

Abstract.—Vertical distribution patterns of haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* are summarized from eight research cruises on Georges Bank, during spring and summer 1981–86. Eggs and larvae were sampled at discrete depths with a 1 m² MOCNESS, pelagic juveniles with a 10 m² MOCNESS, and recently-settled juveniles with a bottom trawl supplemented with submersible observations. In well-mixed waters during early spring, eggs and larvae were distributed throughout the water column. Upon stratification of waters over the outer margin of Georges Bank in mid-May, the larval population was concentrated in the thermocline; the stronger the stratification, the more larvae were confined to this depth zone. At well-mixed shoal sites, pelagic larvae remained distributed throughout the water column.

Differences in day and night distribution patterns provided evidence to indicate that larvae began migrating as small as 6–8 mm; however, clear sampling differences were evident for larvae only at body lengths of >9–13 mm. Larvae tended to be deeper during the day and shoaler by night; larger larvae had a greater vertical range. Pelagic juveniles (>20 mm) occurred deeper in the water column as they grew. By mid-July most juveniles (~40 mm) were associated with the bottom. The transition from pelagic to demersal life (~40–100 mm) probably occurs over a period of 1–2 mo. Recently-settled juveniles remained demersal by day and migrated upwards 3–5 m at night. Their excursions off-bottom decreased in amplitude with larger sizes. Haddock remained closer to bottom both day and night at a smaller size than cod. The diel vertical behavior of cod may be strongly related to the light-dark cycle, whereas behavior of haddock was more variable. Some differences in vertical distributions between haddock and cod can be attributed to morphology and feeding behavior.

Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank*

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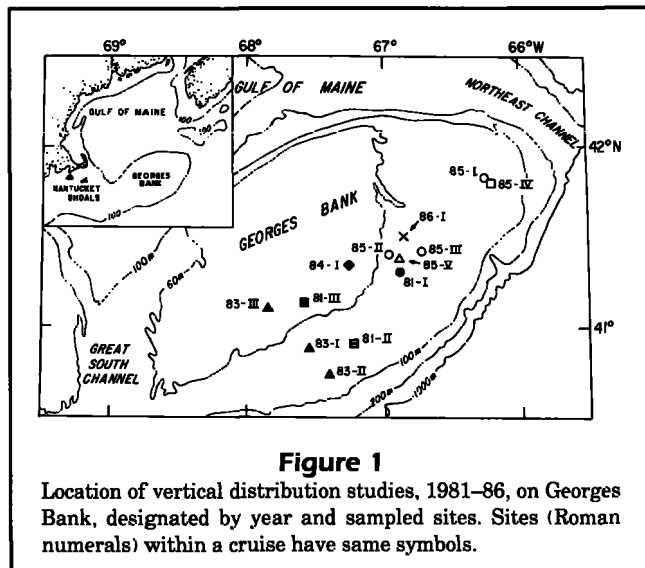
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On Georges Bank off the northeast coast of the United States (Fig. 1, page 293), stocks of haddock *Melanogrammus aeglefinus* L. and Atlantic cod *Gadus morhua* L. historically have been important components of the American and Canadian demersal fishery (Murawski et al. 1983, Overholtz & Tyler 1985). Eggs and larvae of both species are dominant in the spring ichthyoplankton community (O'Boyle et al. 1984, Sherman et al. 1984). Research survey data have shown that the size of a year-class is usually established by the end of the first year of life (Sissenwine 1984). At the Northeast Fisheries Science Center (NEFSC) since 1976, considerable research effort has been focused toward describing the place and time of spawning of haddock and cod, dispersal of eggs and larvae, and survival and recruitment of juveniles on Georges Bank. Field, laboratory, and modeling results were integrated to evaluate important mortality processes during the first year of life. Beginning in spring 1980, a series of interdisciplinary, process-oriented cruises used discrete depth samplers to investigate mortality due to starvation by describing the fine-scale spatio-temporal variability of gadid larvae in relation to their prey during the first few weeks post-hatching (Lough 1984, Laurence & Lough 1985). In 1984, a series of summer and early-fall surveys of ju-

venile gadids was initiated to document the distribution and abundance of the 0-group fish and their transition to the demersal phase when predation may be a dominant mortality factor (Cohen et al. 1988).

Based on these studies, we now have sufficient information to describe the life history of haddock and cod during the first 6–9 mo. Both species spawn on the northeast part of Georges Bank (Fig. 1). Peak spawning time for cod is late February–early March, and early April for haddock. The egg patches drift southwest a few kilometers per day in the clockwise residual drift and hatch within 2–3 wk (Lough 1984). By May, larval concentrations can be found along the southern edge of Georges Bank between the 60 m and 100 m isobath. In late-spring to fall, a seasonal thermocline develops to a depth of 10–30 m in waters deeper than ~60 m. Water shoaler than 60 m is vertically well-mixed throughout the year by the strong (>60 cm/s) rotary tidal currents. Larvae >30 d can be found shoaler than the 60 m isobath as the patch moves southwest, and by late June some fraction of the population has moved onto the shoals of western Georges Bank (Walford 1938,

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Lough 1984, Smith & Morse 1985, Lough & Bolz 1989). By late July–early August, the highest catches of juvenile gadids are usually found on eastern Georges Bank (Lough et al. 1989).

Haddock and cod undergo typical development and morphological transformation at sizes >20 mm standard length (SL, ~2–3 mo post-hatching) (Fahay 1983, Auditore et al. 1993). Their transition from pelagic to demersal life occurs when they are >25 mm in mid-summer (Lough et al. 1989).

Information on larval and juvenile vertical distributions and diel migrations are needed to (a) study their transport by currents, (b) compare vertical distributions of their prey and predators, and (c) make accurate abundance estimates of various stages caught by different sampling gear. In this paper we summarize data on the vertical distribution of 0-group haddock and cod during spring and summer on Georges Bank from 1981 to 1987. The following questions on the early life of haddock and cod were addressed. (1) What is the vertical distribution pattern of larvae and juveniles on Georges Bank? (2) What is the timing and range of diel migratory behavior in relation to development? (3) What is the transition period from pelagic to demersal life for an individual fish? (4) How do light, temperature, salinity, and currents influence vertical distribution and migratory behavior? (5) How does gear selectivity bias vertical distribution patterns?

Methods

Sampling protocol

General cruise objectives and sampling strategy for the larval–juvenile fish studies are described by Lough

(1984). A concentration of larvae on Georges Bank was located by a fine-scale grid of stations using standard bongo-net gear. Based upon real-time sample analyses made during the grid survey, sites were selected within well-mixed and stratified waters for the comparative vertical time-series observations. Haddock and cod were collected by three gear types on eight cruises (Table 1). Pelagic larvae and juveniles were sampled with an electronically-controlled, multiple opening/closing net and environmental sensing system (MOCNESS), with a 1 m² or 10 m² mouth opening (see Wiebe et al. 1976, 1982, 1985). A Yankee 36 bottom trawl was used to sample the recently-settled juvenile fish. The numbers of day, night, and twilight hauls at each site are listed in Table 1.

The MOCNESS used to sample the larval stage has an effective mouth opening of 1 m² when towed at a 45° net angle near 3.7 km/h (2 kn). The unit consists of nine 0.333 mm mesh nets that open and close sequentially on command. Temperature (and salinity beginning in 1985) was obtained simultaneously with standard net-sampling parameters such as depth and volume of water filtered. When a concentration of larvae was located, a drogue was deployed at a depth of 15 m to mark the water mass for further sampling. Thereafter, the 1 m² MOCNESS was used to sample every 3–6 h at the drogue for a period of 24–48 h. Discrete depths were sampled at 10 m intervals from the surface to within 5 m of the bottom within a 5 min period. Each net filtered ~250 m³ of water.

The 10 m² MOCNESS, used to collect the pelagic juveniles, has five 3.0 mm mesh nets. Because juveniles tend to remain localized for at least 2–4 d, sampling was conducted at fixed sites that were determined to contain high concentrations of juveniles. The vertical distribution of pelagic juveniles was sampled every 6 h. Discrete depth strata ranged 10–30 m from the surface to within 5 m of the bottom; each net filtered between 15,000 and 20,000 m³ of water during a 30 min tow.

A Yankee 36 bottom trawl was used to catch recently-settled juveniles. Trawl specifications are found in Azarovitz (1981). The opening height and width of the trawl was 3.2×10.4 m. The trawl had graded stretch mesh of 127–13 mm (mouth to cod-end). Standard roller gear (40.6 cm diameter) was used on the *Albatross IV* 86-03 June 1986 cruise; however, rollers were replaced with a sweep chain of rubber disks (11.4 cm diameter) on the *Delaware II* cruises 85-05 of July 1985 and 85-06 of August 1985, to collect fish close to bottom. The standard bottom-trawl set was made at 6.5 km/h (3.5 kn) for 30 min on the bottom. Trawl sampling was conducted for 24 h.

All specimens were initially fixed in either 4% formaldehyde-seawater solution or 90% ethyl alcohol and

then subsequently preserved in 70% ethyl alcohol and water. Temperature and salinity profiles were obtained from the MOCNESS, XBT drop, or CTD cast.

Data analysis

Larvae and pelagic juveniles were measured to the nearest 0.1 mm SL. Demersal juveniles from the bottom trawl were measured to the nearest mm. Length of haddock and cod were corrected for shrinkage to live-length using the method of Bolz & Lough (1983). Catches from the 1 m² MOCNESS were initially standardized to $n/100 \text{ m}^3$ of water, and 10 m² MOCNESS catches to $n/10,000 \text{ m}^3$. The fish were grouped into size-classes based on developmental characters (Auditore et al. 1993): 2–5, 6–8, 9–13, 14–19, 20–29, 30–39, 40–49, 50–59, and 60–69 mm.

As an initial step, the percent of a size-class at each depth was plotted with the temperature and salinity profile for each tow (figures not shown). Tows were classified as day, night, or (in a few cases) twilight, i.e., 1 h before and after sunrise and sunset. For each pelagic tow, the mean number of fish within a time-block and size-class was calculated for each depth by summing all hauls at that site. Day and night vertical profiles are plotted from these arithmetic means. Also, abundance of larvae was integrated over the water column, in terms of $n/10 \text{ m}^2$ for the 1 m² MOCNESS catches and $n/1000 \text{ m}^2$ for the 10 m² MOCNESS catches. Abundance-weighted mean depth or center of density distributions of size-classes were calculated using the method of Miller et al. (1963). To examine trends, mean depths of selected sites were plotted in time-series with water column thermoclines. Since salinity changes throughout the water column are generally small (<1 psu), temperature usually has a dominant effect on density and stratification of the surface water on Georges Bank (Flagg 1987).

To test for differences in population means between day and night vertical distributions and for interactions among depth, time of day, and size of fish, an unbalanced ANOVA Type-III model was used on all tow data (Dunn & Clark 1974). The linear model is:

$$Y = b_0 + b_1 (D) + b_2 (T) + b_3 (S) + b_4 (D \times T) + b_5 (D \times S) + b_6 (T \times S) + b_7 (D \times T \times S) + e, \quad (1)$$

where Y is fish density (n/m^3), D is depth effect (coded depth level), T is time effect (coded night or day), S is size effect (coded size-class), b is a constant, and e is the normally-distributed residual error term. Transformation of the fish density data by $\log_{10}(x+0.1)$ resulted in a normal distribution of the residuals. Although the interpretation of vertical migration based on ANOVA can be difficult, the depth \times time interaction is generally considered the most useful factor for

detecting diel migrations (Sokal & Rohlf 1969). Summary tables are presented of the factor *F*-values and their level of significance.

For each station, an average temperature and salinity profile was made by summing all the time-series data across the sampled depth levels and calculating the mean, standard deviation, and 95% confidence limits. At sites where stratification of the water column occurred primarily from solar insolation, upper and lower bounds of the thermocline region were determined by inspection for each tow profile. The thermocline was defined as the region of greatest temperature change. In a well-stratified water column, the zone of greatest temperature change was easily identified between the relatively uniform water above and below this zone. In a weakly-stratified water column, determination of the thermocline zone was more subjective. The distribution of larvae within, above, and below the thermocline was estimated for each size-class within a tow at Sites I&II for May 1983. The mean percentage distribution and standard error of each region were calculated on the angular transformation of the tow percentage data: $\text{angle} = \arcsin \sqrt{\text{proportion}}$.

Bottom-trawl catches of recently-settled juvenile haddock and cod were standardized to $n/30 \text{ min haul}$. Length data were grouped by 1 cm size-classes and then grouped by day, night, and twilight catches. Standard statistics (\bar{x} , SD, CV) were calculated on the untransformed data. Differences between population means were tested by the Students' *t*-test on \log_{10} transformed data (Sokal & Rohlf 1969).

Results

Vertical distribution of larvae

Well-mixed water In April 1981, recently-hatched haddock larvae (2–5 mm) and fewer larger larvae (6–8 mm) were distributed throughout the water column (Fig. 2A). Results of the ANOVA for the 2–5 mm haddock (Table 2) showed a significant effect of depth ($p < 0.05$) but not of time of day.

Cod larvae (up to 8 mm) also were distributed through the water column (Fig. 2B). In several vertical profiles the distributions are weakly bimodal. During the day, larger larvae (9–29 mm) were most abundant at mid-depth, 30–40 m, whereas at night they were more abundant above 30 m. Ratios in night-day abundance increased from $\sim 2/10 \text{ m}^2$ or less for the smaller larvae (<14 mm) to $4\text{--}6/10 \text{ m}^2$ for the 14–19 mm and 20–29 mm size-classes. ANOVA for cod larvae showed a significant ($p < 0.05$) interaction effect of time \times size, which was expected since abundance increases at night as cod get larger (Table 2A). A significant ($p < 0.05$) depth \times time interaction occurred only for size-classes >9–13 mm.

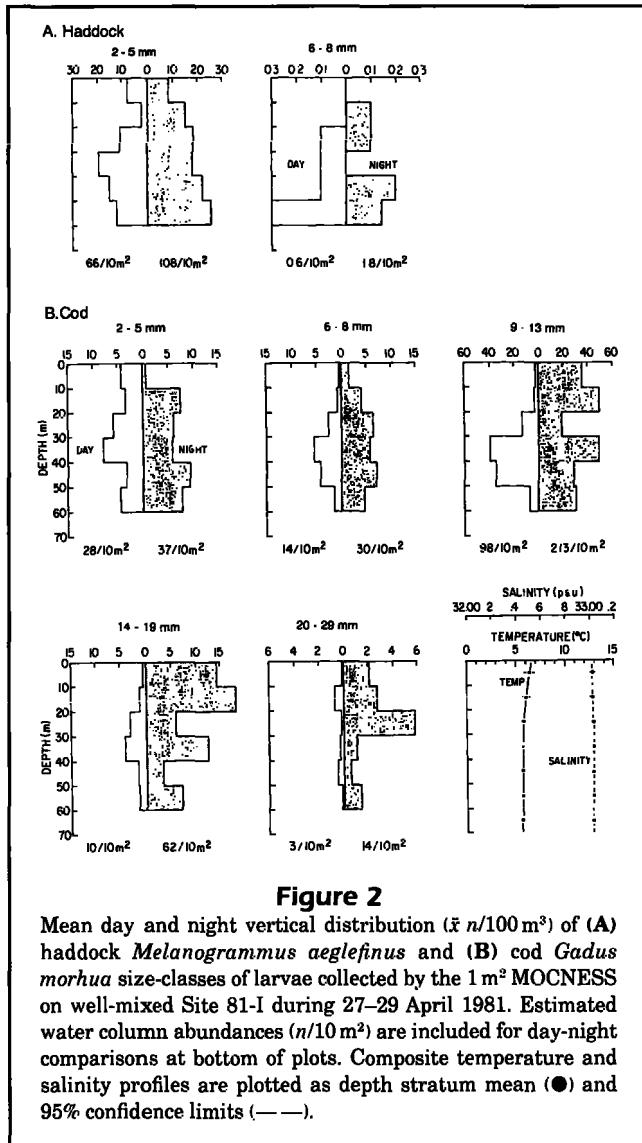


Figure 2

Mean day and night vertical distribution (\bar{x} n/100 m²) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1 m² MOCNESS on well-mixed Site 81-I during 27–29 April 1981. Estimated water column abundances (n/10 m²) are included for day-night comparisons at bottom of plots. Composite temperature and salinity profiles are plotted as depth stratum mean (●) and 95% confidence limits (—).

Mean depths of the four smallest cod size-classes are plotted for each tow within a 24 h period over the 2.5 d of sampling at Site 81-I, and a trend line connects the mean depths of abundance (Fig. 3). There appears to be a daily pattern in vertical distribution. The smaller size-classes, 2–5 mm and 6–8 mm, remained at a depth of ~35 m day and night. In contrast, larger size-classes of cod, 9–13 mm and 14–19 mm, showed a consistent diel migration from a mean depth of 40 m at noon to 20–25 m after sunset.

At the well-mixed shoal (35–58 m) Site 81-III on 27 May 1981, 2–13 mm haddock and 6–13 mm cod larvae were distributed through the water column (Fig. 4) with mean depths of abundance generally at 20 m and 40 m. Because of the limited number of tows, a significant difference in day-night patterns could not be determined.

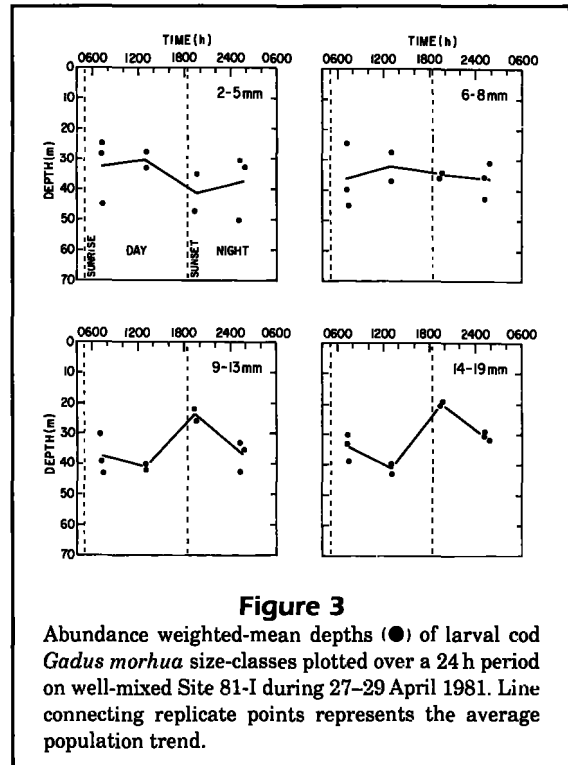


Figure 3

Abundance weighted-mean depths (●) of larval cod *Gadus morhua* size-classes plotted over a 24 h period on well-mixed Site 81-I during 27–29 April 1981. Line connecting replicate points represents the average population trend.

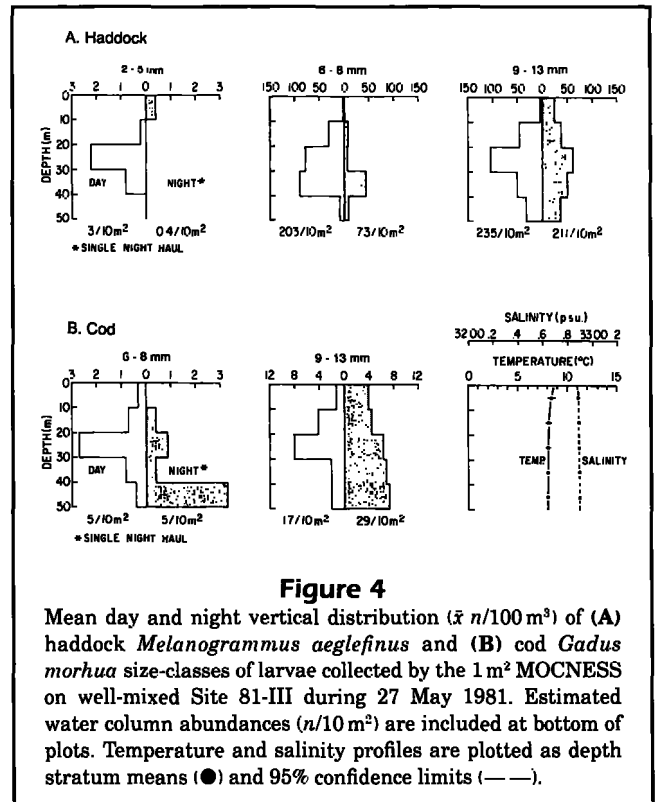


Figure 4

Mean day and night vertical distribution (\bar{x} n/100 m²) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1 m² MOCNESS on well-mixed Site 81-III during 27 May 1981. Estimated water column abundances (n/10 m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

At the well-mixed shoal (34–54 m) Site 83-III on 16–17 May 1983, three size-classes of haddock and cod larvae (6–8, 9–13, 14–19 mm) were distributed through

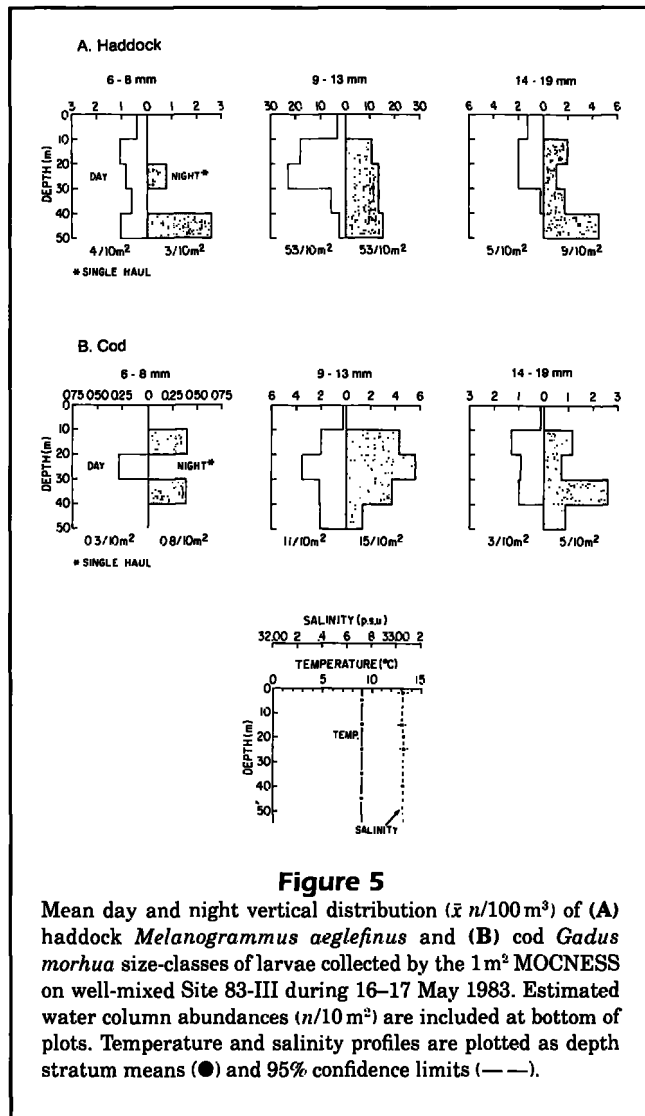


Figure 5

Mean day and night vertical distribution (\bar{x} n/100m³) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1m² MOCNESS on well-mixed Site 83-III during 16–17 May 1983. Estimated water column abundances (n/10m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

the water column (Fig. 5). The single night haul and low densities preclude firm conclusions.

Stratified water On 21 May 1981, when the water column at Site 81-II (75–83 m) was strongly stratified, a single 1 m² MOCNESS night tow found haddock and cod larvae 2–13 mm to be confined almost exclusively to the upper 20 m of the water column, and maximum densities usually were within the strong thermocline gradient at 10–20 m depth (Fig. 6). No recently-hatched cod larvae 2–5 mm were caught in this tow. The surface temperature approached 10°C with a strong thermal gradient at 11–21 m, where the temperature decreased to 5.9°C. An intense storm on 21–24 May 1981, with winds up to 18–21 m/s (35–40 kn) and sea wave heights of 3–5 m (10–15 ft), destroyed the strong thermocline shown in Fig. 6. Following the storm, the water column was well mixed and the larvae were dis-

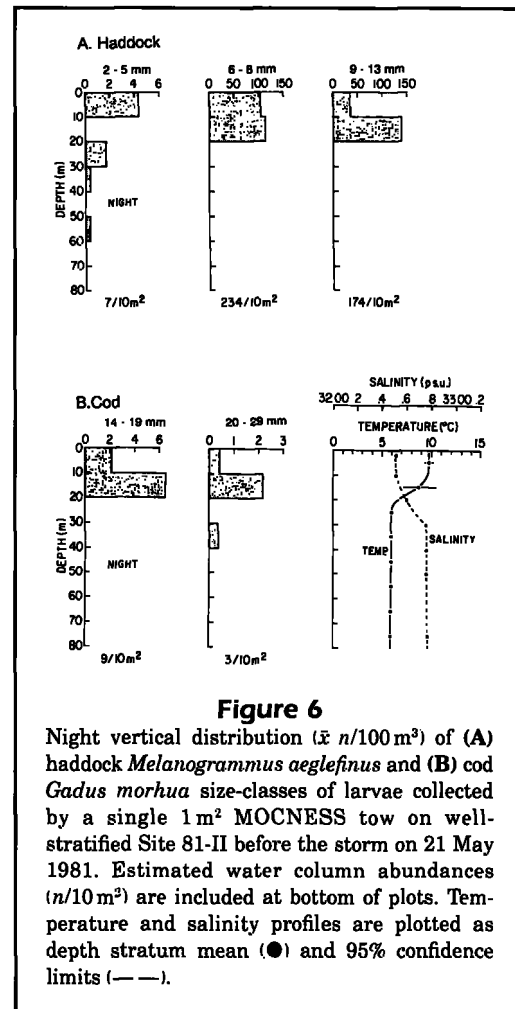


Figure 6

Night vertical distribution (\bar{x} n/100m³) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by a single 1m² MOCNESS tow on well-stratified Site 81-II before the storm on 21 May 1981. Estimated water column abundances (n/10m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum mean (●) and 95% confidence limits (—).

tributed broadly (Fig. 7), but about an order of magnitude more abundant relative to the collections made on 21 May. Differences in mean day and night vertical distributions of larvae during the well-mixed period of 24–26 May 1981 indicate a diel shift in distribution patterns of the larger larvae (Fig. 7), with population centers located deeper in the water column by day (40–60 m) and shoaler by night (10–40 m). This diel shift in vertical distribution is supported by the ANOVA (Table 2B), where both haddock and cod have significant ($p < 0.05$) depth \times time interaction effects. By 28 May 1981, near-surface insolation warming of the upper 20 m occurred, and larvae reaggregated above 20 m near a weak thermocline (Fig. 8).

Mean depths of larvae captured in tows before and after the storm are plotted in Fig. 9 along with depth bounds of the thermocline region. The weak thermocline deepened after 25 May 1981. Mean depths of larval abundance remained below the weak thermocline until 28 May. Tows made on 26 May showed that the larger larvae were mainly located deeper in the

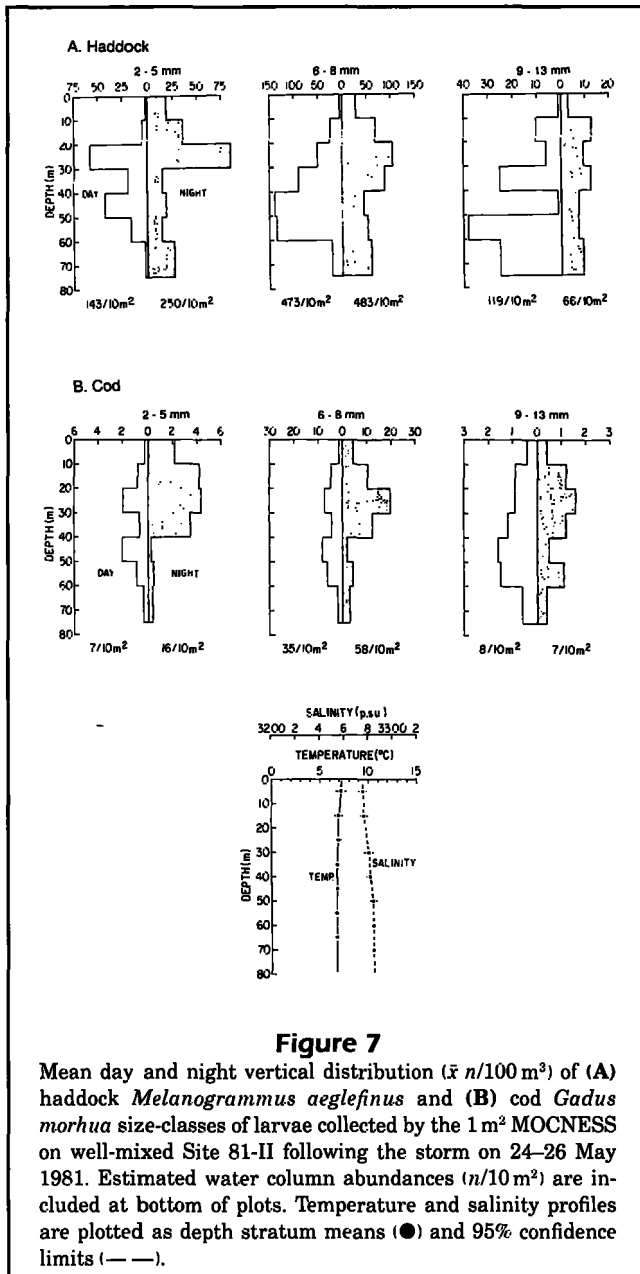


Figure 7

Mean day and night vertical distribution (\bar{x} $n/100$ m³) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1 m² MOCNESS on well-mixed Site 81-II following the storm on 24–26 May 1981. Estimated water column abundances ($n/10$ m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

water column than smaller larvae. However, when the water column was well-stratified on 21 May and weakly-stratified on 28 May, in both day and night all sizes of larvae were located in or above the thermocline. The single day and night tows were not sufficient to base firm conclusions on diel differences.

In mid-May 1983, two sites were sampled in weakly-stratified waters across the southern margin of Georges Bank. At Site 83-I (Fig. 10), mean day and night vertical distributions show haddock and cod larvae distributed broadly through the water column on 13–14 May, but each of the three size-classes had a different depth

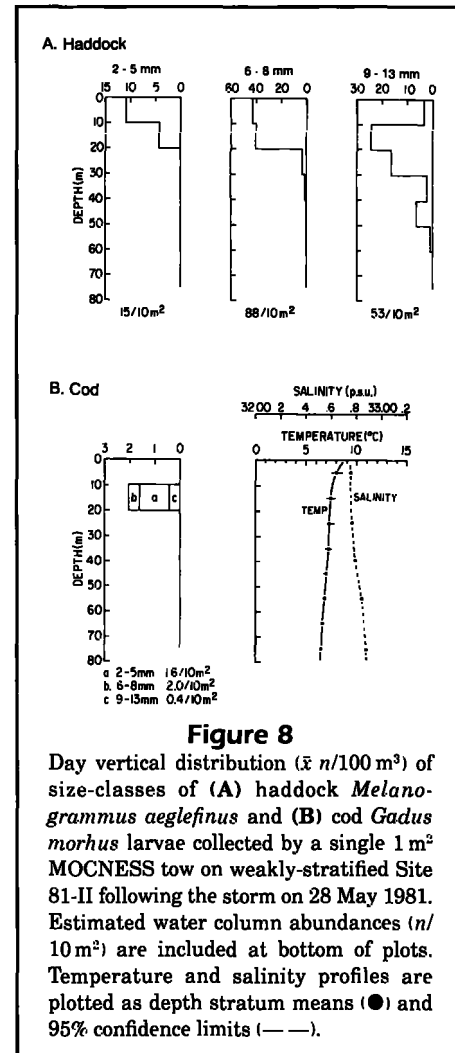


Figure 8

Day vertical distribution (\bar{x} $n/100$ m³) of size-classes of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* larvae collected by a single 1 m² MOCNESS tow on weakly-stratified Site 81-II following the storm on 28 May 1981. Estimated water column abundances ($n/10$ m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

distribution. Recently-hatched larvae (2–5 mm) were most abundant at 10–30 m both day and night. The 6–8 mm size-classes of both species were more broadly distributed and most abundant at 10–50 m depths, with haddock tending to be deeper in the water column by day than cod. The 9–13 mm size-class for both haddock and cod had a pronounced diel shift in day-night distribution patterns: most larvae were in the lower half of the water column by day but in the upper half at night. The maximum density for both species was at 10–20 m. There were significant ($p < 0.05$) interactions for each combination of depth, time, and size (ANOVA; Table 2C).

A time-series of larval catches in relation to the thermocline region at Site 83-I is shown in Fig. 11. Although the mean depth of the thermocline centered at ~20 m, its bounds varied between 10 and 40 m, perhaps due to the tides. While the population centers of cod and haddock larvae tended to be associated with

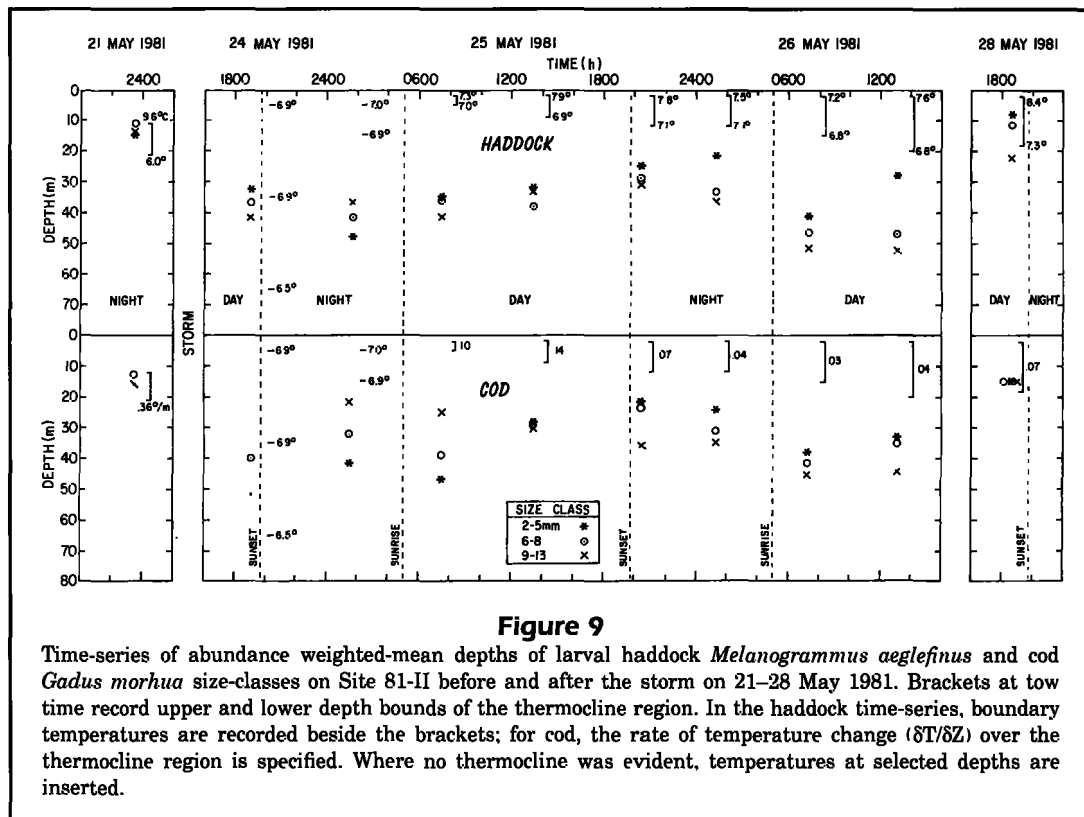


Figure 9

Time-series of abundance weighted-mean depths of larval haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* size-classes on Site 81-II before and after the storm on 21–28 May 1981. Brackets at tow time record upper and lower depth bounds of the thermocline region. In the haddock time-series, boundary temperatures are recorded beside the brackets; for cod, the rate of temperature change ($\delta T/\delta Z$) over the thermocline region is specified. Where no thermocline was evident, temperatures at selected depths are inserted.

the thermocline region, they were not confined exclusively to it, as in May 1981 when the water column was strongly stratified. Larger larvae of both species tended to be found at greater depths during the day, especially the 9–13 mm larvae.

At Site 83-I, >64% of the 9–13 mm size-class for both haddock and cod was found below the thermocline by day, but <28% by night (Table 3A). A significantly ($p < 0.05$) greater percentage of the 9–13 mm size-class was found within and above the thermocline at night. For the 2–5 mm size-classes, haddock and cod larvae were found mostly within or above the thermocline; <15% were located below the thermocline, and there was no significant day-night difference in the profile percentages. For the 6–8 mm size-classes of haddock and cod, the highest percentage of larvae were located within the thermocline. Of the haddock larvae, 40% were found below the thermocline by day, but only 18% at night ($p < 0.005$). There was no significant change in the day-night percentages for 6–8 mm cod.

On 15–16 May 1983, at Site 83-II (88–93 m) near the shelf/slopewater front, thermocline depth was somewhat deeper with a smaller gradient than at Site 83-I. Most haddock and cod larvae were confined to the upper 40 m, the lower bound of the thermocline (Fig. 12). A small percentage of larger larvae (9–13 mm) were

located below the thermocline by day (13% for haddock and 20% for cod) but moved nearer the surface by night (Table 3B). All size-classes of larvae were broadly distributed within the upper part of the water column. There were significant (ANOVA; $p < 0.001$) effects of depth, time, and size for haddock; only depth \times size interaction was significant ($p < 0.01$) for cod (Table 2C). Mean depths of haddock and cod were greater by day for the larger larvae, especially for the 9–13 mm size-classes (Fig. 13), and in all but one night tow the mean depths were located within the confines of the thermocline region.

Vertical distribution of pelagic juveniles

In June 1984, pelagic juvenile haddock and cod were collected at a well-mixed shoal (40–49 m) Site 84-I (Fig. 14). Cod were more abundant than haddock at Site 83-I, and the larger fish (14–29 mm) were caught more abundantly in night tows than day. The three size-classes of haddock were similarly distributed throughout the water column. Few were caught in the upper 10 m; abundance usually peaked near 10–20 m both day and night. Pelagic cod also were caught throughout the water column during the day, with abundance peaks near 10–20 m for the 14–19 mm and 20–29 mm size-classes. They were more abundant in

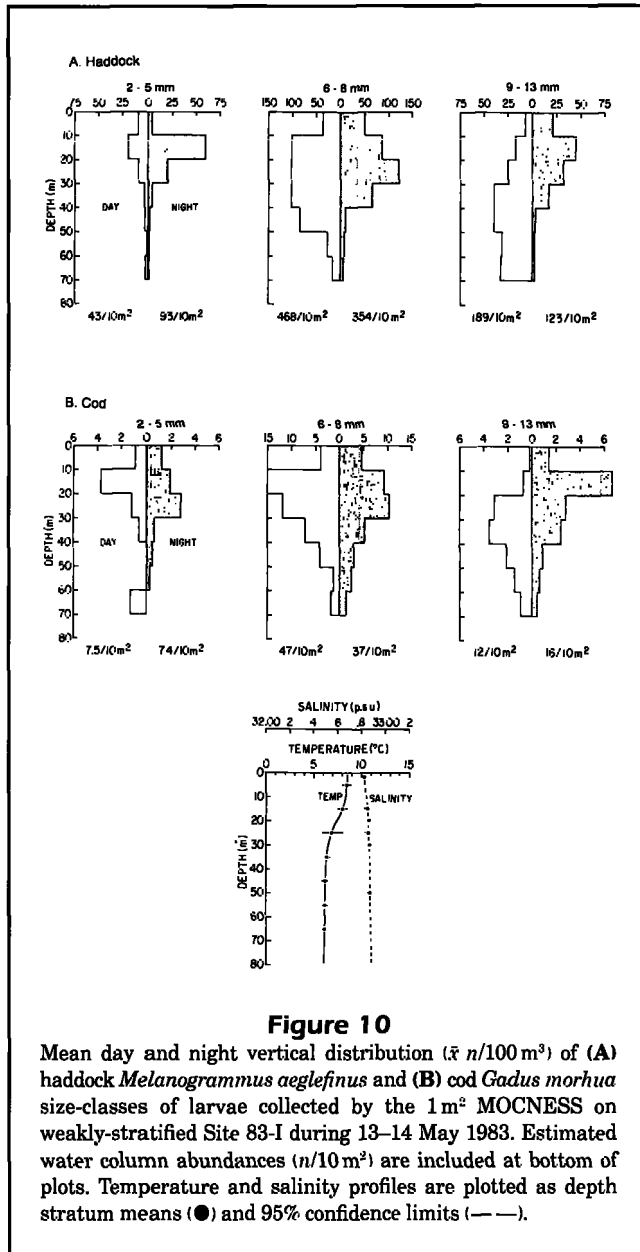


Figure 10

Mean day and night vertical distribution (\bar{x} $n/100$ m³) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1 m² MOCNESS on weakly-stratified Site 83-I during 13–14 May 1983. Estimated water column abundances ($n/10$ m²) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

the upper half of the water column at night, increasing somewhat towards the surface. There were no significant interaction effects in the ANOVA for either cod or haddock (Table 4).

On 18–22 June 1986 at a well-mixed deeper (65–78 m) Site 86-I, cod juveniles 14–49 mm were caught (Fig. 15). Mean day and night vertical distributions show a clear pattern of larger size-classes of cod located progressively deeper in the water column, with the 40–49 mm cod located almost entirely between 50 m and the bottom. Night catches were greater than day catches for all size-classes of cod.

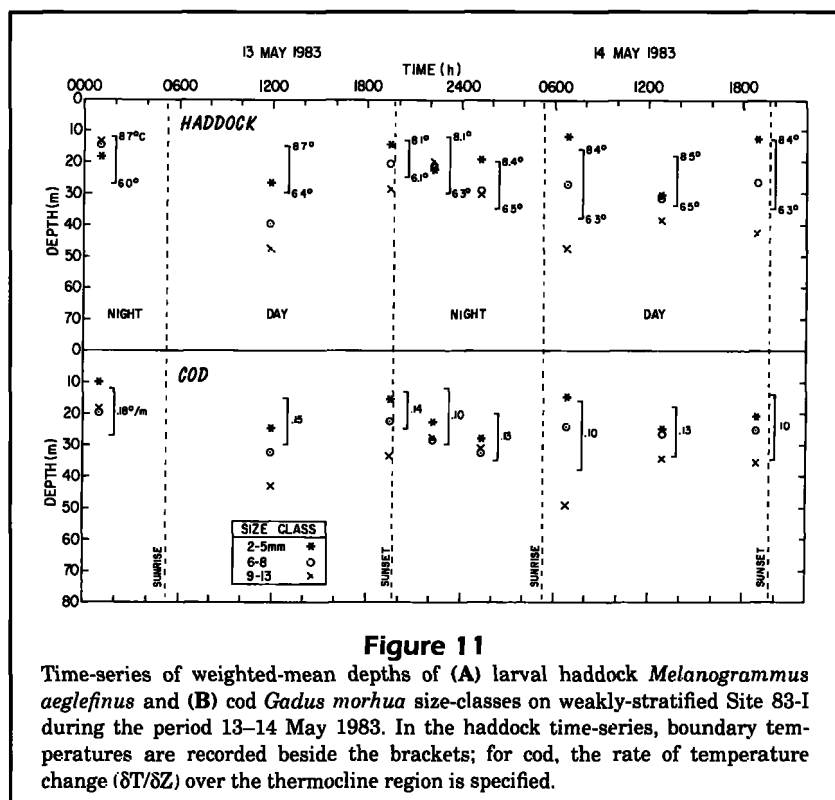
Night mean abundance was significantly greater (ANOVA; $p < 0.01$) than day mean abundance of the 20–29 mm and 30–39 mm size-classes (Table 4). There was no detectable evidence of diel vertical migrations.

By July, relatively few pelagic haddock and cod juveniles were caught. Highest densities of juvenile gadids were located on eastern Georges Bank (Lough et al. 1989). Three sites were sampled in mid-July 1985 on eastern Georges Bank: Site 85-I (82–87 m), stratified; Site 85-II (64–72 m), weakly stratified; Site 85-III (78–83 m), stratified (Fig. 16). The deeper Sites 85-I & 85-III both had a gradual thermocline at 15–30 m depths. Only a few pelagic cod juveniles were caught. Pelagic cod ranging 30–59 mm were caught mostly at night, although a day tow was not made at Site III. Relatively few fish were caught in the upper 30 m, and there was a tendency for the highest densities to be located in the bottom third of the water column. Cod were caught in day tows at Site 85-I in the bottom 60–80 m stratum.

Diel migration of recently-settled juveniles

In 17 bottom trawls (with rollers) at Site 86-I, 25–26 June 1986, demersal cod juveniles with a mean length of 4–5 cm were collected (Table 5). Few were caught in day trawls, but at least an order of magnitude more cod (\bar{x} 103/30 min trawl) were caught in night trawls. During 17–18 July 1985 at Site 85-IV, nine bottom trawls (with rubber disk sweep chain) were made (Table 6; Fig. 17). Both haddock and cod appeared to be caught more abundantly in day trawls than at twilight. Only one haddock juvenile was caught in the single night trawl. The mean length of haddock was 7.1 cm (range 4–10 cm), and 5.5 cm for cod (range 2–12 cm). Mean lengths of both species were the same in day and twilight trawls. The high daylight catches of cod juveniles in this series are in contrast to the high night catches of cod of the same average size, 4–5 cm, in June 1986 using a bottom trawl with rollers. Gear difference (rubber disks vs. rollers) may have been the cause of the different day-night catches, but conclusions cannot be made because in July 1985 only one night trawl was made.

During 16–17 August 1985, 12 bottom trawls (with rubber disk sweep chain) on southeastern Georges Bank (63–71 m), Site 85-V, caught relatively high numbers (210–257/30 min trawl) of 9–19 cm haddock juveniles (Table 7; Fig. 18). The mean number and lengths of fish per trawl were not significantly different ($p > 0.05$) by paired t -tests for the night, day, and twilight catches.



cially after reaching 9–13 mm. Day abundances of haddock are greater than night for the 6–8 mm and 9–13 mm size-classes, which may indicate a different avoidance behavior at this size.

The 10 m² MOCNESS night-day abundance ratios ($n/1000\text{ m}^2$) are shown in Table 9 for size-classes of cod and haddock from study sites in June 1984, 1986, and July 1985. A greater size-range of cod is available than for haddock. For cod, the smallest (9–3 mm) and the largest (50–59 mm) size-classes are not fully vulnerable to the net, due to extrusion of the smallest larvae through the net mesh and distribution of the largest juveniles below the sampling depth. The total night-day ratios for cod are ~2–3 (range 1.49–3.05) for size-classes 14–19 mm through 40–49 mm. Haddock juveniles have night-day ratios of ~3–4 for the 14–19 mm and 20–29 mm size-classes.

Sampler retention and avoidance

The 1 m² MOCNESS sampled effectively on a horizontal scale of 0.2–0.3 km; the 10 m² MOCNESS, 1–2 km; and the bottom trawl, 3–4 km. Minimum length of fish fully retained and not extruded by the various nets was estimated using a model based on the stretch mesh size and a body height-to-length regression (Potter et al. 1990). These estimates indicated that almost all haddock and cod larvae >~4 mmSL are retained by the 1 m² MOCNESS 0.333 mm mesh nets. For the 10 m² MOCNESS, 3.0 mm mesh nets, haddock <17 mm and cod <15–16 mm probably are not fully retained. Minimum size retention of juvenile fish collected by the research bottom trawl is 31–37 mm.

The 1 m² MOCNESS night-day abundance ratios ($n/10\text{ m}^2$) are shown in Table 8, page 307 for size-classes of cod and haddock collected in April and May 1981 and May 1983. The total night-day ratios for cod are ~1.2 for the 2–5 mm and 6–8 mm size-classes, near 2.0 for the 9–13 mm size-class, and to ~4.0–6.0 for the 14–19 mm and 20–29 mm size-classes (Fig. 19). An exponential curve fit appears to adequately describe the increase of night-to-day catch ratios with increasing size of fish. Cod appear to visually avoid the 1 m² MOCNESS net by day at all lengths, espe-

Discussion

The difficulty of detecting vertical migration in planktonic organisms, given the high sampling variability and limited resources for replicate time-series of observations as well as gear limitations, has been discussed by Pearre (1979), Shulenberger (1978), Denman & Platt (1978), and others. We are forced to look for repeatable patterns, often in the absence of statistical proof. Because of these difficulties, diverse observations have been reported in the literature. In this study, the vertical distribution patterns and diel migrations of haddock and cod larvae and juveniles have been documented in stratified and well-mixed waters of Georges Bank in greater detail than previously seen because of electronic MOCNESS samplers and the use of submersibles.

Sampler avoidance

Many investigators have reported night-day catch ratios >1. Net avoidance usually is greater for day than night tows because of visual detection of the net (Morse 1989). In another Georges Bank study using the 10 m² MOCNESS, Potter et al. (1990) reported night catches of pelagic cod juveniles averaging 30 mm to be signifi-

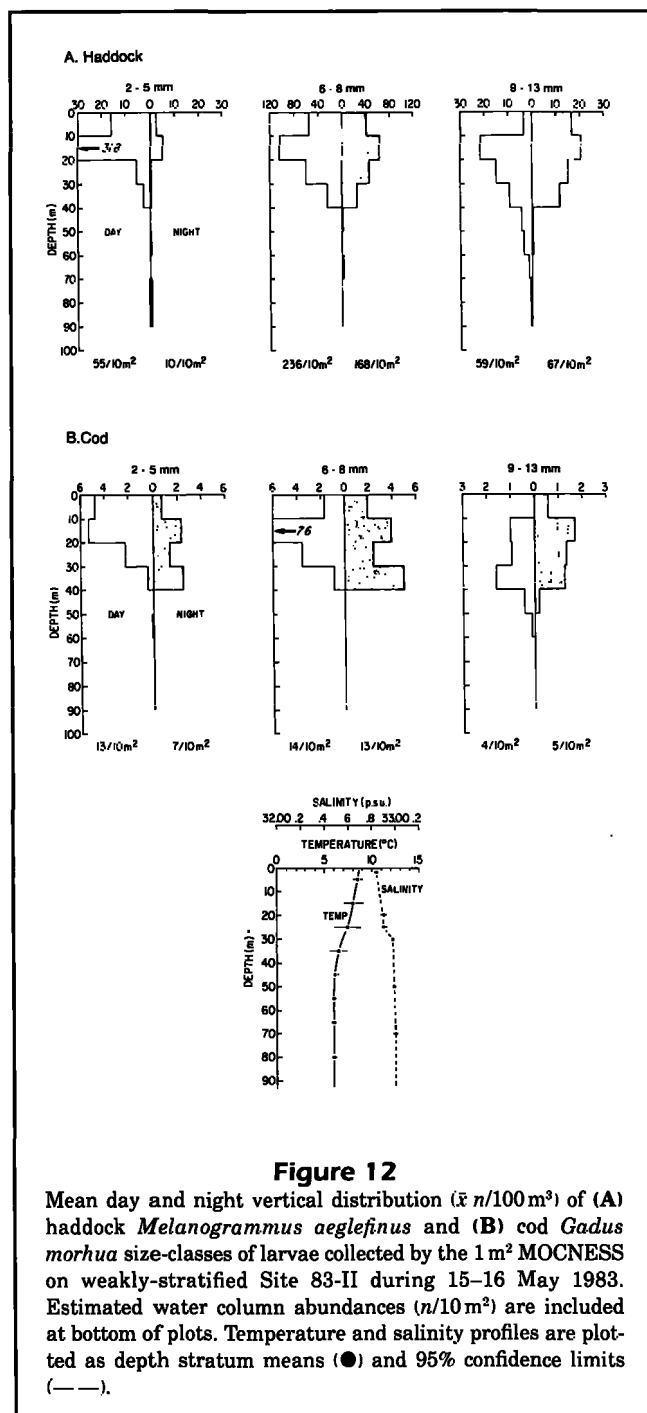


Figure 12

Mean day and night vertical distribution (\bar{x} $n/100\text{m}^3$) of (A) haddock *Melanogrammus aeglefinus* and (B) cod *Gadus morhua* size-classes of larvae collected by the 1 m² MOCNESS on weakly-stratified Site 83-II during 15–16 May 1983. Estimated water column abundances ($n/10\text{m}^2$) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

cantly greater than day catches. Their average night-day catch ratio for 16–45 mm cod was 3.0 (range 1.6–4.7), which is similar to the ratios estimated in this study of cod and haddock pelagic juveniles.

In an extensive study of the northeast U.S. continental shelf ichthyoplankton (an 8 yr time-series of data using a 61 cm diameter bongo net, standard MARMAP double-oblique tows, Morse (1989) found

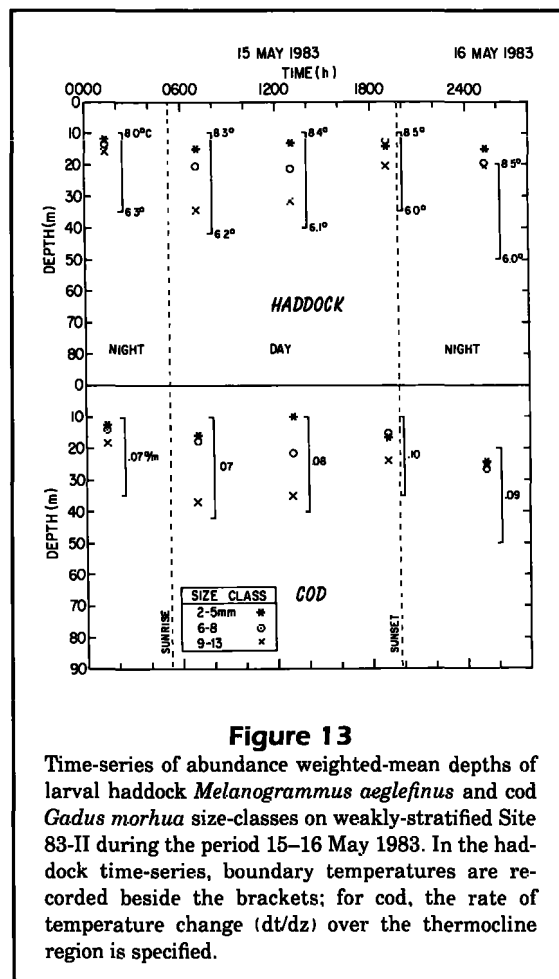
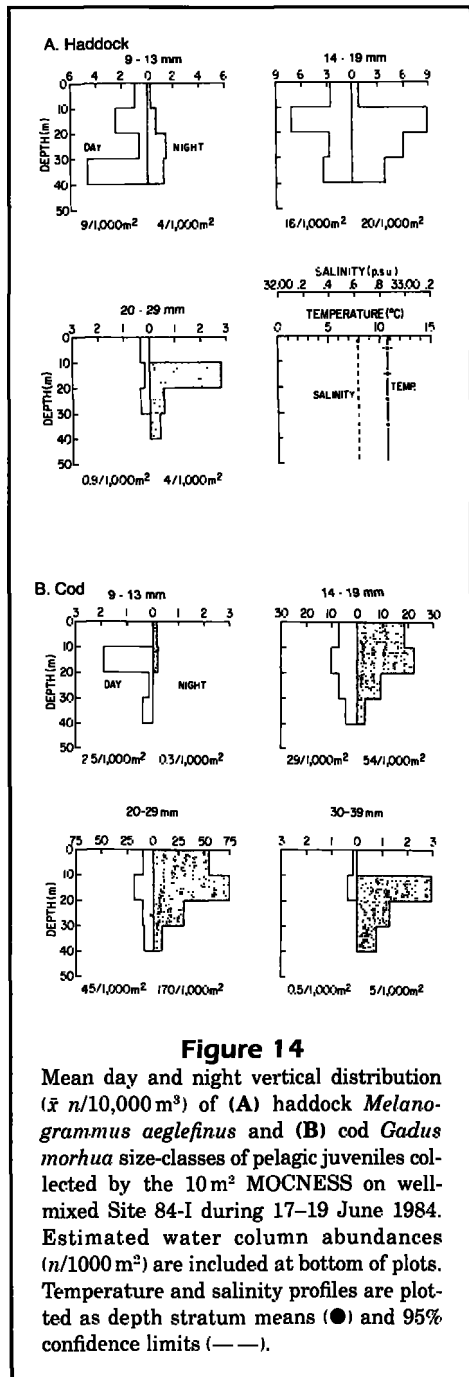


Figure 13

Time-series of abundance weighted-mean depths of larval haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* size-classes on weakly-stratified Site 83-II during the period 15–16 May 1983. In the haddock time-series, boundary temperatures are recorded beside the brackets; for cod, the rate of temperature change (dt/dz) over the thermocline region is specified.

larval haddock to be the exception among most taxa in that day catches exceeded night catches for all lengths of larvae in the range 4–15 mm. Day catches were somewhat greater than night catches for 4–12 mm cod, but for the larger fish (13–20 mm) night catches were equal to or greater than day catches.

Haddock larvae, as well as cod, may remain still during the day to evade predator detection by visual or mechano-reception (Zaret 1980). When both haddock and cod reach a larger size and their sensory systems become more developed, they exhibit a startle response and evade the attacking predator (in this case a net) (Blaxter & Fuiman 1990). Flexion and fin ray development is complete for both species at 15–20 mm (Auditore et al. 1993) and they would be more capable of a powerful darting speed. Perhaps at night without visual stimuli, only the larger juveniles exhibit a startle response to the net-mouth pressure stimulus. Light-aided avoidance is expected to decrease with water depth as a function of light attenuation and the fishes' visual threshold (Blaxter & Fuiman 1990). Pressure



ever, in fish >14 mm, night-day catch ratios are expected to increase to >3 because of light-aided avoidance response. Haddock larvae appear to respond differently to light than cod in their avoidance behavior. A correction factor for cod was not applied from the water-column total abundance ratios. The night-day catch ratios are not suitable for correcting depth strata densities, since net avoidance may be a function of light level which decreases with depth. That is, avoidance may be depth-dependent. We do not have the data suitable for making an appropriate depth correction. Applying a constant correction factor to all depth levels of a given size-class would not change the vertical distribution pattern. We need to know the fishes' reaction distance to the net at the different depth light levels.

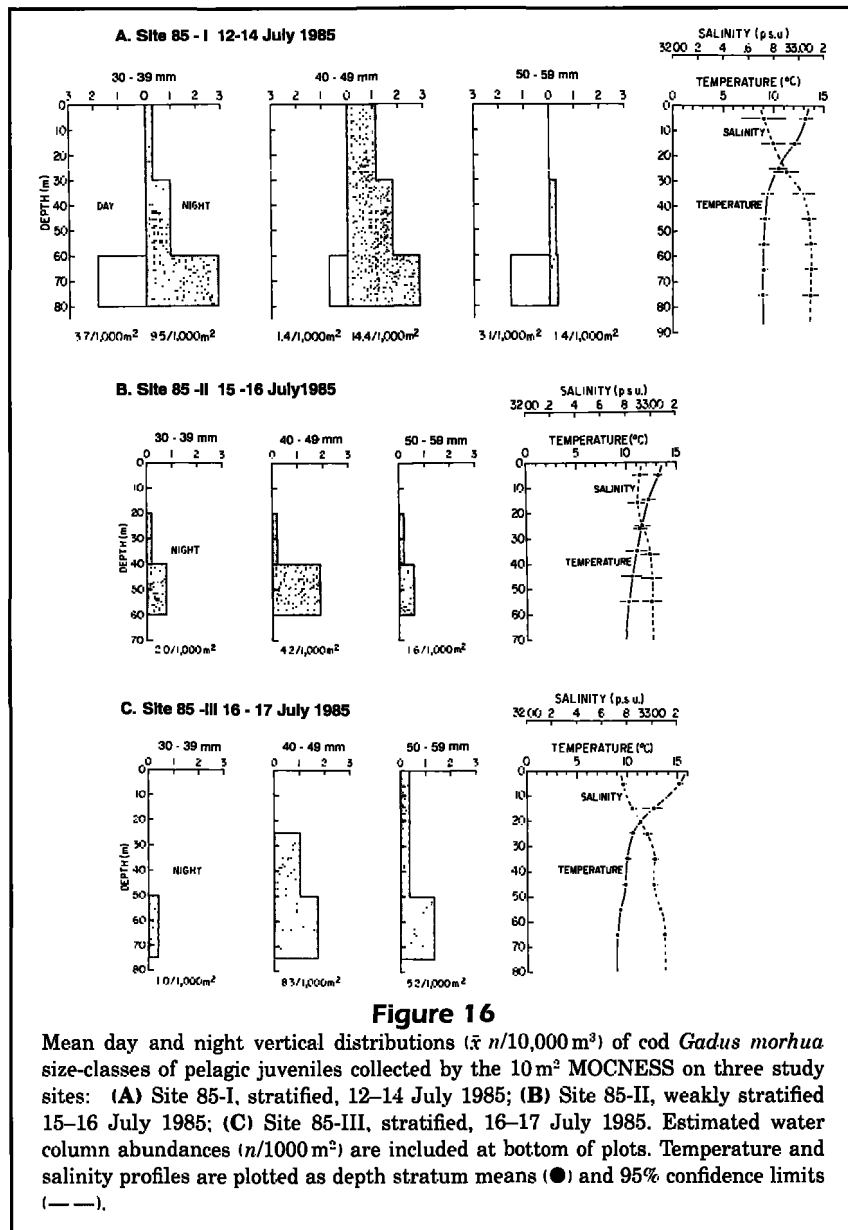
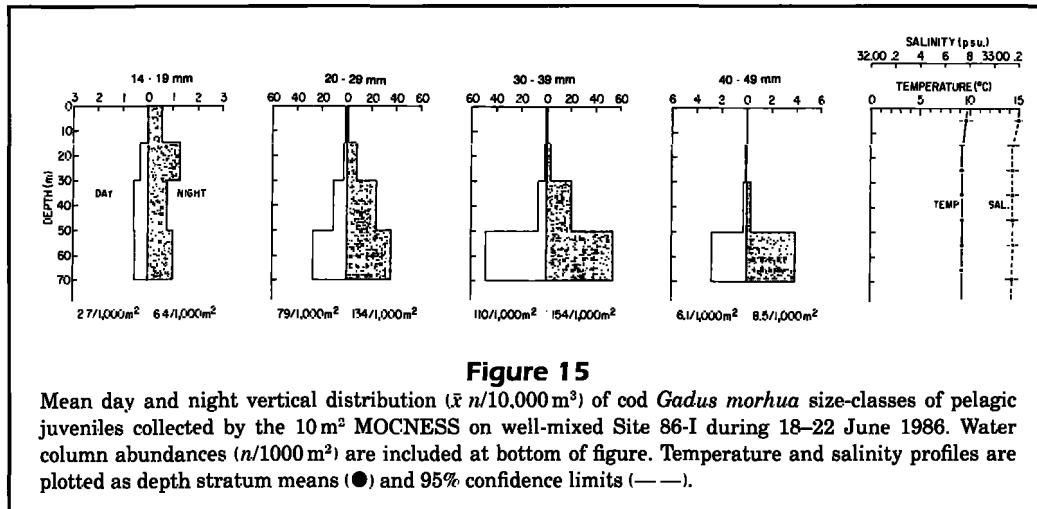
During the fishes' transition from a pelagic to demersal life at ~30–40 mm, they are not fully vulnerable to either pelagic or demersal sampling gear and this contributes to the sampling variability. Scott (1984) studied diel variations in juvenile haddock catch rates from a 24 h bottom-trawl experiment near Sable Island on the Scotian Shelf in July–August. Haddock >6 cm had a marked vertical migration pattern, moving off the bottom at night and returning by daylight. Based on changes in mean lengths, larger fish moved off the bottom in greater proportions than smaller fish. Colton (1965) examined data from bottom-trawl surveys conducted on Georges Bank and found catch-per-tow of 0-group and 1+ yr haddock to be markedly higher during the night than day. He believed the night-day variability was due to escapement from the net during the day and not to avoidance. Lough et al. (1989) conducted submersible studies on eastern Georges Bank in July 1987 and August 1986 and found recently-settled juvenile gadids (mostly cod) 4–12 cm in length close to the bottom (<0.5 m) during the day and a portion of the population rising 1–5 m off the bottom at sunset, drifting with the current. A comparison of standardized research bottom-trawl (with rollers) catches and submersible transect counts showed the extent of undersampling by the bottom trawl. For 4 cm modal-size cod (1987), daylight trawl abundance estimates were at least an order of magnitude lower than the submersible transects, but not significantly different than the night estimates. For demersally-oriented larger fish (7 cm modal length), few fish were caught by daylight trawls, and night trawl catches were still at least an order of magnitude lower than night submersible counts. The larger fish appeared to stay closer to the bottom both day and night, and consequently they are less vulnerable to the bottom trawl with roller gear which may pass over them. Some preliminary results by Cohen et al. (1985) showed that more cod juveniles of 4–5 cm were caught using the bottom trawl with the smaller rubber disc-covered chain sweep than with the larger roller gear. Thus, the bottom trawl catches of recently-settled cod are known to have a significant sampling bias with more cod collected in night trawls than day, and especially for the larger fish escaping the roller gear.

Vertical distribution patterns

The initial depth distribution of recently-hatched larvae is dependent upon the late-stage egg distribution. Some limited egg profile data

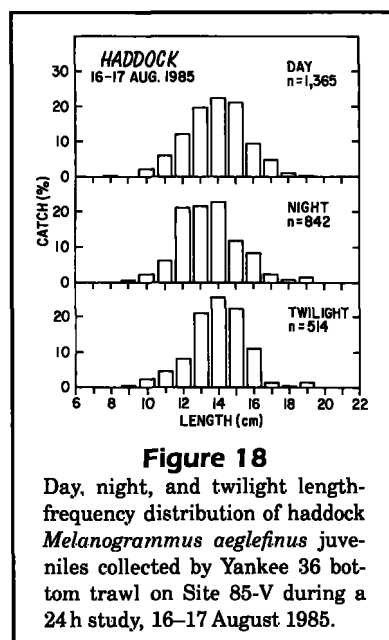
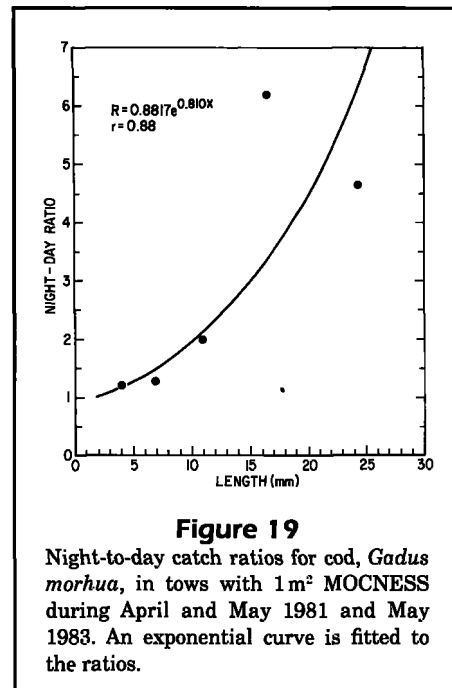
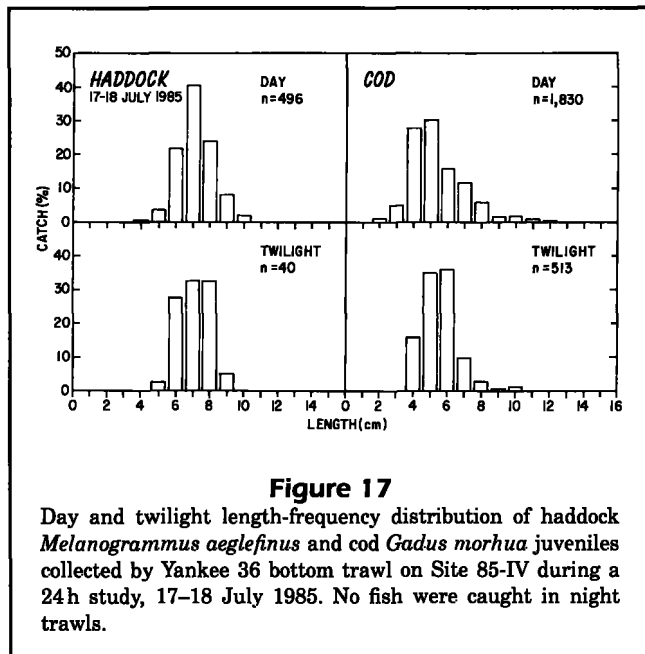
or sound avoidance are expected to be the same over depth, however.

Therefore, for the three smallest size-classes of haddock and cod <13 mm, light-aided avoidance of the 1 m^2 MOCNESS sampler may be relatively small (< factor of 2) as a contributing factor in observed day-night vertical distribution patterns. How-



was reported by Walford (1938), Colton (1965), and Lough (1984) for haddock on Georges Bank. Their results and other regional studies are reviewed by Frank et al. (1989) and Page et al. (1989) in depth distribution studies of haddock eggs on the Southwestern Scotian Shelf. Because haddock eggs increase their specific gravity with age, newly-hatched larvae were generally found at intermediate depths. Furthermore, these studies found the degree of aggregation for late stage-IV eggs was significantly related to the intensity of stratification.

In the present study, in well-mixed waters during early spring, larval haddock and cod were distributed throughout the water column in the same general pattern as the eggs (Lough 1984), with a mode in abundance at mid-depth, 30–40 m. By mid-May, when the surface water is stratified, larvae resided within the thermocline region; the stronger the stratification, the more closely the abundance centers were confined to the thermocline, especially for the smallest larvae. The larval-thermocline coupling is a dynamic process that is frequently perturbed by strong winds and storms but becomes reestablished with a new thermocline. Even under stratified conditions, larger larvae (>9 mm) tend to be found at greater depths during the day. Day-night shifts in their distribution patterns indicate that diel



migrations are fairly well established when larvae reach 9–13 mm length and may be initiated at a smaller size, 6–8 mm, depending on the physical structure of the water column. This pattern of residing deeper by day and shoaler at night continues into the older pelagic juvenile and recently-settled juvenile period.

When larvae reach a length of ~9 mm, the swim bladder may be functionally important in the vertical migration of larvae in both species (Schwartz 1971, Ellertsen et al. 1980, Howell 1984). Haddock and cod have similar developmental patterns; however, there are some important differences (Auditore et al. 1993). At 8–9 mm, haddock have larger and more developed pectoral and pelvic fins than cod. The difference in development is pronounced after 20 mm in length; at 23 mm, the pectoral fins of cod are $\frac{1}{2}$ to $\frac{3}{4}$ the size of haddock, while the pelvic fins of cod are $\frac{1}{2}$ those of haddock. Haddock also possess more total fin rays in the caudal, dorsal, and anal fins than cod. The total number of caudal-fin rays usually determines the overall size of the fin, which is an important means of thrust in gadiform fishes (Cohen 1984). The higher number of caudal- and dorsal-fin rays in haddock, in combination with early paired-fin development, may provide greater maneuverability for haddock. The earlier fin development of haddock larvae compared with cod may allow them to more actively locate high concentrations of prey and stay within these patches. Miller et al. (1963) studied the vertical distribution of larval haddock at three sites on Georges Bank in May 1958. Haddock larvae were found throughout the water column, with maximum concentrations centered at 20–30 m. At all three sites they found periodic changes in the depth distribution of larvae that were related to similar changes in depth of the thermocline. Smaller larvae, 4–8 mm, occurred below the thermocline at each site while >80% of the larger larvae, 9–19 mm, were found in the thermocline. They also found no evidence of diurnal change in the weighted mean depth distribution of larvae, 24 m during the day and 22 m by night. Their observations were in general agreement with those of Frank et al. (1989) for haddock larvae on the Southwestern Scotian Shelf. Frank et al. (1989), using a discrete depth sampler, BIONESS, found recently-hatched haddock larvae in May 1985 and 1986 were concentrated at mid-depth (~30 m) in day and night, and their population centers remained at this level until 20 d post-hatching. The hydrographic conditions were characterized by a density gradient (σ_t) that increased linearly with depth both years. Whereas Miller et al. (1963) and Frank et al. (1989) found had-

dock larvae (<9 mm) below the thermocline, we found both haddock and cod larvae of this size tended to reside mostly within or above the base of the thermocline in May on Georges Bank. Miller et al.'s (1963) ability to discriminate depth changes in larvae was limited because of the small, non-opening/closing samplers (14 cm mouth diameter) that were towed at fixed depth intervals (minimum 9–10 m apart).

Ellertsen et al. (1984) reported on the vertical distribution of cod larvae (4–5 mm) at a strongly-stratified station off the Lofoten Islands, Norway, in May 1982. First-feeding cod larvae were concentrated at 10–20 m depth near the thermocline throughout a 24 h period, but dispersed with the slightest wind mixing. Only under extremely calm conditions were the larvae able to control their vertical distribution and show diurnal migration.

Pelagic juveniles, however, are capable of making extensive migrations through the water column. In our Georges Bank studies, at a well-mixed shoal site in June 1984, pelagic cod juveniles appeared to migrate into the upper half of the water column at night and to remain in the lower water column during the day. Juvenile haddock were much less abundant at this site, and their center of abundance was located at mid-depth with no evidence of day-night migrations like those of cod. The few pelagic cod collected at two stratified sites on eastern Georges Bank in July 1985 were generally found in the lower third of the water column, and few were caught in the thermocline at 15–30 m depth. We have no data on pelagic juvenile haddock at a stratified site for comparison.

Perry & Neilson (1988) studied the vertical distribution of cod and haddock pelagic juveniles in June 1985 on eastern Georges Bank and found a diel migration pattern for both species at a well-mixed shoal site (66 m). At a nearby stratified site in deeper water (80 m), Perry & Neilson (1988) found that juvenile haddock generally remained above 40 m depth with their weighted-mean depth in the thermocline at 20–30 m. In contrast, cod juveniles generally remained deeper than 40 m, below the thermocline, yet still exhibited diel migrations.

Colton (1965) investigated vertical distribution of juvenile haddock using an Isaacs-Kidd midwater trawl in late summer of 1957–58. Over 75% of the pelagic haddock of 27–124 mm occurred between 10 and 40 m depth, with greatest abundance at 20 m at the depth of the thermocline. There was some diel variation in distribution: the weighted-mean abundance was located at 40 m during the day and 30 m at night.

Results from our studies indicate that juvenile haddock and cod change from a pelagic to a demersal existence at a body length of 4–10 cm, and once they reach a demersal stage they stay close to bottom by

day and move off bottom into the water column at night. During the transition period the vertical amplitude of these night excursions decreases with size of fish. The data suggest that cod <6 cm make more extensive off-bottom migrations at night than haddock, with some individuals ranging up to the surface. Haddock appear to assume a more complete demersal life at a smaller size (4–6 cm) than cod, which is consistent with older juvenile and adult behavior. Bailey (1975) found that 6.5–13 cm haddock migrated through the water column at night, whereas larger fish were more confined to the seabed in the northern North Sea during August. Beamish (1966) and Woodhead (1966) reported that adult haddock tend to remain associated with the seabed at night, whereas adult cod make extensive vertical migrations. In contrast, Bailey (1975) concluded that cod juveniles remained on or close to the seabed day and night, because fish caught in midwater were never >7 cm, while those on the seabed ranged up to 13 cm.

Juvenile cod and haddock at ~70–90 mm begin feeding on benthic prey such as polychaetes and crustaceans along with planktonic prey, which is consistent with changes in their mouth (Auditore et al. 1993). The time for juvenile cod and haddock to grow from 40 mm to 70 mm is ~30 d, and from 40 to 90 mm is ~48 d (Bolz & Lough 1988). Therefore, in terms of defining the functional transition period for an individual fish, we consider the transition from a wholly pelagic to demersal existence to take ~1–1.5 mo on average.

Other factors influencing vertical distributions

Neilson & Perry (1990) did a recent review of the literature on diel vertical migrations of marine fishes and concluded that the diversity of vertical migration patterns indicated a facultative process significantly influenced by multiple environmental factors. Prey distributions probably play an important role in the vertical distributions of larvae. Based on Georges Bank data (Buckley & Lough 1987) and simulation models (Laurence 1985), haddock larvae are considerably more food-limited than cod. Stable stratified conditions in the spring, which result in the availability of high concentrations of zooplankton prey, favor growth and survival of haddock larvae. Lough (1984) and Buckley & Lough (1987) found that haddock and cod larvae <~13 mm (mode at 7 mm) were generally associated with the planktonic prey biomass that had a maxima in the thermocline during May 1981 and 1983 along the southern margin of Georges Bank. The stronger the water column stratification, the more closely larvae and prey coincided. At the well-mixed sites where larvae were broadly distributed, prey biomass was

lower and more uniformly distributed through the water column.

Frank & McRuer (1989) also found the condition of haddock larvae off Southwestern Nova Scotia in May 1986 consistent with the well-mixed/stratified regime findings of Buckley & Lough (1987). Larvae were in good condition at the deeper stratified sites and in poor condition at the shallow, well-mixed sites. They also found evidence that the buoyancy of starved larvae (4–7 mm) increased, which frequently resulted in a bimodal depth profile, with larvae in poorer condition nearer the surface. Ellertsen et al.'s (1984) study in the Vesteralsfjord of Norway showed that under calm conditions larval cod appeared to concentrate in the surface layers during the night coinciding with the highest density of copepod nauplii, their preferred prey in the study. They also noted that turbulent mixing dispersed the larvae and prey evenly throughout the water column. Therefore, the vertical distribution of larvae and their prey needs to be evaluated in relation to larval buoyancy and water-column turbulence.

Light plays an important role in the diel migrations of cod and haddock larvae, but it is not known whether larvae follow a specific isolume. There may be a critical light intensity at which visual feeding ceases and vertical migration begins. Minimum light-intensity threshold for larval cod feeding was in the range 0.1–0.4 lux, and maximum feeding incidence at 1.4 lux (Ellertsen et al. 1980). Light regime also can affect the swimming activity and buoyancy of yolk-sac cod larvae by changing their metabolism and utilization of yolk (Solberg & Tilseth 1987).

In Perry & Neilson's (1988) study of pelagic juveniles, the migration pattern of cod appeared to be directly related to the light-dark cycle, whereas that of haddock was more complicated and may have been confounded by periodic changes in the rotary tidal current speed and/or the migratory movements of their preferred mysid prey *Neomysis americana*. Their explanations for the different depth distribution may be related to (1) cod's acclimation to colder waters and haddock's preference for warmer waters, and (2) a possible mechanism for reducing interspecific competition, since their vertical distribution patterns were similar when prey biomass was high and different when prey biomass was low. In our opinion, the differences in vertical distribution between cod and haddock at the stratified site noted by Perry & Neilson (1988) may be attributed to species differences in feeding behavior.

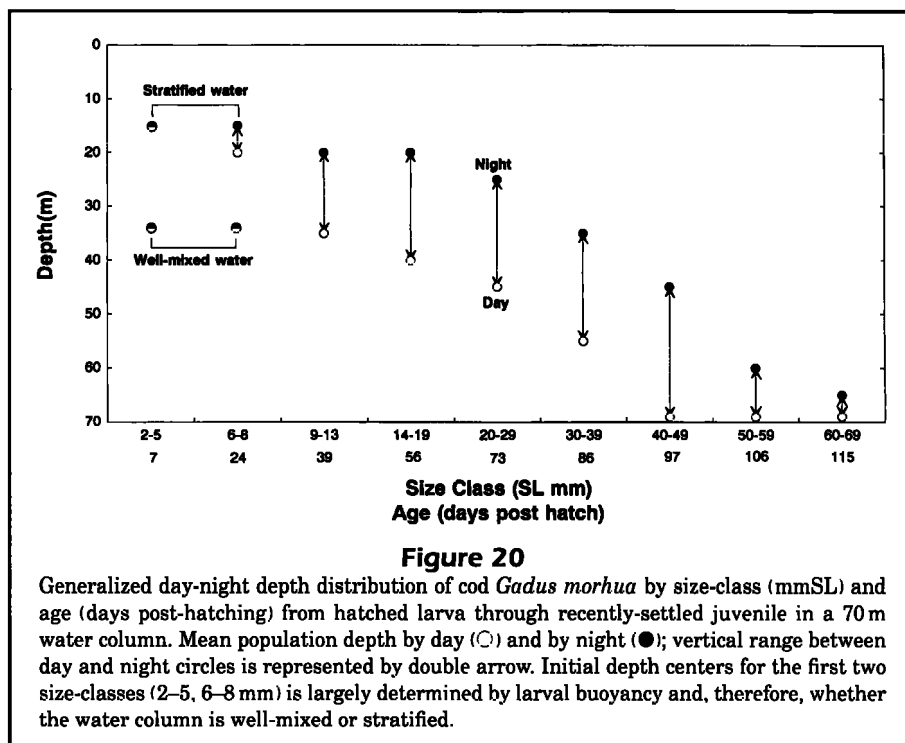
On Georges Bank, planktonic prey selected by both species during settlement at 40–60 mm include copepods, amphipods, euphausiids, and cumaceans (Bowman 1981ab, Koeller et al. 1986, Mahon & Neilson 1987, Lough et al. 1989). Robb (1981) showed that pelagic 0-group gadids in the northern North Sea have

a different feeding behavior reflective of the adult lifestyle, i.e., cod fed on larger active pelagic prey, while haddock concentrated on smaller slower-moving or sedentary organisms. Both Robb's (1981) and Perry & Neilson's (1988) feeding results support the view that haddock feed continuously when prey is available.

A complicating factor in understanding vertical distribution patterns in haddock is their commensal association with the large coelenterate *Cyanea* sp. This association has been reported in the literature for fish up to a length of ~10 cm (Colton & Temple 1961, Mansueti 1963, Rees 1966, Bailey 1975, Koeller et al. 1986). Mansueti (1963) stated that jellyfish serve as a source of food and shelter for young fish between the pelagic and demersal stages. The change from a surface to deeper-water habitat by the fish is believed by Mansueti (1963) to be a factor causing the breakup of the commensal relationship. Koeller et al. (1986) showed *Cyanea* sp. to have been most abundant at the surface, decreasing to near zero below 80 m off Nova Scotia in June 1983. Pelagic juvenile haddock, more so than cod, may require contact with some objects such as jellyfish. Whether jellyfish tentacles also serve as a source of food is not known.

The substrate on which the juveniles settle, (i.e., an unsuitable habitat such as sand) may prolong the transition to demersal life. Lough et al. (1989) hypothesized that a large gravel habitat on northeastern Georges Bank favors survival of recently-settled juvenile fish because of predator avoidance through camouflage and/or increased prey abundance. Pelagic juvenile cod were widespread over eastern Georges Bank in June; and in mid-July when they became demersally oriented, they were present on bottom types ranging from sand to gravel. By contrast, in late July to early August, recently-settled juveniles were abundant only on the large gravel deposit on northeastern Georges Bank and were sparse or absent from the large sand and gravelly sand that cover most of eastern Georges Bank (Lough et al. 1989).

To summarize the vertical distribution patterns observed, we developed a generalized day-night mean depth distribution of cod by size-class, from recently-hatched larvae through recently-settled juveniles (Fig. 20). Cod vertical migrations appear to respond primarily to a day-night cycle, whereas haddock migrations respond to other factors such as prey distribution. Depth centers of the smallest larvae (2–8 mm) appear at two levels—15 and 35 m—depending on whether the water column is stratified or well-mixed (Fig. 20). In order for the water column to be considered sufficiently stratified for larvae to initially reside at 15 m, a change of >0.3 sigma-*t* units would have to occur from surface to the base of a pycnocline. Waters around the flank of Georges Bank are typically



well-mixed in winter, with a seasonal thermocline developing by mid-May subject to perturbations. When larvae reach a length of 9–13 mm, they appear to make day-night migrations regardless of the water-column structure. There is some uncertainty in the day-night migration range of the pelagic juveniles; however, the 20 m range designated is within their swimming capability at this size. Furthermore, we don't know precisely the transition period from a day to night depth. It probably occurs over a 3–4 h period, but it could be shorter. For example, a 10 mm fish swimming at 1 body length/s could transverse 20 m in 1 h. The vertical distribution pattern presented is sufficiently general to be used as a starting point for both cod and haddock at any bottom depth, even though all situations can be interpreted from the data. These studies highlight the need for investigations of behavior-related sampler avoidance and further time-series of observation on fish distributions in different environmental conditions.

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Table 1
Cruises, sampling sites, and gear used for vertical distribution study on Georges Bank, 1981-86.

Vessel cruise no.	Sampling dates	Site	Bottom depth (m)	Gear	No. depth strata sampled	Tows		
						Night	Day	Twilight
<i>Albatross IV</i> 81-03	27-29 April 1981	81-I	67-70	1m ² MOCNESS	6	5	5	0
<i>Albatross IV</i> 81-05	21-27 May 1981	81-II	75-83	1m ² MOCNESS	7-8	4	6	0
		81-III	35-58	1m ² MOCNESS	7-8	1	3	0
<i>Albatross IV</i> 83-03	13-17 May 1983	83-I	66-79	1m ² MOCNESS	7	3	5	0
		83-II	88-93	1m ² MOCNESS	8	2	3	0
		83-III	34-54	1m ² MOCNESS	5	1	3	0
<i>Albatross IV</i> 84-05	17-19 June 1984	84-I	40-49	10m ² MOCNESS	4	3	3	0
<i>Albatross IV</i> 85-06	12-17 July 1985	85-I	80-87	10m ² MOCNESS	2-3	4	3	0
		85-II	64-72	10m ² MOCNESS	3	3	3	0
		85-III	78-83	10m ² MOCNESS	3	2	0	0
<i>Delaware II</i> 85-05	17-18 July 1985	85-IV	80-90	36 Yankee otter trawl with rubber disks	Bottom	1	6	2
<i>Delaware II</i> 85-06	16-17 Aug. 1985	85-V	63-71	36 Yankee otter trawl with rubber disks	Bottom	4	6	2
<i>Albatross IV</i> 86-03	18-22 June 1986	86-I	65-78	10m ² MOCNESS	4	5	6	0
	25-26 June 1986			36 Yankee otter trawl with rollers	Bottom	5	11	1

Table 2

Summary of GLM ANOVA for larval haddock and cod abundance on Georges Bank. *F*-values are denoted by their level of significance.

A. 27-29 April 1981		Site 81-I		
Factor	Haddock^a	Cod^b	Cod^c	Cod^d
Depth (D)	3.15*	8.84***	6.50	8.52
Time (T)	2.07	16.59	39.37	50.92
Size (S)		24.68	31.10	29.09***
D × T	0.49	2.03	3.53***	5.31***
D × S		0.28	1.26	0.93
T × S		3.66*	2.33*	0.14
D × T × S		0.68	0.71	0.76
*** <i>P</i> <0.001		^a 2-5 mm size-class		
** <i>P</i> <0.01		^b 2-5, 6-8, 9-13 mm size-class		
* <i>P</i> <0.05		^c 2-5, 6-8, 9-13, 14-19, 20-29 mm size-class		
		^d 6-8, 9-13, 14-19 mm size-class		
B. 24-26 May 1981		Site 81-II		
Factor	Haddock^a	Cod^a		
Depth (D)	6.71	3.76		
Time (T)	7.72	9.72		
Size (S)	18.17	16.36		
D × T	3.52**	2.90**		
D × S	0.78	0.33		
T × S	1.74	0.69		
D × T × S	0.20	0.19		
*** <i>P</i> <0.01		^a 2-5, 6-8, 9-13 mm size-class		
C. 13-26 May 1983		Site 83-I	Site 83-II	
Factor	Haddock^a	Cod^a	Haddock^a	Cod^a
Depth (D)	4.74	8.17	31.97***	23.84
Time (T)	0.35	0.40	12.11***	0.23
Size (S)	39.67	46.52	15.24***	1.77
D × T	3.13**	0.99	0.86	0.09
D × S	1.25	1.13	1.59	2.29**
T × S	5.33**	0.32	0.13	0.46
D × T × S	1.49	2.31**	1.00	0.93
*** <i>P</i> <0.001		^a 2-5, 6-8, 9-13 mm size-class		
** <i>P</i> <0.01				

Table 3

Average percentage distribution of haddock and cod larvae in relation to the thermocline at Sites 83-I and 83-II on Georges Bank May 1983. Angular transformation was used on the percentage data: angle = arcsin $\sqrt{\text{proportion}}$. Values are presented as the angular mean \pm its standard error followed by a reconverted percentage mean in parentheses.

Angle \pm SE (%)	Larval size-class					
	2-5 mm		6-8 mm		9-13 mm	
	Day	Night	Day	Night	Day	Night
A. Site 83-I 13-14 May 1983						
Haddock						
Above thermocline	43.0 \pm 12.2 (46.6)	40.7 \pm 8.1 (42.6)	22.6 \pm 6.4 (14.8)	27.4 \pm 9.5 (21.1)	9.9 \pm 4.6 (2.9)	25.2 \pm 9.5 (18.1)
Within thermocline	32.0 \pm 9.3 (28.1)	39.4 \pm 4.5 (40.4)	39.5 \pm 5.4 (40.5)	49.7 \pm 6.2 (58.1)	29.9 \pm 4.0 (24.9)	53.4 \pm 4.2 (64.4)
Below thermocline	21.7 \pm 5.5 (13.6)	22.8 \pm 5.8 (15.0)	39.4 \pm 6.1 (40.3)	24.9 \pm 2.5 (17.7)	56.9 \pm 4.8 (70.2)	21.0 \pm 5.1 (12.8)
Cod						
Above thermocline	41.0 \pm 10.5 (43.0)	29.3 \pm 16.9 (23.9)	23.6 \pm 6.3 (16.0)	23.5 \pm 7.5 (15.9)	6.2 \pm 2.8 (1.2)	24.9 \pm 2.1 (17.8)
Within thermocline	44.1 \pm 14.1 (48.4)	47.5 \pm 12.5 (54.4)	45.7 \pm 6.9 (51.2)	45.6 \pm 4.3 (51.1)	35.8 \pm 3.1 (34.3)	46.8 \pm 3.4 (53.2)
Below thermocline	18.7 \pm 6.4 (10.3)	22.0 \pm 3.5 (14.1)	32.6 \pm 5.5 (29.1)	39.7 \pm 4.8 (40.7)	53.1 \pm 3.2 (63.9)	32.0 \pm 5.2 (28.1)
B. Site 83-II 15-16 May 1983						
Haddock						
Above thermocline	31.3 \pm 2.5 (27.4)	48.0 \pm 14.5 (55.1)	23.7 \pm 7.3 (16.1)	34.1 \pm 9.1 (31.4)	12.1 \pm 5.2 (4.4)	31.9 \pm 12.3 (27.9)
Within thermocline	58.4 \pm 2.4 (72.5)	42.1 \pm 14.5 (44.9)	64.8 \pm 6.5 (81.9)	55.7 \pm 8.9 (68.2)	60.5 \pm 2.8 (75.7)	56.0 \pm 11.1 (68.7)
Below thermocline	3.5 \pm 1.7 (0.1)	1.8 \pm 0.0 (0.1)	6.6 \pm 1.7 (1.3)	3.1 \pm 1.3 (0.3)	21.0 \pm 8.0 (12.8)	9.4 \pm 2.4 (2.6)
Cod						
Above thermocline	35.6 \pm 6.7 (33.9)	33.6 \pm 4.7 (30.5)	20.9 \pm 1.9 (12.7)	27.2 \pm 3.1 (20.9)	1.8 \pm 0.0 (0.1)	18.1 \pm 16.3 (9.6)
Within thermocline	54.5 \pm 6.7 (66.1)	45.0 \pm 10.1 (50.0)	69.2 \pm 1.9 (87.4)	62.8 \pm 3.1 (79.1)	63.6 \pm 5.5 (80.3)	72.9 \pm 17.1 (91.3)
Below thermocline	8.1 \pm 0.0 (0.1)	1.8 \pm 0.0 (0.1)	1.8 \pm 0.0 (0.1)	1.8 \pm 0.0 (0.1)	26.4 \pm 5.5 (19.7)	1.8 \pm 0.0 (0.1)

Table 4

Summary of GLM ANOVA for juvenile haddock and cod abundance on Georges Bank. *F*-values are denoted by their level of significance.

A. 17-29 June 1984		Site 84-I			
Factor	Haddock ^a	Haddock ^b	Cod ^c	Cod ^d	
Depth (D)	1.12	0.59	0.24	0.04	
Time (T)	0.48	0.53	0.12	0.06	
Size (S)	11.60***		11.46**	0.34	
D \times T	1.23	0.46	0.34	0.11	
D \times S	0.37		0.10	0.03	
T \times S	0.26		0.49	0.02	
D \times T \times S	0.48		0.09	0.03	
*** <i>P</i> <0.001	^a 9-13, 14-19, 20-29 mm size-class				
** <i>P</i> <0.01	^b 14-19 mm size-class				
* <i>P</i> <0.05	^c 14-19, 20-29, 30-39 mm size-class				
	^d 14-19, 20-29 mm size-class				
B. 18-22 June 1986		Site 86-I			
Factor	Cod ^a				
Depth (D)	41.78***				
Time (T)	9.98*				
Size (S)	4.76*				
D \times T	0.65				
D \times S	1.09				
T \times S	1.91				
D \times T \times S	0.30				
*** <i>P</i> <0.001	^a 20-29, 30-39 mm size-class				
** <i>P</i> <0.01					
* <i>P</i> <0.05					

Table 5

Number and size of juvenile cod (3–9 cm) collected by time of day in bottom trawls, Site 86-I, 25–26 June 1986, *ALBATROSS IV* 86-03.

	No. trawls	\bar{x} n/trawl	SD	CV %	\bar{x} length (cm)	SD	Total no. fish
Night	5	102.8	52.7	51	4.2	0.45	513
Day	11	2.9	1.3	45	4.8	1.48	32
Twilight	1	6.0	—	—	4.4	1.27	6

Table 6

Number and size of juvenile haddock (4–10 cm) and cod (2–12 cm) collected by time of day in bottom trawls, Site 85-IV, 17–18 July 1985, *DELAWARE II* 85-05.

	No. trawls	\bar{x} n/trawl	SD	CV %	\bar{x} length (cm)	SD	Total no. fish
Haddock							
Night	1	1.0	—	—	9.0	—	1
Day	6	84.8	64.6	76	7.1	1.1	496
Twilight	2	20.0	9.9	50	7.1	1.0	40
Cod							
Night	1	—	—	—	—	—	—
Day	6	305.0	391.3	128	5.4	1.6	1,830
Twilight	2	256.6	244.0	95	5.5	1.1	513

Table 7

Number and size of juvenile haddock (3–19 cm) collected by time of day in bottom trawls, Site 85-V, 16–17 August 1985, *DELAWARE II* 85-06.

	No. trawls	\bar{x} n/trawl	SD	CV %	\bar{x} length (cm)	SD	Total no. fish
Night	4	210.5	143.6	68	13.9	1.68	842
Day	6	227.5	114.4	50	13.5	1.76	1,365
Twilight	2	257.0	4.2	2	14.0	1.68	514

Table 8

Night/day abundance ratios ($n/10\text{ m}^2$) for cod and haddock by length size-classes using the 1 m^2 MOCNESS, April and May 1981 and May 1983.

Size-class (mm)	April 1981 Site 81-I	May 1981 Site 81-II	May 1983 Site 83-I	May 1983 Site 83-II	Total	Ratio
Cod						
2-5	37/28	16/7	7.4/7.5	7/13	67.4/55.5	1.21
6-8	30/14	58/35	37/47	13/14	138/110	1.26
9-13	213/98	7/8	16/12	5/4	241/122	1.98
14-19	62/10				62/10	6.20
20-29	14/3				14/3	4.67
Haddock						
2-5	108/66	250/143	93/43	10/55	461/307	1.50
6-8	0.6/1.8	483/473	354/468	168/236	1006/1179	0.85
9-13		66/119	123/189	67/59	256/367	0.70

Table 9

Night/day abundance ratios ($n/1000\text{ m}^2$) for cod and haddock by length size-classes using the 10 m^2 MOCNESS, June 1984, June 1986, and July 1985.

Size-class (mm)	June 1984 Site 84-I	June 1986 Site 86-I	July 1985 Site 85-I	Total	Ratio
Cod					
9-13	0.3/2.5			0.3/2.5	0.12
14-19	54/29	6.4/2.7		60.4/31.7	1.91
20-29	170/45	134/79		304/124	2.45
30-39	5/0.5	154/110	9.5/3.7	168.5/113.5	1.49
40-49		8.5/6.12	14.4/1.4	22.9/7.5	3.05
50-59			1.4/3.1	1.4/3.1	0.45
Haddock					
9-13	4/9			4/9	0.44
14-19	20/16			20/16	3.33
20-29	4/0.9			4/0.9	4.44