991) on 25 May showed a primary density peak of Stage III eggs at 60–50 m depth.

The vertical distribution of small larvae also is determined by their buoyancy in relation

to the vertical structure of the water column since they have limited ability to vertically migrate (Lough and Potter, 1993). Larvae larger than 8 mm can migrate vertically tens of meters daily, and they tend to be deeper during the day and shoaler by night. In May 1983 at a stratified site (83–I) on the southern flank of Georges Bank, Lough and Potter (1993) found most of the 9–13 mm cod and haddock larvae to be below the thermocline ($\sim$20 m) by day, but within or above the thermocline at night. In this study at the SS, only small larvae were present and they were centered on average near 20 m, the base of the pycnocline (Fig. 7). At the MS, the small cod and haddock larvae were distributed throughout the water column at night, but by day their abundance increased markedly with depth, most were located deeper than 20 m (Fig. 8). Larvae larger than 8 mm were fewer in number; larger cod were distributed evenly throughout the water column, while larger haddock maintained the same day–night pattern as the small larvae (Fig. 9). It is possible that the small larvae migrated towards the surface at night, or the day–night patterns may be due to sampling variability.

Larvae feeding and prey abundance

The dominant copepods *Pseudocalanus* spp., *Calanus finmarchicus*, and *Oithona* sp. sampled by the 1/4 m MOCNESS (64 μm mesh) on Georges Bank in May 1992 are typical for the spring conditions (Davis, 1987). Cod and haddock larvae tend to feed on the species of prey which are numerically dominant and within an acceptable size range. Recently-hatched larvae feed on small prey such as copepod nauplii, eggs, phytoplankton, and micro-organisms (Kane, 1984; Auditore *et al.*, 1994). Larvae of 5–8 mm feed on larger prey, typically the copepodite stages. In this study the copepod *Pseudocalanus* spp. was numerically the most important prey. At the SS, nauplii of *Pseudocalanus* spp. were most abundant in the upper 20 m of the water column. During the development of stratification, they were most abundant ($7\ l^{-1}$) in the 20–10 m stratum; following the storm on 26 May 1992, they were most abundant ($6\ l^{-1}$) at the surface 10–0 m. Near this same site in May 1981, Lough (1984) observed larval haddock and cod and their prey ($50\ l^{-1}$) concentrated in the thermocline region at 20–10 m depth. Following a strong storm with winds 35–40 knots, which mixed the entire water column and dispersed larvae and prey, prey densities were reduced to 5–10 l^{-1}. In May 1992, the storm event was not as strong (winds 15–25 knots) as in 1981, so only the surface 20 m was mixed and consequently the relative density of prey remained about the same as before the storm event. The 1/4 m^2 MOCNESS used to sample the micro-plankton integrated the water column in 10-m strata, so it is possible that more discrete and dense layers of prey exist, especially within a less turbulent, stratified zone. Incze *et al.* (1996), using a plankton pump, found higher densities of nauplii (40–160 l^{-1}) in stratified waters prior to the May 1992 storm, generally at 20–10 m depth. Feeding activity based on larval gut contents has been related directly to prey abundance by Ellertsen *et al.* (1984) and Tilseth and Ellertsen (1984b) for cod larvae in the Lofoten area of the Norwegian Sea. Dense concentrations of copepod nauplii (50–100 l^{-1}) could be found under calm conditions, but were mixed to <10 prey l^{-1} after wind events and consequently, feeding success was reduced.

At the MS in this study, copepods were distributed homogeneously throughout the water column, and based on one tow (MOC976), nauplii were slightly more abundant at the surface and near bottom. There were no copepod nauplii in the gut contents of the larvae examined; but predominantly copepod copepodites of the species *Pseudocalanus*. Although

Oithona sp. was common at this site, none were identified in the larval gut contents. The nauplii of *Pseudocalanus* spp. and *Oithona* sp. can not be easily separated; however, the older stages are easily identified and are not preyed upon successfully by gadid larvae (Kane, 1984). In this study the 5–8 mm larval haddock mean number of prey per larva was uniformly low (1.2–1.8 prey larva^{-1}) through the water column at this site; however, the 5–8 mm larval cod mean number of prey per larva was higher near the surface (2.7 prey larva^{-1}). Most of the cod larvae, as well as haddock, of this size were found in the lower part of the water column by day, whereas at night they were more evenly distributed towards the surface. Larvae feed during daylight, and their gut contents probably represent the summation of feeding over the previous 4 h (Tilseth and Ellertsen, 1984a). Therefore, larval cod with the high mean number of prey per larva caught in the surface net after sunset could have fed on prey located at deeper depths. Feeding conditions for small larvae probably were better at the SS where densities of preferred prey, i.e. nauplii, were higher by an order of magnitude above the 20-m pycnocline, within the upper mixed layer. However, recent studies have indicated that small-scale turbulence generated by wind and tides can increase contacts between larval fish and their prey (see MacKenzie and Leggett, 1991; Lough and Mountain, 1996; Werner *et al.*, 1996). The interaction of turbulence and prey density should be considered in feeding success.

Factors influencing larval condition

This pilot field study was designed to examine the relationship between water column structure, prey abundance, and condition of larvae. In contrast to the study of Buckley and Lough (1987), where only integrated tows were used to sample larvae for biochemical analysis, the present study examined larvae sampled at discrete intervals. Also in the Buckley and Lough study, smaller individual fish (< 800 μg dry weight) had to be pooled to meet the larger sample size requirement for analysis. The recent development of fluorometric techniques for determining nucleic acids now allows measurements of these compounds in the smallest larvae, permitting quantitation of variability among individuals.

The ratio of RNA to DNA is a useful biochemical index of the nutritional condition of larvae: the larger the ratio, the greater the potential growth capacity of the larvae and the better the condition of the fish. Laboratory studies have demonstrated that periods of 2 days or longer at different prey levels are required before significant differences in RNA/DNA ratio are observed in fish larvae (Buckley, 1979; Buckley, 1980). Although the activity of ribosomes may decrease immediately upon food deprivation, a reduction in the ribosome number occurs in the range of days (Henshaw *et al.*, 1971; Houlihan *et al.*, 1988). RNA:DNA ratios therefore, are useful as an index of the nutritional condition of a larva over the past 2–3 days. Haddock RNA:DNA ratios from all of the sites combined were broadly and normally distributed (Fig. 18). Cod ratios were some what more narrowly distributed (Fig. 18) and somewhat truncated at the point where starvation mortality would occur, suggesting light predation pressure or death by starvation. In this study, 10% of the total haddock and 1.5% of the total cod had RNA:DNA ratios below 4.1, the level below which larvae are considered to be in poor condition using fluorometric FIA methodology. Clemmesen (1989) sampled herring (*Clupea harengus* L.) from two sites off the coast of Scotland. She determined that at the two stations sampled, 13% and 0% of the larvae were starving based on RNA:DNA ratio. Robinson and Ware (1988) sampled a cohort of Pacific herring larvae over a period of 36 days in the Strait of Georgia. They found no evidence of

mass starvation based on RNA:DNA ratio. RNA:DNA ratio values from these studies can not be directly compared due to differences in methodology.

In this study at the MS, 1.9% of the cod from both sampling periods were in poor condition; however, for haddock, 14.6% were in poor condition on 23 May, but only 4.9% on 26 May (Fig. 19). In this same area of Georges Bank in May 1983, Buckley and Lough (1987) found a higher percentage (50%) of haddock larvae in poor condition at the mixed site. At the Western Transect in this study, none of the cod were observed to be in poor condition while 9.4% of the haddock (Fig. 19) had ratios <4.1. There were no poor condition larvae caught at the Great South Channel Transect.

Both Clemmesen (1994) and Canino *et al.* (1991) reported significant correlations between live length and RNA:DNA ratio of marine larval fish. Canino *et al.* (1991) used length as a covariate in his regression model, and Clemmesen (1994) stressed the importance of using length (or age) dependent ratios to determine minimum values for the evaluation of poor conditioned larvae. In contrast, Buckley (1982) and Buckley *et al.* (1984) showed that for two species of marine fish-larvae reared in the laboratory, the relations among RNA:DNA ratio, temperature and growth rate were unaffected by the size (protein

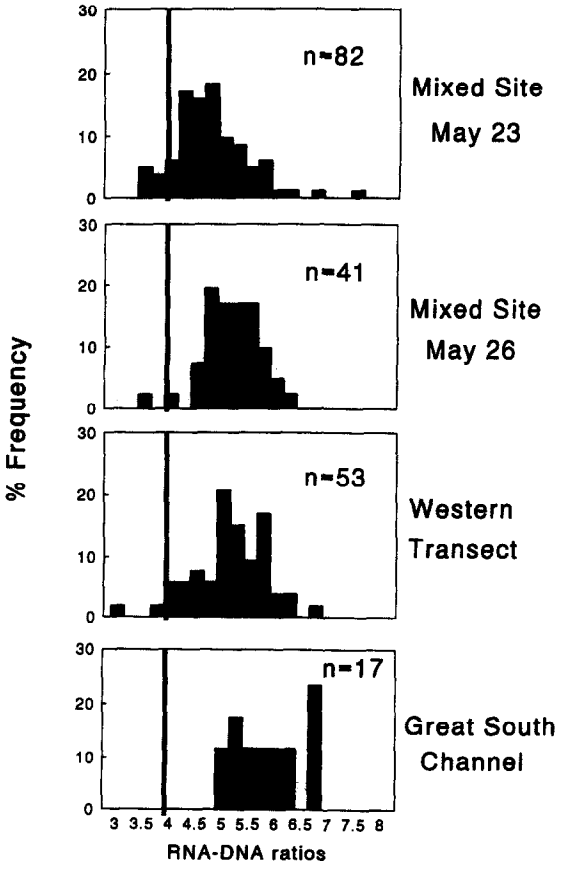

Fig. 19. Per cent frequency distribution of RNA:DNA ratios from haddock larvae collected at each site. Larvae with ratios below 4.1 are considered to be in poor condition.

content) or age of the larvae. They found that when RNA:DNA ratio increased with age, accompanied by a corresponding increase in growth rate. In this study, no correlation between ln length or length and the RNA:DNA ratio of cod or haddock was observed.

The shrinkage algorithm developed by Theilacker (1980) and used in this study for conversion to live standard length is based on a maximum tow time of 20 min. In this study, sampled larvae could remain in the 1-m MOCNESS net from 10–50 minutes depending on the depth of the site and the net it was retrieved from. The relatively poor correlation of ln length with RNA, DNA and protein content could be a result of unaccounted for shrinkage due to the longer duration of the tows, the time spent sorting the larvae, or the freezing of the fish.

RNA:DNA ratios were larger for both cod and haddock from east to west on the bank, i.e. the MS to the Great South Channel Transect (Table 2). Since temperatures at the three sites were similar throughout the study period, the larger RNA:DNA ratio reflect faster growing larvae (Buckley, 1984). The mean length of larvae at the Great South Channel Transect also was larger (and the larvae were presumably older) than larvae at the more eastern sites. This is consistent with their general southwestward transport from the spawning site on northeastern Georges Bank (Lough, 1984). By the time the larvae reach the western end of George's Bank, the poorer condition larvae have disappeared (starved or eaten). Thus, the larvae found in the Great South Channel Transect may represent the better conditioned survivors. It also is possible that copepod prey may have been more abundant in the region. Unfortunately, further conclusions comparing the sites are hampered by the lack of prey data from the transects, and any analysis of the distribution of the ratios is restricted by the small sample size at the transects.

In this study the observations that larvae taken from different depths had statistically different ratios suggests that the larvae had remained together or resided in a similar feeding environment long enough to acquire a unique signature. This is somewhat surprising given the mobility of larger larvae and the wind and tidal mixing characteristics of the water column at these sites. Two mechanisms may account for this suggested segregation of larvae at the different depths: (i) differential buoyancy of small larvae related to chemical composition and condition (Blaxter, 1988; Sclafani *et al.*, 1993), and (ii) vertical migration of larger larvae with aggregation near thermoclines (pycnoclines), tidal fronts, or bottom where food prey may be concentrated (Taggart *et al.*, 1989; Lough and Potter, 1993).

Haddock from the Western Transect (MOC1004) showed a marked decrease in condition in the bottom 30–40 m (RNA:DNA ratio = 4.35, $n = 11$) (Fig. 20). Unfortunately, there were no comparable 1/4 m^2 MOCNESS tows at this site to allow for estimates of the prey field. Although the sample sizes were too small to show complete distributions at each depth, the trend for fish of similar condition to be found together is suggested and should be investigated further.

On 23 May, at the MS, larvae were sampled for biochemical analysis at different depth strata (MOC981). Sixteen hours later, larvae were collected at the same site to examine feeding ratios (MOC985). The condition indices of both cod and haddock reflected their observed mean number of prey per larva. Cod larvae were in better condition in the top 20–0 m than in the bottom 40–20 m (Table 3). Haddock larvae were growing slower than cod collected at the same time; however, no difference with depth was observed. The mean number of prey per larva at the different depths for cod larvae (5–8 mm) were higher from the surface 10–0 m stratum (2.7 prey $larva^{-1}$) than at deeper depths (1.5–1.6 prey $larva^{-1}$); however, for haddock larvae of the same size, the mean number of prey per larva was

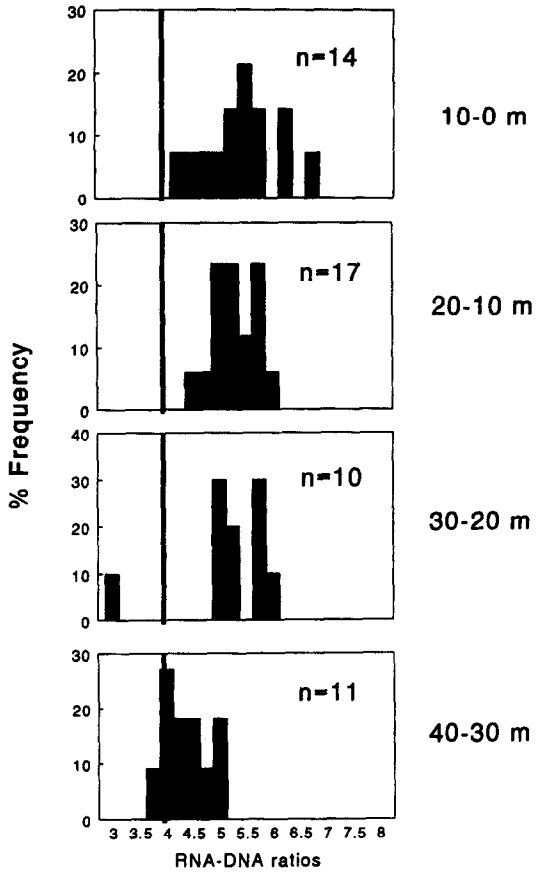

Fig. 20. Per cent frequency distribution of RNA:DNA ratios from haddock larvae collected at discrete depth intervals from the Western Transect. Larvae with ratios below 4.1 are considered to be in poor condition.

uniformly 1.2–1.8 throughout the water column to 40 m depth. Canino *et al.* (1991) compared feeding intensity and mean RNA:DNA ratio values of field-caught walleye pollack (*Theragra chalcogramma*). They found similar trends between the two parameters.

Buckley and Lough (1987) noted that cod larvae were in consistently better condition than haddock at the well-mixed site they sampled. In the present study, cod were in equal or better condition than haddock at locations where samples were taken for biochemistry, essentially in well-mixed waters. Based on prey selectivity studies, Kane (1984) speculated that larval cod may be more aggressive predators that fed on larger prey items at an earlier age than haddock. A comparative study of morphology by Auditore *et al.* (1994) also supports the idea that larval haddock are more passive foragers on smaller prey than cod. Furthermore, in modeling simulations using metabolic and feeding parameters derived from laboratory rearings, Werner *et al.* (1996) have verified field observations that cod grow and survive better at lower prey densities than haddock. Laboratory studies over a range of prey densities have shown that daily specific growth rates of cod were 2–2.5 times greater than haddock when the two species were reared together (Laurence *et al.*, 1981). The poorest

condition larvae (mean RNA:DNA ratio = 4.35) sampled were haddock from 40–30 m at the Western Transect. Haddock larvae apparently grow and survive better in stratified waters where their prey are concentrated (Buckley and Lough, 1987).

The storm on 25 May 1992 with strong northeasterly winds, associated with a strong westward transport of the surface water, appeared to have a differential effect on cod and haddock larvae. Larval cod sampled before (23 May) and after (26 May) the day storm event had indistinguishable RNA:DNA ratios, while larval haddock had significantly higher ratios after the storm. The distributions of the haddock ratios also changed: the mode shifted to a higher ratio, the tail of the distribution appeared to be truncated below a ratio of 4.2, and the ratios were more narrowly distributed (Fig. 19). This difference may be the result of sampling a different population of haddock larvae that was transported from the east, or, possibly prey availability increased after the storm. The near-surface Ekman layer is most subject to wind-induced transport (Werner *et al.*, 1993), so larvae residing in the surface would be advected farther relative to larvae residing deeper in the water column. In this study, haddock larvae had no significant difference in size with depth at the MS; however, most of the haddock resided near bottom during the day and were dispersed throughout the water column by night. Cod, in general, had the same day/night vertical distribution pattern as haddock, but there were large differences in mean lengths between bottom and surface, associated with a difference in condition. The largest and best conditioned cod were found at the surface, and some evidence indicates that their feeding intensity was greater than fish caught at deeper depths. The larger cod larvae are known to be active vertical migrators, moving towards the surface at night and returning to near bottom by day (Lough and Potter, 1993). These larger cod could effectively avoid the surface Ekman layer during a storm by remaining at depth, thereby reducing their horizontal transport. Consequently, vertically migrating cohorts may tend to remain together, experiencing similar conditions that would result in their having more similar RNA:DNA ratios.

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REFERENCES

Auditore P. J., R. G. Lough and E. A. Broughton (1994) A review of the comparative development of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) based on an illustrated series of larvae and juveniles from Georges Bank. *Northwest Atlantic Fishery Organization Scientific Council Studies*, **20**, 7–18.

Berrien P. and J. Sibunka (1996) Distribution patterns of fish eggs in the United States northeast continental shelf ecosystem, 1977–1987, NOAA Technical Report NMFS, 10100–1.

Bisagni J. J. (1992) Differences in the annual stratification cycle over short spatial scales on southern Georges Bank. *Continental Shelf Research*, **12**, 415–435.

Blaxter S. H. S. (1988) Pattern and variety in development. In: *Fish physiology*, W. S. Hoar and D. J. Randall, editors, Academic Press, San Diego, CA.

Bolz G. R. and R. G. Lough (1988) Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. *Fishery Bulletin, U.S.*, **86**, 223–235.

Buckley L. J. (1979) Relationships between RNA:DNA ratio, prey density, and growth rate in Atlantic cod (*Gadus morhua*) larvae. *Journal of the Fisheries Research Board of Canada*, **36**, 1497–1502.

Buckley L. J. (1980) Changes in ribonucleic acid, deoxyribonucleic acid, and protein content during ontogenesis in winter flounder, *Pseudopleuronectes americanus*, and the effect of starvation. *Fishery Bulletin, U.S.*, **77**, 703–708.

Buckley L. J. (1981) Biochemical changes during ontogenesis of cod (*Gadus morhua* L.) and flounder (*Pseudopleuronectes americanus*) larvae. *International Council for the Exploration of the Sea, Rapports et Procès-verbaux des Rèunions*, **178**, 547–552.

Buckley L. J. (1982) Effects of temperature on growth and biochemical composition of larval winter flounder *Pseudopleuronectes americanus*. *Marine Ecology Progress Series*, **8**, 181–186.

Buckley L. J. (1984) RNA:DNA ratio: an index of larval fish growth in the sea. *Marine Biology*, **80**, 291–298.

Buckley L. J. and R. G. Lough (1987) Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhus*) on Georges Bank. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 14–25.

Buckley L. J., S. I. Turner, T. A. Halavik, A. S. Smigielski, S. M. Drew and G. C. Laurence (1984) Effects of temperature and food availability on growth, survival, and RNA:DNA ratio of larval sand lance (*Ammodytes americanus*). *Marine Ecology Progress Series*, **15**, 91–97.

Caldarone E. M. and L. J. Buckley (1991) Quantitation of DNA and RNA in crude tissue extracts by flow injection analysis. *Analytical Biochemistry*, **199**, 137–141.

Canino M. F. (1994) Effects of temperature and food availability on growth and RNA/DNA ratios of walleye pollock *Theragra chalcogramma* (Pallas) eggs and larvae. *Journal of Experimental Marine Biology and Ecology*, **175**, 1–16.

Canino M. F., K. M. Bailey and L. S. Incze (1991) Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Marine Ecology Progress Series*, **79**, 27–35.

Clemmesen C. (1987) Laboratory studies on RNA:DNA ratios of starved and fed herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. *Journal du Conseil pour l'Exploration de la Mer*, **43**, 122–128.

Clemmesen C. (1988) An RNA and DNA fluorescence technique to evaluate the nutritional condition of individual marine fish larvae. *Meeresforschung*, **32**, 134–143.

Clemmesen C. M. (1989) RNA:DNA ratios of laboratory-reared and wild herring larvae determined with a highly sensitive fluorescence method. *Journal of Fishery Biology*, **35A**, 331–333.

Clemmesen C. (1994) The effect of food availability, age or size on the RNA/DNA ratio of individually measured herring larvae: laboratory calibration. *Marine Biology*, **118**, 377–382.

Davis C. S. (1987) Zooplankton life cycles. In: *Georges Bank*, R. H. Backus, editor, The MIT Press, Cambridge, MA, pp. 256–267.

Ellertsen B., P. Fossum, P. Solemdal, S. Sundby and S. Tilseth (1984) A case study on the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten. In: *The propagation of cod* Gadus morhua *L.*, E. Dahl, D. S. Danielssen, E. Moksness and P. Solemdal, editors, Flødevigen rapportser, Vol. 1, pp. 453–477.

Flagg C. N. (1987) Hydrographic structure and variability. In: *Georges Bank*, R. H. Backus, editor, The MIT Press, Cambridge, MA, pp. 108–124.

Frank K. T., F. H. Page and J. K. McRuer (1989) Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 82–92.

Henshaw E. C., C. A. Hirsch, B. E. Morton and B. M. Hiatt (1971) Control of protein synthesis in mammalian tissues through changes in ribosome activity. *Journal of Biological Chemistry*, **246**, 436–446.

Houlihan D. F., S. J. Hall, C. Gray and B. S. Noble (1988) Growth rates and protein turnover in the Atlantic cod, *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 951–964.

Incze L. S., P. Aas and T. Ainaire (1996) Distributions of copepod nauplii and turbulence on the southern flank of Georges Bank: implications for feeding by larval cod (*Gadus morhua*). *Deep-Sea Research II*, **43**, 1855–1873.

Kane J. (1984) The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Marine Ecology Progress Series*, **16**, 9–20.

Laurence G. C., A. S. Smigielski, T. A. Halavik and B. R. Burns (1981) Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. *Rapports et Procès-Verbaux des Reunion Conseil Internationale d'Exploration de la Mer*, **178**, 3034–3311.

Lough R. G. (1984) Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results. In: *The propagation of cod* Gadus morhus *L.*, E. Dahl, D. S. Danielssen, E. Moksness and P. Solemdal, editors, Flødevigen rapportser, Vol.1, pp. 395–434.

Lough R. G. and G. R. Bolz (1989) The movement of cod and haddock onto the shoals of Georges Bank. *Journal of Fish Biology*, **35**, 71–79.

Lough R. G. and D. G. Mountain (1996) Effect of small-scale turbulence on feeding rates of larval cod and haddock in stratified water on Georges Bank. *Deep-Sea Research II*, **43**, 1745–1772.

Lough R. G. and D. C. Potter (1993) Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanngrammus aeglefinus* and Atlantic cod *Gadus morhua*. *Fishery Bulletin, U.S.*, **91**, 281–303.

Manning J., T. Holzwarth-Davis, M. Taylor, T. Rotunno, D. Mountain and G. Lough (1996) Georges Bank Stratification Study: 1992 Data Report, *Albatross IV* 92–04 and 92–05, 27 April–29 May 1992, Woods Hole, Massachusetts, Northeast Fisheries Science Center Reference Document, 95–10, 101 pp.

MacKenzie B. R. and W. C. Leggett (1991) Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Marine Ecology Progress Series*, **73**, 149–160.

Page F. H. and K. T. Frank (1989) Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogramus aeglefinus*) stocks with emphasis on Georges and Browns Bank. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 68–81.

Robinson S. M. C. and D. M. Ware (1988) Ontogenetic development of growth rates in larval pacific herring, *Clupea harengus pallasi*, measured with RNA:DNA ratios in the Strait of Georgia, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1422–1429.

Sclafani M., C. T. Taggart and K. R. Thompson (1993) Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. *Journal of Plankton Research*, **15**, 413–435.

Smith P. K., R. I. Krohn, G. T. Hermanson, A. K. Mallia, F. H. Gartner, M. D. Provenzano, E. K. Fujmoto, N. M. Goeke, B. J. Olson and D. C. Kleak (1985) Measurement of protein using bicinchroninic acid. *Analytical Biochemistry*, **150**, 76–85.

Taggart C. T., K. F. Drinkwater, J. K. McReur and P. LaRouche (1989) Larval fish zooplankton community structure, and physical dynamics at a tidal front. *Rapports et Procès-verbaux des Rèunions Conseil d'Exploration de la Mer*, **191**, 184–194.

Theilacker G. H. (1980) Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. *Fishery Bulletin, U.S.*, **78**, 685–692.

Thompson B. M. and J. D. Riley (1981) Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). *Rapports et Procès-verbaux des Rèunions, Conseil d'Exploration de la Mer*, **178**, 553–559.

Tilseth S. and B. Ellertsen (1984) Food consumption rate and evacuation processes of first feeding cod larvae (*Gadus morhua* L.). In: *The propagation of cod* Gadus morhus *L.*, E. Dahl, D. S. Danielssen, E. Moksness and P. Solemdal, editors, Flødevigen rapportser, Vol.1, pp. 167–182.

Tilseth S. and B. Ellertsen (1984) The detection and distribution of larval Arcto-Norwegian cod, *Gadus morhua*, food organisms by an in situ particle counter. *Fishery Bulletin, U.S.*, **82**, 141–156.

Werner F. E., F. H. Page, D. R. Lynch, J. W. Loder, R. G. Lough, R. I. Perry, D. A. Greenberg and M. M. Sinclair (1993) Influences of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. *Fisheries Oceanography*, **2**, 43–64.

Werner F. E., R. I. Perry, R. G. Lough and C. E. Naime (1996) Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep-Sea Research II*, **43**, 1793–1822.