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Growth and mortality of Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* eggs and larvae on Georges Bank, 1995 to 1999

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ABSTRACT: The egg and larval stages of the Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* populations on Georges Bank, northeastern USA, were sampled monthly from February through July in 1995 and January through June in 1996 to 1999 as part of the US GLOBEC Georges Bank program. The eggs were staged by means of microscopic examination. Larvae were aged by otolith increment analysis. Seasonally averaged rates of egg mortality were estimated for both species and ranged from 9.9 to 20.4 % d^{-1} for cod and 7.8 to 13.4 % d^{-1} for haddock. From the results of a simple drift model, the interannual variability in egg mortality rate is believed to be due largely to wind-driven transport off the southern side of the bank. The estimated number of hatched eggs is strongly correlated with the subsequent recruitment for both the Atlantic cod and haddock stocks. Mortality during the early larval period was estimated for 10 d cohorts within each year, based on the decrease in abundance from egg hatching to the first sampling of the cohort on a survey, when the larvae were on average about 15 d old. For both species, these rates were slowly varying between cohorts within a season, but showed large variation between years. For the 1995 to 1996 period, the annual average mortality rate was about 6.3 % d^{-1} for cod and 10.1 % d^{-1} for haddock, whereas in 1998 to 1999 the values were 3.9 % d^{-1} for cod and 5.4 % d^{-1} for haddock. The lower mortality rates in 1998 to 1999 are believed to be due to higher prey abundance for the larvae in those years. From the larval stage to stock recruitment, haddock appeared to have a survival rate (recruits per larvae) 3 times higher than that for Atlantic cod.

KEY WORDS: Atlantic cod · *Gadus morhua* · Haddock · *Melanogrammus aeglefinus* · Larvae · Growth · Mortality

INTRODUCTION

Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* have been commercially important fish populations in the Georges Bank region off the northeastern USA for over 300 yr. Variation in the annual recruitment of new fish into these populations is believed to be determined largely during the egg, larval and early juvenile life stages. Survival during these early life stages can be significantly influenced by changes in the physical environment and in the plankton food sources available to the larvae and juveniles.

The US Global Ocean Ecosystem Dynamics (GLOBEC) Georges Bank program (GLOBEC 1992) was designed to investigate the influence of a varying or changing climate on the lower trophic levels of the Georges Bank ecosystem, including the early life stages of the Atlantic cod and haddock populations. One component of the program's field work was a monthly (January to June) broad-scale survey that

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sampled the physical conditions and various plankton communities over the Georges Bank region. Analysis of the larval growth and of the egg and larval mortality for cod and haddock during the first 2 yr of the program (1995 and 1996) have been reported by Green et al. (2004) and Mountain et al. (2003). This report builds upon those earlier studies by analyzing the egg and larval growth and mortality during all 5 yr of the program (1995 to 1999).

The basic life histories of the Atlantic cod and haddock populations on Georges Bank have been widely studied and described (e.g. Walford 1938, Lough 1984, Gabriel et al. 1989, Serchuk et al. 1994, Berrien & Sibunka 1999). Spawning by the cod and haddock populations on Georges Bank is concentrated on the northeastern part of the bank in the late winter through spring. The developing eggs and recently hatched larvae are carried to the south and west by the general clockwise circulation. During this transit they are vulnerable to transport off the southern edge of the bank by winds (Lough et al. 1994) or entrainment by warm core Gulf Stream rings (Le Blanc 1986). At an age of 2 to 3 mo the larvae metamorphose to juveniles, become demersal and concentrate in gravel areas on the northern part of the bank (Lough et al. 1989).

The mortality of cod and haddock eggs and larvae has been investigated in a number of field and enclosure studies (Walford 1938, Saville 1956, Harding et al. 1978, Gamble & Houde 1984, Lough 1984, Campana et al. 1989, Heesen & Rijnsdrop 1989, Morse 1989, Sundby et al. 1989). The mortality rates for eggs generally ranged from 10 to 20 % d^{-1} and for larvae from 4 to 12 % d^{-1}. The growth of larvae of both species also has been studied in both the laboratory (Laurence 1978, Geffen 1995) and the field (Bolz & Lough 1983, 1988, Campana & Hurley 1989). While the laboratory studies can track the growth of cohorts, the field derived values rely on changes in the length at age in the sampled wild population, with age being determined by otolith increment analysis (Bolz & Lough 1983). The development of biochemical techniques based on the ratio of RNA to DNA has allowed the recent growth of individual larvae to be determined in field studies (Buckley & Lough 1987, Buckley et al. 2004). Both the laboratory and field results demonstrate that the larval growth varies with temperature, photoperiod and available food. While growth generally increases with temperature, results from RNA/DNA studies suggest that in some years poor feeding conditions in the spring on Georges Bank result in an optimum temperature for growth of about 7°C for both cod and haddock larvae. Above this temperature growth rate tends to level off or even decrease due to temperature-related increased metabolic requirements (Buckley et al. 2004). In other years when larval prey is more abundant, growth continues to increase with temperature.

MATERIALS AND METHODS

As part of the Georges Bank GLOBEC program, monthly surveys of the bank were conducted to sample and document the physical conditions and plankton communities on the bank and in the deeper, adjacent waters. Surveys were conducted from February to July in 1995 and from January to June in 1996 to 1999. A standard grid of stations was occupied on each survey (Fig. 1), although modest modifications were made during the program (e.g. increasing from 38 to 42 stations). The full sampling plan for the surveys is described in Mountain et al. (2003). At all stations the survey included a conductivity, temperature, depth (CTD) profile, a vertically integrated bongo sampler (paired 61 cm diameter nets with 335 µm mesh) tow for ichthyoplankton and a 1 m^2 MOCNESS (MOC1) (Multiple Opening/Closing Net and Environmental Sensing System, Wiebe et al. 1985) tow for vertically discrete samples of both zooplankton (150 µm mesh) and the ichthyoplankton (335 µm mesh). In addition, at approximately one-half of the stations a 10 m^2 MOCNESS (MOC10) (3.0 mm mesh) sampled older fish larvae and other larger planktonic organisms, particularly potential zooplankton and ichthyoplankton predators. To increase the sampling intensity for ichthyoplankton, at the end of some surveys in 1995 a closely spaced grid of bongo tows was conducted where the initial sampling indicated the highest concentration of cod and haddock larvae were located. This strategy did not seem successful, and in the subsequent years a bongo tow was added along the track line at one-half the distance between the standard stations for the January to May surveys. On the June surveys MOC10 tows were done at all of the stations to increase the sampling on the larger larvae and pelagic juveniles of cod and had-

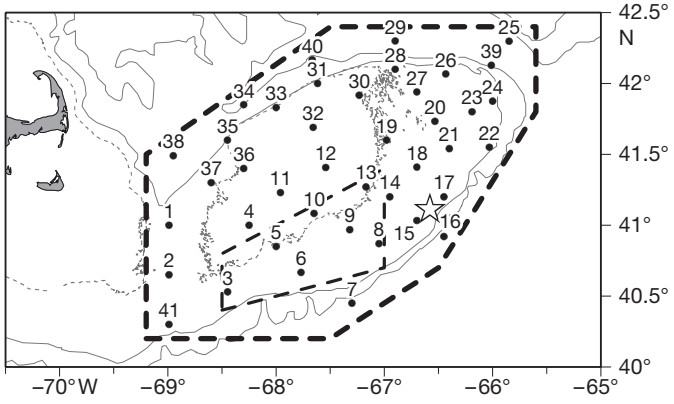

Fig. 1. Standard station locations for the GLOBEC broad-scale survey. The heavy dashed line indicates the area of the kriging grid and the light dashed line encloses the area for which average surface temperature was determined (see text for explanation). The star shows the location of NOAA Buoy 44011

dock and their potential predators. The bongo and MOC1 sampling were completed at most stations on all of the cruises except in January 1997 when only 19 stations covering the bank were done. The MOC10 was the most weather dependent sampling operation and on most cruises a few of the scheduled tows were not accomplished. The sampling of the station grid (Fig. 1) required about 10 to 12 d to complete.

One of the 2 bongo net samples from each tow was preserved in 5% buffered formalin and the other in 95% ethanol. The MOC1 samples were preserved in 95% ethanol. For the alcohol preserved samples the ethanol was changed after 24 h. The formalin samples were sorted for fish eggs and larvae by species. The eggs were then identified to stage according to the protocol described in Mountain et al. (2003) and all larvae were measured to the nearest 0.1 mm standard length (SL). The ethanol-preserved samples were sorted for larvae by species and the lengths of all larvae were measured to the nearest 0.1 mm SL. The MOC10 catches were sieved through 330 µm mesh and individual gadid larvae and juveniles were removed and preserved in 95% ethanol prior to preservation of the rest of the sample in 10% formalin. The lengths of gadids from the MOC10 were measured to the nearest 1.0 mm SL.

Mortality during the egg stage was determined as described by Mountain at al. (2003). In short, for each survey the average densities of early and late stage eggs were determined, where early stage eggs represented the period from fertilization to tail tip twisting and flexing <45° and late stage eggs from the end of the early stage to hatching. The values were normalized by the average duration of those stages, using incubation times by Thompson & Riley (1981) and the observed water temperature, to obtain the number 10 m^{-2} d^{-1}. Linearly interpolating between surveys, daily values were estimated and summed over the season to yield the number of early and late stage eggs produced per 10 m^2 each yr, and from those values, the total abundance of eggs produced on the bank each year. The seasonal average egg mortality rate was calculated by assuming an exponential decline:

$$N_t = N_0 \, e^{-Mt} \quad (1)$$

such that

$$M = -\ln(N_t/N_0)/t \quad (2)$$

and

$$A = 100 \cdot (1 - e^{-M}) \quad (3)$$

where N_0 = early egg abundance, N_t = late egg abundance, t = time between the midpoints of the incubation periods for the 2 stages, M = mortality rate d^{-1} and A = mortality rate expressed % d^{-1}. (NB: Eq. 2 was incorrectly presented in Mountain et al. (2003), see the associated Errata).

The average density of eggs and larvae on each survey was determined by interpolating the log transform of the observed values (number 10 m^{-2}) at each station to a grid of points encompassing the survey region (Fig. 1). This grid, with 2385 points on a 5′ latitude by 5′ longitude spacing and a total area of 55 258 km^2, was developed for use by all of the investigators in the program to provide consistency between the analyses of the various broad-scale data sets. The resulting value at each grid point was retransformed to indicate number 10 m^{-2} and multiplied by the area represented by the grid point. These values were summed for all grid points and divided by the total area of the grid to determine the survey average value. The interpolation to the grid points was done using ordinary kriging (Deutsch & Journel 1998). In the kriging calculations, a single variogram for eggs and a single variogram for larvae was used for all surveys. These were derived using the software package EasyKrig (Chu 1999) to visually determine a best fit variogram for each survey. The variogram parameters for all surveys then were averaged to determine the variograms used in the kriging calculations. Since all years were included in this process, the kriging parameters were different from those used by Mountain et al. (2003). Also, the grid used covers a broader area around the periphery of the bank than that used by Mountain et al. (2003). As a result, the survey abundance numbers for eggs and larvae in 1995 and 1996 were recalculated and differ to some degree from those presented by Mountain et al. (2003). A comparison of kriging with 2 other methods for estimating the average survey abundance values is presented in Appendix A.

For each station the rate of egg hatching was calculated by decreasing the estimated late stage egg density (number 10 m^{-2}) for the mortality expected to occur until the eggs hatched. Since the late stage estimate is assumed to represent the mid-point of that stage, the annual egg mortality rate for that year was applied for one-half the stage duration. This value was divided by the full stage duration to estimate the number of eggs hatched per 10 m^2 d^{-1} at the station. The resulting values for all stations on a survey were kriged and a survey-average hatching rate was calculated. For each year hatching rates for each day were estimated by linearly interpolating between the survey values, which were assumed to represent the calendar day for the mid-point of the survey. The interpolation was extended before and after the survey periods to historic dates for the initiation and cessation of hatching (see Mountain et al. 2003). An annual egg hatching curve was produced by summing the daily values for 10 d intervals (e.g. calendar days 21 to 30). The eggs

hatched during a 10 d interval are referred to as a 'cohort'. In the analyses presented, a 'cohort' is identified by the mid-point of the 10 d interval, so that the '25 d cohort' refers to the larvae that originated from the eggs hatched during calendar days 21 to 30. An egg production curve for each yr was determined similarly using the egg mortality rate and the early stage egg abundance at each station to back-calculate the number of eggs originally spawned.

No biochemical analyses were done to indicate egg condition or viability. As a possible proxy for egg condition, as it might influence subsequent larval mortality, the diameters of cod and haddock eggs were measured to determine if significant differences in size occurred between the years of sampling. Eggs from development stage 6 (embryo greater than full circle round, see Mountain et al. 2003) were used because this is the stage just prior to hatching. Atlantic cod eggs were selected from the March cruise in each year and haddock eggs from the April cruises. A sample of 50 eggs from each selected cruise (10 eggs from each of 5 stations) was the intended protocol. However, in a few instances eggs from additional stations or additional eggs from a single station needed to be taken to obtain the desired 50 eggs. The egg diameters were measured to the nearest 0.01 mm using a Wild M-8 zoom stereo microscope.

The ages of alcohol preserved larvae were estimated following the procedures of Green et al. (2004). Otolith microstructure (enumeration of daily growth increments) was used to determine larval age in days (Bolz & Lough 1988). In samples with few larvae the ages of all the larvae were determined. In samples with a large number of larvae, up to 20 larvae of each species were analyzed from any single sample, ensuring that a representative size range was included in this subsample. Linear and exponential length-at-age or growth models were used for both species to describe larval length as a function of age. The linear model was of the form:

$$Y = a + bX \quad (4)$$

where Y = SL, a = intercept, b = linear or absolute growth rate and X = age in days. The exponential model was of the form:

$$Y = ae^{bX} \quad (5)$$

where Y = SL, a = intercept, b = instantaneous or specific growth rate and X = age in days. The growth model parameters were determined using statistical software SPSS Sigma Plot. The growth analyses done by Green et al. (2004) did not include specimens from the MOC10 samples. For comparison with these analyses, the growth parameters from Green et al. (2004) for June 1995 and May and June 1996 were recalculated to include data from the MOC10 sampling in those months.

For each survey, the hatch date of each larva caught was estimated from its length using the linear growth model for the species and the date of capture. In cases where a growth model was not determined for a survey, the model for an adjacent month's survey was used. No correction for shrinkage was applied to the ethanol preserved samples since the age–length relationships were determined from alcohol preserved larvae. A 3% greater shrinkage was assumed for the formalin preserved larvae relative to those preserved in alcohol, as found by Theilacker (1980) for net caught larvae, and a correction for that shrinkage was applied. Using the hatch dates, the number of larvae in 10 d cohorts (e.g. calendar days 21 to 30, as done previously for egg spawning and hatching) caught at each station was determined. These values were kriged to calculate the survey-average density (number 10 m^{-2}) for each cohort on each survey. Density estimates were not made for cohorts whose hatch dates overlapped the cruise period or had too few larvae caught to provide a meaningful density estimate.

Larval mortality was determined assuming an exponential decrease between population estimates (Eqs. 1 to 3) for 2 situations. First, the mortality was determined by the decrease in abundance between the estimated number of eggs hatched for a cohort (from the egg hatching curves described previously) and the first time the cohort was sampled as larvae on a subsequent survey. These estimates will be referred to as the early larval mortality rate and generally represent approximately the first 15 d post-hatch. Most of the mortality results presented will relate to these early larval values. In the second situation, a cohort abundance was available for 2 successive surveys and the mortality rate was determined by the decrease in larval abundance over the period between the surveys. These values will be referred to as the late larval mortality rate and generally represent the period from about 15 to 60 d post-hatch.

The weighted mean date of the larval catch and its standard deviation (SD) were determined for both species on each survey. The mean date was used to represent the date for the larval abundance estimates in the mortality calculations described above. The average SD of the catch date was 1.7 d for haddock and 2.2 d for cod. Because the majority of the larvae were caught over a period of a few days, no attempt was made to account for mortality during the survey when estimating the larval abundance on a survey.

To investigate the possible loss of small larvae by extrusion through the bongo and MOC1 nets, the total number of cod and haddock larvae caught in 0.5 mm length increments was determined from all 5 yr of sampling. The values were normalized by the total catch to indicate the percent each increment was of the total.

The catch would be expected to increase with decreasing size, and a decrease in catch at small sizes could indicate loss by extrusion. An exponential 'catch' curve was fit to the catch values for the range of sizes from the length increment with the highest catch to the length increment of the largest larvae caught. Using the catch curve, expected catch values were calculated for the smaller size increments. Factors to correct for possible extrusion were determined for those smaller increments by the ratio of the expected catch value to the observed catch at each size increment. However, as explained later, the results did not use a correction for extrusion.

To examine possible daylight avoidance of the nets by the larvae, all bongo and MOC1 samples collected during the program were separated into day and night groupings, as described by Mountain et al. (2003). The ratio of the average number of larvae caught per net tow at night to the average caught in the day was determined for the larvae of each species in 5 mm length increments.

To investigate the influence of the temperature conditions experienced by the larval populations on larval mortality, the surface layer (0 to 30 m) temperature on the southern flank of the bank was determined for each survey (see Fig. 1). Within each year, daily values were determined by interpolating between survey values, which were assumed to represent the mid-date of the survey. A temperature value for the early larval period of each 10 d cohort was calculated by averaging the daily values over 25 d that included the 10 d hatching period for the cohort and the subsequent 15 d that represented the average early larval period. The correlation between the early larval mortality values and the associated temperatures were determined for both species.

The influence of wind-driven transport on egg mortality was investigated in 2 ways. The first correlated the mortality each year with the mean off-bank wind stress during the period of peak egg abundance (mid-February to mid-April for cod and mid-March to mid-May for haddock). The second used a simple wind-driven transport model to simulate the mortality. The transport in the model was determined by the sum of a climatological mean flow and a time-dependent wind-driven Ekman current, as explained in Appendix B. The early stage egg observations for each survey were kriged to the regional grid to determine distributions representing the calendar day of the mid-point for the survey. Daily distributions were then determined by interpolating the value at each grid point between the surveys. These were summed to yield 10 d distributions of the early stage egg abundance. For each 10 d distribution virtual drifters were assigned to each grid point in proportion to its egg abundance. These drifters were advected by the transport model for 17 d, the average time from the early egg stage to hatching. If a drifter crossed the 200 m isobath on the south side of Georges Bank, it was assumed to have been lost from the system. The number of drifters lost for all 10 d periods within the sampling period was determined and expressed as a mortality rate (% d^{-1}) for each year. The wind data used in the model calculations were from NOAA Buoy 44011 on the southeast side of Georges Bank (see Fig. 1). Unfortunately, the buoy did not report winds during the spring of 1996, so the model calculations were done only for the other 4 yr.

To indicate the importance of the early life history processes studied to the ultimate recruitment of the Atlantic cod and haddock stocks, the annual egg and larval abundances are compared with recruitment indices. The number of 1 yr old fish for each year class was estimated from virtual population analyses (VPA) for both cod (Brodziak et al. 2006) and haddock (O'Brien et al. 2006).

RESULTS

Eggs

The estimated egg production curves for Atlantic cod and haddock (Fig. 2a,b, respectively) indicate that the timing of peak spawning varied by about 30 d over the years for both species. The peak for cod ranged from Day 55 in 1996 to Day 85 in 1997, while for haddock the peak occurred about a month later with the earliest peak being Day 85 in 1999 and the latest on Day 115 in 1997 and 1998. The egg distributions for both species on each survey are presented in Sibunka et al. (2007). The timing and location of spawning were similar to that reported in earlier studies (e.g. Lough 1984, Berrien & Sibunka 1999, Lough et al. 2006), with the highest concentration found on the northeastern part of Georges Bank and a much smaller concentration on the northwestern part of the bank.

The seasonal egg mortality rates for both cod and haddock (Table 1) show considerable interannual variability, with a range of about a factor of 2. In each year the cod mortality was higher than for haddock, with the highest values for both species occurring in 1997 and the lowest in 1998. The egg production and hatching curves (Figs. 2 & 3) show that cod egg production was higher than that of haddock, but with lower egg mortality, haddock hatching was greater in some cases. Over the 5 yr period, the spawning abundance for cod, as indicated by the egg production, was almost twice that for haddock, but hatching abundances for the 2 species were similar. The large annual variation in egg mortality resulted in the magnitude of spawning not being a reliable indicator of the number of eggs hatched for either species.

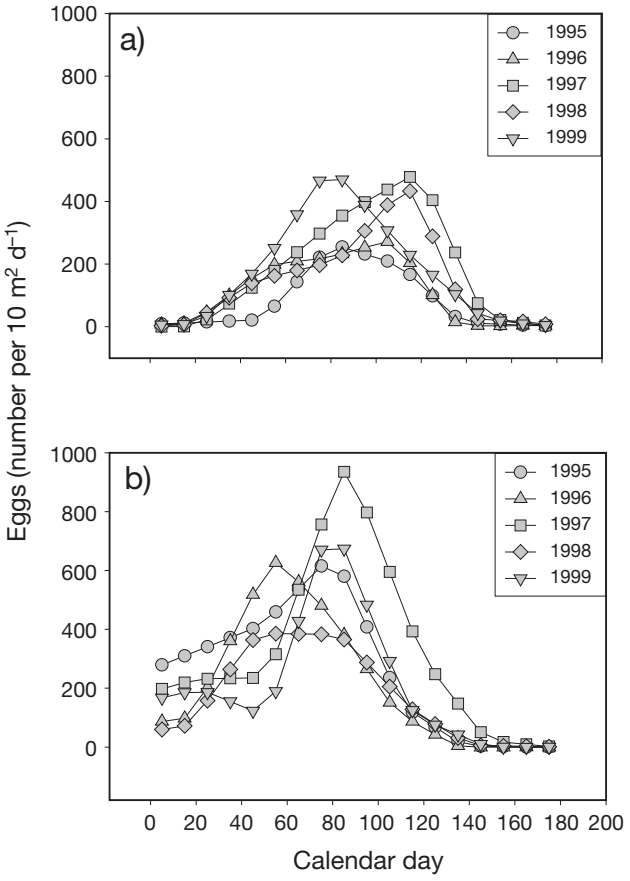

Fig. 2. *Gadus morhua* and *Melanogrammus aeglefinus*. Egg spawning curves (number of eggs per 10 m^2 d^{-1}) for (a) cod and (b) haddock during 1995 to 1999

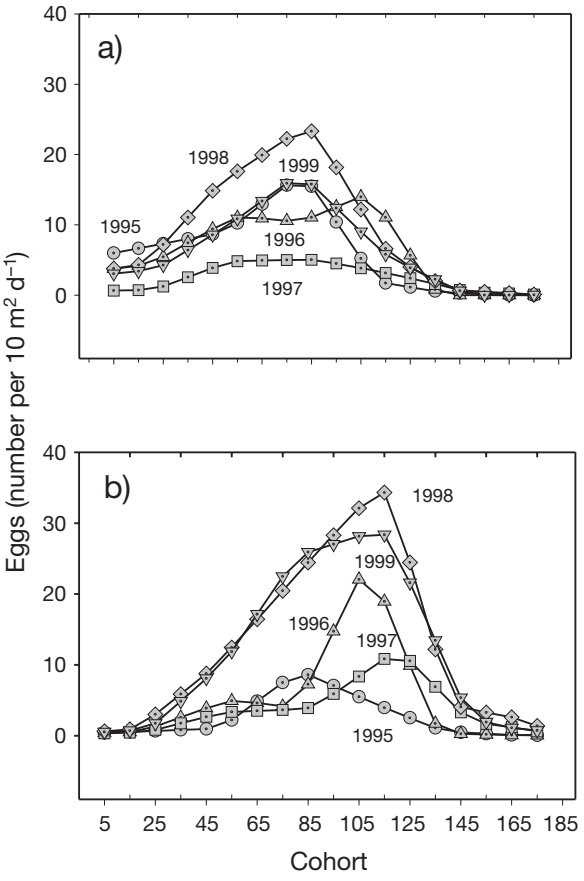

Fig. 3. *Gadus morhua* and *Melanogrammus aeglefinus*. Egg hatching curves (number of eggs per 10 m^2 d^{-1}) for (a) cod and (b) haddock during 1995 to 1999

Table 1. *Gadus morhua* and *Melanogrammus aeglefinus*. Annual egg mortality rates (% d^{-1})

Year	Cod	Haddock
1995	13.7	12.0
1996	12.2	11.3
1997	20.4	13.4
1998	9.9	7.8
1999	15.4	9.9

The annual egg mortality rates appear related to the average off-bank (southeast) wind stress, particularly for cod (Fig. 4a,b), suggesting that off-bank transport was a major factor in the mortality. The mortality rates derived from the wind-driven transport model do exhibit interannual variation similar to the observed rates for Atlantic cod and haddock; the slopes of the regression lines for both species are approximately 1 (Fig. 4c,d). Both regression lines also have intercepts at about 8 to 9% d^{-1}, suggesting that the transport-induced mortality added to an underlying mortality rate of that magnitude from all other sources. While the relationships in Fig. 4, based on only 4 points, are not statistically significant (R^2 ranging from 0.48 to 0.83 and the associated p-values ranging from 0.30 to 0.07), the model results do reflect the high and low events for both species, and wind-driven transport is believed to be a dominant process contributing to egg mortality.

The egg size measurements (Table 2) indicate that the median size for haddock eggs was essentially the same in each year, while for Atlantic cod the size exhibited a slight decrease over the period of the program. A pairwise multiple comparison procedure (Tukey's test) found that the only significant ($p < 0.05$) between-year differences in size occurred for cod; the 1995 eggs were larger than those for both 1998 and 1999. No significant between-year differences in size were found for haddock. To the extent that egg size is a proxy for egg viability, the latter was not a factor in the development of the cod and haddock year classes for any year during the GLOBEC program.

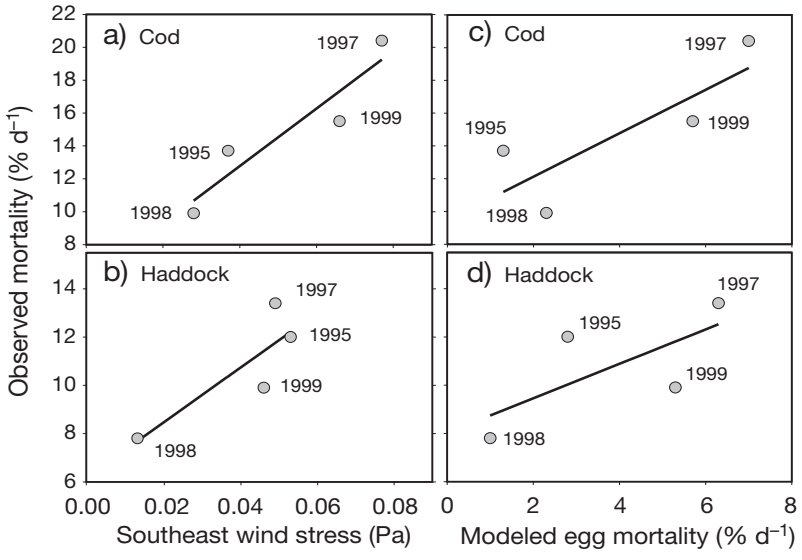

Fig. 4. *Gadus morhua* and *Melanogrammus aeglefinus*. Relationship between the annual egg mortality rate for (a) cod and (b) haddock and the mean southeast wind stress during the period of peak egg abundance for each species, and the relationship between observed and transport model-derived annual egg mortality rates for (c) cod and (d) haddock. Values for 1996 are not included since wind data were not available (see text for explanation)

Table 2. *Gadus morhua* and *Melanogrammus aeglefinus*. Median diameter (mm) of eggs, with 25% and 75% confidence limits (CL)

Year	N	Median	25% CL	75% CL
Cod				
1995	50	1.54	1.5	1.57
1996	50	1.515	1.47	1.57
1997	50	1.5	1.47	1.57
1998	50	1.47	1.46	1.55
1999	50	1.475	1.45	1.54
Haddock				
1995	38	1.47	1.41	1.47
1996	50	1.465	1.41	1.5
1997	50	1.465	1.44	1.47
1998	50	1.47	1.44	1.5
1999	50	1.47	1.42	1.48

Larvae

A total of 28711 larvae were collected and measured (16413 Atlantic cod and 12298 haddock) over the 5 yr of the program. Ages for a total of 4695 larvae (2914 cod and 1781 haddock) were obtained by otolith increment analysis. Comparisons between technicians analyzing the same otolith showed the ages were reproducible to within 8%, comparable to the results reported by Green et al. (2004). As in previous studies of gadid otolith microstructure (Campana & Hurley 1989, Jeffrey & Taggart 2000, Green et al. 2004) significant numbers of otoliths extracted from properly preserved larvae had no distinct increments visible and were not readable. This was particularly true in 1997 and 1999. Thus, the number of otoliths suitable for examination varied from survey to survey and was not necessarily related to the abundance of larvae in samples in each month.

The range of size and age for larvae aged in each month are shown in Table 3 for both species. Cod ranged in size from 1.8 to 44 mm SL and from 4 to 109 d in age. Haddock were from 1.5 to 56 mm and from 4 to 98 d in age. The maximum age of larvae of both species taken in the primary sampling gears (bongo and MOC1) tended to increase through April and May and decrease in June. MOC10 sampling provided additional age data on larger larvae (Table 3). The absence of otoliths with few increments (i.e. indicating <4 d old) is noteworthy and has been encountered in other otolith studies with cod and haddock, but the cause is unknown (see Green et al. (2004) for a discussion of this issue). Regardless, larval cohort abundances were determined only for cohorts whose 10 d time bin did not overlap the dates of a survey, and sampling on the southern and eastern parts of the bank where the highest concentrations of larvae were generally encountered did not occur until a few days into a survey. As a result very few larvae <4 d old were, or would have been, involved in the larval mortality estimates presented.

The linear and exponential growth models derived from the otolith analysis for each survey are provided in Table 4 for Atlantic cod and haddock. In some cases too few larval otoliths were available and/or readable to determine a relationship, particularly for haddock in 1997 when models were determined only for the May and June surveys. The coefficients of determination (R^2) were similar for the linear and exponential models and generally were >0.8. All of the regressions presented for both species were significant, and nearly all were highly significant ($p < 0.001$). The majority of larval cod and haddock available for this study were <60 d old, but inclusion of MOC10 samples from late in the season extended the range of ages to greater than 3 mo.

The night-to-day ratio for the larval catch (Fig. 5) is close to 1 (0.80 to 1.27) for both species at all sizes up to

Table 3. *Gadus morhua* and *Melanogrammus aeglefinus*. Number of cod and haddock larval otoliths examined for age determination by cruise and year, with larval length and age ranges. Numbers in parentheses are from the 10 m^2 MOCNESS sampling. The cruise designations begin with the first 2 letters of the names of the research vessels 'Albatross IV', 'Oceanus' and 'Endeavor'

Year & Month	Cruise	Species	Number	Length range (mm)	Age (d)
1995					
February	EN261	Cod	18	2.1–7.0	7–27
		Had.	1	4.5	16
March	EN263	Cod	392	1.8–15.1	5–57
		Had.	104	1.6–9.9	5–37
April	EN265	Cod	282	2.2–17.3	5–53
		Had.	106	2.3–9.1	6–38
May	AL9505	Cod	142	3.0–18.4	9–56
		Had.	48	3.1–17.6	9–67
June	AL9506	Cod	4 (76)	2.7–26.0 (18–36)	8–53 (38–99)
		Had.	9 (17)	2.6–22.4 (14–36)	4–50 (38–85)
July		Had.	1	11.3	31
1996					
January	EN276	Cod	7	2.5–3.1	8–11
February	EN278	Cod	116	2.4–10.4	7–25
		Had.	30	3.3–5.2	7–16
March	OC275	Cod	207	2.0–12.3	4–43
		Had.	32	2.3–8.3	6–30
April	EN282	Cod	372	2.7–25.0	3–64
		Had.	76	1.7–7.8	5–29
May	AL9605	Cod	21 (127)	5.1–35 (9–40)	29–62 (25–90)
		Had.	(1)	(22)	(56)
June	AL9607	Cod	2 (98)	12.2,16.4 (13–41)	41,57 (34–86)
		Had.	(55)	(11–54)	(33–97)
1997					
January	AL9701	Cod	19	3.0–12.2	8–40
		Had.	1	3.8	17
February	OC298	Cod	19	3.6–18.0	7–47
		Had.	1	3.8	9
March	OC300	Cod	17	3.1–8.3	5–27
		Had.	11	3.0–7.2	4–13
April	OC302	Cod	4	3.3–23.0	6–81
		Had.	3	2.2–3.9	5–12
May	AL9705	Cod	35	2.1–14.0	5–43
		Had.	134	2.4–19.9	7–52
June	AL9707	Cod	2 (30)	2.6,15.0 (14–29)	7,46 (38–75)
		Had.	9 (48)	2.9–10.6 (20–45)	4–35 (47–82)
1998					
January	AL9801	Cod	84	1.7–11.2	4–41
		Had.	2	3.6,3.9	5,7
February	OC317	Cod	175	2.9–19.3	5–68
		Had.	89	2.3–7.7	5–32
March	OC319	Cod	342	2.3–17.6	6–57
		Had.	265	2.3–13.0	7–58
April	OC322	Cod	339 (106)	2.1–23.0 (10–30)	5–67 (34–88)
		Had.	238 (42)	1.5–14.8 (10–27)	5–53 (36–76)
May	AL9806	Cod	22 (17)	3.0–18.8 (20–34)	9–60 (50–79)
		Had.	128 (26)	1.9–15.0 (19.5–36.5)	5–53 (46–86)
June	AL9808	Cod	3 (7)	2.9–5.3 (21–38)	9–14 (59–85)
		Had.	36 (53)	2.3–12.2 (25–56)	6–29 (57–108)
1999					
February	OC366	Cod	45	2.7–27.0	5–85
		Had.	20	2.7–7.0	5–22
March	EN320	Cod	178	2.9–12.2	4–58
		Had.	136	2.9–7.2	4–26
April	OC341	Cod	83	3.0–11.2	7–42
		Had.	94	2.9–10.7	7–39
May	AL9904	Cod	2	4.9,5.9	13,21
		Had.	1	13.3	42
June	AL9906	Cod	(26)	(25–44)	(58–82)
		Had.	(35)	(15–50)	(38–92)

25 mm length for cod and to 20 mm length for haddock. There is no indication of daylight avoidance of the nets by larvae in the size range used in these analyses. Too few larger larvae were caught to determine possible avoidance behavior at larger sizes.

The early larval mortality rates for both Atlantic cod and haddock (Fig. 6) exhibit considerable variability between years. The mortality rates for cod generally range from 0 to 10% d^{-1}, while haddock have a wider range of 0 to 15% d^{-1}. Within each year a seasonal pattern of relatively high values for the early (January to February) and late (April to May) cohorts and lower values in between (March) is evident for cod and to a lesser extent for haddock. An annual mortality value was determined by averaging the values for the 45 to 115 d cohorts for each year, since these cohorts were represented for both species in each year (except for haddock in 1997). These annual mortality rates show a similar pattern for both species of high values in 1995 to 1996 and low values in 1998 to 1999 (Fig. 7). No annual rate was calculated for haddock in 1997 because growth curves were not available for many of the surveys, as noted previously.

The seasonal pattern in the early larval mortality rate, with minimum values for the March cohorts, is similar to that of the surface layer temperature (Fig. 8). Combining all years, the correlation between the early larval mortality estimates and the associated water temperature is highly significant for both species: $R = 0.45$ ($p < 0.01$, $n = 49$) for cod and $R = 0.46$ ($p < 0.01$, $n = 42$) for haddock.

The contribution each cohort made to the total annual larval population was determined by applying each cohort's early larval mortality rate to the cohort's egg hatching abundance for a period of 15 d. The values for all cohorts in each yr were summed to estimate the annual total early larval population (i.e. number of larvae that survived to an age of at least 15 d). The proportion each cohort contributed to that total population was quite consistent among years for cod (Fig. 9a) with a seasonal pattern very similar to the egg hatching curves (Fig. 3a). For haddock, however, the pattern varied among years (Fig. 9b), with the peak contributions in 1995 and 1998 coming in March, while for the other years in April. The April peak is consistent with studies done during other peri-

Table 4. *Gadus morhua* and *Melanogrammus aeglefinus*. Estimated slope (*b*) and intercept (*a*) parameters for the linear (Eq. 4) and exponential (Eq. 5) length-at-age models, with the associated standard errors (SE) and coefficients of determination (R^2)

Year & month	Species	Linear model					Exponential model				
		b	SE	*a*	SE	R^2	*b*	SE	*a*	SE	R^2
1995											
February	Cod	0.21	0.034	1.35	0.43	0.71	0.044	0.0061	2.25	0.22	0.70
March	Cod	0.23	0.004	0.99	0.08	0.89	0.033	0.0007	2.64	0.05	0.81
	Haddock	0.23	0.014	0.70	0.20	0.73	0.043	0.0022	2.00	0.09	0.71
April	Cod	0.23	0.006	1.72	0.13	0.84	0.031	0.0007	3.22	0.07	0.83
	Haddock	0.20	0.010	1.81	0.15	0.79	0.034	0.0016	2.76	0.09	0.75
May	Cod	0.30	0.011	0.07	0.40	0.84	0.030	0.0012	3.53	0.18	0.84
	Haddock	0.23	0.011	1.23	0.30	0.90	0.026	0.0012	3.39	0.16	0.88
June	Cod	0.35	0.017	3.27	1.12	0.84	0.014	0.0010	10.60	0.70	0.77
	Haddock	0.41	0.017	0.33	0.95	0.96	0.022	0.0020	6.19	0.87	0.91
1996											
February	Cod	0.18	0.031	2.56	0.42	0.23	0.036	0.0056	3.04	0.25	0.24
	Haddock	0.14	0.043	2.73	0.53	0.27	0.031	0.0010	3.18	0.07	0.75
March	Cod	0.21	0.008	2.17	0.12	0.77	0.031	0.0010	3.18	0.07	0.75
	Haddock	0.21	0.027	1.43	0.32	0.68	0.043	0.0042	2.28	0.15	0.69
April	Cod	0.25	0.007	1.60	0.20	0.88	0.030	0.0008	3.22	0.11	0.91
	Haddock	0.18	0.020	2.11	0.20	0.50	0.037	0.0032	2.64	0.09	0.52
May	Cod	0.47	0.012	−3.50	0.65	0.92	0.021	0.0006	6.58	0.26	0.91
June	Cod	0.53	0.014	−7.21	0.87	0.94	0.022	0.0005	6.49	0.24	0.95
	Haddock	0.62	0.022	−9.75	1.11	0.93	0.023	0.0006	6.42	0.26	0.94
1997											
January	Cod	0.22	0.026	1.24	0.56	0.83	0.037	0.0030	2.51	0.23	0.89
February	Cod	0.27	0.028	1.27	0.68	0.84	0.034	0.0031	2.99	0.34	0.85
March	Cod	0.17	0.023	3.14	0.30	0.79	0.031	0.0033	3.48	0.21	0.82
April	Cod	0.27	0.011	1.34	0.44	1.00	0.026	0.0007	2.83	0.16	1.00
May	Cod	0.26	0.019	0.50	0.49	0.85	0.039	0.0025	2.44	0.19	0.89
	Haddock	0.30	0.012	−0.88	0.26	0.82	0.045	0.0008	1.98	0.05	0.93
June	Cod	0.37	0.038	0.00	1.96	0.76	0.020	0.0025	6.73	0.93	0.71
	Haddock	0.48	0.018	−3.76	1.03	0.93	0.024	0.0012	5.70	0.44	0.92
1998											
January	Cod	0.20	0.009	1.51	0.15	0.87	0.036	0.0012	2.46	0.08	0.89
February	Cod	0.22	0.006	1.51	0.12	0.88	0.028	0.0005	3.06	0.05	0.91
	Haddock	0.15	0.010	1.88	0.16	0.74	0.034	0.0020	2.47	0.09	0.75
March	Cod	0.21	0.005	1.40	0.11	0.85	0.031	0.0006	2.91	0.05	0.87
	Haddock	0.19	0.005	1.18	0.11	0.84	0.030	0.0008	2.69	0.06	0.81
April	Cod	0.34	0.008	−1.65	0.32	0.81	0.027	0.0006	3.84	0.13	0.81
	Haddock	0.28	0.008	−0.36	0.27	0.81	0.032	0.0008	2.74	0.11	0.85
May	Cod	0.42	0.015	−2.25	0.72	0.96	0.028	0.0014	3.75	0.37	0.95
	Haddock	0.40	0.007	−1.85	0.21	0.92	0.032	0.0007	3.04	0.12	0.93
June	Cod	0.48	0.028	−2.23	1.70	0.97	0.025	0.0034	5.15	1.32	0.94
	Haddock	0.53	0.009	−3.52	0.51	0.98	0.023	0.0008	6.07	0.39	0.94
1999											
February	Cod	0.24	0.010	0.77	0.28	0.93	0.024	0.0007	3.05	0.13	0.95
	Haddock	0.12	0.024	2.06	0.32	0.61	0.034	0.0063	2.33	0.21	0.63
March	Cod	0.17	0.005	2.11	0.08	0.85	0.026	0.0006	3.01	0.05	0.84
	Haddock	0.13	0.010	2.32	0.13	0.53	0.033	0.0023	2.56	0.08	0.57
April	Cod	0.23	0.012	1.40	2.24	0.82	0.036	0.0018	2.83	0.13	0.81
	Haddock	0.22	0.009	1.23	0.17	0.87	0.038	0.0015	2.50	0.09	0.87
June	Cod	0.62	0.102	−13.93	7.33	0.60	0.022	0.0034	6.46	1.60	0.63
	Haddock	0.53	0.057	−5.74	3.92	0.72	0.018	0.0018	8.84	1.18	0.74

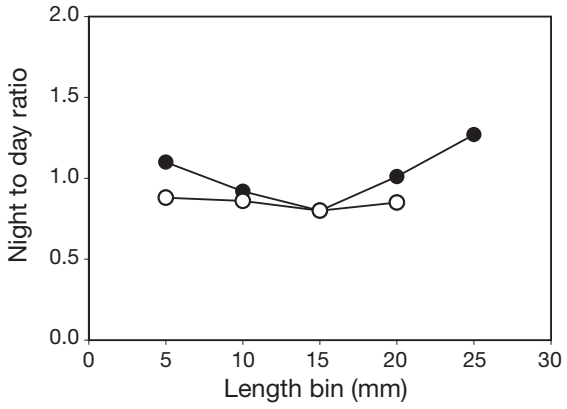

Fig. 5. *Gadus morhua* and *Melanogrammus aeglefinus*. Ratio of night-to-day catch of (●) cod and (○) haddock larvae in 5 mm increments of larval length

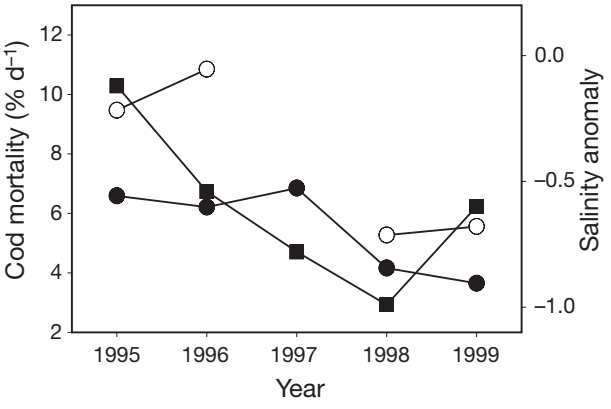

Fig. 7. *Gadus morhua* and *Melanogrammus aeglefinus*. Annual weighted mean early larval mortality rates for (●) cod, (○) haddock and (■) the spring salinity anomaly for the Georges Bank waters

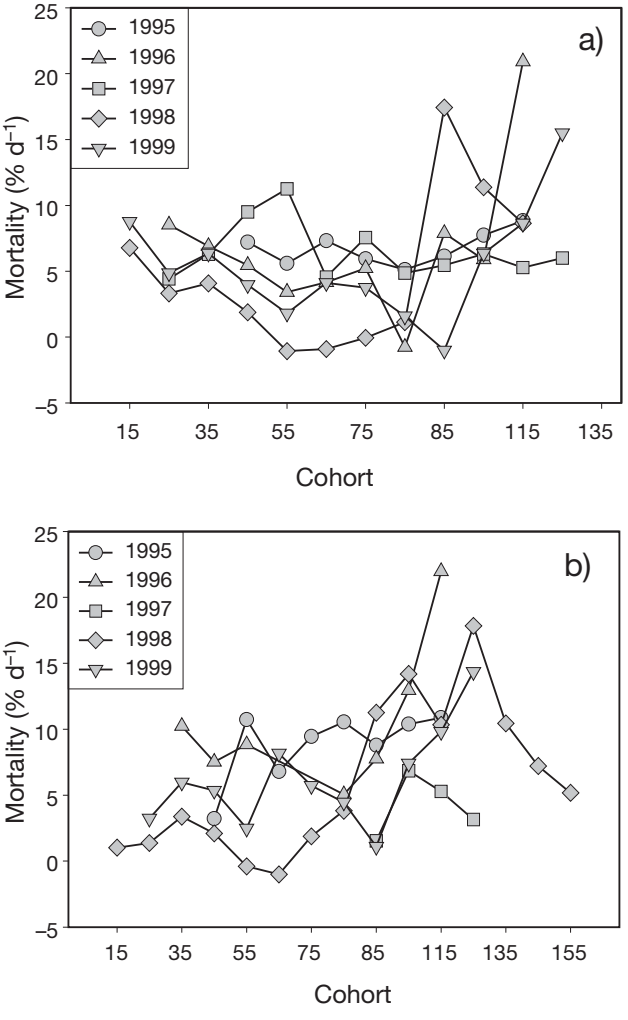

Fig. 6. *Gadus morhua* and *Melanogrammus aeglefinus*. Early larval mortality rates (% d^{-1}) for (a) cod and (b) haddock cohorts in 1995 to 1999

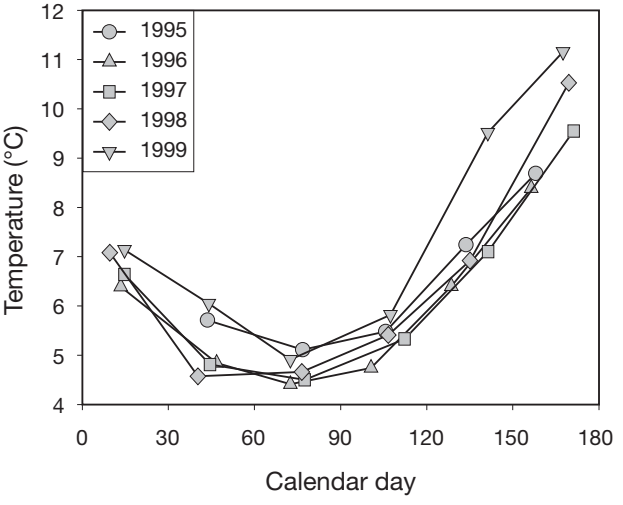

Fig. 8. Mean surface layer (0 to 30 m) temperature on the southern flank of Georges Bank in each year

ods (Berrien & Sibunka 1999). The greater contribution from the earlier (March) cohorts in 1995 is similar to the findings of Lapolla & Buckley (2005), who back-calculated the birth dates of young-of-the-year haddock caught on the Northeast Fisheries Science Center fall trawl survey.

The distribution of larval mortality by age (i.e. average age of the larvae used in the mortality calculation) shows that the mortality rates for older larvae exhibited a narrower range than did those for the early larvae (Fig. 10). For ages greater than about 20 d, the scatter of mortality rates appears to occur around a value of about 7% d^{-1} for cod and 8% d^{-1} for haddock, and with no trend evident for either species as age increased.

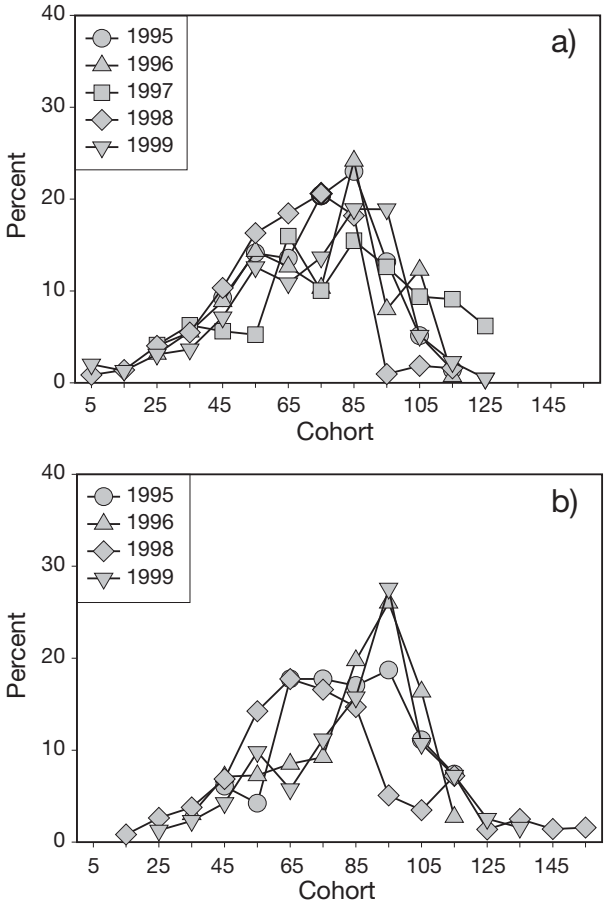

Fig. 9. *Gadus morhua* and *Melanogrammus aeglefinus*. Percentage (%) each cohort contributes to the total annual larval population for (a) cod and (b) haddock

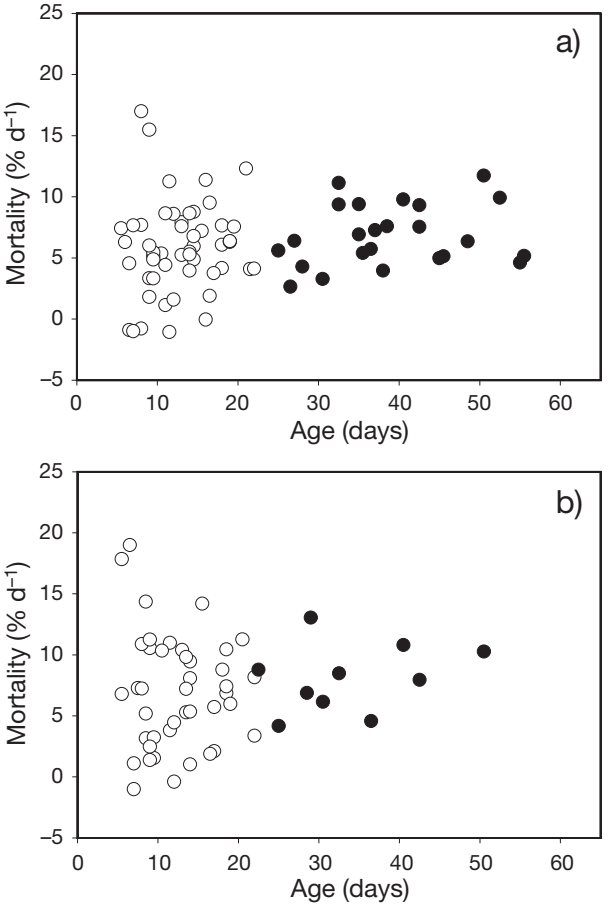

Fig. 10. *Gadus morhua* and *Melanogrammus aeglefinus*. Relationship between larval mortality rate (% d^{-1}) and larval age for (a) cod and (b) haddock, including (○) early larval and (●) older larval mortality values

The histograms of larval catch by size for both Atlantic cod and haddock (Fig. 11) show a decrease in catch abundance below lengths of 4.0 mm, suggesting possible loss of small larvae by extrusion through the nets. Using the catch curves in Fig. 11, multiplicative factors to correct for that loss would be 1.73 at 3.5 mm and 2.93 at 3.0 mm for cod, and 2.32 at 3.5 mm and 4.63 at 3.0 mm for haddock. These small lengths, however, are well within the range of the length at hatch for both species (Laurence & Rogers 1976, Lough 1984), even allowing for up to 20% shrinkage of our samples in preservation. No correction for extrusion was made in calculating the larval abundances used in the analyses presented.

The recruitment of the Atlantic cod and haddock stocks each year was not positively correlated with the number of eggs produced (Table 5). The number of eggs hatched, however, is strongly correlated with recruitment for both cod and haddock, although with only 5 data points the latter is not statistically signifi-

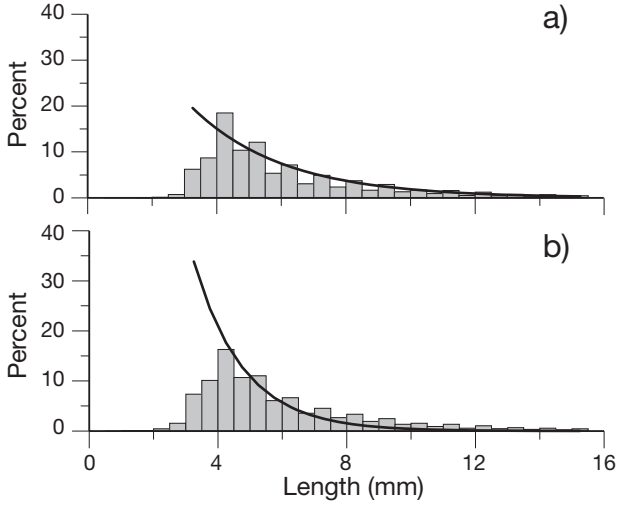

Fig. 11. *Gadus morhua* and *Melanogrammus aeglefinus*. Percent of total larval catch (1995 to 1999) by 0.5 mm length increments for (a) cod and (b) haddock (shaded bars). The solid lines represent exponential catch curves (see text for explanation)

Table 5. *Gadus morhua* and *Melanogrammus aeglefinus*. Correlation (R), and the associated probability level (p) between egg production, egg hatching and larval abundance and the subsequent recruitment for the cod and haddock populations

	Cod		Haddock	
	R	p	R	P
Egg production to recruitment	−0.91	0.03	0.06	0.92
Egg hatching to recruitment	0.90	0.04	0.71	0.18
Larval survival to recruitment	0.90	0.04	0.64	0.36

cant. The number of larvae reaching 15 d of age did not provide a better indicator of recruitment than did the egg hatching abundance. The high negative correlation between cod egg production and recruitment (Table 5) is believed to be spurious. It results from the highest cod egg production occurring in 1997 when the egg mortality happened to be highest, promoting low survivorship, and the lowest egg production occurring in 1998 when egg mortality happened to be lowest, promoting high survivorship. There is no evident mechanism to connect variation in egg production with variation in egg mortality, particularly since the latter is believed to be associated with variation in wind-driven transport of eggs off the bank.

DISCUSSION

The egg mortality rates for both species varied by a factor of up to about 2 among years (Table 1), which is apparently attributable to differences in the wind-driven transport of eggs off the bank (Fig. 4). In modeling of the egg transport, the rate of egg loss from the bank averaged in 10 d periods was fairly consistent within each year and not dominated by a few intense events. As a result, the mean southeast wind stress was a good proxy for the integrated effect of the time-dependent transport process. The importance of off-bank transport (and of the southeast winds) was shown many years ago by Chase (1955), who used a weighted index of the daily atmospheric pressure difference between Nantucket, Massachusetts and Yarmouth, Nova Scotia (a proxy for the southeast component of the winds on Georges Bank) during the spring to explain about 50% of the variance in haddock recruitment over the period from 1928 to1951.

The probability that an egg would be retained or lost from the bank is influenced by where on the bank the egg is spawned. The transport model results (not shown) indicate that eggs on the southeastern part of the bank had a lower probability of remaining on the bank than those from the western part, similar to the results of Lough et al. (2006). The percentage of eggs that originated on the western half of the bank (west of 67.5° W) varied considerably among years (Table 6), particularly for haddock. This change in the proportion of eggs from the western part of the bank probably contributed to the interannual variability in the observed egg mortality. For example, the proportion was highest and the observed mortality rate was lowest for both species in 1998.

The early larval mortality rates (Fig. 6) are comparable to the mortality rates reported in the other studies of Atlantic cod and haddock identified in the Introduction. However, this is the first study able to delineate the seasonal pattern of mortality during the larval period over a number of years. With a few exceptions (discussed later) the mortality rates are coherent or smoothly varying between successive cohorts within each year, indicating that mortality is more chronic than episodic. Overall, the major variability in mortality was between years, not cohort to cohort within a year.

A number of processes could have contributed to the observed variability in mortality. As indicated previously, wind-driven transport of eggs off the bank is believed to be responsible for much of the interannual variability in the egg mortality rates. The same transport model was applied to the early larval period from egg hatching to the first sampling of each cohort as larvae. The results (not shown) found no relationship between wind-driven transport and the annual early larval mortality rates (Fig. 7). While the eggs are mainly in the near-surface layer (Pepin et al. 2005), the larvae are distributed throughout the water column and less vulnerable to wind-driven transport.

Another mechanism causing advective loss of larvae is the entrainment of water from Georges Bank by warm core rings. A review of satellite imagery for rings with entrainment features in close proximity to larval distributions suggest at least 2 situations where entrainment may have contributed to a high larval mortality rate. In April 1998 the distribution of late-stage haddock eggs extended off the southern flank of the bank into a ring entrainment feature. The asso-

Table 6. *Gadus morhua* and *Melanogrammus aeglefinus*. Percent (%) of eggs originating west of 67.5° W on Georges Bank

Year	Cod	Haddock
1995	11.9	3.8
1996	8.8	18.5
1997	15.8	7.6
1998	18.6	29.8
1999	16.5	9.2

ciated loss of eggs and hatching larvae could be responsible for the increased mortality rate for haddock hatched in April (the 95, 105 and 115 d cohorts in Fig. 6b). Cod had a similar spatial distribution in April 1998 and also exhibited high mortality rates for the same 3 cohorts. Similarly, in 1997 a ring with an obvious entrainment feature moved westward along the southern flank of the bank during February and March and may have contributed to the high mortality rates for the cohorts of cod hatched in those months (Fig. 6a). While the association of entrainment features and larval distributions with higher mortality rates is suggestive, the actual loss of larvae due to entrainment cannot be quantified from the available data.

Differences in larval mortality could be related to changes in larval condition or growth rate. The slopes of the linear length-at-age models (Table 4) represent a growth rate (mm d^{-1}). These rates, however, are not for individual larvae, but instead represent the population sampled at the time of the survey. Since older larvae would have experienced conditions over a wider time period than the young larvae, comparison of the slopes or growth rates from different months or years should involve models based on comparable age ranges. The length-at-age relationships for January through April in the different years are based on comparable age ranges. The slopes are of similar magnitude (0.20 to 0.25 mm d^{-1} for cod and 0.18 to 0.23 mm d^{-1} for haddock) with no evident pattern in variability between months or years, and thus do not suggest a relationship between growth and the observed mortality. For May and June overall, and for April 1998, the slopes are higher, but are based on older larvae, making a direct comparison with the results for January through April inappropriate.

Other GLOBEC studies did investigate the larval condition for the same Atlantic cod and haddock populations using biochemical techniques. Buckley et al. (2006) estimated starvation mortality rates from low RNA/DNA values in young cod and haddock larvae during April of 1995, 1997 and 1999. For both species, 1995 had the highest mortality rate, while 1997 and 1999 exhibited substantially lower rates, and the rates for cod were lower than those for haddock. This pattern of mortality is similar to the annual mortality rates for 1995 and 1999 in Fig. 7. In a related study, Buckley & Durbin (2006) show that the larval prey abundance on Georges Bank, particularly *Pseudocalanus* sp., was low in 1995 and high in 1998 and 1999. Food availability probably was a major factor in causing the annual differences in larval condition reported by Buckley et al. (2006) and in the larval mortality reported in this study.

The salinity of the Georges Bank waters exhibited large interannual variability during the GLOBEC years (Smith et al. 2001, Mountain 2003), with the March to April salinity anomaly decreasing by almost 1 PSU from 1995 to 1998, before increasing moderately in 1999 (Fig. 7). Buckley & Durbin (2006) indicated that the variability in the larval prey abundance showed a close inverse relationship to changes in salinity. The annual averaged early larval mortality rates for haddock and cod also show interannual variability similar to that of salinity (Fig. 7), with low mortality associated with low salinity and (from Buckley & Durbin 2006) high larval prey abundance. The changes in salinity are not believed to be important physiologically for either the larvae or their zooplankton prey, but instead are a proxy for other factors associated with the changing water mass properties. The salinity changes did not originate locally, but occurred across the entire Gulf of Maine and resulted primarily from changes in amount of Scotian Shelf water entering the gulf around Cape Sable (Smith et al. 2001, Mountain 2003). The change in the source waters could have involved changes in the nutrient levels and/or in the plankton community advected into the region. Together, the results of these different studies suggest connections from changes in the regional flow patterns to changes in the production of local zooplankton populations and to changes in the growth and survival of the larval cod and haddock populations on Georges Bank. Identifying and documenting the mechanisms and rates responsible for these apparent connections will be an important topic for future analyses in the GLOBEC program.

The early larval mortality rates were positively correlated with water temperature, i.e. lower mortality at lower temperature. The Georges Bank has the southern most cod stock in the North Atlantic Ocean and colder temperatures might be expected to have a positive effect on overall survival and recruitment. In a study of temperature–recruitment relationships for 9 stocks around the North Atlantic, Planque & Fredou (1999) found that stocks in warmer waters exhibited increased recruitment with colder temperatures, and the reverse was true for coldwater stocks. However, the Georges Bank water temperatures were in the middle of the range considered, and no relationship was evident between temperature and recruitment for Georges Bank cod. In a study across many species, Houde (1989) showed larval mortality generally increased with temperature, assumedly due to increased metabolic requirements at higher temperatures and resulting food limitation. Buckley et al. (2004) found that larval Atlantic cod on the bank did exhibit lower growth rates, probably from food limitation, at temperatures above 7°C. However, for most of the cohorts considered here (Fig. 6) the early larval period ended before calendar day 140 and only a few (6 of 91) mortality values were associated with temperatures above

7°C (Fig. 8). The temperature–mortality relationship found in this study is not believed to be due to food limitation at higher temperature. While the cause is not known, a possible explanation is that at lower temperatures the metabolism and food requirements of the larval predators were lower and predation mortality was reduced.

The larval mortality rates for both species (Fig. 10) did not show a decreasing trend with increasing age, as is characteristic of many other species (Bailey & Houde 1989, Houde 1997) and found in other studies of Atlantic cod (e.g. Sundby et al. 1989). While in some cases the early larval mortality rates reported here were higher than for the older larvae, in other cases the early mortality rates were much lower. This variation in the trend of mortality with larval age is similar to that observed by Voss et al. (2001) for Baltic cod *Gadus morhua callarias*. In 1988, they found that the very young larvae had a mortality rate of about 20% d^{-1} and the older larvae about 7% d^{-1}, while in 1991 the situation was reversed, with the early mortality rate being low (0.08% d^{-1}) and the older rate higher (22% d^{-1}). The explanation for the large change in early larval mortality was that compared with 1988, 1991 had better environmental conditions that benefited the early larvae. Similarly, as explained previously, the very low early mortality rates on Georges Bank in 1998 and 1999 are believed to be related to high food prey abundance, which may have been related to regional changes in environmental conditions.

An important goal for the GLOBEC program is to determine the influence of variations in early life history characteristics (particularly abundance and mortality) on the ultimate recruitment of the Atlantic cod and haddock populations. As shown in Table 5, variability in both the number of eggs hatched and the number of larvae is strongly correlated with recruitment for cod, and to a lesser degree (with lesser confidence) for haddock. The range of egg mortality rate among years (Table 1) would cause a change in survivorship during the egg stage by a factor of 6.6 for cod and 2.7 for haddock. The range of annual early larval mortality (Fig. 7) would cause a change in survivorship by a factor of 1.5 for cod and 2.1 for haddock in the early larval stage. For cod, the egg mortality made a much larger contribution to variation in overall survivorship than did the larval mortality. For haddock, contributions from the egg and the larval mortalities were comparable. Although not directly studied here, processes during the late larval–juvenile stage were also important in determining the recruitment. Averaged over the 5 yr of the program, the haddock stock (omitting 1997, since an annual larval estimate is not available) produced 9.2 recruits per 10^5 larvae, while the cod stock had only 2.8 recruits per 10^5 larvae. This indicates that haddock had an overall survival rate in the late larval–juvenile period 3.3 times higher than that for cod. In the range of larval abundance that occurred in these years, both Atlantic cod and haddock exhibited an increase in recruitment with increasing larval abundance (Fig. 12). While the regression for haddock is not statistically significant (see Table 5), the ratio of the regression slopes for haddock and cod is 2.7 (Fig. 12), about the same as the ratio above for the total populations. The cause of this difference between species in late larval–juvenile survival is not known, but it probably contributed to the greater increase in the haddock stock abundance during these years than occurred for cod.

No confidence limits are given for the abundance or mortality rate estimates presented. Combining catches from 2 sampling gears (bongo and MOC1) with different numbers of samples collected by both gears on each survey makes a rigorous determination of confidence limits problematic. The early larval mortalities for a cohort were derived from the difference between egg hatching abundance determined by one method (annual egg hatching curves) and the larval abundance determined by a different method (identifying the cohort population on a survey using a length-at-age curve). It is not surprising that in a few cases more larvae were estimated for a cohort than hatching eggs, resulting in a negative mortality rate (e.g. Fig. 6). In comparing and contrasting mortality rates between cohorts and between years, the relative differences in values are more important than the specific values themselves. To indicate the sensitivity of the mortality estimates to the methods used, all of the abundance and mortality calculations were redone using the correction for possible extrusion and using the exponential length-at-age curves (Table 4) (with and without

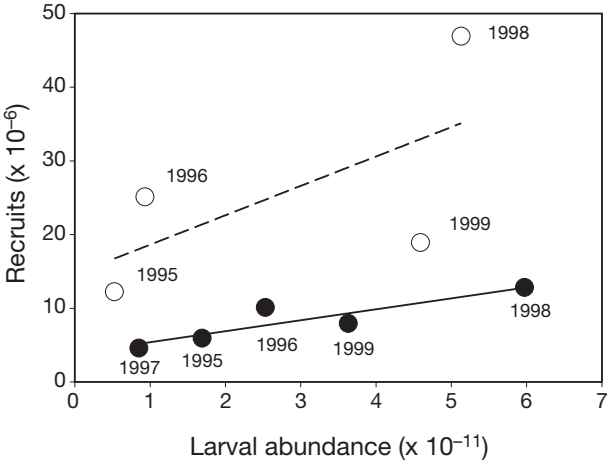

Fig. 12. *Gadus morhua* and *Melanogrammus aeglefinus*. Recruitment as a function of larval abundance (15 d post-hatch) for (●) cod and (○) haddock

correction for extrusion). While a few points in Figs. 6, 7 & 10 would move slightly, all of the basic results and conclusions presented would be unchanged. Similarly, Appendix A indicates that while estimates of abundance for a cohort may vary depending on the spatial interpolation method used, the mortality estimates would be essentially the same. This insensitivity to methodology and the consistency in the early larval mortality rates between adjacent cohorts in Fig. 6 suggest that the mortality estimates are reasonably precise and reliable.

In summary, the major conclusions from this study are: (1) The egg mortality varied by about a factor of 2 between years and was higher for Atlantic cod than for haddock. The interannual variation appeared due, in large part, to wind-driven advection of eggs off the southern flank of the bank. (2) The mortality rate during the early larval period was smoothly varying within a year, but varied considerably among years. Haddock experienced a wider range of mortality rate than did cod. (3) The interannual variability in the average early larval mortality rate for both species was similar to the variability in the salinity of the Georges Bank waters and believed to be due to changes in food availability that, in turn, were associated with the changes in water properties. (4) For both species, the number of eggs hatched was strongly correlated with the variation in subsequent recruitment. The number of larvae surviving to an age of 15 d did not provide a better indicator of recruitment variation. (5) The survivorship during the post-larval, juvenile period appeared to be higher for haddock than for cod by about a factor of 3.

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Appendix 1. Comparison of interpolation methods

The egg and larval abundance values were determined by interpolating the observed values (number 10 m^{-2}) at the original station locations to a grid (Fig. 1) using a kriging algorithm. The products of the interpolated value at each grid point times the area that grid point represented were then summed for the whole region. Other methods are available to determine the regional abundance value; however, an important question remains as to the sensitivity of the resulting abundance and mortality values to the method used. To investigate this, 2 additional methods were applied. The first was to interpolate the grid point values using a simple inverse distance squared weighting of the stations nearest to the grid point. The second was a non-spatial method based on the delta statistic (Pennington 1983). This approach assumes that the value at each station represents a random draw from a population that includes zero values and whose non-zero values are log-normally distributed. The delta statistic provides a non-biased estimator of the mean and variance of such a population.

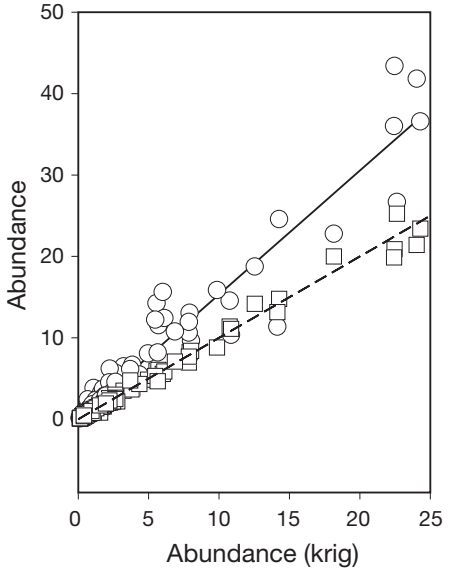

Fig. A1. Comparison of larval abundance values determined by kriging with those determined by (□) the distance squared interpolation method and (○) the delta-distribution method. The dashed line has a slope of 1, and the solid line a slope of 1.7

The abundance of all of the larval cohorts used in the mortality estimates presented in Fig. 6a were determined by delta and the distance squared methods. The corresponding mortality rates were also determined for both methods. Comparing the abundance values with the values determined by kriging (Fig. A1) showed that the distance squared values were essentially the same as the kriging values (R^2 = 0.9, slope = 0.95). The delta method consistently yielded higher abundance estimates than kriging by a factor of about 1.7 (R^2 = 0.9, slope = 1.7). The mortality estimates derived by the distance squared method were essentially the same as those for kriging (squares in Fig. A2), while the delta mortality estimates (circles in Fig. A2) showed a bit more scatter, but in nearly all cases the estimates were within ± 1 to 2% d^{-1} of each other.

The kriging method was chosen for the analyses presented in this study because the abundance values appeared to have a spatial pattern and it could rigorously include the spatial statistics of that pattern in the interpolation calculations. Regardless, while the abundance estimates may vary by method, the resulting mortality estimates are quite similar. Therefore, the conclusions presented are not sensitive to or dependent upon the method used for determining the regional abundance estimates.

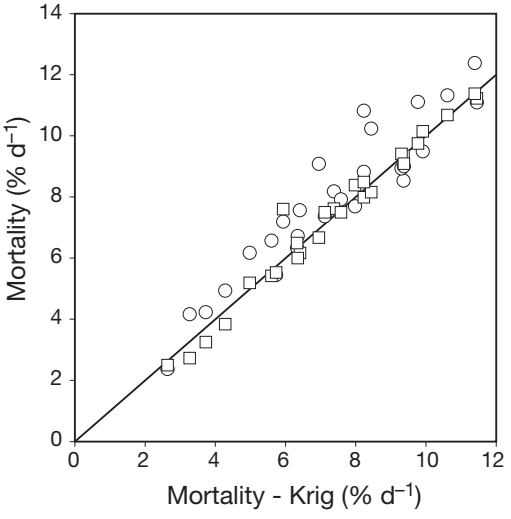

Fig. A2. Comparison of the mortality rates derived from the larval abundance values determined by kriging with those determined by (□) the distance squared interpolation method and (○) the delta distribution method. The dashed line has a slope of 1

Appendix 2. Wind-driven transport models

The correlation of egg mortality with SE wind stress (Fig. 4a,b) suggests that the time-dependent response of the ocean to the wind forcing is important in the transport of eggs off the southern flank of the bank. To estimate the time-dependent flow field, a time-dependent wind-driven current is added to a bi-monthly climatological flow field derived from a circulation model (Naimie 1995). The wind-driven current is derived from a solution to the time-dependent Ekman equations (Jilsaniaski 1970). If the winds are assumed to be piece-wise constant (e.g. for hourly wind values the wind is assumed constant over the hour period), the contribution to the present current from the wind some hours earlier is determined by a rotation coefficient and a magnitude coefficient applied to the wind vector (Mountain & Mooney 1979). The contributions from all of wind velocities in the wind history used (e.g. the previous 72 h) are independent and can be summed to derive the wind-driven current. Once the coefficients are calculated, the wind-driven current is easily calculated for any time series of wind values.

The wind data from NOAA Buoy 44011 on eastern Georges Bank was used for this analysis, with the wind stress calculated using Large & Pond (1981) as described by Manning & Strout (2001). To reflect the movement of the upper layer of the water column, the calculated surface wind-driven current speed was multiplied by 0.5 since the average Ekman speed over the upper 20 m is approximately one-half of the surface value.

Using an Ekman current and adding it to a climatological velocity is a convenient and numerically efficient method to approximate the actual flow field, although it is not a fully rigorous solution. The important issue is how well does it work in the case of Georges Bank? To test this, the movements of satellite tracked buoys deployed in the GLOBEC program (R. Limburner pers. comm.) were used. The drift tracks were reviewed to identify 3 cases in which buoys were on the eastern or southern part of the bank (where the high concentrations of developing eggs are observed) when a major wind event occurred and there would have been a significant time-dependent adjustment of the surface layer flow field. The observed drift tracks are compared with model derived tracks, calculated both for the wind-driven model (Ekman + climatology) and for climatology alone (Fig. A3). The model was initiated about 2 d before the wind event occurred and the resulting change in the direction of drift is evident. The wind-driven model tracks capture the cross-isobath movement quite well, although they somewhat overestimate the along-isobath movement. For estimating the wind-driven loss of eggs from the bank, the movement across the isobaths is most important, while movement along isobath is not. The comparisons in Fig. A3 indicate that the wind-driven model used here provides a reasonable estimate of the cross-isobath movement. Note that neither the climatology nor the Ekman components include the tidal motions that are quite evident in the observed drift tracks.

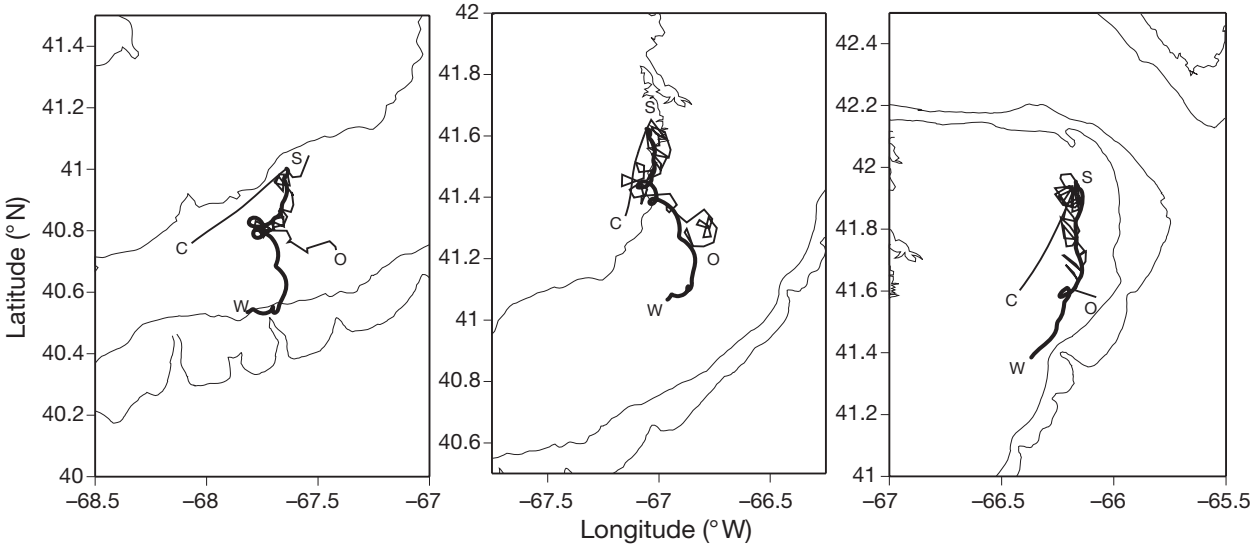

Fig. A3. Comparison of the observed drift (O) for 3 satellite tracked buoys with modeled drifts using only the climatological flow field (C) and using the combination of climatology and the time-dependent Ekman wind-driven flow (W)

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