Abstract—Ichthyoplankton surveys have been used to provide an independent estimate of adult spawning biomass of commercially exploited species and to further our understanding of the recruitment processes in the early life stages. However, predicting recruitment has been difficult because of the complex interaction of physical and biological processes operating at different spatial and temporal scales that can occur at the different life stages. A model of first-year life-stage recruitment was applied to Georges Bank Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks over the years 1977–2004 by using environmental and density-dependent relationships. The best life-stage mortality relationships for eggs, larvae, pelagic juveniles, and demersal juveniles were first determined by hindcasting recruitment estimates based on egg and larval abundance and mortality rates derived from two intensive sampling periods, 1977–87 and 1995–99. A wind-driven egg mortality relationship was used to estimate losses due to transport off the bank, and a wind-stress larval mortality relationship was derived from feeding and survival studies. A simple metric for the density-dependent effects of Atlantic cod was used for both Atlantic cod and haddock. These life stage proxies were then applied to the virtual population analysis (VPA) derived annual egg abundances to predict age-1 recruitment. Best models were determined from the correlation of predicted and VPA-derived age-1 abundance. The larval stage was the most quantifiable of any stage from surveys, whereas abundance estimates of the demersal juvenile stage were not available because of undersampling. Attempts to forecast recruitment from spawning stock biomass or egg abundance, however, will always be poor because of variable egg survival.

Life-stage recruitment models for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank

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Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) co-occur in many regions of the North Atlantic and show moderate levels of synchrony in recruitment within regions, indicating that common environmental conditions affect both species (Fogarty et al., 2001). Recruitment in these species is generally correlated with the abundance of the late larval stage and more so by age-0 juveniles. However, the large year classes of haddock on Georges Bank resulted from different early life history survival rates, indicating that they were driven by different causes (Rothschild et al., 2005).

Although recruitment control of Atlantic cod (hereafter, cod) and haddock has generally been believed to be set at the juvenile stage (Myers and Cadigan, 1993; Fogarty et al., 2001), the importance of the contribution of survivors from the egg and larval stages has been variable and uncertain. A recent review concluded that no life stage or process can be singled out as the primary contributor for recruitment variability in marine fish (Houde, 2009). Recruitment levels can be controlled by environmental factors on eggs and larvae in some species and years but are regulated on late-stage larvae and juveniles in other species and years. Recruitment is not necessarily set at a particular stage because it is an integrated, cumulative process. Forecasting recruitment will depend on our knowledge of the process, mechanisms that regulate recruitment, and our ability to monitor these processes.

Environmental variables have been incorporated into stock and recruitment models to help explain additional variability (e.g., Maunder and Watters, 2003; Fogarty et al. 2008; Hare et al., 2010; Mantzouni et al., 2010). Individual based models (IBMs) with specific species early life-stage behaviors have been embedded in hydrodynamic models to simulate variability in egg and larvae transport and survival (see Miller [2007] for review). Process-based forecasting models are needed to link adult egg production with juvenile stages. Recruitment can be viewed in terms of stage-specific contingency survival. Recent conceptual models of recruitment view the complex process as the interactions between small-scale activating factors and larger-scale constraining factors (Stenseth et al., 1999; Bailey et al., 2005). Activating factors are high-frequency (stochastic) events that affect larval survival, the cumulative result of many episodic events such as early larval feeding in relation to wind-induced turbulence, and invertebrate predation. Constraining factors tend to limit population size through low frequency events, physical barriers, and density-dependent processes, such as competition for prey and limited space, predation, and cannibalism.

On Georges Bank, the lower recruitment variability of cod (standard deviation [SD] of residuals of

Ricker curve=0.52) was related to a combination of broader spawning in time and space, a higher tolerance to environmental factors, and stronger density-dependent mechanisms, especially intraspecific predation (Fogarty et al., 2001). The higher recruitment variability of haddock (SD=1.07) and more restricted spawning later in the season, coupled with different morphological and physiological features and feeding strategies indicate that activating factors (e.g., environmental effects) during the larval stage play a more important role in recruitment than constraining factors (e.g., density-dependent predation) during the juvenile period.

The Northeast Fisheries Science Center (NEFSC) has been conducting groundfish and plankton surveys on the northeast continental shelf over the last 50 years (O'Brien et al.[1]; Brodziak et al.[2]). Ichthyoplankton data from two intensive sampling efforts, the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys from 1977 to 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys from 1995 to 1999, have provided abundance estimates of eggs and larvae, their transport patterns in the currents, growth and mortality rates, and prey and predators. Process cruises were embedded within the standard surveys to focus on specific mechanisms to learn more about the recruitment process in the first year of life, the period when the size of the year class is usually established. A long-term goal was to develop readily obtainable environmental indices in future monitoring programs that could be used in models to provide a better estimate of recruitment. Because typical stock projections of 3–5 years require an assumption that recruitment will stay constant, any prior knowledge will be important for specifying annual catch limits between assessments.

Our objective was to develop early-stage mortality relationships to hindcast recruitment of age-1 cod and haddock on Georges Bank. The primary hypotheses investigated were the following: 1) the abundance of eggs retained on the bank is a function of wind-driven transport; 2) larval-stage mortality is a function of wind-induced turbulence that promotes feeding, hence better survival; 3) the abundance of pelagic juveniles is related to the number of larvae that survive; and 4) the survival of demersal juveniles to age-1 recruits is a function of density-dependent predation. These and other recruitment hypotheses were also explored for Georges Bank haddock in Friedland et al. (2008). The ichthyoplankton data from the two intensive sampling

periods, MARMAP and GLOBEC, were first used to hindcast recruitment, and were then compared with the virtual population analysis (VPA) recruitment estimates (O'Brien et al.[1]; Brodziak et al.[2]) to determine the best life-stage mortality relationships. Then, by using the seasonal egg abundance estimated from the VPA-derived spawning stock biomass, proxies for egg, larval and juvenile mortality rates were applied to all years, 1977–2004, to estimate age-1 recruitment.

Materials and methods

Historically, peak cod spawning occurs on the northeastern part of Georges Bank in February–April and in March–April for haddock (Fig. 1), and their eggs and larvae are transported south and west along the southern flank of Georges Bank but some part of the cohort is retained on the more shoal, central part of the bank. These commercially important species on Georges Bank have been monitored by the NEFSC annually by spring and fall bottom trawl and plankton surveys. Time series data are available since 1978 on spawning stock biomass (SSB) and recruitment (R) at age 1, as well as egg and larval abundances. The ichthyoplankton surveys have been used to produce estimates of the total seasonal production of eggs that then could be compared with the VPA-derived estimates of egg production given sufficient information (Lough et al., 2008).

Life-stage recruitment model

The model estimates the number of age-1 recruits from the initial abundance of eggs decreasing through various life-stage mortality rates to survivors at recruitment. In this study, the estimated mortality rates were initially used for each stage (without attempting to incorporate stochastically determined mortality processes) by using the following equation:

$$R = E*e-(m_1*t_1 + m_2*t_2 + m_3*t_3 + m_4*t_4), \qquad (1)$$

where R = number of predicted recruits;
E = initial number of eggs spawned or hatched;
m_1 = the observed instantaneous mortality over the egg period t_1;
m_2 = the larval observed mortality rate over the period t_2;
m_3 = the pelagic juvenile mortality over the period t_3; and
m_4 = the demersal juvenile mortality over the period t_4.

The egg-stage duration (t_1) of 19 days to hatching is used for both cod and haddock and is based on development time at a typical winter water temperature on Georges Bank of 5°C. The larval- and juvenile-stage durations were based on the length-at-age curves in Bolz and Lough (1988). Hatching of cod eggs to first larvae occurs in mid-March and for haddock in mid-April.

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[1] O'Brien, L., N. Shepherd, and L. Col. 2006. Assessment of the Georges Bank Atlantic cod stock for 2005. NMFS NEFSC Ref. Doc. 06-10, 148 p. Available from Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1097.

[2] Brodziak, J., M. Traver, L. Col, and S. Sutherland. 2006. Stock assessment of Georges Bank haddock, 1931–2004. NMFS NEFSC Ref. Doc. 06-11, 114 p. Available from Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1097.
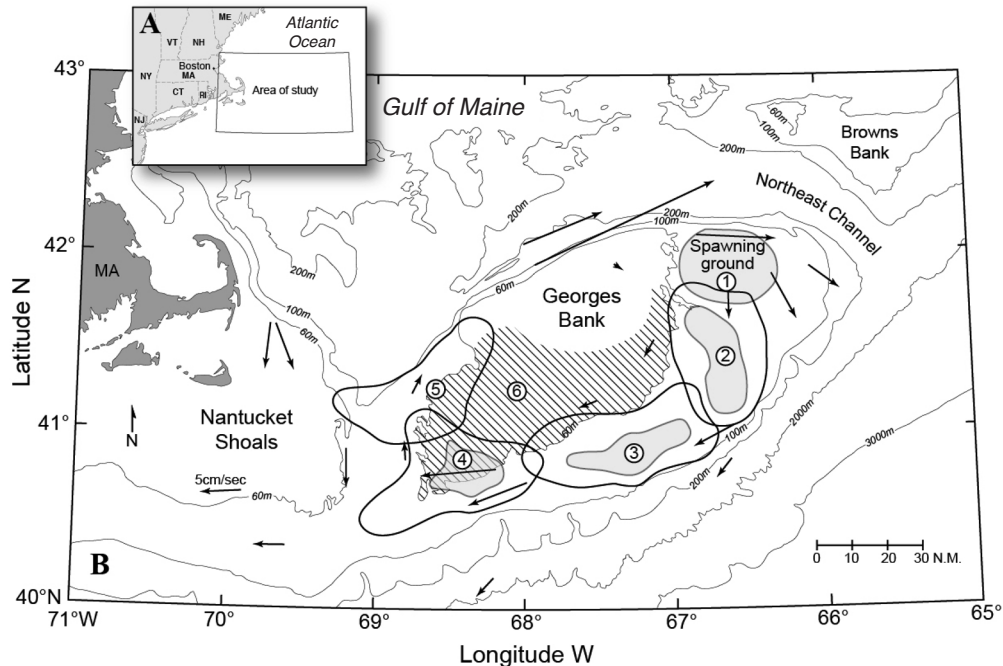
Figure 1

(**A**) Map of the northeast coast of the United States showing the Georges Bank study area. (**B**) Generalized distribution of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) eggs (1), larvae (2, 3), and pelagic juveniles (4, 5) during their first 3–4 months of life in the clockwise circulation over Georges Bank. The shaded areas within the stage patches represent the areas of highest density. Cross-hatching indicates where the highest abundance of recently-settled, demersal juveniles (6) may be found in early-summer. The arrows represent the direction and relative speed of mean summer water column flow. A reference arrow of 5 cm/s in length is located on Nantucket Shoals. Figure is redrawn from Lough et al. (2005, fig. 1). Depth contours are given in meters (m).

Larvae of both species take approximately 30 days to grow to 10 mm standard length (SL) (t_2). Pelagic cod juveniles take 90 and haddock juveniles take 70 days to reach 5 cm SL (t_3). The demersal juvenile stage (t_4) for cod takes 241 days to reach 26 cm SL, and 210 days for haddock to reach 20 cm SL. January 1 is the date when fish are considered to be 1 year old. The demersal juvenile duration was estimated from the mid-date of the pelagic juvenile stage (Lough, 2010). Stage duration specified above, which is dependent on growth and temperature, was not varied in this study.

The initial recruitment predictions were based on estimates of spawning and hatching abundances and life-stage mortality rates derived from the MARMAP and GLOBEC surveys (Tables 1 and 2). Revised hatching abundances for GLOBEC years were used so that the methods were the same as those used for the MARMAP years (Mountain and Kane, 2010).

With this life-stage recruitment model, estimates of age-1 recruitment from the initial egg and hatching (larval) abundances were determined and correlated with the VPA-derived age-1 recruitment for Georges Bank cod and haddock. Simulations based on randomization of parameters were not done for confidence limits of the age-1 recruits because the potential range of the parameters was so wide as to be meaningless.

VPA-derived egg abundance

Spawning stock biomass (SSB) and recruitment (R) for Georges Bank cod and haddock were obtained from assessments conducted by using the adaptive framework for the estimation of population size (ADAPT) virtual population analyses (VPA) calibration method (Parrack, 1986; Conser and Powers, 1990). The VPAs were calibrated with indices of abundance from spring and fall research bottom trawl surveys through 2005 (O'Brien et al.[1]; Brodziak et al.[2]). SSB was estimated by using NOAA Fisheries Toolbox, Virtual Population Analysis, vers. 3.0 software (NOAA, 2008) as the product of the numbers of fish in the first year of the period in question, the mean weight at age (as determined from commercial fishery catch statistics), and the variable proportion of mature fish-at-age summed over all age classes. Maturation ogives were estimated with logistic regression of maturity data collected during NEFSC spring bottom trawl research surveys (O'Brien et al.[1]; Brodziak et al.[2]).

Table 1

Yearly spawning egg and hatching abundances and life-stage mortality rates used in the Atlantic cod (*Gadus morhua*) age-1 recruitment hindcasts by program surveys. Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys occurred from 1977 and 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys occurred from 1995 to 1999. Survey egg and larval abundances and mortality rates are from Lough et al. (2006) and Mountain and Kane (2010). Pelagic juvenile mortality was specified as 6%/d. Demersal juvenile mortality rates were estimated from Equation 7.

Survey and year	Spawning abundance (no.×10^{12})	Egg mortality (%/d)	Hatching abundance (no.×10^{12})	Larval mortality (%/d)	Pelagic juvenile mortality (%/d)	Demersal juvenile mortality (%/d)
MARMAP						
1977	No egg data		7.209	8.6	6.0	3.00
1978	No egg data		33.395	16.2	6.0	2.27
1979	28.817	17.1	2.063	5.5	6.0	2.19
1980	59.081	2.7	33.030	12.3	6.0	2.12
1981	58.783	13.5	3.214	5.4	6.0	2.54
1982	55.048	19.6	0.553	16.0	6.0	2.07
1983	4.761	9.5	0.876	10.4	6.0	1.91
1984	3.980	2.3	2.644	9.8	6.0	2.26
1985	4.935	4.0	2.278	7.6	6.0	1.89
1986	8.940	12.3	0.830	10.1	6.0	2.57
1987	8.282	13.2	0.607	10.0	6.0	2.04
GLOBEC						
1995	22.056	13.7	1.269	8.2	6.0	1.78
1996	17.186	12.2	1.269	7.1	6.0	1.83
1997	33.470	20.4	0.366	6.3	6.0	1.92
1998	11.015	9.9	1.520	5.5	6.0	1.81
1999	19.304	15.4	0.880	5.1	6.0	1.97

For Georges Bank cod, annual fecundity was estimated with the NEFSC autumn research survey mean lengths-at-age in an exponential fecundity-at-length model from fish sampled on Georges Bank in February and March of 1999 and 2000 (McIntyre and Hutchings, 2003). For Georges Bank haddock, annual fecundity was estimated by using mean length-at-age from the NEFSC autumn research surveys in a fecundity-length model based on fish collected on Georges Bank during January through March, 1972–73 (Lough et al., 2008). In a more recent study by Alonso-Fernández et al. (2009), the autodiametric method was used to estimate potential fecundity of cod and haddock on Georges Bank. Fish were captured in early March 2006, 2007, and 2008. Their derived fecundity-length relationships were plotted and compared with the above referenced studies and found to be surprisingly close. The cod fecundity estimate by Alonso-Fernández et al. (2009) begins to increase slightly for fish 60 cm and longer compared with that of McIntyre and Hutchings (2003); whereas the Alonso-Fernández et al. (2009) haddock fecundity estimate was slightly lower at all sizes than that of Lough et al. (2008). We decided to use the McIntyre and Hutchings (2003) and Lough et al. (2008) fecundity-length models because the fish were captured closer in time to the MARMAP and GLOBEC studies. Fecundity estimates at length and ages are known to vary annually, especially for cod, but this information has not been collected routinely; therefore, a single fecundity model was applied for each stock under the assumption that fecundity did not change significantly.

To account for differences in egg viability, cod egg production was multiplied by a factor of 0.10 for first-time spawners, and 0.60 for second-time spawners (Trippel, 1998). For haddock, egg production was multiplied by 0.033 for first-time spawners and 0.20 for second-time spawners (Lough et al., 2008). For both cod and haddock, annual egg production was estimated from fecundity at age, summed over ages one to ten.

Ichthyoplankton-survey–derived egg abundance

Estimates of hatching abundance from the NEFSC's ichthyoplankton surveys for spawning cod and haddock included the MARMAP period 1977–87 (Lough et al., 2006, Mountain et al., 2008) and the GLOBEC period 1995–99 (Mountain et al., 2008). Egg data were lost for the 1977 and 1978 seasons. In terms of survey coverage during the various sampling periods, the region was

Table 2

Yearly spawning egg and hatching abundances and life-stage mortality rates used in the haddock (*Melanogrammus aeglefinus*) age-1 recruitment hindcasts by program surveys. Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys occurred from 1977 and 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys occurred from 1995 to 1999. Survey egg and larval abundances and mortality rates are from Lough et al. (2006) and Mountain and Kane (2010). Pelagic juvenile mortality was specified as 6%/d. Demersal juvenile mortality rates were estimated from Equation 7.

Survey and year	Spawning abundance (no.×1012)	Egg mortality (%/d)	Hatching abundance (no.×1012)	Larval mortality (%/d)	Pelagic juvenile mortality (%/d)	Demersal juvenile mortality (%/d)
MARMAP						
1977	No egg data		7.017	10.1	6.0	3.00
1978	No egg data		12279.967	29.9	6.0	2.27
1979	7.988	10.3	2.032	14.0	6.0	2.19
1980	80.803	17.2	2.071	11.5	6.0	2.12
1981	13.317	9.3	2.192	11.3	6.0	2.54
1982	4.004	16.5	0.090	17.8	6.0	2.07
1983	13.488	9.7	2.397	19.1	6.0	1.91
1984	1.651	0.0	2.394	16.6	6.0	2.26
1985	3.025	3.7	1.534	9.2	6.0	1.89
1986	2.492	5.3	0.978	10.5	6.0	2.57
1987	2.224	0.8	2.078	11.0	6.0	2.04
GLOBEC						
1995	7.274	12.0	0.580	10.3	6.0	1.78
1996	10.866	11.3	1.030	11.5	6.0	1.83
1997	12.286	13.4	0.700	9.1	6.0	1.92
1998	9.160	7.8	1.920	4.7	6.0	1.81
1999	16.512	9.9	1.740	6.1	6.0	1.97

sampled bimonthly with about 30 standard stations during the MARMAP period (Fig. 2). The GLOBEC sampling period provided the best coverage of the spawning seasons because surveys were conducted at about 40 standard stations monthly from January through June throughout the Georges Bank region (Fig. 2B). Other years outside the MARMAP and GLOBEC time series were surveyed only once or rarely twice during the spawning season so that we have the least confidence in those years for estimating egg abundance during the spawning season.

Sampling methods and data procedures for the ichthyoplankton time series are described in full detail elsewhere (Lough et al., 2006; Mountain et al., 2008; Mountain and Kane, 2010). Fish eggs were identified, staged, and counted from quantitative 61-cm bongonet hauls. Counts of staged eggs were normalized to the number of eggs per 10 m^2 per day (no./[10 m^2×d]). Egg densities were averaged by survey, and survey means were expanded by the number of days represented by each survey and summed over the season's beginning and end times to estimate the total number of eggs spawned (Fig. 3). Only late-stage cod and haddock eggs can be visually identified, and therefore the abundances of earlier stage eggs were approximated by the proportion of the late-stage eggs. Differential egg mortality between the two species may have introduced a systematic bias in the yearly egg production estimates—a bias that varies with their relative biomass. This bias is discussed in Lough et al. (2008) but cannot be readily corrected.

Egg stage

Another method for estimating egg mortality was the use of a simple wind-driven transport model developed by Mountain et al. (2008) for the GLOBEC years, which was redone for the time series 1979–2005 (Mountain[3]). Particles simulating the egg distributions were allowed to drift in the modeled flow for 17 days (egg duration) and were considered lost to Georges Bank if they crossed the 200-m isobath. The percentage transport loss of particles was determined from mid-February to mid-April for cod and from mid-March to mid-May for haddock and converted to a daily mortality rate (%/d). The observed survey egg mortality rates from the GLOBEC and MARMAP years were regressed against

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[3] Mountain, D. 2008. Unpubl. data. Northeast Fisheries Science Center, Woods Hole, MA 02543-1097.
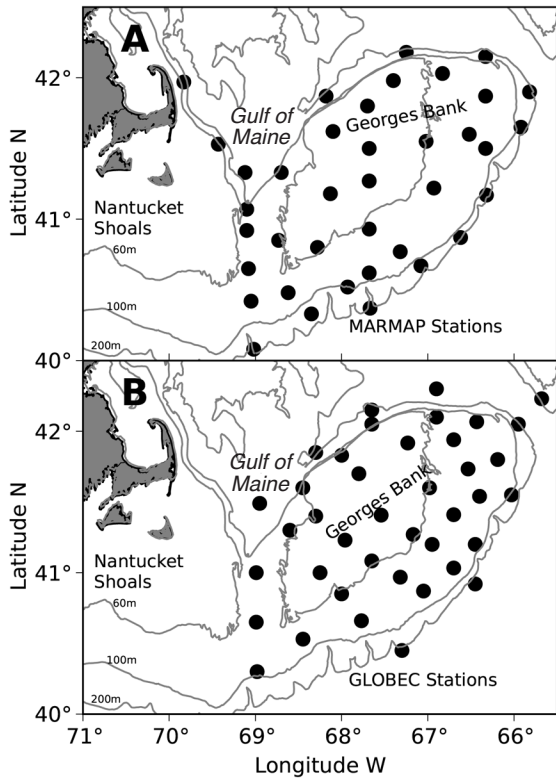
Figure 2

(**A**) Marine Resource Monitoring, Assessment, and Prediction (MARMAP) standard sampling stations on Georges Bank from 1977 to 1987, and (**B**) the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) broad scale standard sampling stations surveyed from 1995 to 1999. Depth contours are given in meters (m).

Figure 3

Comparison of yearly egg abundance derived by the virtual population analysis (VPA) spawning stock biomass method, with that estimated from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) ichthyoplankton surveys for Georges Bank (**A**) Atlantic cod (*Gadus morhua*), and (**B**) haddock (*Melanogrammus aeglefinus*).

the modeled mortality rates to estimate the underlying on-bank loss due to starvation and predation. The equations used to estimate egg mortality ($M_{observed}$) were as follows:

Cod
$$M_{observed} = 8.59 + 1.50 \, (M_{modeled}),$$
$$r^2 = 0.49, \, n = 11; \quad (2)$$

Haddock $\quad M_{observed} = 5.76 + 1.06 \, (M_{modeled}),$
$$r^2 = 0.17, \, n = 11. \quad (3)$$

The intercepts were used as the constant on-bank mortality and added to the yearly off-bank modeled mortality for an estimate of the total yearly mortality rate. Although the regressions were not highly significant, they appeared to be a reasonable adjustment. About 6–9 %/d of the total egg mortality can be attributed to *in situ* processes leaving 10–14 %/d due to transport loss. Mountain et al. (2008) used just four years from the GLOBEC data and found similar on-bank mortality of 8–9 %/d from the regression intercepts.
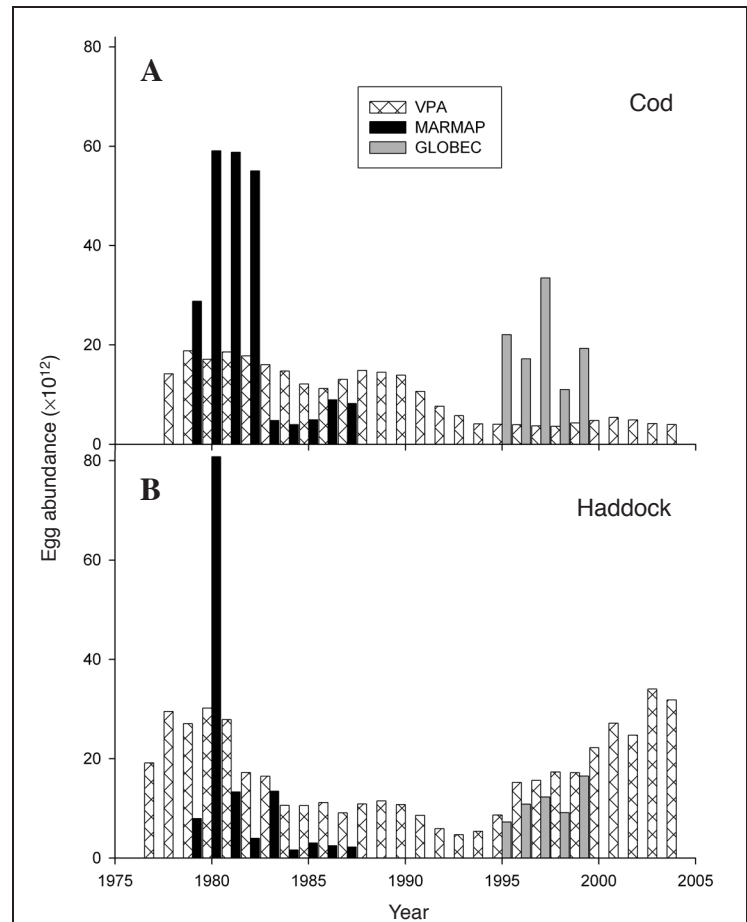
Larvae

Mountain et al. (2008) found an inverse relationship between early larval cod and haddock mortality and a Georges Bank spring salinity anomaly for the GLOBEC years, which also was related to larval prey abundance (Buckley and Durbin, 2006). Mountain et al. (2008) also found a positive relationship between larval mortality and Georges Bank water temperatures for the same years; however, there was no relationship between temperature and recruitment. Nevertheless, we were not able to find a relationship between salinity or temperature and larval mortality when they were averaged over a spawning season. Estimating larval mortality without adequate survey data is difficult because of the complex interaction between growth and mortality and the increasing ability of the larvae to limit transport,

forage, and avoid predators as they grow. A positive correlation was found between prey biomass concentration and growth rates for larval cod and haddock collected on Georges Bank during the GLOBEC surveys (Buckley and Durbin, 2006). Increased larval growth would reduce stage duration and presumably enhance survival. Wind stress was used as an indication of wind mixing or turbulence because it can affect larval encounter rates with zooplankton prey and subsequent feeding, growth, and survival for each cohort. Field studies indicated that the highest feeding ratio (mean number of prey per larval gut) for larval cod occurred when wind exceeded 10 m/s (Sundby and Fossum, 1990; Sundby et al., 1994). Modeled simulations indicated that maximum ingestion occurred at wind speeds near 15.3 m/s (MacKenzie et al., 1994). In a Georges Bank field study, Lough and Mountain (1996) found that the feeding ratio of haddock larvae increased with wind speed up to 7.1 m/s in the upper 20 m. There was an interaction between turbulence and prey density; the mean prey per gut increased with prey density at lower turbulence. Weekly vector-averaged wind stress (in pascals, [Pa]) from January through June 1995–99 (Fig. 4) was used from a combination of NOAA buoys 44-005, 44-008, and 44-0011

Figure 4

Weekly vector-averaged wind stress (in pascals, [Pa]) from January through June 1995–99 obtained from a combination of NOAA buoys 44-005, 44-008, and 44-0011 versus larval cohort day of the year from 1 January. Wind stress was used to derive a relationship with larval cohort mortality in Figure 5. Larval cohort mortality rates were estimated from 10-day hatching bins (January–June) from Georges Bank U.S. Global Ocean Ecosystems Dynamics (GLOBEC) broadscale surveys, 1995–99.

(Manning and Strout, 2001) to correlate with larval mortality. Larval cod and haddock cohort mortality rates were estimated from 10-day hatching bins (January–June) from Georges Bank GLOBEC broadscale surveys, 1995–99 by Mountain et al. (2008). Cohort mortality represents the first 15 days of early life from hatching to about 6-mm standard length (SL). Trend lines were fitted to the mortality and wind stress data for all years and for the high larval growth years 1998–99 and the low growth years 1995–96. Insufficient data were available for 1997, and therefore this year was omitted from the analysis. Both cod and haddock showed a decreasing mortality rate with increasing wind stress; however, the correlation was not significant for cod. For haddock, the best fit based on the coefficient of determination was for the high growth years 1998–99 ($r^2 = 0.57$, Fig. 5), where mortality declined with wind stress until about 0.15 Pa and then increased after about 0.20 Pa. Wind stress of 0.15–0.20 Pa is equivalent to a wind speed of 9–12 m/s. The trend line for all years combined (not shown) was similar to the 1998–99 fit, but less significant ($r^2 = 0.24$).

For 1998 and 1999, the lowest cohort mortality was associated with the highest wind stress (0.15–0.20 Pa) that occurred from January to early March (Fig. 4). Wind stress declined uniformly throughout the spring. For 1995 and 1996, there was generally lower wind stress than optimal for survival, except for a brief period of high wind stress in February and a higher wind stress in April (Fig. 4). It is interesting that in both of these years there was an intense storm period in early
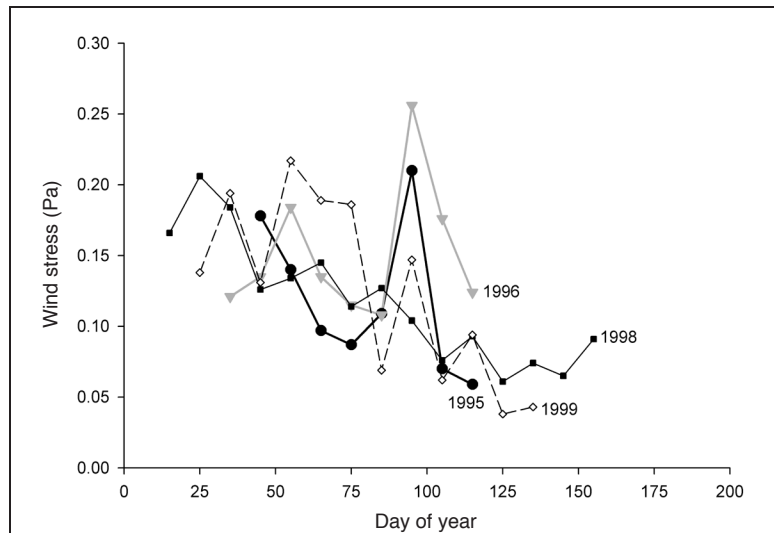
April (day 95). Larval mortality rates for the haddock April 5 (day 95) cohort were 8.8 and 7.8 %/d for 1995 and 1996, respectively, and 11.3 and 1.1 %/d for 1998 and 1999. Cod mortality rates for the same cohort were 6.1 and 7.9 %/d for 1995 and 1996, respectively, and 1.1 and 0.0 %/d for 1998 and 1999. Mortality rates for the haddock April 15 (day 105) cohort were 10.4 and 13.0 %/d for 1995 and 1996, and 14.2 and 7.4 %/d for 1998 and 1999. Cod mortality rates for the April 15 (day 105) cohort were 7.7 and 5.9 %/d, for 1995 and 1996, and 11.4 and 6.4 %/d for 1998 and 1999. Larval cod growth rates based on otolith daily ring analysis also were slightly better in April and May 1996 than 1995 (Mountain et al., 2008), consistent with the lower mortality in 1996.

Because the haddock mortality-wind relationship for 1998–99 best fitted the reported studies of feeding as related to wind stress, this relationship also was used to estimate larval stage mortality for both cod and haddock:

$$M = 741.70 \ W^2 - 249.29 \ W + 23.75,$$
$$r^2 = 0.57, \ n = 27, \quad (4)$$

where W = wind stress (Pa).

Pelagic juveniles

There is little information on pelagic juvenile mortality, and because it is expected to be less that larval-stage

mortality on average, a rate of 6 %/d was used for all years (Lough, 2010).

Demersal juveniles

Considering the demersal stage or age-0 group juveniles, density-dependent mortality is considered to be important in many prerecruit fish populations. Cannibalism has been thought to be especially significant for cod because strong year classes seldom follow each other, most likely the result of age-1 fish preying on the age-0 group. Moreover, there is direct evidence of cod raised in captivity cannibalizing smaller individuals (Laurence et al., 1981; Folkvord et al., 1994). For the Georges Bank time series of cod year classes, age-1 recruits declined by as much as 50–70% from the previous year's age-1 recruits when stocks were high, indicating density dependence. Direct evidence of cannibalism was observed from gut contents of field-caught cod on Georges Bank, especially by fish longer than 100 cm (Link and Garrison, 2002).

Time-series analyses

Autocorrelation functions with consecutive time lags (12 years) using STATISTICA™ vers. 9.1 (StatSoft, Inc., Tulsa, OK) software did not indicate any significant
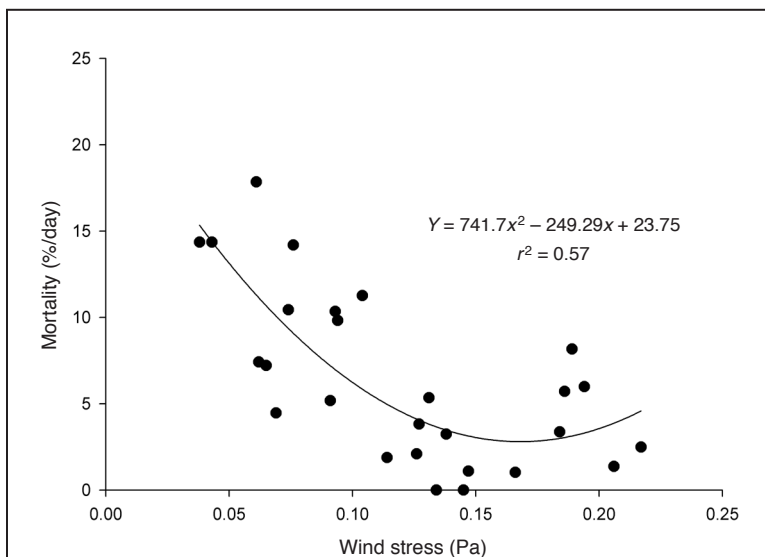

Figure 5

Haddock (*Melanogrammus aeglefinus*) larval cohort mortality (%/d) versus wind stress (Pa) on Georges Bank for 1998–1999. Cohort mortality represents the first 15 days of early life from hatching to about 6-mm standard length (SL). For the mortality-wind relationship, cohort mortality is assumed to be related to feeding, which is based on previous studies showing turbulence-increased contact between larvae and their prey, generated by the wind, is a dome-shaped relationship. Mortality rates declined with wind stress until about 0.15 Pa (9 m/s) and then increased after about 0.20 Pa (12m/s), consistent with theoretical underpinnings.

(P<0.05) annual time lags for either cod or haddock over the full time series. However, there was a negative correlation (r=−0.50, P=0.14, n=11) for cod when the VPA-derived recruitment at age 1 was lagged one year for the MARMAP years (1977–87) that had some large year classes. Nevertheless, for the short-time series compared in this study, we were interested in the year-to-year variability and did not want to remove autocorrelation if evident. Also, note that Mantzouni et al. (2010) found that there was no significant autocorrelation for the Georges Bank cod survival index (log[R/SSB]) for the years 1978–2004. Therefore, the first method used in this study was to assign a mortality rate of 3.0 %/d if the previous year had better than average recruitment; if less than average recruitment, a mortality rate of 2.5 %/d was assigned.

A second method for estimating density-dependent demersal juvenile mortality was by first predicting the abundance of the pelagic juvenile stage for each of the years where hatching abundance and larval mortality rates were available for years 1977–87 (Lough et al., 2006) and for 1995–99 (Mountain and Kane, 2010). The yearly demersal juvenile-stage mortality rate (Z) was calculated by the exponential loss between the beginning of the demersal stage and age-1 recruitment:

$$Z = -\ln(N_t/N_0)/t , \qquad (5)$$

where N_0 = the abundance of demersal juveniles;
N_t = the number of age-1 recruits; and
t = the duration of the demersal juvenile stage.

The percent mortality rate per day was calculated as

$$M \text{ (in \%/day)} = 100 (1-e^{-Z}). \qquad (6)$$

Regressions were made for all years and separately for MARMAP years (1977–87) and GLOBEC years (1995–99). The regressions were not highly significant (P>0.05), but all showed the same trend of juvenile mortality rates increasing with size of the previous year's recruits. The MARMAP years had the best correlation because there was higher recruitment than during the GLOBEC years when the stocks were depressed. The regression for the MARMAP years (Fig 6) was used to adjust the demersal juvenile cod mortality rates in the time series:

$$Y = 0.020 \text{ (cod age-1 } R) + 1.716, \\ r^2=0.18, n=10, \quad (7)$$

where Y = mortality (%/day); and
R = previous year's number of recruits (10^6).

The same cod regression (Eq. 7) was used for haddock because cod are considered to be their main predator (Tsou and Collie, 2001). Demersal juvenile mortality rates derived by this method are listed in Tables 1 and 2.

Results

The yearly initial egg abundance derived from the MARMAP and GLOBEC ichthyoplankton surveys were within the same order of magnitude as those derived from the VPA SSB fecundity relationships, but for the most part, the values did not track each other (Fig. 3). Estimates determined from the GLOBEC surveys for haddock had the best correspondence with the VPA estimates. Egg abundance for cod was higher than the VPA estimate in 9 of 14 years (Fig. 3A), whereas egg abundance determined for haddock was higher in only two years, 1980 and 1983 (Fig. 3B). There was no significant correlation between the survey egg abundance and age-1 recruits for either species; however, there was a significant correlation between age-1 recruits and both larval and pelagic juvenile abundance (Tables 3 and 4).

Correlations between recruitment of cod predicted with the various life-stage models and the cod VPA age-1 recruitment are shown in Table 5 and Figure 7. Starting from the spawning abundance time series, the best recruitment correlation was obtained from the GLOBEC years ($r=0.94$, $P<0.05$) with the demersal juvenile mortality rate based on regression of the previous year's recruitment, although both methods produced similar results. The recruitment values predicted from the GLOBEC years were nearly identical to those predicted by the VPA; however, there was more disparity between the two values during the MARMAP years (Fig. 7A). The recruitment values predicted by the VPA were consistently somewhat higher than those predicted from the spawning abundance model. The years 1983 and 1987 did not track the pattern of these values estimated by the VPA as did the other years. Note there was no egg abundance data for 1977 and 1978.

The hatching abundance models produced similar correlations with the recruitment values from the VPA as the spawning abundance models. The GLOBEC years had the best correlation ($r=0.93$, $P<0.05$) with nearly identical predictions (Fig. 7B). The MARMAP year's recruitment values were lower than VPA values, especially again for 1983 and 1987, and the two additional larval years, 1977 and 1978. The GLOBEC years provided a more reliable comparison than the MARMAP years since surveys were conducted monthly with more sampling stations than the bimonthly MARMAP surveys.

Starting from the seasonal egg abundance derived from the VPA SSB and using the derived proxies for estimating egg and larval mortality estimates to predict
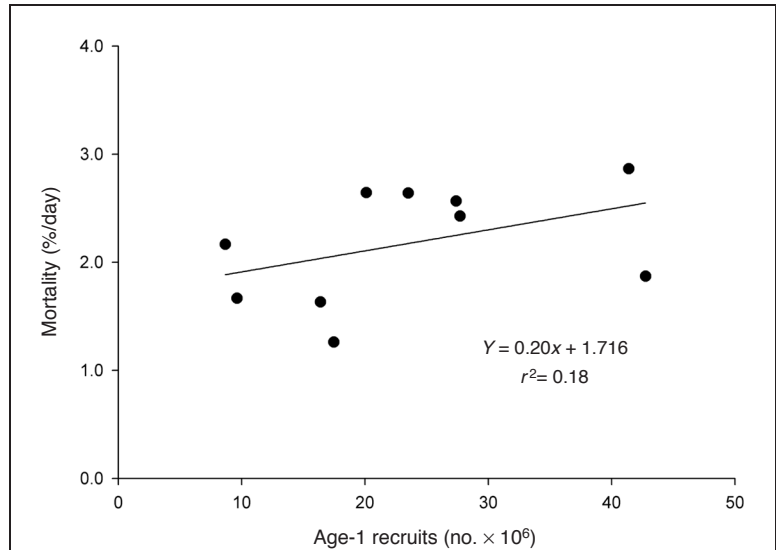

Figure 6

Demersal juvenile Atlantic cod (*Gadus morhua*) mortality rate versus the previous year's age-1 recruits on Georges Bank between 1977 and 1987. The yearly demersal juvenile mortality rates were estimated by the exponential loss between the beginning of the demersal stage and the age-1 recruits. The density-dependent regression was used to adjust the demersal juvenile cod mortality rates in the time series.

Table 3

Coefficients of correlation (r) among Atlantic cod (*Gadus morhua*) early life-stage abundances determined from ichthyoplankton surveys, and recruitment at age-1 based on virtual population analysis abundances for 1977–87, and 1995–99. Life-stage abundances were $\log_{10}$ transformed. Correlations where $P<0.05$ are starred.

Life stage	Eggs	Larvae	Pelagic juveniles	Recruits age-1
Eggs	1.00			
Larvae	0.23	1.00		
Pelagic juveniles	0.15	0.70*	1.00	
Recruits age-1	−0.20	0.57*	0.36	1.00

recruitment, we calculated the correlations with VPA recruitment values for the MARMAP and GLOBEC years, and for the full time series, 1977–2004 (Table 5). Egg mortality was based on the wind stress model. The demersal juvenile mortality rate based on regression of recruitment from the previous year was used because it generally produced a better correlation. The low correlation ($r=0.37$) for the full time series is evident in Figure 7C, poorer for the MARMAP years ($r=0.25$), and even poorer for the GLOBEC years ($r=0.05$).

Correlations between the various predictions of recruitment values with the haddock life-stage models and the haddock VPA age-1 recruitment values are

shown in Table 6 and Figure 8. Starting from the spawning abundance time series model predictions of recruitment, compared with the recruitment values predicted by the VPA, the highest correlation resulted from the GLOBEC years (r=0.83) using the demersal juvenile mortality rate based on regression of previous year's recruitment, although both methods produced similar results. The recruitment values predicted from both the GLOBEC and MARMAP years were nearly identical to the recruitment values predicted by the

VPA, except for the years 1979, 1983, 1987, and 1996, where the life-stage model recruitment values were lower than the VPA recruitment values (Fig. 8A). Note there was no egg abundance data for 1977 and 1978.

The hatching abundance models of predicted recruitment from the MARMAP years resulted in a high spurious correlation with the recruitment values predicted by the VPA (not shown) due to the large 1978 year class. After eliminating the 1978 recruitment values, the correlations were not significant, but better (r=0.45) with the demersal juvenile mortality rate based on regression of recruitment from the previous year (Fig. 8B). Correlation for the GLOBEC years was significant(r=0.89, P<0.05), but 1996 still was the most underestimated year compared to the recruitment estimated by the VPA. For both eggs and larvae, using the demersal juvenile rate based on regression of previous year's recruitment provided a slightly better correlation.

Starting from the seasonal egg abundance derived from the VPA SSB and using the variable egg and larval mortality proxies, we found very poor correlations for the full time series 1979–2004 (r=0.36) (Fig. 8C) even after the very large 2003 year class recruitment values were deleted. There was essentially no predicted recruitment correlation for the MARMAP years (r=−0.16) and GLOBEC years (r=−0.08). The two largest recruitment year classes in the time series, 1978 and 2003, were underestimated by a factor of 4−6. The

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Table 4

Coefficients of correlation (r) among haddock (*Melanogrammus aeglefinus*) early life-stage abundances determined from ichthyoplankton surveys and recruitment at age-1 based on virtual population analysis abundances for 1977–87 and 1995–99. Life-stage abundances were $\log_{10}$ transformed. Correlations where P<0.05 are starred.

Life stage	Eggs	Larvae	Pelagic juveniles	Recruits age-1
Eggs	1.00			
Larvae	0.18	1.00		
Pelagic juveniles	0.16	0.66*	1.00	
Recruits age-1	0.31	0.51*	0.47	1.00

Table 5

Correlations (r) between the various Atlantic cod (*Gadus morhua*) life-stage model predictions of recruitment (R) and the cod virtual population analysis (VPA) for age-1 recruitment (R). Base case models start from either annual spawning abundance of eggs or hatching abundance of larvae with life-stage mortality rates derived from Marine Resource Monitoring, Assessment, and Prediction (MARMAP) or U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys. The third base case is the abundance of eggs derived from the VPA spawning stock biomass (SSB). The annual survey egg and larval mortality rates used for each model can be found in Table 1. For egg-and larval-stage mortality, a function of wind stress is designated as "$f(W)$ Eq." and refers to the equation number in the text. Pelagic juvenile mortality used a constant 6%/d for all models. The demersal juvenile mortality rate was determined by two methods: 1) Demersal juvenile mortality rate of 2.5%/d was used if that year was below mean recruitment (R) in the full time series 1978–2004 from previous year's R^{-1}, or a mortality rate of 3.0%/d was used if that year was above mean R from previous year's recruitment (<> mean R^{-1}); 2) Demersal juvenile mortality used as a function of the previous year's R^{-1} from Equation 7 is designated as $f(R^{-1})$ Eq. 7. Correlations (r) P<0.05 are starred. Associated figures for some of the models are referred to in parentheses.

Time series	No. parameters	Egg mortality	Larval mortality	Demersal juvenile mortality	r	r^2	
MARMAP 1979-87	4	Table 1	Table 1	<> Mean R^{-1}	0.66*	0.44	
	4	Table 1	Table 1	$f(R^{-1})$ Eq. 7	0.76*	0.58	
GLOBEC 1995-99	4	Table 1	Table 1	<> Mean R^{-1}	0.94*	0.88	
	4	Table 1	Table 1	$f(R^{-1})$ Eq. 7	0.94*	0.88	(Fig. 7A)
MARMAP 1977-87	3		Table 1	<> Mean R^{-1}	0.73*	0.53	
	3		Table 1	$f(R^{-1})$ Eq. 7	0.70*	0.49	
GLOBEC 1995-99	3		Table 1	<> Mean R^{-1}	0.93*	0.86	
	3		Table 1	$f(R^{-1})$ Eq. 7	0.93*	0.86	(Fig. 7B)
MARMAP	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.25	0.06	
GLOBEC	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.05	0.002	
1978–2004	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.37	0.14	(Fig. 7C)

1978 recruitment from the VPA was 84×10^6 versus the predicted 15×10^6. There were no egg data available from the 1978 surveys, but the larval abundance was the highest of the time series $12,280 \times 10^{12}$ (see Table 2), which would indicate that the VPA SSB derived egg production was significantly underestimated, or there was an unusual survival of eggs. The 2003 VPA R was 789×10^6 versus the predicted 192×10^6. For this year class there was no egg or larval data available to compare with the VPA SSB derived egg production estimate.

With the use of these simple models with proxies, the results indicated that forecasting recruitment for individual years can best be made if there is good survey coverage of the larval stage as conducted for the GLOBEC years. Forecasts would be poorer if only survey coverage of the egg stage or seasonal egg abundance derived from the VPA SSB were used.

Discussion

Cod recruitment had not fully recovered in recent years from the low recruitment of the 1990s with only a moderate year class in 2003 and weak year classes in 2000, 2002, and 2004 (O'Brien et al.[1]; and see Lough et al., 2008, fig. 2). A relatively strong cod year class occurred in 1980 and more moderate year classes in 1985 and 1988. Older year classes (>age 5) were greatly reduced after the 1980s. Spawning stock biomass had only increased slightly since closure of the fishery in 1994. Environmental conditions may have been especially favorable for early survival of the 1985 and 2003 year classes according to the recruitment survival index (R/SSB).

High haddock year classes occurred in 1963, 1975, 1978, and 2003, generally from intermediate spawning stock biomasses (see Lough et al., 2008, fig. 3). After closure of the Georges Bank fishery in 1994, haddock SSB steadily recovered, and with older age classes entering the population, recruitment increased to moderate levels with the 1998 and 2000 year classes. The 2003 year class of haddock was the highest recorded recruitment since 1963 (Brodziak et al. [2]). The recruitment survival index generally followed the trend in recruitment (Friedland et al., 2008).

Both estimates of egg and larval production and SSB and recruitment based on survey data are inherently imprecise. Coefficients of variation (CV) for the egg and larval abundance estimates from the MARMAP surveys ranged between 20 and 60% (Lough et al., 2006). They are especially sensitive to the interval be-
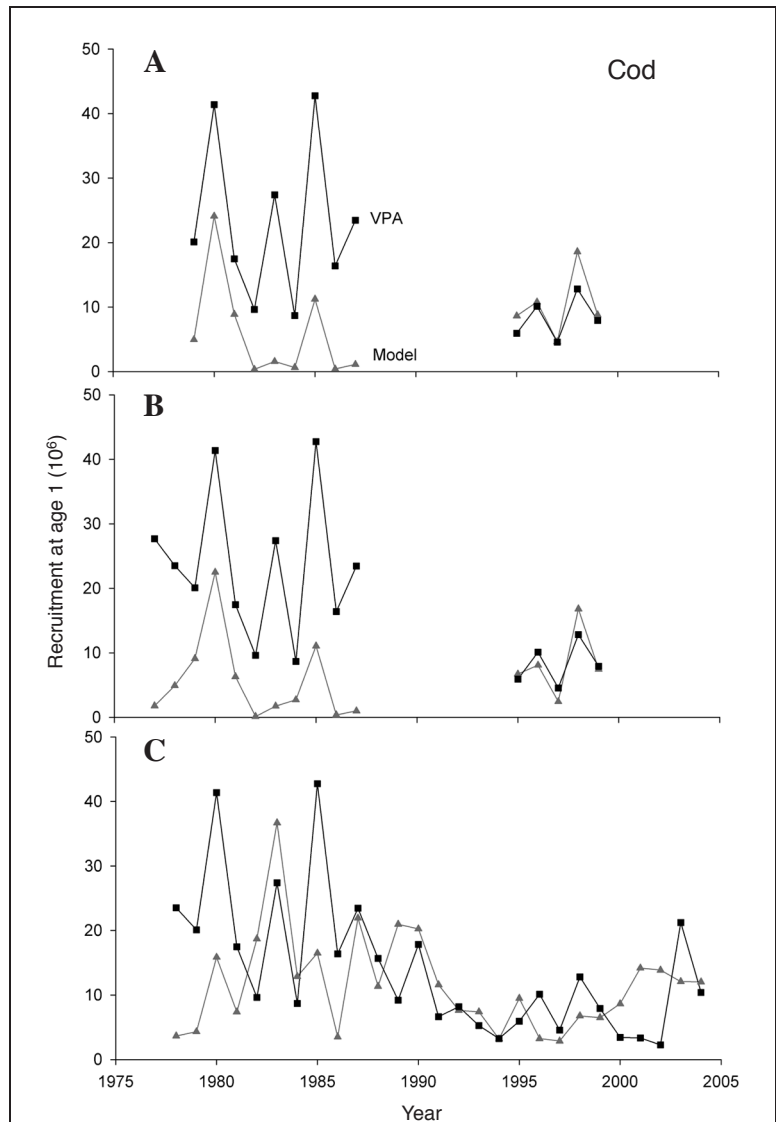

Figure 7

Yearly comparison of the various cod (*Gadus morhua*) life stage model predictions of recruitment (triangles) with the Georges Bank cod virtual population analysis (VPA) for age-1 recruitment (squares). Life-stage model predictions of recruitment start from the annual survey spawning abundance of eggs (**A**), the survey hatching abundance of larvae (**B**), and the abundance of eggs derived from the VPA spawning stock biomass method (**C**). Ichthyoplankton survey data were used from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) study (1977–87) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) study (1995–99); egg data were lost for the 1977–78 seasons.

tween surveys in relation to the timing and duration of the egg and larval stages, and the number of samples within a cruise (Pennington and Berrien, 1984; Hauser and Sissenwine, 1991). The monthly GLOBEC egg and larval surveys provided the best abundance assessments, whereas the bimonthly MARMAP surveys were less definitive. VPA-derived recruitment abundance

of age-1 fish in the time series was not provided with an estimate of their variability, but CVs of SSB and recruitment are likely to be similar to those derived from the ichthyoplankton surveys (*cf.* Brander, 2003). Georges Bank age-1 cod and haddock CVs based on the terminal year assessment are about 58% (O'Brien et al.[1]; Brodziak et al.[2]).

Hindcasting cod and haddock age-1 recruitment from the field egg and larval abundances was remarkably close to VPA estimates for the GLOBEC years, 1995–99, in part owing to the better sampling coverage, compared with that of the MARMAP years, 1977–87. The MARMAP field recruitment estimates for cod were less than the VPA recruitment, especially for the 1983 and 1987 seasons from eggs and 1977 and 1978 seasons from larvae. Under-sampling is a possible explanation because the MARMAP surveys were only conducted bimonthly. Episodic events, such as transport off the bank, could be missed with under-sampling. During April and May 1987, an unusual westward transport of shelf water may have carried a large portion of eggs and larvae from Georges Bank to Nantucket Shoals (Polacheck et al., 1992). Hindcasting recruitment of haddock for 1996 from both eggs and larvae did not follow the trend in the VPA recruitment, and Mountain et al. (2003) mentioned a possible loss off the bank owing to a strong March wind event. The 1983 and 1987 hindcasts also were lower than the VPA recruitment starting from

either eggs or larvae. However, the hindcasts starting with larvae were very close for the 1977 and 1978 seasons. Haddock recruitment in 1978 was high and both retention indices also were relatively high for eggs and larvae to remain on Georges Bank that year (Lough et al., 2006; Friedland et al., 2008).

Abundance at hatching (larvae) was a better predictor of age-1 recruitment than initial egg abundance. There is greater uncertainty in egg abundance and mortality because the early stage eggs are usually undersampled (late-stage eggs are more dispersed) and the identification of the early stages is based on the proportion of cod-to-haddock late-stage eggs. Also, initial egg abundances may have been underestimated owing to off-bank loss. Mountain et al.'s (2008) wind-transport modeled estimate of egg mortality suggested transport off the southern side of Georges Bank to be 12–14 %/d, leaving about 6–8 %/d on-bank mortality due to predation or morbidity.

In the present study there was no correlation between initial egg abundance and recruitment, but there was a significant positive relationship between initial larval abundance and recruitment for both cod and haddock. Initial abundance of pelagic juveniles was still positively correlated with recruitment, but was less significant. These correlations would suggest that recruitment was largely established by the larval stage in some years; however, Lough (2010) compared the 1986 and 1987 cod
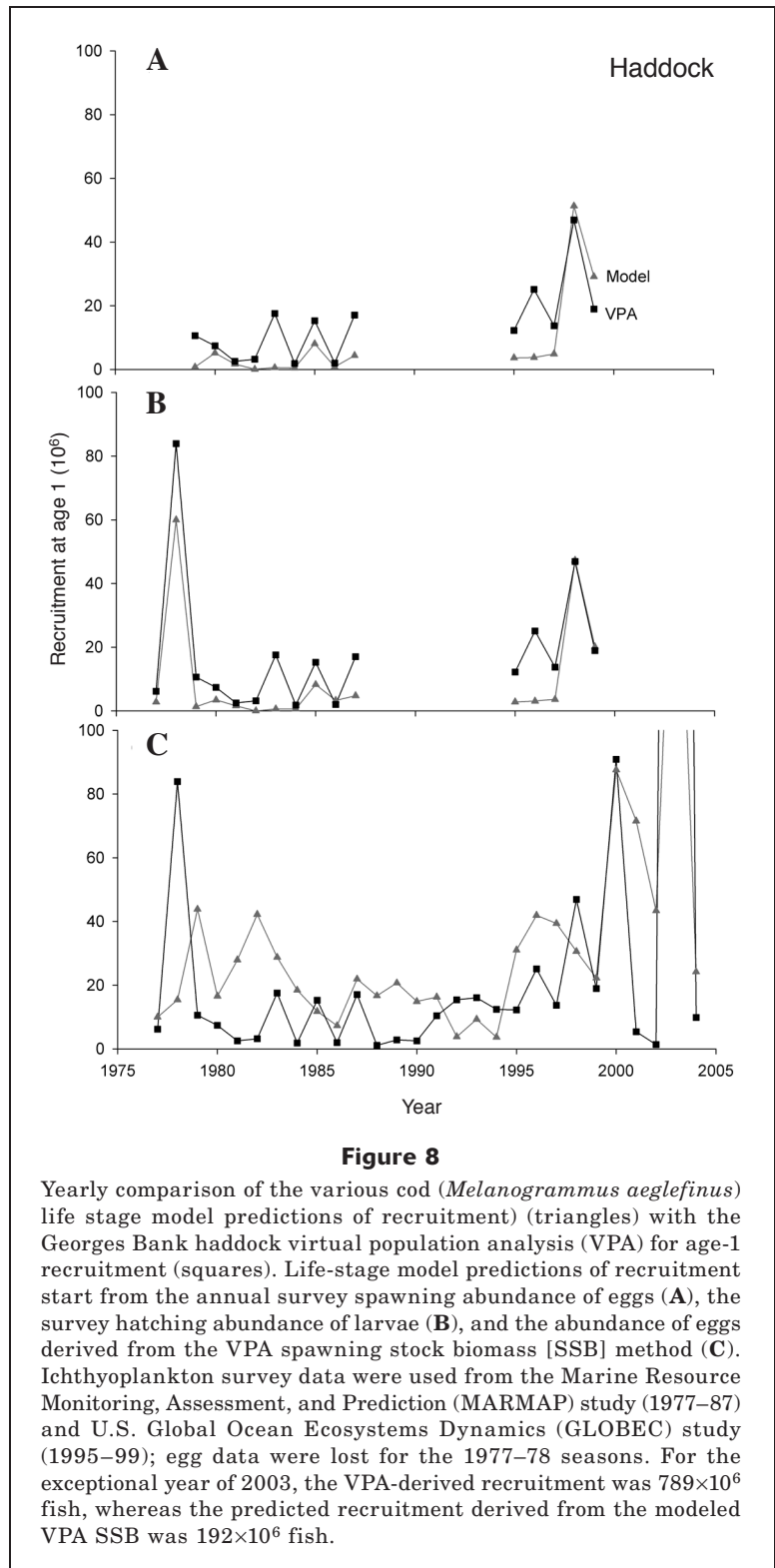
Table 6

Coefficients of correlation (*r*) between the various haddock (*Melanogrammus aeglefinus*) life stage model predictions of recruitment (R) and the cod virtual population analysis (VPA) for age-1 recruitment (R). Base case models start from either annual spawning abundance of eggs or hatching abundance of larvae using the stage mortality rates derived from Marine Resource Monitoring, Assessment, and Prediction (MARMAP) or U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys. The third base case is the abundance of eggs derived from the VPA spawning stock biomass (SSB). The annual survey egg and larval mortality rates used for each model can be found in Table 2. Egg- and larval-stage mortality used a function of wind stress is designated as "$f(W)$ Eq." and refers to the equation number in the text. Pelagic juvenile mortality used a constant 6%/d for all models. The demersal juvenile mortality rate was determined by two methods: 1) Demersal juvenile mortality rate of 2.5%/d was used if that year was below mean recruitment (R) in the full time series 1978–2004 from previous year's R^{-1}, or a mortality rate of 3.0%/d was used if that year was above mean R from previous year's R (<> mean R^{-1}); 2) Demersal juvenile mortality used as a function of the previous year's R^{-1} from Equation 7 is designated as $f(R^{-1})$ Eq. 7. Correlations (*r*) $P<0.05$ are starred. Associated figures for some of the models are referred to in parentheses.

Base case	Time series	No. parameters	Egg mortality	Larval mortality	Demersal juvenile mortality	*r*	r^2	
Spawning abundance	MARMAP 1979-87	4	Table 2	Table 2	<> Mean R^{-1}	0.38	0.13	
		4	Table 2	Table 2	$f(R^{-1})$ Eq. 7	0.49	0.24	
	GLOBEC 1995-99	4	Table 2	Table 2	<> Mean R^{-1}	0.72	0.52	
		4	Table 2	Table 2	$f(R^{-1})$ Eq. 7	0.83	0.69	(Fig. 8A)
Hatching abundance	MARMAP 1977-87	3		Table 2	<> Mean R^{-1}	0.07	0.05	
		3		Table 2	$f(R^{-1})$ Eq. 7	0.45	0.02	
	GLOBEC 1995-99	3		Table 2	<> Mean R^{-1}	0.82	0.67	
		3		Table 2	$f(R^{-1})$ Eq. 7	0.89*	0.79	(Fig. 8B)
Eggs VPA SSB	MARMAP	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	−0.16	0.03	
	GLOBEC	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	−0.08	0.01	
	1978-2004	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.36	0.13	(Fig. 8C)

early life stages, when the pelagic juveniles also were surveyed on Georges Bank and showed that events during the juvenile stage may still alter the course of recruitment.

Hindcasting age-1 recruitment from the VPA SSB-derived seasonal egg abundance with egg, larval, and juvenile mortality proxies resulted in the general trend in recruitment predicted by the VPA, but less so for individual years. A comparison of cod and haddock egg production from ichthyoplankton surveys and VPA SSB-derived data did not correspond closely for individual years. VPA SSB-derived egg production is generally considered to be an overestimate of potential reproductive output, particularly if the reduced age structure of a population includes a greater proportion of first- or second-time spawners that produce significantly fewer viable eggs and larvae (Murawski et al., 2001). As cod declined on Georges Bank, a greater percentage of females matured at an earlier age (O'Brien et al.[1]). Additional corrections were made in this study for the higher egg mortality estimates of the first- and second-time spawners. However, the few length-fecundity studies reported in the literature that were applied to the entire time series may still vary considerably from year to year. Moreover, there is no estimate of the difference between potential and realized fecundity. After spawning there is additional mortality before eggs are sampled by nets. Factors that may have influenced the spawning biomass estimates, including the differential mortality of cod and haddock egg stages, are discussed in Lough et al. (2008).

Larval mortality rates generally increase with increasing temperature, and within a narrow temperature range, they increase with decreasing growth rates (Morse, 1989; Buckley et al., 2010). The increasing seasonal growth rate in larval cod on Georges Bank in the spring was most related in generalized additive models (GAMs) to the increasing photoperiod and less so for the increasing temperature (Buckley et al., 2006). Growth rates were low in late-winter spring 1995, but comparatively higher in 1997–99, corresponding with the increasing trend in prey abundance, especially that of *Pseudocalanus* spp. (Buckley and Durbin, 2006), and decreasing larval mortality rates (Mountain et al., 2008). Larval cod and haddock mortality rates were high in 1995 and 1996 and low during 1997–99. The larger haddock recruited year class of 1998 had the lowest egg and larval mortality in the GLOBEC time series. A combination of favorable events appeared to have been associated with the 1998 haddock year class. The increased older

Figure 8

Yearly comparison of the various cod (*Melanogrammus aeglefinus*) life stage model predictions of recruitment) (triangles) with the Georges Bank haddock virtual population analysis (VPA) for age-1 recruitment (squares). Life-stage model predictions of recruitment start from the annual survey spawning abundance of eggs (**A**), the survey hatching abundance of larvae (**B**), and the abundance of eggs derived from the VPA spawning stock biomass [SSB] method (**C**). Ichthyoplankton survey data were used from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) study (1977–87) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) study (1995–99); egg data were lost for the 1977–78 seasons. For the exceptional year of 2003, the VPA-derived recruitment was 789×10^6 fish, whereas the predicted recruitment derived from the modeled VPA SSB was 192×10^6 fish.

spawners in the population benefited from good feeding conditions the previous fall leading to higher egg production and more viable eggs and larvae (Friedland et al., 2008). Likewise increased growth rates of larvae in the spring associated with higher prey abundance and

the increased retention on the bank were also considered to be contributing factors to lower egg and larval mortality that year.

Although faster growing larvae generally experience greater survival, their timing in the seasonal cycle appears to be critical. Buckley et al. (2010) have taken a more detailed and theoretical approach to the seasonal trends in mortality and growth of cod and haddock larvae from the GLOBEC years. The ratio of mortality to growth (M/G) was examined as an index of seasonal changes in cohort biomass that provides the greatest window of opportunity for survival. Variability in M/G can be related to photoperiod, temperature, and prey and predator abundance. Although the critical factors affecting M and G are tied to the fixed seasonal cycle, their deviations can have complex pathways. Predation is thought to be the most likely critical factor affecting M. Although the temperature range experienced by most larvae from a minimum in March to May is only a few degrees (4–7°C), there was an extremely large increase in M (0.03 to 0.15)—greater than can be accounted for by metabolic processes alone. Predators also increase with the seasonal cycle and their consumption rates increase with temperature and day length. However, there was no direct correlation between temperature and M; the two warmest years, 1999 and 1995, had low M and high M, respectively.

Planktivorous fish such as Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) could have a major impact on larvae and pelagic juveniles as they migrate northward in the spring and overlap with patches of larvae on the southern flank of Georges Bank (Garrison et al., 2000). Potentially high mortality can occur at the time of settlement during July–August where there is limited gravel-complex habitat on eastern Georges Bank to provide protection from predation (Lough, 2010). Demersal juvenile fish are preyed upon by many piscivorous fish such as spiny dogfish (*Squalus acanthias*), silver hake (*Merluccius bilinearis*), larger Atlantic cod, and longhorn sculpin (*Myoxocephalus octodecemspinosus*) (Link and Garrison, 2002). Tsou and Collie (2001) applied an eight-species multispecies virtual population analysis (MSVPA) on six important fish species on Georges Bank for 1978–92 to estimate predation mortalities of age-0 and age-1 fish. Silver hake accounted for more than 40% of predation on age-0 cod, and cannibalism and predation by spiny dogfish contributed another 30%. Cannibalism was high before 1983, increasing slightly with increasing stock biomass. Haddock also experienced high predation at age-0 with its main predator being cod. We reanalyzed a time series (1974–2002) of the Georges Bank piscivorous biomass data (silver hake, spiny dogfish, cod) published by Steele et al. (2007, fig. 5b); however, no significant correlations were found for cod and haddock age-1 recruits, pelagic juvenile abundance, or demersal juvenile mortality rates.

Cod and haddock appear to have different controls leading to recruitment. Populations in the low latitudes of Georges Bank respond differently than other stocks.

In this study cod recruitment appears to be set during the larval stage during years of low stock abundance, but during the juvenile stage when the previous year's recruits are high, indicating a density-dependent predation of age-1 fish preying on age-0 group juveniles. Young haddock, however, have different morphology, physiology, and behavior that allow them to grow rapidly and survive when prey are abundant, and therefore environmental effects, especially during the larval stage, can have the greatest control. It is still possible for haddock to be controlled during the juvenile stage when cod stocks are high. Friedland et al. (2008) examined the correlation between the Georges Bank haddock 1962–2004 survivor ratio ($\log_{10} R/SSB$) and the egg-larval retention, feeding conditions, juvenile size, and estimated hatch date, timing, and magnitude of spring and fall phytoplankton blooms and only found a significant relationship for the magnitude of the fall bloom and exceptional year classes during the 1998–2004 period, primarily due to the strength of the 1998, 2000, and 2003 year classes. They hypothesized that the increased production provided increased benthic prey for the maturing adults. Their analysis did not rule out the contribution of survivors during early life stages because the available data were limited and highly variable. Also, their March–April zooplankton prey data still show a positive trend with the survivor ratio and the correlations are only marginally nonsignificant.

Mountain and Kane (2010) showed that the survivorship of Georges Bank cod and haddock larvae changed between the 1980s and 1990s, coincident with change in the zooplankton from a dominant *Calanus fimarchicus* community to smaller species such as *Pseudocalanus* spp. The smaller species may have increased the growth and survival of haddock larvae in the 1990s because haddock prefer smaller prey for a longer duration, whereas the larger *Calanus* community in the 1980s may have favored cod, which are more selective pursuit predators.

Comparison with other gadoid populations

For Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment, it has been suggested that the relative dominance of activating or constraining factors is responsible for the transition from larvae to juveniles (Bailey et al., 2005). During periods of changing climate, such as observed for the North Pacific, recruitment control for pollock could shift between larvae and juveniles owing to the dominant mechanisms controlling survival (Ciannelli et al., 2005). A more recent study (Coyle et al., 2011) showed that the change from cold to warm periods was associated with a shift from large to small copepods and that the low survival of age-0 pollock was due to poor feeding and increased predation by large predators.

For Atlantic cod in the high latitude Barents Sea, higher recruitment at age-3 tended to be associated with warmer years when the spawning sites moved northward along the west coast of Norway (Sundby and Nakken, 2008). Svendsen et al. (2007) modeled the ef-

fects of Atlantic water inflow and primary production and found that the combination of inflow of larvae into the Barents Sea and high primary production accounted for 70% of the variability in cod recruitment. At high latitudes, environmental forcing is stronger, productive seasons are shorter, and there are fewer trophic links than at low latitudes (Kristiansen et al., 2011).

Recruitment of cod in the North Sea is known to be related negatively to temperature (O'Brien et al., 2000) and positively to plankton abundance. Beaugrand et al. (2003) developed a plankton index of larval cod survival that was correlated with age-1 recruits. An improved plankton index based on three indicators (*C. finmarchicus*, *Pseudocalanus* spp., and euphausiids) improved its applicability to other cod stocks (Beaugrand and Kirby, 2010). Daewel et al. (2011) explored the bottom-up trophic processes on larval cod in the North Sea using a larval fish individual based model and a three-dimensional ecosystem model to provide the prey field for three years. Their most important finding was that larval survival was most related to the timing and overlap of species-specific prey. Retention of larvae within the prey field and temperature also interacted to promote growth and survival. At this location colder years were more correlated with larval survival because the lower wind stress decreases dispersal and delays the onset of first-feeding larvae overlapping with their prey. On the other hand, top-down control was reported by Fauchald (2010), who found North Sea cod recruitment, together with abundance of *Calanus finmarchicus,* to be negatively correlated with the SSB of herring, a main competitor of cod, over a 44-year time series. Herring stock size appeared to affect cod recruitment over decadal periods, whereas *C. finmarchicus* appeared to explain the annual recruitment, although the principle prey of larval cod in the North Sea is *Pseudocalanus* spp. (Heath and Lough, 2007).

Shelf ecosystems near the southern limit of cod and haddock distributions have been hypothesized to be controlled by bottom-up processes where there is a positive correlation between predators and prey (Frank et al., 2007). On these southern banks, water temperature is warmer and species richness is higher than on more northern shelves. Variability in the spring bloom and copepod prey, believed to support greater growth and survival of larvae, has been related to the size of the haddock year class on Browns Bank (Platt et al., 2003; Head et al., 2005). Conversely, Friedland et al. (2008) did not find any correlation between the timing of the spring bloom on Georges Bank and the haddock survivor index. However, they did find that the magnitude of the fall bloom before the spawning year class of haddock on Georges Bank was correlated with subsequent recruitment—the hypothesis being that enhanced conditions for prespawning adults of increased benthic productivity, specifically their main prey, brittle stars, improved their egg quality and quantity and resulted in a higher survival of eggs and larvae.

Top-down control of recruitment has been implicated for the Scotian Shelf (Frank et al., 2005) and North Sea

(Fauchald, 2010) when the large predatory fish are removed and the ecosystem becomes dominated by pelagic fish. The demise of cod has allowed the resurgence of herring, which prey on the eggs and larvae of cod and other species. A similar trophic switching occurred on Georges Bank where groundfish (cod, haddock) shifted to small pelagic species (herring, mackerel) in the 1980s (Link et al., 2009). A Georges Bank food web study (Steele et al., 2007) showed the importance of bottom-up forcing for fish yields; however, the authors emphasized that both bottom-up and top-down processes operate at the same time and no single process determined the observed patterns for the three fish categories over four decades. Mueter et al. (2009) also found evidence for bottom-up control of fish yield for the Gulf of Maine and Georges Bank region since the 1980s. Mueter et al. (2009) compared different ecosystems (Bering Sea, Gulf of Alaska, Norwegian Sea, Barents Sea, Gulf of Maine, Georges Bank), and concluded that zooplankton can be controlled by both bottom-up and top-down processes leading to regime shifts caused by direct and indirect effects of fishing and climate.

Toward better forecasting

Cod and haddock recruitment depend on a unique combination of spawning stock attributes and environmental effects on the early life stages as exemplified in this study. Projected recruitment, based on annual egg production derived from VPA SSB-fecundity relationships or egg surveys, is less reliable than that derived from surveys of the larval stage. Intensive surveys of larvae and pelagic juveniles, however, may be sufficiently accurate for annual forecasts.

The challenge is to provide easily obtainable indices of environmental conditions that will link egg production with survival through the larval and juvenile stages. There are many factors contributing to mortality rates in most years and that are difficult to separate (e.g., advective loss, feeding and growth, predation), except in years of strong environmental forcing. We now can estimate an approximate loss rate of eggs transported off Georges Bank, given wind direction, strength, and duration, using recently developed circulation models, as well as possible upstream (Scotian Shelf) contributions of spawned eggs. Estimating the annual average larval mortality rate is more tenuous without survey abundance data.

The greatest life-stage mortality can occur during the demersal juvenile stage of almost nine months where a small change in mortality rate over this long duration can have a significant impact on survivors. A simple metric for the density-dependent effects of cod was used in this study. However, it is unlikely we will be able to fully assess predation mortality for the juveniles because it is so variable, and it is difficult to quantitatively survey the recently settled juveniles owing to escapement. Auster and Link (2009) and Steele et al. (2007) recommended that feeding guilds be considered for monitoring as a management resource because sig-

nificant changes in some of the guilds within the fish community were observed over the last four decades in the Gulf of Maine and Georges Bank region.

Conclusion

These simplistic life-stage recruitment models with known life-stage abundance and mortality rates, have predicted age-1 recruitment of Georges Bank cod and haddock to be close to recruitment derived by VPA methods. However, starting with annual egg abundance derived from the VPA SSB and using proxies for the egg, larval, pelagic juvenile, and demersal juvenile-stage mortality, the models could at best predict trends in recruitment for both species. Survey abundance estimates of the larvae used in these models can be used to forecast recruitment reasonably close with VPA estimates for some years. The larval period is the most quantifiable pelagic stage in terms of estimating abundance and mortality; it eliminates the need to survey the egg stage, and is closer in time to the demersal juvenile stage. Without such survey data it is difficult to assess the magnitude of mortality for these stages.

Acknowledgments

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