

# Seasonal trends in mortality and growth of cod and haddock larvae result in an optimal window for survival

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**ABSTRACT:** Changing climate and global depletion of fish stocks have added urgency to the century-old quest to understand the factors controlling fish production. The leading hypotheses advanced to explain the large (orders of magnitude) inter-annual variability in recruitment of young fish emphasize rapid growth and a match to prey production in the first weeks after hatching, although avoiding predators may be of equal or greater importance. Here we show for 2 important North Atlantic groundfish (Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*) that seasonal patterns in growth ( $G$ ) and mortality ( $M$ ) rates of young larvae combine in some years to yield a window of opportunity when  $M$  falls below  $G$  within days after hatching and cohort biomass increases rapidly possibly leading to high recruitment. Contrary to expectations, this window occurs early in the seasonal production cycle (February to March) when temperatures are near their annual minimum, fish larvae and their prey are relatively scarce, and  $G$  is low. In most cases examined, later, faster-growing cohorts appear to be rapidly lost to a suite of vertebrate and invertebrate predators whose abundance, metabolism, and consumption increase through the spring with increasing water temperature. In this seasonally varying environment, size on year day may be critical to minimizing  $M/G$ . Our data demonstrate the importance of rapid growth throughout the season cycle, but particularly early in the season when temperatures, potential prey, and predators are at seasonal low levels. These findings reinforce the importance of management practices protecting larger, older females that begin spawning earlier in the season and produce larger, more viable eggs and larvae.

**KEY WORDS:** Transition size · Vital rates · Photoperiod · Seasonal trends · Atlantic cod · Haddock

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## INTRODUCTION

Marine fishes invest a large proportion of their body mass in reproduction each year; most produce thousands to millions of small (~1 mm) eggs. The reproductive rate of females (gamete weight / body weight) frequently approaches 50% and can exceed 100% yr<sup>-1</sup> in some species (e.g. bay anchovy *Anchoa mitchilli*, Luo & Musick 1991). Many species are serial batch spawners (Murua & Saborido-Rey 2003), and a single female may produce numerous batches of eggs over a period of weeks to months (e.g. Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*), with egg production of a stock extending over even longer time

periods. Typically larger, older individuals initiate spawning earlier in the season and produce a larger number of egg batches over a longer period of time than do smaller, younger individuals (Parrish et al. 1986, Lambert 1990, Wright & Gibb 2005). In other species (total spawners), females release eggs over a period of hours and are spent for the year (e.g. Atlantic herring *Clupea harengus* and striped bass *Morone saxatilis*). Production of multiple egg batches over an extended period of time is sometimes described as a bet-hedging strategy to ensure that at least some of the offspring are released into a favorable environment. Alternatively, serial batch spawning may be an adaptation allowing the female to produce more eggs annu-

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ally than can be contained within the body at any one time.

Given the variability of the marine environment across time and space scales, selection on a variety of traits including spawning time and location is likely to vary among years and over longer time scales in response to changes in climate. Comparisons between the hatch-date distributions of the initial larval population, estimated from egg and larval surveys or an analysis of the adult spawning stock, and that of survivors collected later in life have revealed both positive (favoring late-hatched individuals) and negative (favoring early-hatched individuals) selection on hatch date depending upon the species, year class, or life stage examined. Positive selection on hatch date has been reported for sprat *Sprattus sprattus* (Baumann et al. 2006, Voss et al. 2006) and Atlantic cod (Hinrichsen et al. 2002) spawning in the Baltic Sea. These investigators used hydrodynamic models to recreate the environmental history of larvae and in the case of sprat attributed the positive selection to favorable feeding conditions for older larvae later in the year. Negative selection on hatch date was demonstrated for anadromous striped bass (Secor & Houde 1995, Limburg et al. 1999) in 2 different estuaries with prey abundance apparently playing a role in at least 1 system. In both the North Sea (Wright & Gibb 2005) and the Northwest Atlantic (Lapolla & Buckley 2005), negative selection on hatch date has been reported for haddock. In the North Sea, the disproportionately large contribution of age-2, first-time spawners to egg production late in the season and their presumed lower egg viability was implicated in the observed negative selection on hatch date. Overall, the timing and agents of selection on hatch date are largely unexplored, particularly the role of post-larval patterns of selection and integration of selective processes over the full life history.

Spawning is usually timed to a particular phase in the seasonal cycle. In temperate and boreal waters, strong seasonal forcing results in a dynamically changing environment that is somewhat predictable on average but highly variable annually. Climatic forcing affects both the mean and variance of the seasonal pattern on longer time scales. Protracted spawning is seen as an adaptation to ensure that at least some portion of the progeny survive in a dynamic and unpredictable environment. The primary environmental queues for the timing of spawning in most temperate and boreal marine fishes are photoperiod and secondarily temperature (Davie et al. 2007). The timing and intensity of the annual production cycle (phytoplankton-zooplankton) are affected by photoperiod, temperature, nutrients, and water column structure, among other factors. Many recruitment hypotheses emphasize a match between first-feeding larvae shortly after hatch and

the production of suitable prey, usually the various life stages of copepods (Cushing 1990), although a mismatch in space or time with potential predators may be equally important. In fact, there is likely a trade off between maximizing growth and minimizing mortality. Pope et al. (1994) described an approach to modeling growth and mortality in a seasonally perturbed size spectrum where survival was maximized by hatching at the right time and growing to stay within a wave of abundant smaller prey, while avoiding a 'co-evolving wave' of larger predators.

Since development in marine fishes is strongly linked to size, stage-specific survival is determined by the weight-specific growth rate ( $G$ ) and the instantaneous mortality rate ( $M$ ) according to the equation:

$$N_1/N_0 = (W_1/W_0)^{-M/G} \quad (1)$$

where  $N_0$  and  $N_1$  are the numbers alive at the beginning and end of a stage bounded by weights  $W_0$  and  $W_1$ , respectively. The ratio  $M/G$  is an index of the change in biomass of a cohort and has been referred to as the 'single process' (Cushing 1975) and the 'physiological mortality rate' (Beyer 1989). The instantaneous rate of change in biomass ( $B$ ) is  $G - M$ , such that

$$B_1 = B_0 \times e^{(G-M)t} \quad (2)$$

where  $t$  is the stage duration (i.e.  $\ln[W_1/W_0]/G$ ). Prior to first feeding, embryos and larvae rely on maternal stores for nutrition and  $M$  is always  $> G$ . Eventually  $M$  should decrease with increasing size, although any trends in  $M$  during the larval stage have been difficult to document. Typically  $G$  is stable or increases during the larval period and eventually decreases later in life. The 'transition size' at which  $M = G$  signals the point where the biomass of the cohort stabilizes. Houde (1997) compiled much of the available field data on  $M/G$  for fish larvae and emphasized its importance in determining the fate of a cohort or year class. For the most part, these data were annual means or represented a small window in time (a single cruise). To date, seasonal trends in  $M/G$  have received little attention, in part due to difficulty in serially sampling shelf species. Consequently, the best available data on seasonal trends in  $M/G$  are for more accessible estuarine species such as bay anchovy (Rilling & Houde 1999) and striped bass spawning in Chesapeake Bay (USA) tributaries where for the latter a U-shaped relationship was observed between water temperature and larval  $M/G$  with minimum values near 18°C (Rutherford & Houde 1995, Secor & Houde 1995).

Across species over a broad temperature range, a positive relationship is expected between growth and mortality rates largely because both increase with temperature (Pepin 1991, Houde & Zastrow 1993). Species inhabiting warm waters typically have higher  $M$  and  $G$

than species inhabiting colder waters. However, as pointed out by Ware (1975) and later confirmed experimentally with larvae reared at prey levels from starvation to excess (Buckley et al. 1993), within a species over a narrow range of temperatures,  $G$  and  $M$  are inversely related (normal to the overall  $G$ - $M$  regression among species), with rapidly growing cohorts enjoying a survival advantage over cohorts growing more slowly at similar temperatures. Nevertheless, even within a species,  $G$  and  $M$  are responsive to a number of factors including photoperiod, temperature, prey, and predator abundance that may vary spatially, seasonally and inter-annually, resulting in variability in  $M/G$ .

The US GLOBEC: Northwest Atlantic Georges Bank Program afforded the opportunity to study shelf populations of fish and zooplankton with a level of seasonal and spatial coverage over a 5 yr period not previously undertaken. Here we combined data on the seasonal and inter-annual variability in mortality rates of Atlantic cod and haddock obtained from 24 cruises (Mountain et al. 2003, 2008) with comparable data on the seasonal and ontogenetic trends in larval growth rates (Buckley & Durbin 2006, Buckley et al. 2006). We examined models relating  $M$  to hatch date, photoperiod, and water temperature. We then investigated seasonal and inter-annual trends in the stage-specific or 'physiological' mortality rate ( $M/G$ ) and cohort biomass and their role in recruitment variability and previously observed selection on birth date (Lapolla & Buckley 2005).

## MATERIALS AND METHODS

Our approach to modeling the seasonal trends in  $M/G$  and biomass of cohorts hatching between 1 February (Year day [DOY] 31) and 1 May (DOY 121) was first to fit suitable models to the mortality data from Mountain et al. (2008). Data on mortality and its seasonal trend for the period 1995 to 1999 were based on the GLOBEC Northwest Atlantic, Georges Bank time series with 6 cruises each year between January and June (Mountain et al. 2008). A standard grid of 40 stations was sampled on each survey with a vertically integrated bongo sampler (paired 61 cm diameter nets with 335  $\mu\text{m}$  mesh) and a 1  $\text{m}^2$  MOCNESS (335  $\mu\text{m}$  mesh). Additional samples were taken with the bongo between stations. Also, at about half of the stations, a 10  $\text{m}^2$  MOCNESS (3 mm mesh) sampled older fish larvae and other planktonic organisms. The full sampling plan and methodology can be found in Mountain et al. (2003, 2008). The density and total abundance of hatching larvae were estimated from the distribution of late stage eggs corrected for estimated egg mortal-

ity. A subset of larvae from each cruise was aged based on otolith daily-ring counts. Each larva was then assigned an age based on age-length relationships specific to each cruise. Following Mountain et al. (2008), larvae were grouped into 10 d cohorts (e.g. larvae hatched between DOY 31 and 40 inclusive were assigned to cohort 35). Early larval mortality was estimated from the difference between the estimated number of a 10 d cohort at hatching and the number when the same cohort was first sampled as larvae on a subsequent cruise assuming an exponential decrease, thus yielding a single estimate of early larval mortality for each cohort over approximately the first 15 d post hatch. In the few instances when the larval abundance estimate was greater than the estimated number of eggs hatched for a cohort, we set the mortality rate to 0.001 for our analyses. We did not use the more limited data of Mountain et al. (2008) on late larval mortality (about 15 to 60 d post hatch).

Mountain et al. (2008) provided plots of early larval mortality ( $M$ ) versus cohort hatch date (their Fig. 6) and of water temperature versus calendar day (their Fig. 8) but did not publish models relating  $M$  to environmental variables. They reported that the seasonal pattern in  $M$ , with minimum values in March, was similar to that of surface water temperature (0 to 30 m). Moreover, significant positive linear relationships were observed between temperature ( $T$ ) and  $M$  for both cod and haddock larvae. Also,  $M$  exhibited considerable variability among years, with annual mortality values (average of the 45 to 115 d cohorts for each year) higher in 1995 and 1996 and lower in 1998 and 1999 for both species. They saw no trend in  $M$  with larval age for either cod or haddock (their Fig. 10).

Given the grouping of years, the similarity in the seasonal trends in all years except 1997 and the inherently large errors associated with estimates of  $M$  in fish larvae, we chose to combine data for the years 1995, 1996, 1998, and 1999. We then fit the data to a fixed effect model (Demidenko 2004) treating the cluster (year)-specific coefficients as fixed and using ordinary regression analysis with a dummy variable (DV) coding for membership in a low- (1995, 1996) or high-mortality year (1998, 1999). This approach to mixed effects models is appropriate when the number of clusters is small and the number of observations per cluster is large. DV was assigned a value of 1 in 1995 and 1996, and 0 in 1998 and 1999 based on the findings of Mountain et al. (2008). This approach benefited from using all available data to establish the shape of the seasonal mortality curve, while the dummy variable served to displace the curve vertically on the  $y$ -axis, that is, to increase mortality by a constant for high mortality years. Because of the low number of observations for  $M$  in 1997 for haddock larvae and the physical conditions

that year, we considered the 1997 data separately. Mortality rates of cod larvae for 1997 stood out as an exception to the seasonal trend, possibly because of elevated off-bank transport due to wind-driven advection or to loss of eggs and larvae from the bank due to an entrainment feature associated with encroachment of a warm-core ring along the southern flank in February and March that year (Mountain et al. 2008). For cod, mortality rates in 1997 were intermediate between the low- and high- $M$  year groupings. Consequently, we did not model 1997 haddock larval mortality rates and used the mean mortality rate ( $0.07 \text{ d}^{-1}$ ) that year for cod (i.e. no seasonal trend).

We used an information theoretic approach, the Akaike Information Criterion (AIC), to evaluate linear models incorporating all combinations of temperature, cohort hatch day, photoperiod, and a dummy variable for membership in a low- or high-mortality year (Wagenmakers & Farrell 2004). Square and cubic terms were also included for the environmental variables. AIC is particularly helpful in determining the number of independent variables to include in the final model, providing an objective measure of the trade off between the loss in degrees of freedom and the increase in  $r^2$  with the addition of independent variables to the model.

We reasoned that cohort hatch day was most likely serving as a proxy for position in the annual seasonal cycle of physical and biotic variables, such as day length, temperature, and predator and food availability. Given this background, we then evaluated mortality models incorporating only day length, day length cubed, surface water temperature, and the dummy variable for low- and high-mortality years. We chose to use day length rather than cohort hatch day to make the models more generally applicable to cod and haddock stocks that occur over a wide range of latitudes. Also, day length usually explained just slightly more of the observed variability in  $M$  than did cohort hatch date. For the purpose of modeling seasonal changes in  $M/G$  and biomass, we used the models with the highest AIC score corrected for the number of observations ( $\text{AIC}_c$ ).

Data on larval growth rates and their seasonal trend for the period 1995 to 1999 were taken from Buckley et al. (2006). Growth rates were estimated for individual larvae based on their RNA/DNA content and water temperature using a laboratory calibration for a series of experiments with cod and haddock reared at different temperatures and prey levels (Caldarone et al. 2003, Caldarone 2005). Larval growth rates showed strong ontogenetic and seasonal trends in both Atlantic cod and haddock (Buckley et al. 2006). Growth rates were variable among years, with the lowest growth rates observed in 1995 and higher growth

rates in 1997, 1998, and 1999. Growth rates increased with larval size and year day between March and May. For modeling purposes, we used the years 1995 and 1999 as representative of low- and high-growth years, respectively, since these were the only years in our time series when larval sampling was completed on process cruises in March, April, and May; consequently, we have the highest confidence in the growth models for these years. Growth rates prior to 15 March were estimated using the photoperiod value for 15 March, assuming no effect of photoperiod between 1 February and 15 March. This assumption was based on 2 factors: (1) on Georges Bank, the greatest change in growth rate with photoperiod was seen in April, with a smaller change in the second half of March (Buckley et al. 2006), and (2) growth rate data from Mountain et al. (2008) showed no effect of either water temperature or year day on growth rate prior to March. Their growth estimates were based on size-at-age estimated from otolith daily-ring counts.

Separate size- and photoperiod-dependent growth (SPPDG) models of the form:

$$G = m_1 \times \text{PP} + m_2 \times \ln(\text{Pro}) + C \quad (3)$$

were fit to the  $G$  data on individual larvae for the years 1995 and 1999 for both species, where PP is the photoperiod, defined as the day length in hours between civil sunrise and civil sunset and Pro is the protein content in  $\mu\text{g}$  (Buckley et al. 2006, their Table 5),  $m_1$  and  $m_2$  are fitted regression coefficients, and  $C$  is a fitted constant.

To model changes in  $M/G$  and cohort  $B$ , the low and high  $M$  models were used with SPPDG models (Buckley et al. 2006) for the years 1995 (low  $G$ ) and 1999 (high  $G$ ) to yield 4 scenarios (low  $M$ -low  $G$ , low  $M$ -high  $G$ , high  $M$ -low  $G$ , and high  $M$ -high  $G$ ). For cod, a fifth scenario was considered with constant 1997 mortality and the high 1999 growth (constant  $M$ -high  $G$ ). An additional consideration for inclusion of the fifth scenario is that constant mortality is often assumed when seasonal data are not available.

$M/G$  was estimated for newly-hatched larvae using the estimated instantaneous growth rate for a larva with  $34 \mu\text{g}$  protein on a given day (photoperiod) and estimated mortality rate for a cohort starting out on that day. 'Transition size' was estimated by setting  $G = M$  (Eq. 3 = Eq. 4) and solving for protein content (see 'Results' for Eq. 4). Changes in  $B$  were modeled using an MS Excel spreadsheet starting with 1 million larvae and an initial size of  $34 \mu\text{g}$  protein or an initial  $B$  of  $34 \text{ g}$  protein for both cod and haddock on Day 0. For each consecutive day, the number alive, their size, and  $B$  were estimated based on day length and, in the case of  $G$ , larval protein content, by applying the modeled  $G$  (Eq. 3) and  $M$  (Eq. 4) to the previous day's estimates.

Modeled cohorts were started on the first day of each month between February and May.

The temperature values for each 10 d cohort were taken from Mountain et al. (2008). Briefly, they estimated the surface layer (0 to 30 m) temperature on the southern flank of the bank for each survey. Daily values within each year were determined by interpolating between the survey values. The temperature value assigned to each 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.

Linear models were fit by least squares, and AIC parameters were estimated using the SAS PROC REG (SAS v8.2). For AIC, selection was set to rsquare aic.

## RESULTS

### Mortality 1995–1999

In most years when water temperature (see Mountain et al. 2008, their Fig. 8) and  $M$  of larval cod (Fig. 1a) were plotted against year day, both followed a similar U-shaped trend with minimum values in March. Mortality of haddock larvae (Fig. 1b) did not show the descending leg of the U and had minimum values earlier in the year. Mortality rates of cod larvae for 1997 stood out as an exception to this trend. For cod in 4 of the 5 yr examined (1995, 1996, 1998, 1999), mortality rates were positively related to temperature ( $p \leq 0.05$ ). When data on cod were combined

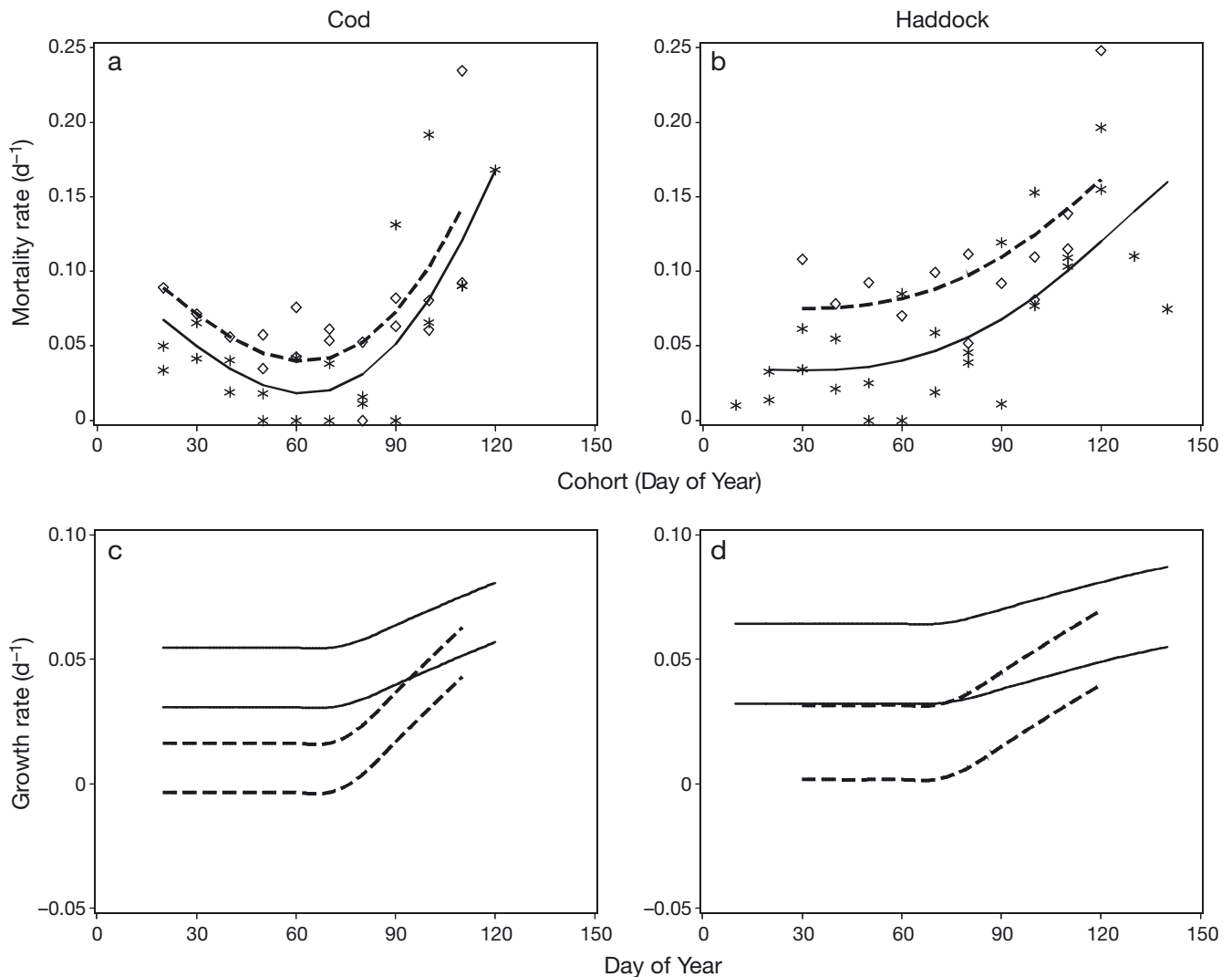


Fig. 1. *Gadus morhua* and *Melanogrammus aeglefinus*. Mortality ( $M$ ) and growth ( $G$ ) rates ( $d^{-1}$ ) of cod and haddock early larval cohorts on Georges Bank: (a) observed and modeled early mortality of cod in high- $M$  years (1995 and 1996;  $\diamond$ , ---) and low- $M$  years (1998 and 1999;  $*$ , —); (b) observed and modeled early mortality of haddock in high- $M$  years (1995 and 1996;  $\diamond$ , ---) and low- $M$  years (1998 and 1999;  $*$ , —); (c) modeled growth of 34  $\mu g$  (bottom curve in pair) and 200  $\mu g$  protein cod larva in 1995 (---) and 1999 (—); (d) modeled growth of 34 (bottom curve in pair) and 200  $\mu g$  protein haddock larva in 1995 (---) and 1999 (—)

for all 5 yr, the relationship between temperature and  $M$  was significant at  $p \leq 0.001$  (Tables 1 & 2). For haddock in 3 of the 4 yr examined (1996, 1998, 1999),  $M$  was significantly related to temperature ( $p \leq 0.05$ ). When data on haddock were combined for all years, the relationship between temperature and  $M$  was significant ( $p \leq 0.01$ ). During the 5 yr GLOBEC study period,  $M$  of young larvae differed among years. Mortality rates in both species were higher in 1995 and 1996 than in 1998 and 1999 (Mountain et al. 2008).

AIC indicated that for cod larvae the best mortality model was of the form:

$$M = m_1 \times PP + m_2 \times PP^3 + m_3 \times DV + C \quad (4)$$

where DV was a dummy variable assigned a value of 0 for the years 1998 and 1999 or 1 for 1995 and 1996,  $m_x$  are regression coefficients, and  $C$  is a fitted constant (Table 1). For haddock larvae, a model with 2 independent variables ( $PP^3$  and DV) was marginally better (lower adjusted AIC value) than Eq. (4). However, for modeling purposes we chose to use Eq. (4) for both species due to the higher  $r^2$  values and consistency between species. Interestingly, the best model for either species did not include a temperature term, although for haddock a model incorporating  $T$ ,  $PP^3$ , and DV was a very close second. Models incorporating

Table 1. *Gadus morhua* and *Melanogrammus aeglefinus*. Fit statistics and Akaike Information Criterion (AIC) evaluation of selected models of early larval mortality rate in cod and haddock for the years 1995, 1996, 1998, and 1999. Based on reported mortality rates, the dummy variable (DV) was set to 0 for 1998 and 1999 and to 1 for 1995 and 1996. Although all combinations of the independent variables temperature ( $T$ ), photoperiod (PP),  $PP^3$ , and DV were considered, only the 2 best models (lowest AIC) with 1, 2, and 3 dependent variables are presented.  $N = 38$  each for cod and haddock.  $K$  is the number of estimated parameters.  $AIC_c$  is the AIC value corrected for  $N$ .  $\Delta AIC$  is the difference from the best candidate model. Akaike weight ( $w_i$ ) approximates the model probability.

Model parameterization is presented in Table 2

Independent variables	$r^2$	AIC	K	$AIC_c$	$\Delta AIC$	Akaike weight ( $w_i$ )
<b>Cod</b>						
$T$	0.300	-235.7	2	-235	11	0.00
$PP^3$	0.280	-234.7	2	-234	12	0.00
PP, $PP^3$	0.485	-245.4	3	-245	1	0.36
$T$ , DV	0.400	-239.7	3	-239	7	0.02
PP, $PP^3$ , DV	0.534	-247.3	4	-246	0	0.69
$T$ , PP, $PP^3$	0.492	-244.0	4	-243	3	0.13
$T$ , PP, $PP^3$ , DV	0.534	-245.3	5	-243	3	0.18
<b>Haddock</b>						
$PP^3$	0.405	-231.7	2	-231	5	0.04
PP	0.392	-231.0	2	-231	6	0.03
$PP^3$ , DV	0.518	-237.5	3	-237	0	0.64
PP, DV	0.497	-236.0	3	-235	2	0.29
PP, $PP^3$ , DV	0.540	-237.3	4	-236	1	0.44
$T$ , $PP^3$ , DV	0.540	-237.3	4	-236	1	0.43
$T$ , PP, $PP^3$ , DV	0.544	-235.6	5	-234	3	0.13

Table 2. *Gadus morhua* and *Melanogrammus aeglefinus*. Parameterization for selected linear models of early larval mortality rate in cod and haddock for the years 1995, 1996, 1998, and 1999. The value of the dummy variable (DV) was set to 0 for 1998 and 1999 and to 1 in 1995 and 1996. Fit statistics are presented in Table 1. Slopes ( $m_x$ ) are numbered in order of the independent variables listed.  $C$  is a fitted constant

Independent variables	$m_1$	$m_2$	$m_3$	$C$
<b>Cod</b>				
$T$	0.0331			-0.1202
$PP^3$	0.0000446			-0.0319
PP, $PP^3$	-0.2114	0.000476		1.7434
$T$ , DV	0.0379	0.0334		-0.1612
PP, $PP^3$ , DV	-0.2265	0.000506	0.0228	1.8620
$T$ , PP, $PP^3$	-0.00987	-0.25807	0.000580	2.1724
<b>Haddock</b>				
$PP^3$	0.0000466			-0.02513
PP	0.0236			-0.22610
$PP^3$ , DV	0.0000456	0.03780		-0.03610
PP, DV	0.02285	0.03639		-0.2289
PP, $PP^3$ , DV	-0.05804	0.0008947	0.01361	0.39627
$T$ , $PP^3$ , DV	0.01246	0.00003175	0.04430	0.04003

just  $T$  and DV were significant but not among the best 2 parameter models for either species. For both cod and haddock, the best model included a DV term.

The photoperiod-dependent mortality (PPDM) model (Eq. 4) was used to estimate the seasonal trend in  $M$  (Fig. 1 a, b) for low- (DV = 0) and high-mortality years (DV = 1) for both cod and haddock larvae. Despite the inclusion of the  $PP^3$  term, the PPDM model for haddock reflects the low and flat trend in  $M$  early in the season for haddock.

### Growth rates 1995–1999

Modeled larval growth rates showed strong ontogenetic and seasonal trends in both Atlantic cod and haddock larvae. For cod, modeled growth was initially negative ( $-0.003 \text{ d}^{-1}$ ) for a newly hatched (34  $\mu\text{g}$  protein) larva in 1995, becoming positive by 18 March with increasing photoperiod (Fig. 1c). The 1999 SPPDG cod model yielded minimum growth estimates of  $0.03 \text{ d}^{-1}$ . Growth rates of haddock larvae followed similar trends (Fig. 1d), with growth rates for haddock generally higher than those for cod of the same size on a given year day.

The seasonal trends in mortality and growth combined to produce strong seasonal trends in the  $M/G$  ratio (Fig. 2a,b). Of the 5 scenarios examined for cod, only the low  $M$ -high  $G$  and constant  $M$ -high  $G$  scenarios yielded  $M/G$  ratios  $<1$  for first-feeding cod larvae ( $34 \mu\text{g}$  protein) and then only for a period centered on 1 March for the low  $M$ -high  $G$  scenario and later in the year for the constant  $M$ -high  $G$  scenario.  $M/G$  values for first-feeding haddock were lowest in February when they approached unity for the low  $M$ -high  $G$  scenario. Under all but the constant  $M$ -high  $G$  scenario, cohorts hatching in April and May lost biomass ( $M < G$ ). The February to March period corresponds with the time of the annual minimum in water temperature on Georges Bank. Slow growth (1995 model) shifted the minimum  $M/G$  toward the beginning of April in cod and even later for haddock first-feeding larvae. Even when coupled with low mortality, growth in 1995 was insufficient to yield  $M/G < 1$  in young larvae at any point in the seasonal cycle for either species. When coupled with high mortality, the fast 1999 growth was insufficient to yield  $M/G < 1$  in young larvae at any point in the seasonal cycle for either species, although values did fall below 1.4 in early March in cod and approached 2 in February for haddock.

Since larval growth rates are size dependent and  $M$  was independent of size as modeled following the observations of Mountain et al. (2008), estimated  $M/G$  ratios are also size dependent. For each scenario, it is possible to estimate the 'transition size' at which  $M = G$  on any day during the period of larval drift (Fig. 2c,d), although at times (e.g. the high  $M$ -low  $G$  scenario), the estimated 'transition size' corresponds to the juvenile stage. Larvae less than the transition size fall below the curve and have  $M/G > 1$ , while larvae above the curve have  $M/G < 1$ . In the few instances where  $M < G$  in first-feeding larvae, the estimated transition size is less than the size at hatch. Because growth was size dependent, the number of days during the period of larval drift when  $M/G < 1$  increases with larval size under each scenario. For cod, the transition size dropped below  $100 \mu\text{g}$  protein for a period of days centered on early March for both fast growth scenarios (low and high  $M$ ). With constant mortality, the transition size was  $>1000 \mu\text{g}$  of protein until late April. For haddock larvae, only low mortality coupled with fast growth yielded transition sizes  $<100 \mu\text{g}$  protein with the lowest values in February. The high  $M$ -low  $G$  scenario yielded transition sizes  $>1000 \mu\text{g}$  for both species.

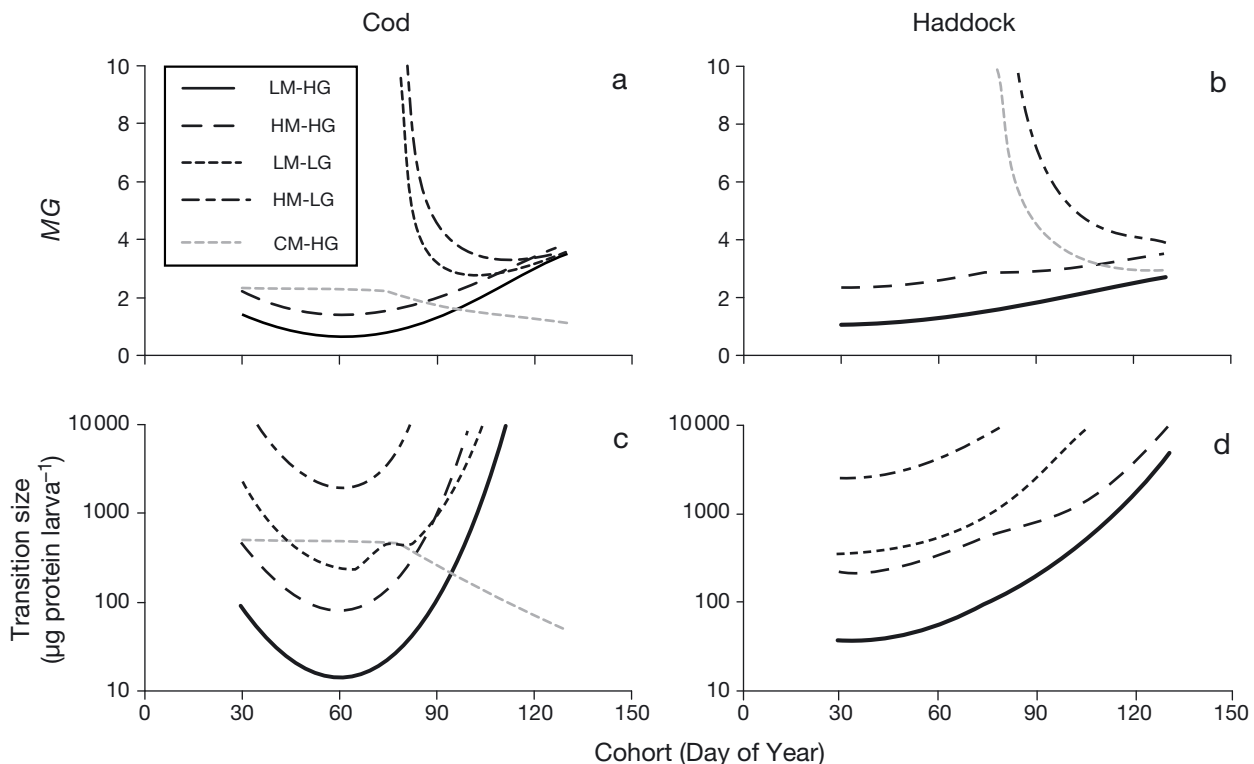


Fig. 2. *Gadus morhua* and *Melanogrammus aeglefinus*. Mortality ( $M$ )/growth ( $G$ ) ratios of newly hatched larvae ( $34 \mu\text{g}$  protein) and transition size for cod and haddock on Georges Bank: (a) estimated  $M/G$  of newly hatched cod larvae for the years with low  $M$  and high  $G$  (LM-HG), high  $M$  and high  $G$  (HM-HG), low  $M$  and low  $G$  (LM-LG), high  $M$  and low  $G$  (HM-LG), and constant  $M$  and high  $G$  (CM-HG); (b) estimated  $M/G$  of newly hatched haddock larvae; (c) transition size (protein content in  $\mu\text{g}$  larva<sup>-1</sup>) for cod at which  $M = G$ ; and (d) transition size for haddock larvae

These models were used to follow the fate of cohorts hatching on 1 February, 1 March, 1 April, and 1 May under each scenario (Fig. 3). Most cohorts rapidly lost biomass. For cod, only the February and March cohorts in the low  $M$ -high  $G$  scenario and the May cohort in the constant  $M$ -high  $G$  scenario increased in biomass during the first 30 d after hatching. With seasonally varying mortality, biomass of the February and March

cohorts were approximately equal after 30 d and higher than that of the April and May cohorts. With seasonally varying mortality, the May cohort yielded the lowest biomass at 30 d despite larvae having the highest growth rates. For the February and March cohorts of cod, the high  $M$ -high  $G$  scenario yielded higher biomass after 30 d than did the low  $M$ -low  $G$  scenario.

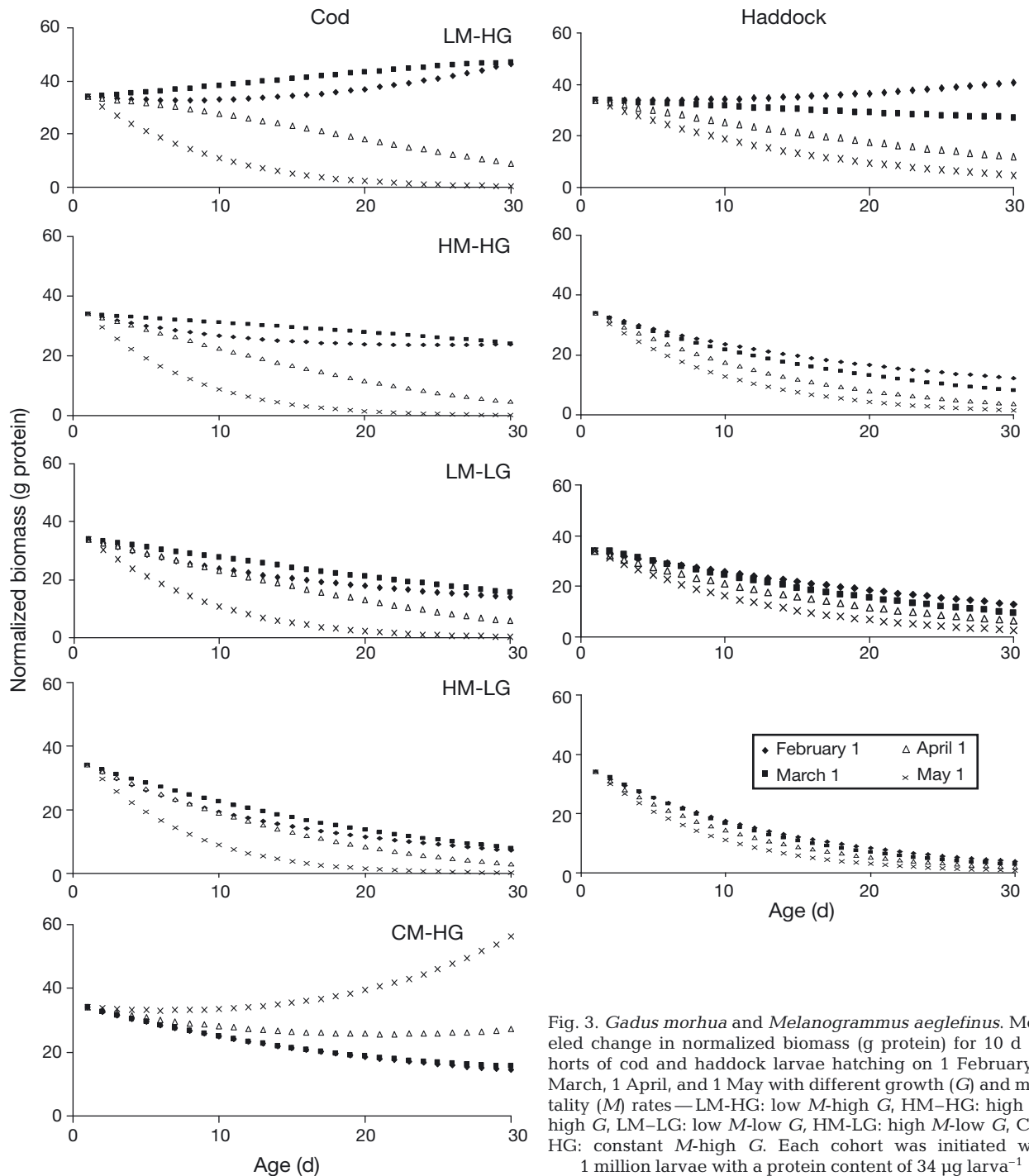


Fig. 3. *Gadus morhua* and *Melanogrammus aeglefinus*. Modeled change in normalized biomass (g protein) for 10 d cohorts of cod and haddock larvae hatching on 1 February, 1 March, 1 April, and 1 May with different growth ( $G$ ) and mortality ( $M$ ) rates—LM-HG: low  $M$ -high  $G$ , HM-HG: high  $M$ -high  $G$ , LM-LG: low  $M$ -low  $G$ , HM-LG: high  $M$ -low  $G$ , CM-HG: constant  $M$ -high  $G$ . Each cohort was initiated with 1 million larvae with a protein content of  $34 \mu\text{g larva}^{-1}$



For haddock, only the February cohort in the low  $M$ -high  $G$  scenario increased in biomass during the first 30 d after hatching. For all 4 scenarios, biomass of the February cohort was greatest, followed by the March cohort. In every scenario, the May cohort yielded the lowest biomass at 30 d, despite larvae having the highest growth rates. For all haddock cohorts, the low  $M$ -low  $G$  scenario yielded slightly higher biomass after 30 d than did the high  $M$ -high  $G$  scenario.

Our analysis suggests that a cohort of cod larvae hatching on 1 March, under the low  $M$ -high  $G$  scenario, would increase in biomass for just over 30 d (not shown). By about 35 d post hatch (dph) at a size of about 140  $\mu\text{g}$  protein, estimated  $M$  would exceed  $G$  and the biomass of the cohort would begin to decrease. This fate could be avoided either by faster growth or reduced mortality. For example, a cohort growing just 10% faster would increase in biomass until 40 dph at a size of 275  $\mu\text{g}$  protein. Eventually  $M$  should decrease with increasing size.

## DISCUSSION

Selective processes operate throughout the early life stages to determine the number and composition of the incoming year class. For haddock, 2 studies comparing the hatch dates of eggs to those of survivors collected some months later as demersal juveniles showed a pronounced shift in the distributions towards individuals hatching early in the year (Lapolla & Buckley 2005, Wright & Gibb 2005). In the case of North Sea haddock (Wright & Gibb 2005), the large contribution of age-2, first-time spawners to egg production later in the season (based on an analysis of commercially caught fish) was implicated as an agent for the negative selection on birth date, although other factors such as prey levels and seasonal trends in predator abundance and activity likely contributed. First-time spawners of a number of fish species have been shown to produce smaller and less viable eggs than larger repeat spawners (Trippel et al. 1997).

For both cod and haddock on Georges Bank, the strong ontogenetic and seasonal trends in growth and mortality of young larvae seen during the GLOBEC study period should result in selection on hatch date, although factors acting later in life could mitigate this early selection. For cod, in most years, this selection should favor larvae hatched in a window centered on early March when water temperatures are near their seasonal minimum. For haddock, seasonal trends in  $M$  and  $G$  favored larvae hatched in February and March. If our initial assumption of no effect of photoperiod on growth rate prior to 15 March is false and  $G$  was estimated by extending our SPPDG models into the early

portion of the year, then the survival window for both species would be centered on March. Since peak hatch of haddock is usually seen in April about 1 mo later than the minimum in early-larval mortality (Lough et al. 2006, Mountain et al. 2008), these trends would contribute to the observed negative selection on birth date, although other agents acting later on pelagic and demersal juveniles may contribute to the observed selection. Peak hatch of cod centered on early March in most years (Lough et al. 2006, Mountain et al. 2008) more closely matched the survival window for larvae, based on trends in  $M$  and  $G$ . Problems with reliably counting otolith daily rings in juvenile cod thus far have precluded direct estimation of the hatch dates of demersal juveniles on Georges Bank (L. Buckley unpubl.).

The trends in growth and early larval survival of cod and haddock on Georges Bank during the GLOBEC study period appear to rule out a large contribution of larvae hatched in May. With only 1 exception (cod 1997—constant  $M$ ), the May cohorts of both cod and haddock rapidly lost biomass, despite their rapid growth compared to earlier cohorts. The estimated hatch dates of haddock demersal juveniles on both Georges Bank and the North Sea appear to confirm this finding (Wright & Gibb 2005, Lapolla & Buckley 2005). Interestingly, when Pope et al.'s (1994) model of growth and mortality in a seasonally perturbed size spectrum was parameterized for North Sea cod, cohorts hatching after April rapidly lost biomass to an overtaking 'co-evolving wave' of larger predators. They concluded that 'the optimal 'fish' strategy is to start life in advance of the prey wave and thus to stay in front of the predator wave for as long as possible' (p. 47), thereby passing through the predator wave at the largest practical size. This appears to be the strategy adopted by cod and haddock on Georges Bank. Peak hatch of both cod and haddock is ahead of the peak abundance of their copepod prey in May (Buckley & Durbin 2006). Predators of larval cod and haddock reach maximum densities later in May and June when mackerel and herring move onto the Bank (Garrison et al. 2000) and developing invertebrate predators of a suitable size increase in abundance (Davis 1984).

The timing of critical growth and mortality may differ in early life. Even if the critical mortality that determines recruitment occurs during the late-larval and juvenile periods, large size on year day and rapid growth during the early larval period may be requisite to avoiding predation mortality at these later stages. The relative survival advantage of early cohorts may help to explain the correlation observed between the magnitude of the fall bloom on Georges Bank and recruitment of haddock spawned the following winter and spring (Friedland et al. 2008), since favorable feed-

ing conditions for the adults may result in earlier spawning in addition to higher egg quality and higher realized fecundity (Ware 1975, Kjesbu 1994).

Given the relatively large errors associated with estimating mortality in fish larvae and the variability in both  $M$  and  $G$ , it is likely that some larval cohorts would experience vital rates quite different than our smoothed model predictions. Where  $M$  was lower and  $G$  higher than predicted, this variability could lead to episodic recruitment of lucky cohorts. However, the relatively smooth hatch date distributions observed for haddock young of the year (YOY)-juveniles on Georges Bank during 1995 to 1999 (Lapolla & Buckley 2005) suggest that this was a rare event during the GLOBEC study period, with the possible exception of 1997, a season of apparent high wind loss off the Bank.

Indirect estimates of hatch-date distributions based on age-length relationships derived from larvae and pelagic juveniles and length of YOY juvenile cod and haddock surviving to the fall on Georges Bank show examples of positive, negative, and neutral selection on hatch date depending on the species and year, over the period 1978 to 1987 (Lough et al. 2006). However, these calculations assume that growth rates are similar among years and that differences in size in the fall are indicative of differences in age rather than growth rate or some combination of the 2 factors, which is more likely the case. While these indirect estimates of hatch dates are not as reliable as direct otolith daily ring counts, they do raise questions relative to changes in the Georges Bank ecosystem over time and the phenology of predator and prey species. In some recent years (GLOBEC), conditions appear to have favored larvae hatched early in the season, while in previous decades that had different temperature regimes and spawning stock structure, larval survival may have been more favorable for mid- and late seasonal spawning.

What factors account for the seasonal trends in  $M$  and  $G$  during the period of larval drift on Georges Bank? Growth and mortality of cod and haddock on Georges Bank reflect changes in water temperature, photoperiod, and the abundance of prey and predators. For both cod and haddock, position in the fixed solar cycle, as indexed by year day or photoperiod, explained a larger portion of the observed variability in both  $M$  and  $G$  than did observed water temperature, although in the case of  $M$ , a day length cubed term was needed to capture the observed U-shape with a minimum in March for cod. Moreover, addition of actual water temperature or residual water temperature (the difference between modeled and observed water temperature) to mortality and growth models that already incorporate year day or photoperiod resulted in little reduction in the residual mean square error. This

would seem to imply that the critical factors affecting  $M$  and  $G$  were more closely tied to the fixed seasonal cycle rather than the actual water temperature. While water temperature certainly affects both  $M$  and  $G$ , deviations from the seasonal temperature cycle on Georges Bank do not appear to affect  $G$  or  $M$  in a simple, predictable fashion that can be captured in our regression models. For example, 1999 and 1995 were the 2 warmest years during our study period, yet 1999 had low  $M$  and high  $G$ , while 1995 had high  $M$  and low  $G$ .  $G$  in 1999 was an exception in that residual  $G$  (observed  $G$  – predicted  $G$  based on larval size and photoperiod) was strongly correlated with residual temperature (observed  $T$  – predicted  $T$  based on year day). This would seem to imply that larval prey was abundant in 1999, allowing larvae to benefit from the warmer temperatures through faster growth.

The most likely environmental factors critically affecting  $G$  are prey availability, photoperiod, and water temperature (Buckley & Durbin 2006, Buckley et al. 2006). Photoperiod determines the portion of the day with sufficient light for feeding and consequently directly affects the daily ration. Photoperiod also affects growth through the endocrine system and bioenergetics (Jobling 1994). Water temperature directly affects digestion rates and other molecular and physiological processes. Both water temperature and photoperiod also indirectly affect larvae through effects on the prey production.

The most likely critical factor affecting  $M$  is predation, although water temperature and photoperiod likely play important roles. While starvation of early larvae may be important at specific times (e.g. March 1995), in most years direct starvation mortality of cod and haddock larvae appeared minimal (Buckley et al. 2006). Both vertebrate and invertebrate predators of cod and haddock larvae on Georges Bank follow a seasonal trend, most increasing in abundance as the water warms and the day lengthens (Davis 1984, Garrison et al. 2000). Moreover, increasing water temperature increases the metabolic rates of predators, resulting in increased consumption rates when sufficient prey is available. Photoperiod and light intensity also affect consumption rates of visual predators, predator avoidance, and escape reactions

The change in water temperature during the period of larval drift on Georges Bank is small. Greater than 90% of all cod and haddock larvae are collected at water temperatures between 4 and 7°C, although surface water may warm to ~9°C or higher in May, once the seasonal stratification develops. Our data suggest that in most years,  $M$  increases from ~0.03 at 4.5°C to ~0.15 at 6.5°C, a 5-fold increase over 2°C or a  $Q_{10} > 100$ . The extremely large increase in  $M$  with temperature implies that it is not due to a simple kinetic or physio-

logically based process, such as starvation or an increase in predator consumption due to temperature. If this were the case, the  $Q_{10}$  would be much lower, on the order of  $\sim 2$  to 5 (Jobling 1994). Increasing loss (transport) from the bank is even less likely to play a role in the seasonal increase in  $M$ , since, if anything, recirculation and retention increase during the spring (Lough et al. 2006). Rather, a dramatic increase in the abundance of predators would appear to be necessary to account for the large increase in  $M$  seen in most years as waters warm in the spring.

Most recruitment hypotheses (match-mismatch, member-vagrant, growth-mortality, and 'bigger is better') have some degree of validity but are most often insufficient to explain the variability seen in recruitment. All life stages are critical, and a number of factors must be optimized to produce a strong year class. Highly fecund species experience high mortality during the early life stages and high selection pressure to optimize reproductive parameters for maximum fitness. As a result of this optimization process for many stocks, no single stage, process, or event dominates recruitment success across many years (Lough et al. 2006)

The 'bigger is better' hypothesis holds that individuals that grow rapidly and are larger at age have a higher probability of avoiding predation and therefore are more likely to survive. By extension, factors that increase size at age should result in increased recruitment. The 'stage duration hypothesis,' sometimes referred to as the 'single process' (Cushing 1975, 1990), holds that individuals that grow rapidly through the highly vulnerable larval period are more likely to survive. By extension, factors that increase growth rate should result in increased recruitment. These hypotheses are variants of the same theme, since growth rate is one determinant of size at age, the other being size at hatch. Some factors, such as temperature and photoperiod, that have a strong effect on  $G$  also affect  $M$ . These factors would result in increased survival to metamorphosis or recruitment only when the net effect is a decrease in the  $M/G$  ratio.

Several lines of evidence suggest that size and timing in the seasonal cycle together have a strong effect on survival and recruitment in a seasonally varying environment (Pope et al. 1994, Nishimura et al. 2007). A strong year class of walleye pollock was characterized by early hatch and slower growth compared to 2 smaller year classes with later hatch dates but faster growth of survivors (Nishimura et al. 2007). In addition to hatch size and growth rate, spawning time and hatch date determine size on year day. In ecosystems with strong seasonal cycles in physical and biotic variables, hatch date and size on year day can be particularly important to recruitment success. The high sur-

vival of Georges Bank haddock hatched early in the season relative to those hatched later provides strong evidence of the importance of hatching time and by inference size on year day (Lapolla & Buckley 2005). In these instances, it was the slower-growing, early cohorts that were large on a given year day that enjoyed the survival advantage over later, faster-growing cohorts. However, the fate of the early cohorts in 1995, which experienced slow growth and rapid loss of biomass compared to corresponding cohorts in 1999, illustrate the importance of rapid growth to survival. Moreover, both theory and observations suggest that within a cohort, faster-growing individuals experience a survival advantage over slower-growing individuals (Meekan & Fortier 1996, Nielsen & Munk 2004).

Over the 5 yr examined, the rates of growth and mortality appeared to be inversely related during the larval stage. Two years had rapid growth and low mortality (1998 and 1999), while 2 years had slow growth and high mortality (1995 and 1996). Interestingly, the copepod prey available to larval cod and haddock was higher in 1997, 1998, and 1999 compared to 1995 and 1996 (Buckley & Durbin 2006). Growth in both species was high in 1997, while mortality of cod larvae was intermediate compared to the other years, with no apparent seasonal trend and relatively low values late in the season. Data for the few cohorts of haddock larvae available for 1997 also indicated that  $M$  was relatively low late in the season. These data suggest that later cohorts may have been favored in 1997 compared to the other years. However, while the 1997 haddock YOY-juveniles had the latest estimated mean hatch date (18 March), the May cohorts appeared to make only a small contribution to recruits that year (Lapolla & Buckley 2005). Recruitment was poor in 1997 for both cod and haddock, possibly because of off-bank transport of eggs and larvae due to winds and warm-core rings (Mountain et al. 2008).

Our data for cod and haddock early life stages on Georges Bank suggest that the fixed seasonal cycle explains a large portion of the observed variability in both growth and mortality rates. The strength of the seasonal cycle relative to inter-annual variability suggests that the seasonal cycle must be removed or otherwise accounted for when looking at inter-annual variability or longer-term trends. Year day or photoperiod explained a larger portion of the variability in  $M$  and  $G$  than did actual water temperature, demonstrating that the seasonal cycle is more than a temperature effect on vital rates and that other aspects of the seasonal cycle must also be considered. Size on year day is seldom considered but could strongly affect survival and recruitment of marine fishes. The strong performance of early cohorts highlights the importance of feeding condition for the spawning stock over the fall

and winter and the value of older repeat spawners that initiate spawning earlier in the seasonal cycle, produce larger eggs, and have higher relative fecundity compared to younger first-time spawners.

We are not saying that water temperature has no effect on *G* and *M* of larval fish or even that photoperiod has a larger direct effect than temperature. During the spring in temperate marine waters, a number of important physical and biotic variables change with the seasonal cycle. Both water temperature and photoperiod covary with these variables and can be considered proxies (Heath & Gallego 1997). Our data suggest that on Georges Bank photoperiod or year day explain a larger portion of the observed variability in *M* and *G* than does water temperature and are the better proxies.

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