Variation in ocean colour may help predict cod and haddock recruitment

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ABSTRACT: Characteristics of the spring and fall phytoplankton blooms in spawning areas on the Scotian Shelf, Canada, were estimated from remote sensing data. These blooms, along with anomalies in the North Atlantic Oscillation, were used to explain variation in the recruitment of 4 populations of cod and haddock. We tested the effects of the timing of the bloom using the chlorophyll *a* (chl *a*) signal, the maximum amount of chl *a*, the timing of the diatom bloom, and the maximum relative dominance of diatoms on the recruitment (to Age 1) of cod and haddock on the Scotian Shelf. Models were run separately for the effects of the spring and fall blooms. Only 3 of 10 models tested (0-lag) explained significant (80 to 92 %) variation in recruitment. However, the performance of these models was not consistent across populations or species, suggesting that generalities about how spring and fall phytoplankton blooms affect recruitment cannot yet be made. The differences among models suggest that fish larvae are probably adapted locally to food production and thus indirectly to the characteristics of the phytoplankton bloom, which in turn are influenced by regional (meso-scale) oceanographic conditions.

KEY WORDS: Recruitment · Phytoplankton bloom · Diatom bloom · Ocean satellite imagery · NAO · Cod · *Gadus morhua* · Haddock · *Melanogrammus aeglefinus*

INTRODUCTION

Recruitment to fish populations is notoriously variable among years, and explaining this variability has been a long-standing goal of fisheries science (Cushing 1982, Bakun 1996, Govoni 2005). Mortality is often high in the first days, weeks and months of life (Peterson & Wroblewski 1984, McGurk 1986, Bailey & Houde 1989, Lorenzen 1996), and it is likely that a combination of factors affects the survival of early life-stages. Particularly good or poor recruitment could be caused by a mismatch between the timing of spawning and food abundance (Cushing 1969, 1982, 1990), the degree to which larvae are retained within areas of high food production (Iles & Sinclair 1982, Sinclair & Iles 1988), and losses due to predation (Dingsør et al. 2007, Kempf et al. 2009). If unfavourable, any of these factors could cause low re-

cruitment, but all (and probably several others) may have to be favourable for larval growth and survival to produce an exceptional year-class. Much of the early work was on the first feeding of larval fish, but survival of juveniles and maternal effects can also have strong effects on recruitment (Houde 2008, Friedland et al. 2008). Recruitment variability results from a complex array of physical processes and trophic dynamics operating over many temporal and spatial scales (Houde 2008). Many attempts have been made to explain larval survival using environmental covariates, but often only for a single species and over a restricted spatial-temporal domain (e.g. Campana et al. 1989, Friedland et al. 2008, but see Mertz & Myers 1994 and Fogarty et al. 2001). Monitoring of environmental effects needs to be at appropriate spatial and temporal scales (seasonal dynamics over 1000s of km^2 and multiple years) to be able to make accurate pre-

dictions of high or low recruitment (Stige et al. 2006, Svendsen et al. 2007, Smart et al. 2012).

The first few days, weeks and months may be a critical period for survival (Hjort 1914), but larval surveys are intermittent, so studies of interannual variability in recruitment must estimate recruitment from a stock assessment model, which then includes the early part of the juvenile stage. In stock assessment, recruitment is often defined as the number of 1- or 2-year olds in a given year and is usually calculated from a model fit to the commercial catch-at-age, and from a survey while accounting for the size of fish selected by the commercial and survey gear. Recruitment has been related to spawning stock biomass (SSB) for many stocks around the world (Myers et al. 1995). These stock–recruitment relationships, however, are highly variable and recruitment can also be related to environmental conditions, such as bottom (Myers et al. 1997) and sea surface temperature (O'Brien et al. 2000, Kempf et al. 2009), salinity (Myers et al. 1993), the Pacific Decadal Oscillation (PDO; Clark & Hare 2002), and the North Atlantic Oscillation (NAO; Brander & Mohn 2004, Stige et al. 2006). Beaugrand et al. (2003) found that sea surface temperature was correlated with a measure of plankton abundance derived from the continuous plankton recorder and with cod recruitment in the North Sea. Building a predictive model of recruitment which links oceanographic conditions to phytoplankton and zooplankton production and to larval survival and year-class strength could greatly improve stock projections and contribute to the long-term sustainable management of fish stocks. For example, the recruitment of Pacific halibut is so closely related to the PDO that recruitment is projected as a direct function of the PDO index (Clark & Hare 2002, 2007).

The Cushing-Hjort match-mismatch hypothesis states that larval survival is highest when the timing of reproduction is well matched with the timing of peak food production (Hjort 1914, Cushing 1969, 1982, 1990). Larval cod and haddock feed on zooplankton (primarily *Pseudocalanus* and *Calanus* spp.) the first few weeks after hatching (McLaren & Avendaño 1995). Platt et al. (2003) found that higher survival rates of juvenile haddock occurred in years when the spring phytoplankton bloom started earlier. Haddock recruitment was the highest in 1999, a year in which the phytoplankton bloom started earlier and *Calanus finmarchicus* reproduced early, making resources particularly abundant for larval haddock (Head et al. 2005). The coincidence of these events suggests that an early bloom leads to earlier and increased zooplankton production and higher survival of juvenile haddock: a sort of 'double-match' hypothesis. Friedland et al. (2008) looked at a variety of factors thought to affect haddock larval survival on Georges Bank, including the characteristics of the spring and fall bloom. They found that the magnitude of the fall bloom prior to subsequent spring spawning affected year-class strength and proposed a 'parental condition' hypothesis.

The NAO is an indicator of interannual climate variability over the North Atlantic and Northwest European Shelf seas (Hurrell et al. 2003). In particular, the shelf-slope front is positioned closer to the Scotian Shelf when the NAO index (January) is high, which affects the mixed layer depth and nitrate concentrations on the shelf, and ultimately, characteristics of the phytoplankton bloom (Zhai et al. 2011). Given these links, the NAO index can be viewed as a large-scale driver of phytoplankton dynamics on the Scotian Shelf. Therefore, we build our models explaining the variation in cod and haddock recruitment by entering the winter NAO index first, followed by measures of the phytoplankton bloom.

Satellite remote sensing provides a synoptic view of ocean conditions, and as technology improves, the data are produced at increasingly fine spatial and temporal resolution. Ocean colour has been routinely used to estimate primary production (IOCCG 2008), and more recently, to decompose autotrophic biomass into components based on functional types (Nair et al. 2008). An algorithm exists for the North West Atlantic (Sathyendranath et al. 2004) to discriminate diatoms (an important functional type) from ocean-colour records. These data allow for a closer look at bottom-up forcing on recruitment variability.

Here, we use the NAO winter index, satellite-derived colour data (time series which provide a proxy for characteristics of the phytoplankton bloom) and estimates of SSB to test if the match-mismatch hypothesis can explain variation in cod and haddock recruitment. We extend the work of Platt et al. (2003) by using a hierarchical model to examine the effects of the NAO and satellite-derived ocean colour data on the recruitment of cod and haddock on the Scotia Shelf of Canada. We examine both the spring and fall bloom, and we separately examine the effects of diatoms which are known to be an important food source for *Calanus* (Harris et al. 2000).

MATERIALS AND METHODS

Cod and haddock stocks on the Scotian Shelf are assessed in 2 management units, the Eastern Scotian Shelf (ESS) (Northwest Atlantic Fisheries Organiza-

tion [NAFO] Divisions 4VsW), and the Western Scotian Shelf (WSS) (NAFO Division 4X). A critical input to the assessment of these stocks has been the annual bottom-trawl research surveys which have been used to monitor groundfish stocks on the Scotian Shelf for over 40 years (Clark et al. 2010). Each area has different oceanographic conditions and fish communities (Zwanenburg et al. 2002), and tagging studies have shown that cod and haddock form relatively distinct populations (Martin 1962, Hurley et al. 1998, Stobo & Fowler 2006).

A statistical catch-at-age stock assessment model was developed for each area, and the SSB and recruitment to Age 1 was estimated. Annual recruitment was estimated as a free parameter and a Ricker stock–recruitment (S–R) relationship assuming log-normal error was fit externally to the assessment model (post hoc; Fig. 1). In 2004, only a partial groundfish survey was done. This created problems with our estimate of SSB and recruitment, and consequently, this year was removed from the analysis. The residuals of the S–R curve, which are a measure of larval survival after accounting for the non-linear effects of SSB, were correlated with annual indices of

phytoplankton dynamics. Recruits per spawner can also be used as an index of survival (Platt et al. 2003): this measure is highly correlated with the residuals of a stock recruitment relationship (e.g. ESS cod: r = 0.97, p < 0.001), but does not account for the non-linear effects of SSB (Myers et al. 1995). Both measures of survival produced similar results, and the choice of index did not change our conclusions.

Typically, cod and haddock spawn in the spring, but cod also spawn in the fall in inshore and offshore locations on the Scotian Shelf (McKenzie 1940). Here, we focus on the offshore spawning component because it is thought to have the largest contribution to stock recruitment, and because phytoplankton dynamics are more clearly delineated by remote sensing on the offshore. An examination of ichthyoplankton and length frequency data shows that fall spawning makes the largest contribution to year-class strength as the spring spawning component on the ESS has been lost (Frank et al. 1994). On the Western Scotian Shelf, cod and haddock spawn on Browns Bank (Hurley & Campana 1989, Page & Frank 1989, Waiwood & Buzeta 1989, Brander & Hurley 1992). Cod and haddock on the ESS tend to spawn in broader, poorly defined
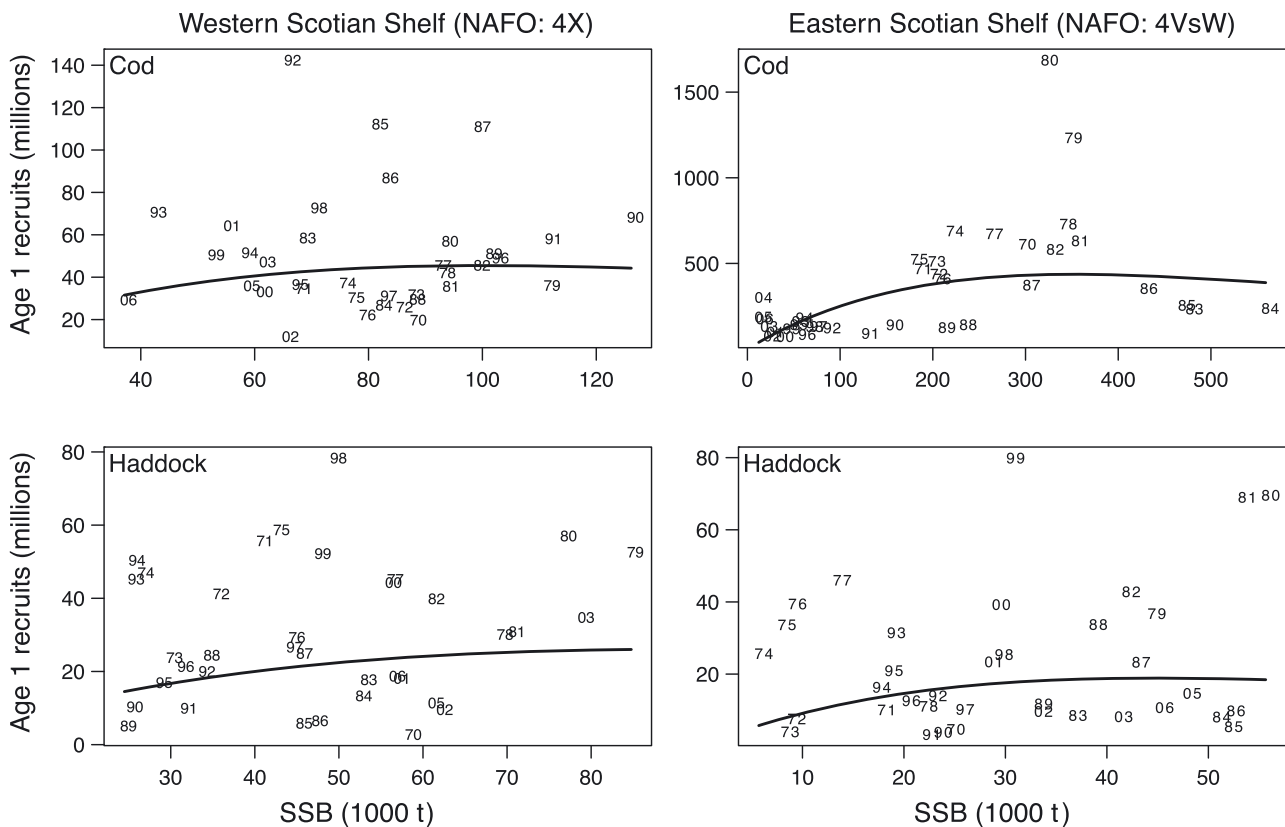

Fig. 1. Stock–recruitment relationships for cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* on the Eastern and Western Scotian Shelf. Recruitment is estimated to Age 1, but points are labelled by year of birth. SSB: spawning stock biomass

areas (Brander & Hurley 1992, Frank et al. 1994). Here, we considered 2 spawning areas for cod: Middle Bank, and a large area that includes Emerald, Western and Sable Island Banks, which we refer to as 'Greater Western Bank'. For haddock we consider a smaller area, which includes Emerald and Western Banks. Within each of these areas we estimated the characteristics of the phytoplankton bloom.

Chlorophyll concentration and probability of occurrence of diatoms were derived from single passes Level 2 data (i.e. remote-sensing reflectances) from the Sea-viewing Wide Field-of-view Sensor (Sea-WiFS) launched by the National Aeronautics and Space Administration (NASA, http://oceancolor.gsfc.nasa.gov). First, a polynomial equation was applied to remote-sensing reflectance ratios measured in the visible part of the solar spectrum (blue to green ratio) to obtain chlorophyll a (chl a) concentration—an index of phytoplankton biomass (O'Reilly et al. 1998). Second, an algorithm based on the absorption properties of diatoms was used to identify waters dominated by diatoms (Sathyendranath et al. 2004). The algorithm compares chl a concentrations computed using different remote-sensing reflectance ratios as inputs to look-up-tables for diatom-dominated waters and waters populated by a mixture of phytoplankton groups, on the basis of which the pixel is classified as being dominated by diatoms (value of 1) or not (value of 0). The algorithm was applied to daily images projected on a regular grid of 1.5 × 1.5 km resolution, which were then composited by quarter month (8 d unit) for the period January 1998 to December 2007 over each of the study areas. The results obtained over the period of observation, which are the average of 0 (mixture of phytoplankton) and 1 (diatoms), are presented as a probability that the pixel was dominated by diatoms during each 8 d time interval.

For each year and each fishing bank, we estimated 4 characteristics of the spring and fall bloom: the timing of the bloom using the chl a signal, the maximum amount of chl a, timing of the diatom bloom, and the maximum relative dominance of diatoms. Platt & Sathyendranath (2008) reviewed these and other measures that can be derived from remote sensing data. Our methods differ slightly from those of Platt et al. (2003) and Platt & Sathyendranath (2008). Instead of fitting a Gaussian distribution to the bloom, we take our measures directly from the data. The timing of the spring bloom was defined simply as the sample day on which the minimum level of chl a (or relative dominance of diatoms) was recorded in a window spanning 5 sampling intervals (~6 wk) prior to when the maximum chl a was recorded. The maximum amount of chl a in the spring or fall was simply the highest chlorophyll concentration (or relative dominance of diatoms) recorded during the season. The fall bloom is longer and less well defined, but we used the same methods, though with a wider sampling window (~10 wk), to determine the start of the bloom. These measures were chosen because they tended to indicate different aspects of the bloom (low correlation among indices) and for their ease of interpretation. Each measure of the bloom was standardised to a mean of zero, and the anomalies were used to explain variations in recruitment. The results of this method corresponded highly with those of Platt & Sathyendranath (2008) (r = 0.80, p = 0.005) and had the advantage of being automated.

The effects of the NAO and measures of the phytoplankton bloom were tested using generalized linear models. The residuals from the stock recruitment curve were re-scaled to be positive, and were modeled assuming a quasi-Poisson distribution that estimated the degree of overdispersion. The effects of the spring and fall bloom on recruitment were tested separately. Initial models included the full set of parameters: NAO, timing of the chl a bloom, max. chl a, timing of the diatom bloom and max. relative dominance of diatoms and non-significant variables were removed. Models were tested for 2 periods (spring and fall), for 4 spawning areas (Browns, Middle, Greater Western Bank, Emerald and Western Banks), within 2 populations (Eastern and Western Scotian Shelf) of 2 species (cod and haddock). Consequently, 10 models were tested. We ran a suite of 5 separate models specifically to test the maternal effect hypothesis (Friedland et al. 2008). Bloom magnitude (sum or integral of chlorophyll concentrations during the blooms) and diatom bloom magnitude (sum or integral of the proportion of diatoms during the blooms) was calculated. NAO winter index, bloom magnitude and diatom bloom magnitude were lagged, and the effect of the fall bloom on spring spawning and recruitment (or spring bloom on fall spawning and recruitment in the case of 4VsW cod) was tested. A few combinations were not plausible and were not tested; for example, there is not a large spawning component of haddock on Middle Bank.

RESULTS

Typically, the spring bloom occurred over a well-defined 2 to 3 wk period, whereas the fall bloom was less well defined, extended over a longer period, and sometimes was nearly absent (Figs. 2 & 3). When
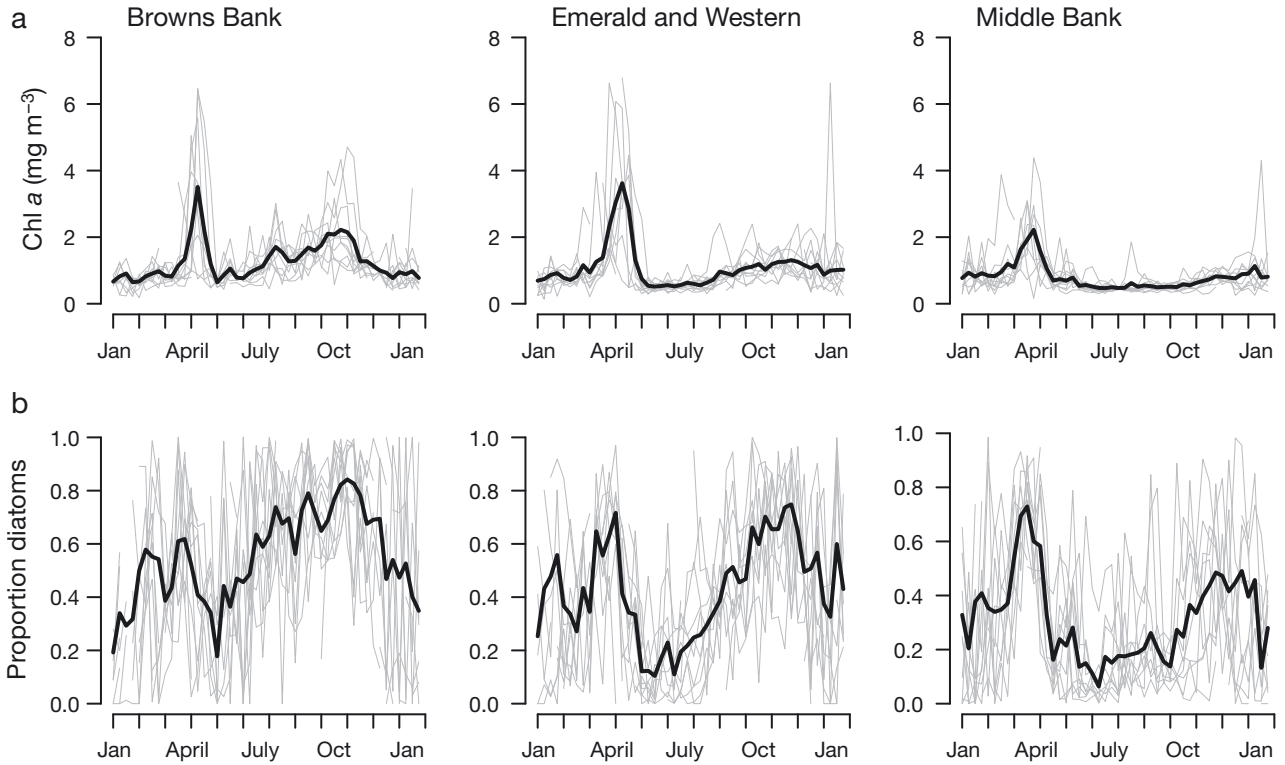
Fig. 2. Mean (thick, dark line) and annual estimates (thin lines) of (a) chl *a* and (b) proportion of diatoms on Browns, Emerald and Western, and Middle Bank of the Scotian Shelf
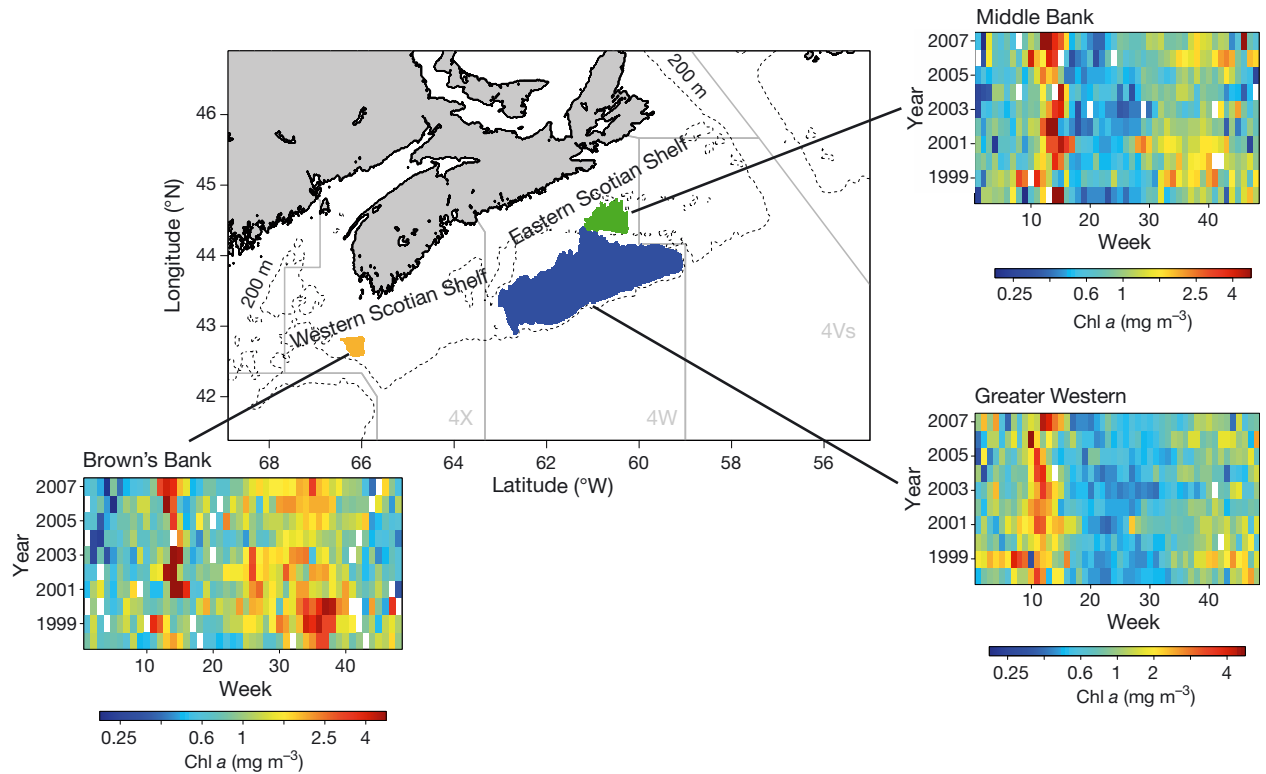

Fig. 3. Remote sensing estimates of chl *a* on Browns, Emerald and Western, and Middle Bank. Grey lines delineate Northwest Atlantic Fisheries Organization divisions. Week refers to an 8 d sampling interval. White cells are weeks without data

each year is overlaid and a long-term weighted mean is calculated (weighted by the number of 1.5 km^2 pixels which contained data), one can see that all banks have a spring bloom peaking in late March or early April (Fig. 2a). Browns Bank also has a fall bloom peaking in late September and early October. The banks on the ESS show a slow increase in chl *a* after the spring bloom, but a less well-defined fall bloom.

Diatoms made up a large proportion of the spring and fall blooms, and there was large variation in their relative dominance, but typically 50 to 60% of the spring bloom and 70 to 80% of the fall bloom were estimated to be dominated by diatoms. On Browns Bank there was large interannual variation in the timing of the spring diatom bloom, and a fall bloom occurred every year. The spring and fall diatom blooms are better defined on Middle and Emerald and Western Banks with a noticeable decrease in diatom dominance during the summer (Figs. 2b & 4).

Large recruitment tended to occur at higher SSB for cod, but recruitment was less related to the SSB of haddock (Fig. 1). The S-R parameters are better estimated for cod because there is a wider range of variation of SSB (600 t cod vs. 60 t haddock) and more data at low SSB which help better determine the slope at the origin (Table 1). The ESS has had particularly low cod SSB and below average recruitment since the moratorium in 1993. In comparison, cod recruitment was above average in 4 years on the WSS (1998, 1999, 2001, 2003), since 1993 (Fig. 1).

Only 3 of the 10 (0-lag) models tested explained a significant proportion of the variation in recruitment, indicating that the effects of the phytoplankton bloom are not general, but are likely specific to regions, season and species. None of the relationships tested on the WSS were significant. On the ESS, a simple 2-parameter model explained 87.4% of the variation in haddock recruitment: recruitment was greater at positive values of the NAO index and when the spring diatom bloom started earlier on Emerald and Western Bank (Table 2, Fig. 5). A model with only the timing of the spring diatom bloom also explained a significant proportion of variation (p = 0.01, result not shown). Haddock recruitment also tended to be larger when diatoms were dominant in the fall bloom (0-lag) (slope = 8.63, dispersion parameter = 5.4, p = 0.006), but the relative dominance of diatoms in the fall bloom (same year as recruitment) did not significantly improve the model above that based on the spring bloom. We did not find an effect of the bloom magnitude in the fall on haddock recruitment in the
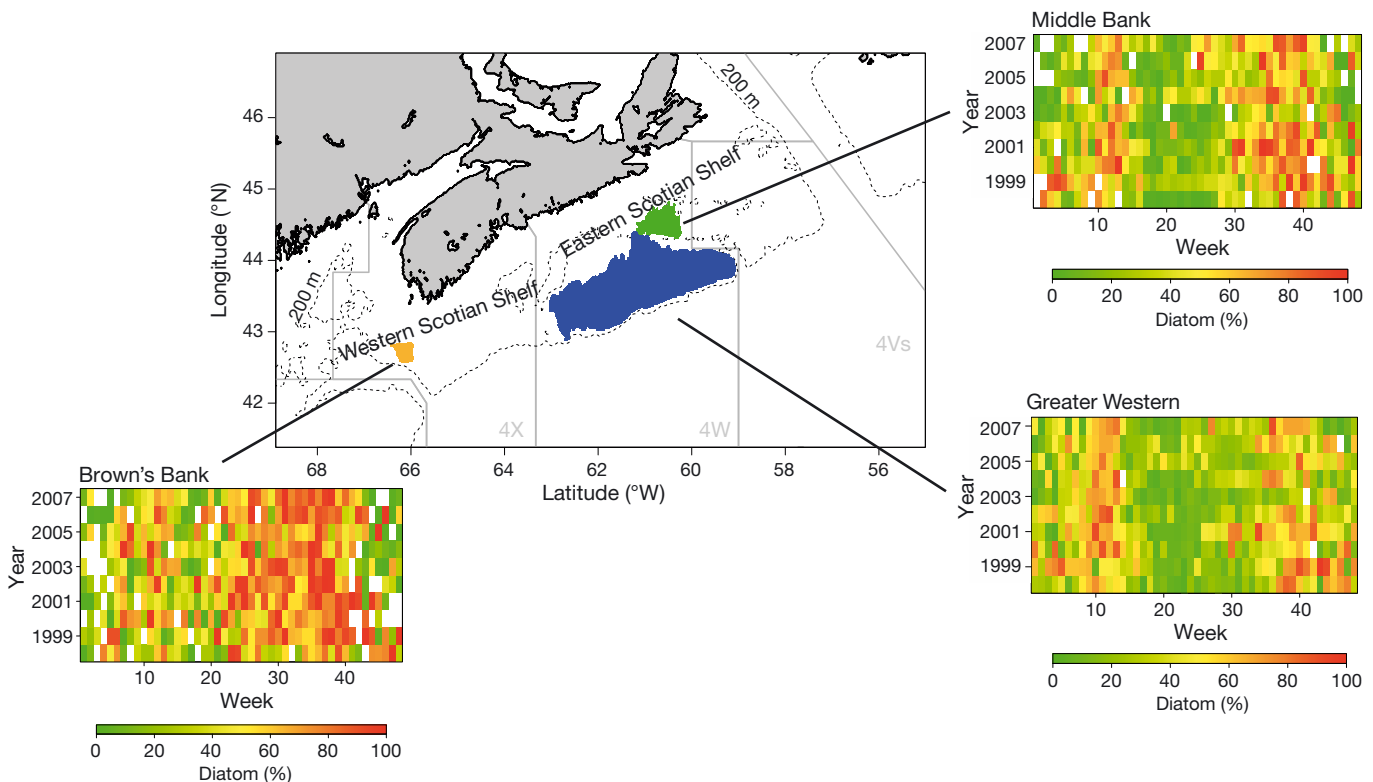

Fig. 4. Remote sensing estimates of percent diatoms on Browns, Emerald and Western, and Middle Bank. Grey lines delineate NAFO divisions. Week refers to an 8 d sampling interval. White cells are weeks without data

Table 1. Ricker stock–recruitment parameter estimates assuming log-normal error. Spawning stock biomass in 1000 t and recruitment in millions; nll = negative log likelihood. Stock references refer to Northwest Atlantic Fisheries Organization divisions

Species	Stock	Parameter	Estimate	95% CI	
				Lower	Upper
Cod	4X	α	109.54	48.24	248.73
		β	45.20	36.31	56.28
		σ	0.513		
		nll	166.93		
Cod	4VsW	α	358.19	233.51	549.44
		β	438.10	335.08	572.79
		σ	0.721		
		nll	245.34		
Haddock	4X	α	91.79	31.57	266.88
		β	26.13	17.44	39.14
		σ	0.789		
		nll	155.95		
Haddock	4VsW	α	44.75	24.47	81.83
		β	18.89	14.12	25.26
		σ	0.890		
		nll	147.17		

Table 2. (a) Analysis of deviance and (b) parameter estimates for a model of haddock recruitment on the Eastern Scotian Shelf. The NAO index is the average of winter months (Dec—Mar inclusive). D.start measures the anomalies in timing of the diatom bloom at Emerald and Western Bank in the spring; dispersion parameter = 4.00; Pr: probability

(a) Parameter	df	Deviance	F	Pr < F
NULL	7	154.20		
NAO	1	54.09	13.51	0.014
D.start	1	80.76	20.16	0.006

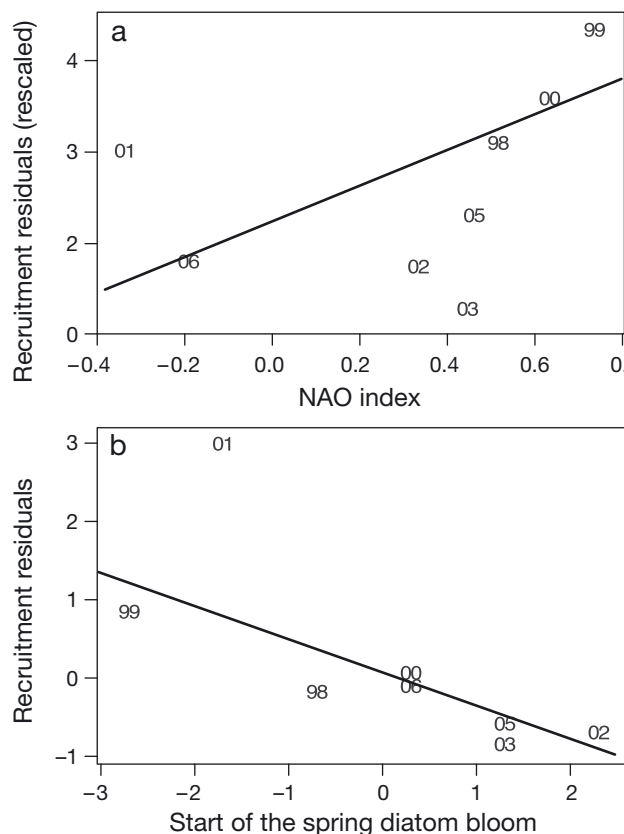| (b) Parameter	Estimate	SE	t-value	Pr > |t|
Intercept	2.44	0.27	9.3	0.0003
NAO	1.08	0.47	2.3	0.07
D.start	−0.42	0.1	−4.3	0.007

Fig. 5. Relationships between haddock *Melanogrammus aeglefinus* recruitment (points are labelled by year of birth) on the Eastern Scotian Shelf and (a) the NAO index, and (b) the timing of the spring diatom bloom on Emerald and Western Bank in weeks (zero representing the mean week of start of diatom bloom), such that positive (negative) values correspond to a late (early) bloom. Residuals (y-axis) are on the Poisson transform (log link)

This 2-parameter model explained 91.2% of the variation in cod recruitment. A model with only the timing of the spring diatom bloom also explained a significant proportion of variation (p = 0.03, result not shown). Although an effect of the timing of the spring diatom bloom on the recruitment of a fall spawning population might indicate a maternal effect, we did not find an effect of bloom magnitude in the spring on cod recruitment in the fall (maternal effect hypothesis; Friedland et al. 2008).

DISCUSSION

We show that fish recruitment is related to the NAO and the timing of the diatom bloom as measured by remote sensing colour data at the broad scale of spawning banks. Diatoms are known to be an important source of food and energy for lower level

following spring (maternal effect hypothesis; Friedland et al. 2008).

Cod recruitment on the ESS was not correlated with any characteristics of the spring bloom, and was correlated with the fall phytoplankton bloom on Middle Bank but not on Greater Western Bank. Cod recruitment was lower when the maximum amount of chl *a* during the fall bloom was higher, and when the fall diatom bloom started later (Table 3, Fig. 6).

heterotrophs such as *Calanus* spp. and fish larvae (Harris et al. 2000). Remotely-sensed indices of the diatom bloom explained more variation than the

Table 3. (a) Analysis of deviance and (b) parameter estimates for a model of cod recruitment on the Eastern Scotian Shelf. Max. = the anomalies in maximum amount of ch *a* during the fall bloom; D.start = the anomalies in timing of the diatom bloom on Middle Bank in the fall; dispersion parameter = 3.67

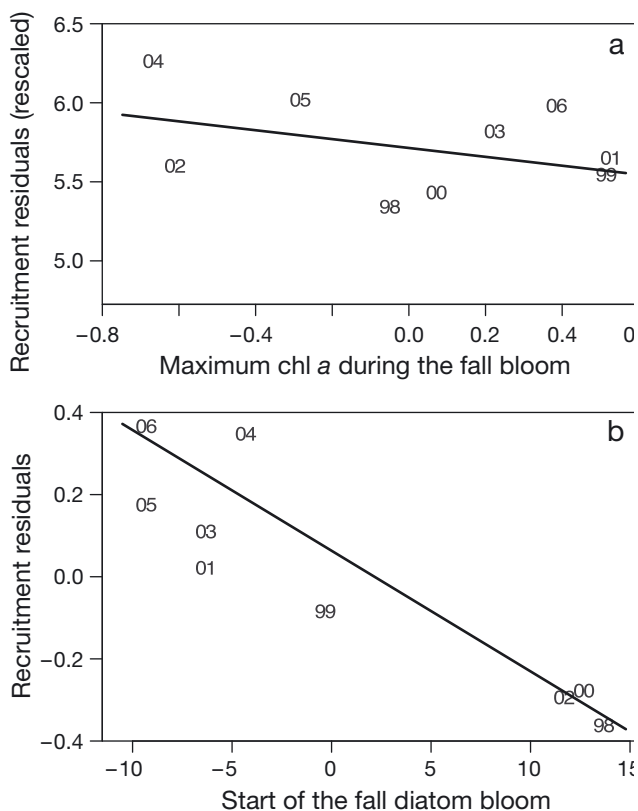| (a) Parameter	df	Deviance	*F*	Pr < *F*
NULL	8	249.53		
Max	1	43.02	11.74	0.014
D.start	1	184.58	50.35	0.0004
(b) Parameter	Estimate	SE	*t*-value	Pr > | *t* |
Intercept	5.74	0.04	156.0	<0.0001
Max	−0.42	0.08	−5.2	0.002
D.start	−0.03	0.004	−6.9	0.0005

Fig. 6. Relationships between cod *Gadus morhua* recruitment (points are labelled by year of birth) on the Eastern Scotian Shelf and (a) the maximum chl *a* (mg m^{-3}) measured during the fall bloom, and (b) the timing of the fall diatom bloom on Middle Bank. Residuals (y-axis) are on the Poisson transform (log link)

NAO index or the chl *a* signal, further supporting the key role of diatoms in the ecosystem and the utility of partitioning out diatoms and primary production into functional types (Sathyendranath et al. 2004, Nair et al. 2008). Further, we have improved upon the relationship between phytoplankton and haddock recruitment found by Platt et al. (2003) by incorporating the NAO and by measuring the characteristics of the spring and fall diatom bloom.

Our results indicate that we cannot make general statements about how the variability in phytoplankton bloom affects cod and haddock recruitment on the Scotian Shelf, given current data. We were unable to explain any of the variation in cod and haddock recruitment on the Western Scotian Shelf. This is a curious result and raises the question: What makes recruitment in this area so difficult to explain? On the ESS, different factors correlated with variation in cod and haddock recruitment. The fall bloom does not appear to be a better predictor than the spring bloom, and the NAO index explained variation in haddock recruitment but not cod recruitment. The differences among models suggest that fish larvae are probably adapted locally to food production and thus indirectly to the characteristics of the phytoplankton bloom, which in turn are influenced by regional (meso-scale) oceanographic conditions. Longer time series and the inclusion of other factors may be needed to reach more general conclusions (Houde 2008).

Nevertheless, our 2-parameter models were able to explain a large proportion of variation in haddock recruitment. Partitioning out the diatom signal is an improvement from the overall chl *a* signal used to explain haddock recruitment by Platt et al. (2003). When the NAO index was also included, the model explained 87% of the variation in haddock recruitment. It has been shown that the NAO affects both oceanographic conditions on the ESS and characteristics of phytoplankton bloom (Zhai et al. 2011). When the NAO index is high, the timing of the spring diatom bloom is earlier, which leads to higher larval survival (Fig. 5). At least that was the case in 1999, but a low NAO index in 2001 was followed by an early diatom bloom and high survival. Although data from 2001 may appear to contradict our conclusion, they are congruent with the model and observations in Platt et al. (2009). They found that the timing and amplitude of the spring and fall bloom had a 2 yr periodicity at mid-latitudes. This suggests that a more complex model is needed before the NAO index can be used to predict haddock recruitment.

We found that cod recruitment on the ESS was uncorrelated with the winter NAO index, consistent

with the results of Brander & Mohn (2004) and Stige et al. (2006) who found significant effects of the NAO in other areas. The strongest predictor of cod recruitment was the timing of the fall diatom bloom, where an early bloom was correlated with higher cod recruitment (Fig. 6). Since cod spawning occurs predominately in the fall (Frank et al. 1994), this correlation supports the match-mismatch explanation more than maternal condition, but that interpretation must remain tentative because the proportion of spring spawners has not been examined recently and they may now be contributing a larger proportion to overall recruitment. A similar (although not directly comparable) result was found between cod recruitment and primary production in the North Sea in the spring (Svendsen et al. 2007), suggesting that this line of work should be pursued throughout the North Atlantic. The ESS cod stock has been greatly depleted since the closure of the fishery in 1993. Continued monitoring of phytoplankton and recruitment trends may be important in understanding the potential for stock recovery (Myers et al. 1997, Frank et al. 2011).

Variation in ocean colour can be used to help predict cod and haddock recruitment, but predictions are stock specific and local in nature. These results may indicate that the mechanisms affecting fish recruitment may be partially driven by large-scale oceanographic forces, but that survival is fundamentally affected by local conditions (i.e. food availability and quality, advection, predation). Longer time series of phytoplankton production will undoubtedly help in this exploration, but this avenue of research is dependent on having consistent and high quality data collected and analysed for generations to come (i.e. remote sensing data, fish surveys). It is expected that better predictions of recruitment will result from stronger linkages between the climate, broad-scale oceanographic conditions and primary production (e.g. Platt et al. 2009, Zhai et al. 2011) and a deeper understanding of the energy transfer from phytoplankton to fish larvae.

Our analyses are only a partial step to a larger hierarchical and meta-analytic approach. Such an approach would include a greater array of covariates to explain recruitment in a hierarchy from broad scale (e.g. NAO) to local scale factors (e.g. food availability, temperature, growth, and predation) and include more stocks and species, which should help us better understand contingencies and uncover any generalities. For example, meta-analyses of cod recruitment showed that the effect of the NAO (and sea surface temperature) on recruitment depends on geographic area, with a positive effect on the recruit-ment of some stocks and a negative effect on others (Planque & Fredou 1999, Brander & Mohn 2004). At the local scale, temperature mediates larval feeding and survival. Warm temperatures negatively affect larval growth and survival when there is a mismatch between the timing of reproduction and food availability, whereas cold temperatures help larvae bridge a gap in resources (Laurel et al. 2011).

It is now becoming evident that the composition of the phytoplankton community affects larval growth, development and survival and overall ocean productivity. The relative proportions of dinoflagellates and diatoms affect the ratios of fatty acids (ratios of DHA and EPA) available to zooplankton and ultimately can affect larval growth (St. John et al. 2001, Copeman & Laurel 2010). Favourable conditions in the Pacific produced a large proportion of diatoms, which was reflected in lipid and fatty acid composition of forage fish, suggesting that energy transfer from phytoplankton to higher trophic levels was higher when diatoms dominated the bloom (Litz et al. 2010). We show that the timing of the diatom bloom affects fish recruitment in some areas, and we suggest that diatom production continue to be monitored and possibly incorporated into stock assessment and fish harvest plans. Diatoms may not only affect the quality of the food supply for larvae, but they probably also impact adult health. Lipid storage in the liver affects the health and reproduction of cod (Marshall et al. 2000), and in the Baltic, the maturation and the timing of spawning (Røjbek et al. 2012). Increased adult health also translates into positive maternal effects creating a positive feedback on egg production, larval survival and potentially recruitment (Trippel et al. 2005, Friedland et al. 2008, Grote et al. 2011).

After 100 years of research on the factors affecting recruitment, the one thing we have learned is that there are few generalizations that broadly apply across species and stocks. Perhaps broader generalizations exist and we have been unable to elucidate them, or maybe we should direct our efforts to understanding the contingencies of oceanography, food production and predation unique to specific areas. A predictive model can be formed for specific areas (as above), but these models should not be applied to other areas—at least not yet. Any general approach should consider multiple spatial and temporal scales and consider factors to be hierarchical from small to large scales (and/or vice versa; Levin 1992, Houde 2008). Indices of large-scale oceanographic conditions such as the NAO and PDO are likely to explain some variation, as will smaller scale measures of the phytoplankton bloom.

LITERATURE CITED

Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. California. Sea Grant College System, University of California, La Jolla

Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Adv Mar Biol 25:1–83

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Brander K, Hurley PCF (1992) Distribution of early-stage Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and witch flounder (*Glyptocephalus cynoglossus*) eggs on the Scotian Shelf: a reappraisal of evidence on the coupling of cod spawning and plankton production. Can J Fish Aquat Sci 49:238–251

Brander K, Mohn R (2004) Effect of the North Atlantic Oscillation on the recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 61:1558–1564

Campana SE, Smith SJ, Hurley PCF (1989) A drift-retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns bank. Can J Fish Aquat Sci 46(Suppl 1):s93–s102

Clark D, Emberley J, Clark C, Peppard B (2010) Update of the 2009 summer Scotian Shelf and Bay of Fundy research vessel survey. Res Doc 2010/008, DFO Canada Science Advisory Secretariat, Ottawa, ON

Clark WG, Hare SR (2002) Climate and stock size on recruitment and growth of Pacific halibut. N Am J Fish Manag 22:852–862

Clark WG, Hare SR (2007) Assessment of the Pacific halibut stock at the end of 2006. Int Pac Halibut Comm Report of Assessment and Research Activities 2006:97–128

Copeman LA, Laurel BJ (2010) Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Mar Ecol Prog Ser 412:259–272

Cushing DH (1969) The regularity of the spawning season of some fishes. J Cons Int Explor Mer 33:81–97

Cushing DH (1982) Climate and fisheries. Academic Press, London

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293

Dingsør GE, Ciannelli L, Chan KS, Ottersen G, Stenseth NC (2007) Density dependence and density independence during the early life stages of four marine fish stocks. Ecology 88:625–634

Fogarty MJ, Myers RA, Bowen KG (2001) Recruitment of cod and haddock in the North Atlantic: a comparative analysis. ICES J Mar Sci 58:952–961

Frank KT, Drinkwater KF, Page FH (1994) Possible causes of recent trends and fluctuations in Scotian Shelf/Gulf of Maine cod stocks. ICES J Mar Sci Symp 198:110–120

Frank KT, Petrie B, Fisher JAD, Leggett WC (2011) Transient dynamics of an altered large marine ecosystem. Nature 477:86–89

Friedland KD, Hare JA, Wood GB, Col LA and others (2008) Does the fall phytoplankton bloom control recruitment of Georges Bank haddock, *Melanogrammus aeglefinus*, through parental condition? Can J Fish Aquat Sci 65: 1076–1086

Govoni JJ (2005) Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. Sci Mar 69(Suppl 1):125–137

Grote B, Hagen W, Lipinski MR, Verheye HM, Stenevik EK, Ekau W (2011) Lipids and fatty acids as indicators of egg condition, larval feeding and maternal effects in Cape hakes (*Merluccius paradoxus* and *M. capensis*). Mar Biol 158:1005–1017

Harris RP, Irigoien X, Head RN, Rey C and others (2000) Feeding growth and reproduction in the genus *Calanus*. ICES J Mar Sci 57:1708–1726

Head EJH, Brickman D, Harris LR (2005) An exceptional haddock year class and unusual environmental conditions on the Scotian Shelf in 1999. J Plankton Res 27: 597–602

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe. Rapp P-V Reun Cons Int Explor Mer 20:1–228

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70

Hurley PCF, Campana SE (1989) Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwest Nova Scotia. Can J Fish Aquat Sci 46(Suppl 1):s103–s112

Hurley PCF, Black GAP, Comeau PA, Mohn RK, Zwanenburg K (1998) Assessment of 4X haddock in 1997 and the first half of 1998. Res Doc 98/136, DFO Canadian Stock Assessment Secretariat, Ottawa, ON

Hurrell JW, Kushnir G, Ottersen G, Visbeck M (eds) (2003) The North Atlantic Oscillation: climate significance and environmental impact. Geophysical Monograph No 134. American Geophysical Union, Washington, DC

Iles TD, Sinclair M (1982) Atlantic herring: stock discreetness and abundance. Science 215:627–633

IOCCG (International Ocean-Colour Coordinating Group) (2008) Why ocean colour? The societal benefits of ocean-colour technology. In: Platt T, Hoepffner N, Stuart V, Brown C (eds) Reports and monographs of the international ocean-colour coordinating group. IOCCG Report No. 7, Dartmouth, NS

Kempf A, Floeter J, Temming A (2009) Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006: the interplay between climate influence and predation. Can J Fish Aquat Sci 66:633–648

Laurel BJ, Hurst TP, Ciannelli L (2011) An experimental examination of temperature interactions in the match–mismatch hypothesis for Pacific cod larvae. Can J Fish Aquat Sci 68:51–61

Levin S (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Litz MNC, Brodeur RD, Emmett RL, Heppell SS, Rasmussen RS, O'Higgins L, Morris MS (2010) Effects of variable oceanographic conditions on forage fish lipid content and fatty acid composition in the northern California Current. Mar Ecol Prog Ser 405:71–85

Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J Fish Biol 49:627–647

Marshall CT, Yaragina NA, Ådlandsvik B, Dolgov AV (2000) Reconstructing the stock−recruit relationship for North-

east Arctic cod using a bioenergetic index of reproductive potential. Can J Fish Aquat Sci 57:2433–2442

Martin WR (1962) Canadian research report, 1961. C. Haddock. Int Comm Northwest Atl Annu Rep 12(Part III):46

McGurk MD (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar Ecol Prog Ser 34:227–242

McKenzie RA (1940) Nova Scotian autumn cod spawning. J Fish Res Board Can 5a:105–120

McLaren IA, Avendaño P (1995) Prey field and diet of larval cod on Western Bank, Scotian Shelf. Can J Fish Aquat Sci 52:448–463

Mertz G, Myers RA (1994) Match/mismatch predictions of spawning duration versus recruitment variability. Fish Oceanogr 3:236–245

Myers RA, Drinkwater KF, Barrowman NJ, Baird JW (1993) Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can J Fish Aquat Sci 50:1599–1609

Myers RA, Bridson J, Barrowman NJ (1995) Summary of worldwide spawner and recruitment data. Can Tech Rep Fish Aquat Sci No. 2024

Myers RA, Mertz G, Fowlow PS (1997) Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fish Bull 95:762–772

Nair A, Sathyendranath S, Platt T, Morales J and others (2008) Remote sensing of phytoplankton functional types. Remote Sens Environ 112:3366–3375

O'Brien CM, Fox CJ, Planque B, Casey J (2000) Fisheries: climate variability and North Sea cod. Nature 404:142

O'Reilly JE, Maritoreana S, Mitchell BG, Siegel DA and others (1998) Ocean color chlorophyll algorithms for SeaWiFS. J Geophys Res 103:24937–24953, doi:10.1029/98JC02160

Page FH, Frank KT (1989) Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns bank. Can J Fish Aquat Sci 46(Suppl 1):68–81

Peterson I, Wroblewski JS (1984) Mortality rate of fishes in the pelagic ecosystem. Can J Fish Aquat Sci 41:1117–1120

Planque B, Frédou T (1999) Temperature and recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56:2069–2077

Platt T, Sathyendranath S (2008) Ecological indicators for the pelagic zone of the ocean from remote sensing. Remote Sens Environ 112:3426–3436

Platt T, Fuentes-Yaco C, Frank KT (2003) Spring algal bloom and larval fish survival. Nature 423:398–399

Platt T, White GN III, Zhai L, Sathyendranath S, Roy S (2009) The phenology of phytoplankton blooms: ecosystem indicators from remote sensing. Ecol Model 220:3057–3069

Røjbek MC, Jacobsen C, Tomkiewicz J, Støttrup JG (2012) Linking lipid dynamics with the reproductive cycle in Baltic cod *Gadus morhua*. Mar Ecol Prog Ser 471:215–234

Sathyendranath S, Watts L, Devred E, Platt T, Caverhill C, Maass H (2004) Discrimination of diatoms from other phytoplankton using ocean-colour data. Mar Ecol Prog Ser 272:59–68

Sinclair M, Iles DT (1988) Population richness of marine fish species. Aquat Living Resour 1:71–83

Smart TI, Duffy-Anderson JT, Horne, JK, Farley EV, Wilson CD, Napp JM (2012) Influence of environment on walleye pollock eggs, larvae, and juveniles in the southeastern Bering Sea. Deep-Sea Res II 65–70:196–207

St. John MA, Clemmesen C, Lund T, Köster T (2001) Diatom production in the marine environment: implications for larval fish growth and condition. ICES J Mar Sci 58:1106–1113

Stige LC, Ottersen G, Brander K, Chan KS, Stenseth NC (2006) Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. Mar Ecol Prog Ser 325:227–241

Stobo WT, Fowler GM (2006) Canadian tagging of commercial groundfish and small pelagic fish in the vicinity of the Scotian Shelf and Gulf of St. Lawrence, 1953-1985. Can Tech Rep Fish Aquat Sci 2669:xii + 137 p

Svendsen E, Skogen M, Budgell P, Huse G and others (2007) An ecosystem modeling approach to predicting cod recruitment. Deep-Sea Res II 54:2810–2821

Trippel EA, Kraus G, Köster FW (2005) Maternal and paternal influences on early life history traits and processes of Baltic cod *Gadus morhua*. Mar Ecol Prog Ser 303:259–267

Waiwood KG, Buzeta MI (1989) Reproductive biology of southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can J Fish Aquat Sci 46:153–170

Zhai L, Platt T, Tang C, Sathyendranath S, Hernández Walls R (2011) Phytoplankton phenology on the Scotian shelf. ICES J Mar Sci 68:781–791

Zwanenburg KCT, Bowen DW, Bundy A, Drinkwater K and others (2002) Decadal changes in the Scotian Shelf large marine ecosystem. In: Sherman K, Skjoldal HR (eds) Large marine ecosystems of the North Atlantic: changing states and sustainability. Elsevier Science, Amsterdam, p 105–150