Contribution to the Special Issue: ‘Commemorating 100 years since Hjort’s 1914 treatise on fluctuations in the great fisheries of northern Europe’

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Autumn bloom phenology and magnitude influence haddock recruitment on Georges Bank

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Received 2 July 2013; revised 1 April 2014; accepted 4 April 2014; advance access publication 3 June 2014.

The haddock (Melanogrammus aeglefinus) stock on Georges Bank in the Northwest Atlantic is characterized by extremely large recruitment events relative to spawning-stock biomass. Recent work has indicated that the dynamics of the preceding autumn bloom may have explanatory power to describe these events. In this paper, we examine the hypothesis that autumn phytoplankton dynamics affect the recruitment of haddock, examine the temporal and spatial characteristics of the autumn phytoplankton bloom on Georges Bank, and correlate individual sex-specific condition measurements of haddock made in spring to recruitment patterns. Autumn bloom characteristics vary considerably across Georges Bank with earlier-occurring and larger-integral blooms occurring on the northern flank. On average, autumn blooms start on day 273 (29 September) and persist ≏50 days. There was a significant negative correlation detected between bloom start date and recruitment and a significant positive correlation of bloom integral and recruitment. The survivor ratio loge(R/SSB) was positively and significantly correlated with individual condition of females in spring. The analysis of autumn bloom on Georges Bank provides a predictive index for recruitment strength of haddock and has utility for the assessment of this stock.

Keywords: bloom timing, haddock, parental effects, phenology, recruitment.

Introduction

Understanding the mechanisms responsible for the variation in year-class strength of harvested marine populations continues to be one of the primary challenges to fisheries oceanographers, as it was to Hjort in the early days of the science (Hjort, 1914; Houde, 1987; Cushing and Horwood, 1994). A comprehensive understanding of the causes of recruitment variation remains elusive, although it is a “characteristic feature” (Hjort, 1914) of many stocks. Similarly, the ability to make quantitative predictions of year-class strength is difficult because a variety of abiotic and biotic forcing mechanisms interact (Begg and Marteinsdottir, 2002; Govoni, 2005; Pitchford et al., 2005; Payne et al., 2009a). These factors influence stock productivity at all phases of ontogeny, providing a wealth of potential juncures or “bottlenecks” in the reproductive cycle where recruitment may be determined (Houde, 2008). It has been a challenge to identify where these recruitment bottlenecks occur, both because many recruitment factors are seemingly disparate and can co-vary with other biological and physical forcing variables (Myers, 1998; Miller et al., 2011). One approach to increasing the performance in the prediction of year-class strength is the identification of tractable short- and long-term ecosystem drivers that co-vary with the observed fluctuations of the stock (Fritz et al., 1990). Such an approach is appropriate given the long-term empirically derived and modelled time-series of both oceanographic conditions and fish abundance that now exists for some areas and fish stocks (Greenstreet and Hall, 1996; Klyashtorin, 1998; Fogarty et al., 2001; Hare and Able, 2007). Georges Bank, which is part of the US Northeast continental shelf ecosystem, is a well-studied area with respect to its resident fish populations and oceanographic conditions. The ecosystem is highly productive and supports commercial fisheries on a number of finfish
and shellfish species. Of the groundfish species, Georges Bank haddock (Melanogrammus aeglefinus) is a valued fisheries target, which exhibits marked variation in annual year-class strength (Overholtz et al., 1986; Fogarty et al., 2001). The recruitment dynamics of Georges Bank haddock are characterized by punctuated events of extremely large year-classes, which are critical for sustaining harvestable biomass. Although haddock recruitment is positively correlated with stock size, there is considerable variation in this relationship (Brodziak et al., 2001). The source of variation in Georges Bank haddock recruitment has been the subject of considerable debate, the importance of which has been underscored by the occurrence of yet another large year class in 2010 (Northeast Fisheries Science Center, 2012).

Haddock possess a complex life history and a number of potential recruitment bottlenecks has been identified and investigated. Recruitment strength of haddock has been associated with spring bloom productivity and its role in the survival of larval haddock (Platt et al., 2003; Munk, 2007; Buckley et al., 2010). These studies have addressed both spatial and temporal aspects of the spring bloom and the benefits that high levels of primary productivity have to increase larval feeding opportunities. Mountain and Kane (2009) have found an association of larval survivorship of haddock and zooplankton community structure, suggesting that shifts in size spectra of zooplankton may affect haddock recruitment success. That larval retention may be important to recruitment and determined by water circulation patterns on Georges Bank has been suggested as well (Smith and Morse, 1985; Myers and Drinkwater, 1989). It is clear that spawning haddock on Georges Bank are concentrated in an area that favours larval retention and presumably enhances their access to prey and preferred settlement habitats (Page et al., 1999; Lough et al., 2006; Lough and O’Brien, 2012). The timing of haddock spawning has also been investigated, suggesting that earlier hatched haddock have a greater likelihood of surviving to become juvenile recruits (Head et al., 2005; Lapolla and Buckley, 2005). Episodic recruitment events have also been associated with the autumn bloom on Georges Bank the year before spawning, suggesting that parental condition is important to the observed contrast in recruitment (Friedland et al., 2008). It is this later hypothesis we examine further, in the light of the additional recruitment events that have occurred since it was first suggested and mindful of the fact that the former hypotheses of recruitment control are with foundation. We believe all these factors work in concert to control Georges Bank haddock recruitment. The outstanding issue is which of these has the best predictive power to describe the recruitment dynamics of this population.

The parental condition hypothesis suggests that year-class strength in haddock is determined by prespawner provisioning (Friedland et al., 2008). Blooms of large magnitude, the intensity of which is defined as the integral, result in a flux of energy to the benthos. Since juvenile and adult haddock consume primary detritivores (Wigley and Theroux, 1965), large dimension blooms will provide energy to this prey source. We hypothesize that the trophic response of haddock to this input of energy is to shunt more energy into somatic growth and gonad formation during the months before spawning. The result being an increase in production, the production of more gametes (Rickman et al., 2000) or the production of gametes of greater quality (Martensdottir and Steinarsson, 1998; Donelson et al., 2008), or a combination. In this study, we evaluate the effects of autumn bloom phenology and spatial dynamics on haddock recruitment. We accomplish this by spatially stratifying the Georges Bank ecosystem, guided by a qualitative analysis of bloom patterns and on a regular grid. We describe the temporal productivity dynamics on Georges Bank and relate estimated bloom parameters to recruitment. Finally, we examine how recruitment correlates to indices of sex-specific individual condition, measured in spring.

Material and methods

To describe how the phenology and spatial extent of the autumn phytoplankton bloom on Georges Bank influences haddock recruitment, we first evaluated the relationship of recruitment and stock size for the entire time-series of these data (1960–2010). Two models, Cushing (1971) and Ricker (1954), were used to describe the relationship between stock size (S, 10,000 mt) and recruitment (number of age-1 recruits). The Cushing model is \( f(S) = \alpha S^g \), and the parameters are \( \alpha \), which controls the steepness of the curve, and \( g \), which controls the shape of the curve (the relationship is linear for \( g = 1 \)). The dome-shaped Ricker (1954) model is defined as \( f(S) = \alpha S^2 e^{-\beta S} \), and the model parameter \( \alpha \) is the slope of the function near stock size of zero and the spawning-stock size at maximum recruitment is \( 1/\beta \).

Year-specific survivor ratio for haddock for the period for which environmental (ocean colour) data were available was calculated as the age-1 abundance (number of individuals) divided by the spawning-stock biomass of the previous year (SSB, mt, Northeast Fisheries Science Center, 2008, 2012). These data included recruitment years 1998–2010 and were obtained from age-structured population assessment. Following Friedland et al. (2009), the recruitment data were log$_e$ transformed.

Chlorophyll \( a \) measurements were made on Georges Bank 1997–2009 using ocean–colour images taken by the Sea-viewing Wide Field of View (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) sensors. The spatial extent of the analysis was limited to the Georges Bank region and was evaluated at various spatial scales (Figure 1). Data from these two sensors provide an overlapping and nearly uninterrupted time-series of ocean colour images from 1997 to present. We used level-3 processed data and completed a quantitative analysis of the autumn phytoplankton bloom on Georges Bank. We conducted an analysis of variance of these data to describe the productivity of the bloom and the spatial extent of the bloom during the period of interest. The analysis was performed using the Cusanuck software package (Cusanuck, 2009).

Figure 1. Map of the Georges Bank area of the US Northeast continental shelf. The highlighted area is the Georges Bank ecoregion, which is subdivided into four subregions (1–4) qualitatively identified by examining the first principal component of the monthly chlorophyll \( a \) concentration, shown as contours within the ecoregion. Dashed lines mark a regular 0.5° sample grid that overlaps the ecoregion. The dotted line is the 100 m isobath.

\[ S_{g} = \frac{\text{number of age-1 recruits}}{\text{spawning-stock biomass of the previous year}} \]

\[ f(S) = \alpha S^g e^{-\beta S} \]

\[ g \] the slope of the function

\[ \alpha \] controls the steepness of the curve

\[ \gamma \] controls the shape of the curve
data, at 9 km and 8-d spatial and temporal resolution, respectively, from the Ocean Color website (oceancolor.gsfc.nasa.gov).

We examined autumn bloom patterns at three levels of spatial resolution: (i) the Georges Bank ecoregion; (ii) a set of four subregions of the ecoregion determined by temporal patterns in the chlorophyll concentration; and (iii) a regular spatial grid of 0.5° resolution (Figure 1). The ecoregion-level analysis reflects the division of the regional shelf sea into production units (Ecosystem Assessment Program, 2012). We divided the ecoregion into subregions based on monthly aggregated composite images of chlorophyll a concentration and identified areas that shared similar autumn bloom characteristics. Principal component analysis (PCA) was performed on these data and the first principal components of each time-series were plotted. We used kriging interpolation and identified regions on Georges Bank with similar values in the integral of their first principal components. These were qualitatively aggregated as unique subregions within the larger Georges Bank ecoregion. The 0.5° square grid included all grid locations that overlapped the ecoregion.

The chlorophyll a value at each 8-d period, for all levels of resolution, was calculated by taking the average of the constituent pixel elements. Regardless of the spatial resolution, we used linear interpolation to fill in any single missing values within the extent of the data and filled missing values at the beginning and end of the time-series with first and last observations, respectively, thus completing each chlorophyll a time-series. Because we were interested in the autumn bloom dynamics, we limited the analysis to the second half of the year and used the 23 8-d chlorophyll periods starting on day 185 and ending on day 361 (beginning of July to the end of December).

Characterization of autumn bloom dynamics was determined using a sequential averaging algorithm called STARS or "sequential t-test analysis of regime shifts" (Rodionov, 2004, 2006). The method has been used in previous analyses of Georges Bank autumn blooms (Friedland et al., 2008, 2009) and elsewhere (Friedland and Todd, 2012). The STARS algorithm is a filtering method that involves processing the time-series under investigation to identify statistically significant structural changes in the mean. The STARS algorithm requires that three parameters be specified. The first is the α-level for a change in the mean to be considered significant and this was set to α = 0.05. The second parameter is the length criteria, the number of time-steps (the duration of a time-step in this analysis is 8 d) to use when calculating the mean level of a new regime, this was set to 5. Finally, the Huber weight parameter was set to 3; this parameter determines the relative weighting of outliers in the calculation of the regime mean. We considered a bloom to have occurred if there was an 8-d period bracketed by a positive and negative structural change and a structural change (positive or negative) could not occur in the first or last two 8-d periods to be scored. Finally, a recognized bloom could not exceed nine 8-d periods (∼2.4 months). This scoring rule was based on preliminary analysis of Georges Bank autumn blooms. We found that the median bloom duration was six 8-d periods and the inter-quartile range of bloom duration was five to eight 8-d periods. Bloom lengths exceeding or equal to nine 8-d periods were determined to be basically different in their structure to the typical, discrete blooms observed during the autumn. We considered these longer, seasonal changes in chlorophyll concentration to have different ecological implications to the benthos, specifically, the reduced ability to export energy.

For each detected bloom, we extracted statistics to characterize bloom timing and dimension. Bloom start was defined as the day of initiation of the autumn bloom: The first day of the 8-d period that exhibited bloom conditions. Bloom average is the average chlorophyll concentration during the bloom period and bloom integral was the integral of the chlorophyll concentrations for the bloom period. In some years and locations, no distinct autumn bloom period was detected by the STARS algorithm. When no bloom was detected, the bloom average and integral were based on chlorophyll concentrations from a climatological bloom period and bloom start was treated as a missing value. The climatological bloom period was based on the mean start and end dates of observed blooms. The Pearson product–moment correlation was used to test the direction and magnitude of the correlation of survivor ratio to bloom start, average and integral.

As a further characterization of the effect of bloom dynamics on haddock, we evaluated the relationship of recruitment and condition. We determined the Pearson product–moment correlation of survivor ratio, log (R/SSB), and mean sex-specific condition of Georges Bank haddock collected in spring (April) to determine

<table>
<thead>
<tr>
<th>Year</th>
<th>SSB, mt</th>
<th>R, 10^3</th>
<th>R/SSB</th>
<th>log R/SSB</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>50 807</td>
<td>49 156</td>
<td>0.968</td>
<td>-0.014</td>
</tr>
<tr>
<td>1999</td>
<td>59 528</td>
<td>11 668</td>
<td>0.196</td>
<td>-0.708</td>
</tr>
<tr>
<td>2000</td>
<td>73 600</td>
<td>90 866</td>
<td>1.235</td>
<td>0.092</td>
</tr>
<tr>
<td>2001</td>
<td>87 872</td>
<td>5 551</td>
<td>0.063</td>
<td>-1.199</td>
</tr>
<tr>
<td>2002</td>
<td>100 258</td>
<td>2 870</td>
<td>0.029</td>
<td>-1.543</td>
</tr>
<tr>
<td>2003</td>
<td>119 310</td>
<td>412 375</td>
<td>3.456</td>
<td>0.539</td>
</tr>
<tr>
<td>2004</td>
<td>108 126</td>
<td>7 985</td>
<td>0.074</td>
<td>-1.132</td>
</tr>
<tr>
<td>2005</td>
<td>126 290</td>
<td>28 833</td>
<td>0.228</td>
<td>-0.641</td>
</tr>
<tr>
<td>2006</td>
<td>225 173</td>
<td>7 123</td>
<td>0.032</td>
<td>-1.500</td>
</tr>
<tr>
<td>2007</td>
<td>252 065</td>
<td>9 365</td>
<td>0.037</td>
<td>-1.430</td>
</tr>
<tr>
<td>2008</td>
<td>238 744</td>
<td>4 773</td>
<td>0.020</td>
<td>-1.699</td>
</tr>
<tr>
<td>2009</td>
<td>210 557</td>
<td>7 605</td>
<td>0.036</td>
<td>-1.442</td>
</tr>
<tr>
<td>2010</td>
<td>167 279</td>
<td>748 016</td>
<td>4.472</td>
<td>0.650</td>
</tr>
</tbody>
</table>

![Figure 2. Relationship of SSB (×10 000 mt) and recruitment (number of age-1 individuals) for the Georges Bank haddock stock with Cushing (solid line) and Ricker (dashed line) stock recruitment curves. Extraordinary year classes 1998, 2000, 2003, and 2010 (closed circles) are identified.](https://academic.oup.com/icesjms/article-abstract/71/8/2017/2804375/Downloaded-from-som southern missing user on 07 March 2018)
if a positive relationship existed. Condition is a morphological weight–length index of nutritional and health status of an individual (Richter et al., 2000). Individual condition was calculated using Fulton’s condition factor, $K = 10000 \times W/L^3$, where $W$ is the weight of an individual haddock (kg) and $L$ the fork length of an individual (mm) collected in spring (April) from 1992 to 2010 on Georges Bank (Froese, 2006). The number of haddock analysed for each year, for each sex, ranged from 41 to 449 individuals (the

![Figure 3](https://academic.oup.com/icesjms/article-abstract/71/8/2017/2804375/Downloadedfromhttps://academic.oup.com/icesjms/article-abstract/71/8/2017/2804375)

**Figure 3.** Time-series of three-period moving average smoothed of 8-d chlorophyll $a$ measurements (mg m$^{-3}$, points) and STARS algorithm fit to time-series (solid line) for the years 1997–2009 (a to m, respectively) and for data climatology (n) over autumn season (days 176–361).
Table 2. Table of the average autumn bloom dynamics for the entire Georges Bank region and for each of the designated subareas established in this study.

<table>
<thead>
<tr>
<th>Local</th>
<th>Observed blooms</th>
<th></th>
<th></th>
<th></th>
<th>Climatological bloom</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Start</td>
<td>End</td>
<td>Number</td>
<td>Duration</td>
<td>Start</td>
<td>End</td>
<td>Integral</td>
<td>Average</td>
</tr>
<tr>
<td>Georges Bank</td>
<td>272.3</td>
<td>312.3</td>
<td>11</td>
<td>6.0</td>
<td>273</td>
<td>313</td>
<td>9.58</td>
<td>1.62</td>
</tr>
<tr>
<td>Area 1</td>
<td>257.0</td>
<td>301.0</td>
<td>6</td>
<td>6.5</td>
<td>257</td>
<td>297</td>
<td>13.38</td>
<td>2.17</td>
</tr>
<tr>
<td>Area 2</td>
<td>274.1</td>
<td>314.1</td>
<td>7</td>
<td>6.0</td>
<td>273</td>
<td>313</td>
<td>7.45</td>
<td>1.29</td>
</tr>
<tr>
<td>Area 3</td>
<td>255.9</td>
<td>297.0</td>
<td>7</td>
<td>6.1</td>
<td>257</td>
<td>297</td>
<td>8.18</td>
<td>1.35</td>
</tr>
<tr>
<td>Area 4</td>
<td>277.6</td>
<td>319.9</td>
<td>7</td>
<td>6.3</td>
<td>281</td>
<td>321</td>
<td>9.28</td>
<td>1.51</td>
</tr>
</tbody>
</table>

The mean autumn bloom start day, end day, and duration is the average of the available years (Number) from (1997 to 2012) for which an autumn bloom was detected. The climatological period is the nearest 8-d start and end day to the observed bloom period. The integral and average for all years is the mean mg m⁻³ chlorophyll a for all autumn blooms.

Figure 4. Boxplots of bloom integral (mg m⁻³) binned by bloom start date for blooms detected in 0.5° grid locations for all years over Georges Bank.

Table 3. Correlation table of the log₁₀ of the number of age-1 recruits (× 10⁶) per SSB (mt) and the integral (mg m⁻³) and average (mg m⁻³ d⁻¹) of chlorophyll a and the start date of autumn blooms in the entire Georges Bank region and for each of the designated subareas established in this study from 1998 to 2009.

<table>
<thead>
<tr>
<th>Local</th>
<th>Magnitude</th>
<th>Average</th>
<th>Start date</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>p-value</td>
<td>R</td>
</tr>
<tr>
<td>Georges Bank</td>
<td>0.80</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Area 1</td>
<td>0.70</td>
<td>0.01</td>
<td>0.30</td>
</tr>
<tr>
<td>Area 2</td>
<td>0.21</td>
<td>0.49</td>
<td>0.23</td>
</tr>
<tr>
<td>Area 3</td>
<td>0.47</td>
<td>0.11</td>
<td>0.22</td>
</tr>
<tr>
<td>Area 4</td>
<td>0.00</td>
<td>0.99</td>
<td>-0.11</td>
</tr>
</tbody>
</table>

The p-value is the probability value of the regression. R is the Pearson product–moment correlation coefficient. Values in bold font indicate that the p-value of the correlation is less than 0.05.

Results

The first principal component of the monthly chlorophyll a time-series, evaluated on Georges Bank at 0.5 × 0.5° resolution, indicates that there is heterogeneity in chlorophyll concentration patterns within the region (Figure 1). Our spatial unit of analysis is indicated by the boundaries of the polygon in Figure 1, and these boundaries are generally coincident with the Georges Bank haddock stock management boundaries and the bathymetry of the Bank. We identify four areas on Georges Bank with distinct properties in the PCA analysis of monthly aggregated chlorophyll a dynamics.

Haddock recruitment has varied greatly in relation to SSB from 1960 to 2010 (Figure 2). The patterns of estimated SSB and recruitment revealed four large year classes that occurred between 1998 and 2010 (Figure 2, Table 1) including the first and last years of the period and the years 2000 and 2003. The fit of the Cushing model to the entire time-series, 1960 to 2010, indicated a generally positive relationship of SSB and recruitment (Figure 2), but this relationship was not statistically significant (p > 0.05). There is very little difference in the expected mean magnitude of recruitment and SSB among the two model forms analysed (Cushing and Ricker) and both of these model fit the data poorly (Cushing R² = 0.07 and Ricker R² = 0.06).

The STARS estimates of autumn chlorophyll a patterns of Georges Bank resulted in simplified patterns of the 8-d point estimates, from which the average, integral, and phenology could be determined (Figure 3). Variation in the timing of initiation of autumn bloom conditions was evident and ranged from days 233 to 305 (20 August to 31 October). The mean start day was 271 (27 September) and the bloom was terminated, on average, at day 313 (8 November). Autumn bloom phenology in 1999 and 2009 were the earliest recorded, occurring at day 233 (20 August). Autumn bloom initiation for 2002 was the second earliest, occurring at day 257 (13 September). The 3 years for which early start dates of autumn bloom were identified also had the longest bloom duration of seven to eight 8-d periods. Autumn bloom in 1997 lasted seven 8-d periods and was the only year which had estimated bloom duration longer than five 8-d periods. There were also absences in the detection of autumn bloom in 2004 or 2008 (Figure 3h and I). The mean value of chlorophyll a in the time-series was 1.62 mg/m² chlorophyll a across the entire Georges Bank region (Table 2). The largest mean peak chlorophyll a values occurred in 1997, 2001, and 2006 with integrals ranging from 1.74 to 1.94 mg/m² chlorophyll a. The mean value of chlorophyll a from autumn blooms in years 1999, 2002, and 2009 was similar to that of chlorophyll a for all autumn blooms examined, ranging from 1.52 to 1.69 mg/m² chlorophyll a. The integrated chlorophyll a for the identified bloom period was greatest for autumn blooms in 1997, 1999, 2002, and 2009, ranging from 13.50 to 14.77 mg/m² chlorophyll a. These were the only blooms that had integrals exceeding 10.0 mg/m² chlorophyll a.
Spatial differences exist in the phenology and magnitude of the chlorophyll a bloom dynamics of the four regions identified on Georges Bank (Table 2, Figure 3). Areas 1 and 3 are characterized by early bloom initiation relative to the other subregions and the whole of Georges Bank. Area 1 is unique in the large bloom average it exhibits, which results in an elevated chlorophyll a integral relative to the other subregions. Our ability to detect autumn blooms in each of the subregions was reduced \( (n = 6–7) \), relative to the detection of the entire region \( (n = 11) \). We detected a weak negative relationship of autumn bloom integral and day start (Figure 4).

The subregion and whole Georges Bank patterns in phenology and integral of observed autumn blooms are correlated with the observed recruitment time-series (Table 3). The integral and phenology of autumn bloom on Georges Bank is strongly and positively correlated with the annual recruitment index \( R \times 10^5/\text{SSB} \times 10^4 \) (Figure 5). Only Area 1 of Georges Bank has a significant correlation to the recruit index (Table 3): the integral of autumn bloom in this area is positively correlated with recruitment.

Gridded, kriged spatial analysis indicates that Area 1 is a centre of autumn bloom phenology and the characteristic dynamics that are correlated with recruitment success (Figure 6). Area 1 exhibits earlier dates of autumn bloom initiation and greater bloom average and integrals than other areas. Autumn bloom start dates increase (occur later) to the south and west on Georges Bank. Similarly, regions to the south and west of area 1 have a decrease in average and integral across most of the region except the area located farthest west.

We found a correlation between the mean annual condition of haddock on Georges Bank collected in April and survivor ratio of the year class using the Pearson product–moment correlation. The positive relationship was weak for both males \( (r = 0.424) \) and females \( (r = 0.517) \), but the relationship of female mean Fulton’s condition factor and the survivor ratio was statistically significant \( (p = 0.023) \). The notable year classes in 1998, 2000, 2003, and 2010 are not consistently associated with greater magnitudes of Fulton’s \( K \) values, ranking fifth, third, and tenth greatest, respectively, of the condition estimates \( (n = 19) \).

Discussion

Autumn phytoplankton blooms on Georges Bank are conspicuous features during some years and, like the observed pattern of haddock recruitment, are marked by interannual variability. The primary finding in this work is that autumn blooms occurring on the northern edge of Georges Bank are especially important to the recruitment dynamics of haddock and that recruitment is facilitated by blooms that occur early in autumn season and are of large magnitude. The proposed mechanism of trophic transfer to females is supported by the observed positive and significant correlation of recruitment and individual condition of females. Autumn blooms have been shown to be important to haddock recruitment success on Georges Bank and we provide a mechanism of this process, maternal provisioning, by analysing the spatial and temporal dimensions of autumn bloom, condition dynamics, and recruitment patterns.

Our assessment that some metrics of autumn bloom are important to haddock year-class strength has a spatial component. Large integral blooms, which are positivity correlated with year-class strength, are centred on the north-central and northern flank areas of Georges Bank. Bloom conditions in this area supply particulate organic carbon to the northeast peak region via clockwise gyre circulation observed on the Bank (Butman et al., 1982). The northeast peak of Georges Bank has been recognized as an area of aggregation for prespawning haddock (Lough et al., 2006; Lough and O’Brien, 2012). Early bloom conditions should allow more time for transport of surface production to benthic foodwebs (Townsend and Cammen, 1988) and long-lasting blooms may provide the most energy to benthic primary and secondary consumers which are a major prey item of haddock (Wigley and Theroux, 1965). The identification of subregions of Georges Bank, where productivity and oceanographic characteristics act at different stages of ontogeny to maximize recruitment of haddock, is a necessary step to understanding the environmental dynamics that influence population productivity.
Maternal somatic and reproductive condition in some fish species has been shown to be influenced by environmental conditions (Ventresca et al., 1995) and improvement in maternal condition has been shown to increase egg size and egg quality. These characteristics relate to larval viability (Donelson et al., 2008). For example, Marteinsdottir and Steinarrson (1998) reported that Atlantic cod (Gadus morhua) larval size at hatching increased with egg size, and that measures of larval viability, including feeding success, swimbladder development, and growth rates at age 15 days, were positively correlated with egg size and weight. Probst et al. (2006) examined parental effects on the life history traits of haddock. They found that maternal influences on larval standard length and yolk area were significant. Maternal provisioning may provide the proximal cause of larval survival because larger larvae are better at evading predators due to greater swimming speeds (Batty et al., 1993) and have increased sensory development (Fuiman, 1989). Our assessment that the survivor ratio is positively correlated with female condition is indicative that the trophic mechanism of increased productivity in autumn provisions spawning females, leading to increases in individual condition and reproductive output.

Large autumn blooms on Georges Bank are a cause for and a consequence of large-scale biological and oceanographic dynamics. Autumn phytoplankton blooms, like those in spring, are driven by oceanographic processes at large spatial and temporal scales (Song et al., 2010). The connectivity of bloom conditions to these dynamics implies that there may be alternative mechanisms to maternal provisioning and that these may be responsible for the observed strong haddock year-classes following an early and large-integral autumn bloom. One potential alternative hypothesis is that strong autumn bloom conditions promote survival of overwintering of the copepod Calanus finmarchicus (Meise-Munns et al. 1990), the eggs of which are major prey species of haddock larvae (Kane, 1984). Another alternative is that the large-scale oceanographic factors that promote productive autumn bloom conditions are responsible for spring conditions that promote retention of larvae on Georges Bank. Page et al. (1999) and Lough et al. (2006) have reported the importance of cod and haddock larvae being retained on Georges Bank during spring such that they will settle in optimal habitats.

Before the strong year class in 2000, the haddock stock in Georges Bank was characterized by low SSB and generally poor year classes relative to stock size (Overholtz et al., 1986). Episodic recruitment events, such as those most recently observed in 2010, are critical for fishery sustainability and the two strong year classes observed in 2000 and 2003 provided the biomass to build the stock to its current level, above the SSB at MSY (Northeast Fisheries Science Center, 2008, 2012). We find that the integral and timing of autumn phytoplankton bloom on Georges Bank is significantly correlated with haddock recruitment. The potential effects of maternal provisioning have not been widely studied for wild fish stocks and we suggest that such a mechanism may be important to the recruitment dynamics of other spring-spawning fish.

The results of this work indicate that autumn bloom timing and integral is a potentially powerful predictive tool for forecasting haddock recruitment. Our results further support the hypothesis that maternal provisioning is the mechanism that leads, in part, to strong year classes of haddock on Georges Bank. This conclusion is consistent with an expanded interpretation of Cushing’s (1990) match–mismatch hypothesis: that fitness is maximized when predator requirements maximally overlap, in time and space, prey

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**Figure 6.** Contour maps of autumn bloom mean start day of the year (a), mean bloom average (b), and mean bloom integral (c) based on 0.5° grid data over the Georges Bank ecoregion for the period 1997–2011. Units: average (mg m\(^{-3}\)) and integral (mg m\(^{-3}\) 8-d).
availability during some critical life stage (Durant et al., 2007). Historically, this critical life-stage has been recognized as the larval stage; however, we show that a potential bottleneck for the Georges Bank Haddock may occur earlier in ontogeny.

Acknowledgements
This work was supported by funding from the National Marine Fisheries Service Fisheries (NMFS) Fisheries and the Environment (FATE) program. We particularly thank M.J. Fogarty for his thoughtful review of an early draft of the manuscript.

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![Figure 7. Mean male and female Fulton’s condition factor (error bars are 1 s.d.) for spring (April) from 1992 to 2010. The calculation of the mean and standard deviation of each annual sex-specific condition factor was based on n = 43–420 measurements for males and n = 41–441 measurements for females.](https://academic.oup.com/icesjms/article-abstract/71/8/2017/2804375)
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Handling editor: Manuel Hidalgo