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Do environmental factors affect recruits per spawner anomalies of New England groundfish?

Jon Brodziak and Loretta O'Brien

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We evaluated the influence of environmental factors on recruits per spawner (RS) anomalies of 12 New England groundfish stocks. Nonparametric methods were used to analyse time-series of RS anomalies derived from stock-recruitment data in recent assessments. The 12 stocks occur in three geographic regions: the Gulf of Maine (cod *Gadus morhua*, redfish *Sebastes fasciatus*, winter flounder *Pseudopleuronectes americanus*, American plaice *Hippoglossoides platessoides*, witch flounder *Glyptocephalus cynoglossus*, and yellowtail flounder *Limanda ferruginea*), Georges Bank (cod, haddock *Melanogrammus aeglefinus*, and yellowtail flounder), and Southern New England (summer flounder *Paralichthys dentatus*, yellowtail flounder, and winter flounder). Randomization tests were applied to detect years when RS anomalies were unusually high or low for comparison with oceanographic conditions such as the 1998 intrusion of Labrador Subarctic Slope water into the Gulf of Maine region. Randomization methods were also used to evaluate the central tendency and dispersion of all RS anomalies across stocks. Average RS anomalies were significantly positive in 1987 across stocks and regions, indicating that environmental forcing was coherent and exceptional in that year. Responses of RS values of individual stocks to lagged and contemporaneous environmental variables such as the North Atlantic Oscillation (NAO) index, water temperature, windstress, and shelf water volume anomalies were evaluated using generalized additive models. Overall, the NAO forward-lagged by 2 years had the largest impact on RS anomalies. This apparent effect is notable because it could provide a leading indicator of RS anomalies for some commercially exploited stocks. In particular, the three primary groundfish stocks on Georges Bank (cod, haddock, and yellowtail flounder) all exhibited positive RS anomalies when the NAO_2 variable was positive.

Keywords: environmental forcing, generalized additive models, New England groundfish, North Atlantic Oscillation, randomization test, recruits per spawner, shelf water volume, water temperature, windstress.

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J. Brodziak and L. O'Brien: National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA 02543, USA. Correspondence to J. Brodziak: tel: +1 508 495 2365; fax: +1 508 495 2393; e-mail: jon.brodziak@noaa.gov.

Introduction

Understanding the impact of environmental changes on recruitment is important for predicting sustainable fishery yields from marine ecosystems. Environmental conditions affect the recruitment strength of fish stocks. Often several environmental factors will be important determinants of survival rates during early life history. For example, strong windstresses and resulting geostrophic currents may alter the retention of fish larvae in suitable shelf areas for settlement (Polacheck *et al.*, 1992) or alter the timing of the spring phytoplankton bloom, subsequent plankton productivity, and the amount of food available for newly-hatched larvae (Mann, 1993). Alternatively, water temperature anomalies may alter average metabolic conditions or available prey field of larval fish (Houde, 1997). Survival rates during early life history stages can either increase or decrease due to changing environmental factors. However, it is difficult to generalize about the relative importance of environmental factors because the impacts are specific to each ecosystem.

Many studies have evaluated the relative impacts of environmental conditions on recruitment in the North Atlantic (see, for example, ICES, 1994, 1998, 1999). Correlative relationships suggesting recruitment synchrony among North Atlantic stocks have been suggested (see for example, Templeman, 1972; Koslow, 1984), but often, such correlations have not persisted through time (Mann, 1993), in part owing to the lack of analysing potential influences of biotic and abiotic factors on recruitment (Myers *et al.*, 1995; Myers, 1998). Clearly, accounting for both biotic and abiotic factors is important for understanding the variability of recruitment. In a recent analysis, O'Brien *et al.* (2000) suggested that the substantial decline in the North Sea cod stock over the past decade was due to the joint effects of overfishing and the warming of North Sea waters. Their finding, that both overfishing and environmental change were important factors in reducing fishery productivity, highlights the fundamental challenge of dealing with multiple causal mechanisms in determining the relative importance of maternal and environmental factors on recruitment strength. To address the issue of confounding of maternal and environmental factors, we used recruits per spawner anomalies to evaluate the influence of environmental factors on recruitment success. In this context, an anomaly represents the deviation of observed recruitment per unit of spawning output from the expected relationship under a stock-recruitment relationship. The use of recruits per spawner anomalies attempts to avoid inherent confounding of maternal and environmental factors by adjusting observed survival ratios during early life history to account for the maternal impact, to the extent practicable.

We analysed recruits per spawner anomalies to investigate the influence of environmental factors on recruitment of 12 commercially exploited groundfish stocks in the northeast USA continental shelf ecosystem. Time-series of recruits per spawner (RS) anomalies were computed using stock-recruitment data from the most recent assessment of each stock. The 12 stocks were distributed in three distinct geographic regions: the Gulf of Maine (cod *Gadus morhua*, redfish *Sebastes fasciatus*, winter flounder *Pseudopleuronectes americanus*, American plaice *Hippoglossoides platessoides*, witch flounder *Glyptocephalus cynoglossus*, and yellowtail flounder *Limanda ferruginea*), Georges Bank (cod, haddock *Melanogrammus aeglefinus*, and yellowtail flounder), and Southern New England (yellowtail flounder, summer flounder, and winter flounder). Two nonparametric techniques were used to evaluate potential synchrony of RS anomalies across years in these regions and also to investigate the relative importance of alternative environmental factors on survival of early life history stages. First, randomization methods were applied to detect years where RS anomalies were unusually high or low for comparison with atypical oceanographic conditions such as the 1998 intrusion of Labrador Sea Slope Water into the Gulf of Maine (Pershing *et al.*, 2001). Randomization methods were also used to evaluate the central tendency and dispersion of total RS anomalies across stocks. Second, generalized additive models were fitted to evaluate the responses of RS values of individual stocks to lagged and contemporaneous environmental variables such as the North Atlantic Oscillation, water temperature, windstress, and for some stocks, shelf-water volume anomalies. We discuss the evidence for recruitment synchrony and compare the relative importance of alternative environmental factors on recruits per spawner anomalies of the selected stocks.

Material and methods

Recruits per spawner anomalies

Stock-recruitment data were obtained from recent stock assessments (NEFSC, 2002a). The longest time-series of stock-recruitment data was for Georges Bank haddock ($n = 71$, 1931–2001), while the shortest was for Cape Cod–Gulf of Maine yellowtail flounder ($n = 16$, 1985–2000). RS anomalies were computed based on the stock-recruitment function used in the stochastic projections for each stock. For some stocks, the stochastic projections were based on random resampling of observed recruitments (R_j) (NEFSC, 2002b). In this case, the stock-recruitment function was based on the average RS value over the range of observed spawning biomass (S_j). For other stocks, a parametric Beverton–Holt relationship with random error was used in the stochastic projections (Brodziak *et al.*, 2001; NEFSC, 2002b). In this case, the stock-recruitment function was the deterministic stock-recruitment curve. In either case, the annual RS anomaly (RS_j) was computed as the difference between the observed RS value (R_j/S_j) and the predicted RS from the stock-recruitment function divided by the standard deviation of the observed RS values (σ_{RS}):

$$RS_j = \frac{\left(\frac{R_j}{S_j}\right)^{OBS} - \left(\frac{R_j}{S_j}\right)^{PRED}}{\sigma_{RS}} \quad (1)$$

We standardized the RS anomalies to ensure that values were comparable across stocks (Figure 1). This was important because the coefficient of variation of observed RS values ranged from roughly 50% (summer flounder and Southern New England winter flounder) to over 200% (redfish and Southern New England yellowtail flounder). As calculated, the RS anomalies represent the combined effects of environmental variation and trophic interactions on the observed production of recruits per spawner.

For each year (j) and area, we derived the expected RS anomaly ($E[RS_j]$) across the number of stocks in the area (n), indexed by k, in that area:

$$E[RS_j] = \frac{1}{n}\sum_k RS_{j,k} \quad (2)$$

This average provides a measure of whether a particular year had above- or below-average survival anomalies across stocks. A synchronous pattern of expected RS anomalies would suggest that a common factor or set of factors affected juvenile fish survival in that year. Thus, the $E[RS_j]$ values provide a measure of the central tendency of

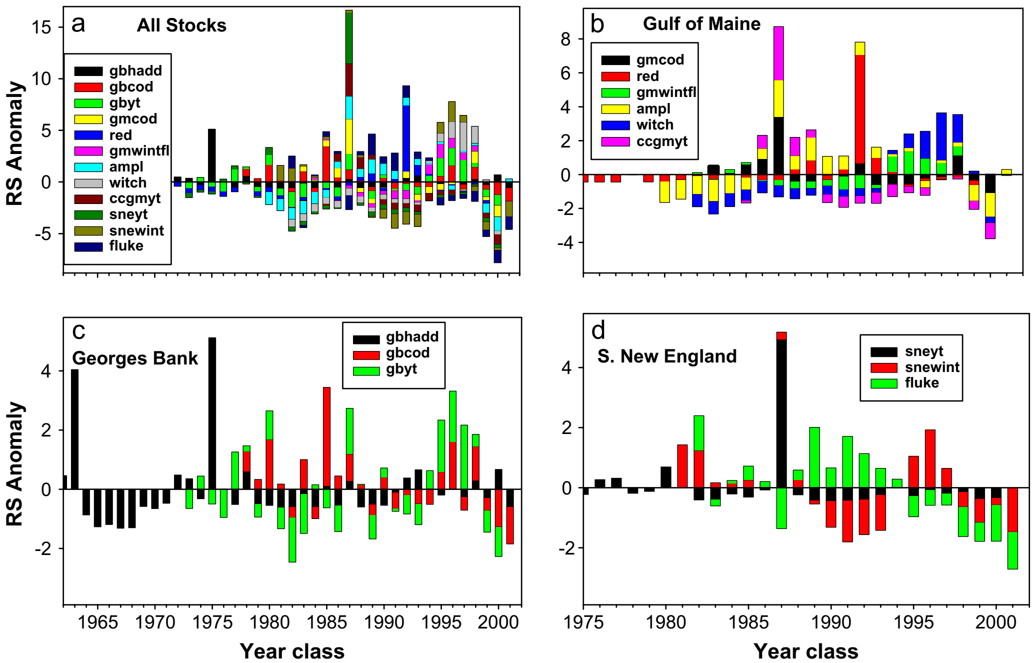

Figure 1. Standardized recruits per spawner (RS) anomalies for all 12 groundfish stocks (a), Georges Bank stocks (b), Gulf of Maine stocks (c), and Southern New England stocks (d), using acronyms for Georges Bank haddock (gbhadd), cod (gbcod), and yellowtail flounder (gbyt), Gulf of Maine cod (gmcod), redfish (red), winter flounder (gmwintfl), American plaice (ampl), witch flounder (witch), and Cape Cod–Gulf of Maine yellowtail flounder (ccgmyt), and Southern New England yellowtail flounder (sneyt), winter flounder (snewint), and summer flounder (fluke).

the effect of environmental conditions on fish survival in each region. We also computed two measures of annual dispersion for the RS anomalies in each region. The first was the variance of the RS anomalies by year (Var[RS_j]):

$$\mathrm{Var}[RS_j] = E[RS_j^2] - E[RS_j]^2 \quad (3)$$

This indicates whether the RS values were more or less variable in a given year. The second measure of dispersion was the sum of the absolute deviations of annual RS anomalies (D[RS_j]) where

$$D[RS_j] = \sum_k |RS_{j,k}| \quad (4)$$

In this case, larger values of D[RS_j] indicate that the sum of both positive and negative impacts on recruits per spawner was greater in a given year. This provides an index of whether environmental effects were more extreme in a given year and region.

Environmental factors

We selected a suite of environmental factors that may have a potentially important influence on early life history stage survival of groundfish. These included the North Atlantic Oscillation index (Parsons and Lear, 2001; Brander and Mohn, 2004), water temperatures (Laurence and Rogers, 1976), windstresses in nursery areas (Mann, 1993; Mountain *et al.*, 2003), and a measure of the volume of continental shelf water in the northeast USA continental shelf ecosystem (Mountain, 2003).

Values of the North Atlantic Oscillation (NAO) index were obtained from Jones *et al.* (1997, see updated data at http://www.cru.uea.ac.uk). We averaged December (year − 1) through March (year) values to produce an annual index (Figure 2a). These months were used because the NAO exerts a strong influence on North Atlantic winter storm frequency and temperatures (Parsons and Lear, 2001).

We used shelf-water volume anomalies (Mountain, 2003) to reflect the relative intensity of the southward flow of shelf water in the Mid-Atlantic Bight region (Figure 2a). The effect of the volume anomaly on recruits per spawner was investigated for the Mid-Atlantic Bight stocks of Southern New England winter and yellowtail flounder, and summer flounder.

Values of regional temperature anomalies were developed using research survey data and methods developed by Mountain *et al.* (2004). Anomaly series were available for Georges Bank, western and eastern Gulf of Maine, and the northern and southern Mid-Atlantic Bight. Bottom and surface water temperature anomalies were available during both spring (1968–2003) and autumn (1963–2003), with

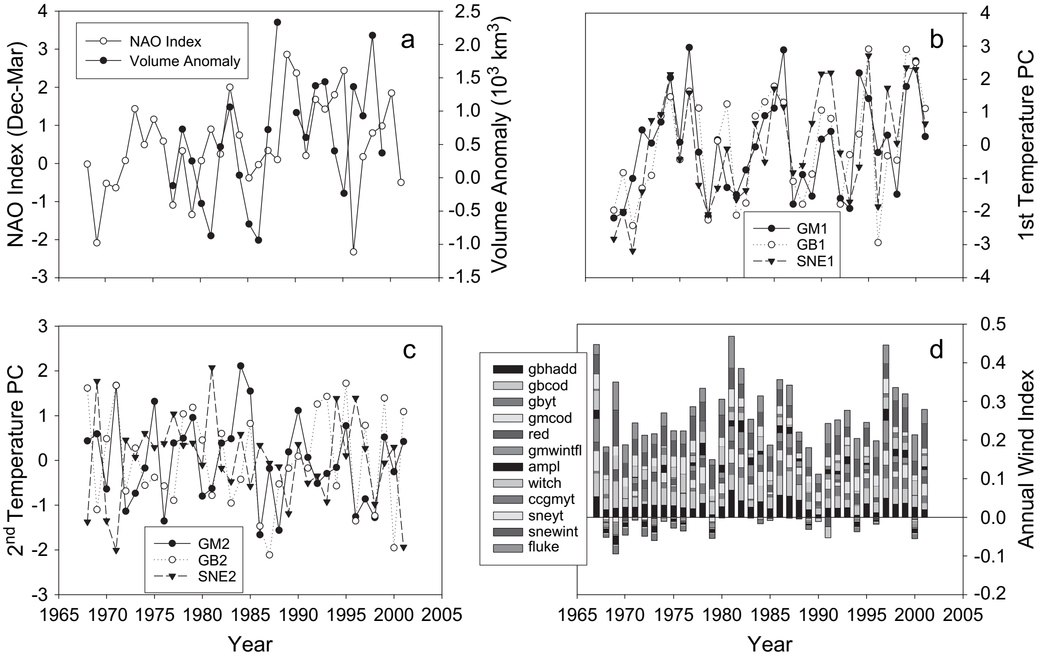

Figure 2. Environmental factors investigated as potential predictive variables for recruits per spawner anomalies were the North Atlantic Oscillation (NAO) index and shelf water volume anomaly (a), the first principal components of regional water temperature anomalies (b), the second principal components of regional water temperature anomalies (c), and a wind-induced current index of larval retention for each stock (d), using acronyms for Georges Bank haddock (gbhadd), cod (gbcod), and yellowtail flounder (gbyt), Gulf of Maine cod (gmcod), redfish (red), winter flounder (gmwintfl), American plaice (ampl), witch flounder (witch), and Cape Cod−Gulf of Maine yellowtail flounder (ccgmyt), and Southern New England yellowtail flounder (sneyt), winter flounder (snewint), and summer flounder (fluke).

the exception of a few years with missing measurements. Temperature anomalies for the entire Gulf of Maine were computed as a weighted average of the western (53%) and eastern (47%) Gulf of Maine anomaly values; the relative weights were based on the total survey area for the eastern and western subregions. Similarly, temperature anomalies for the Mid-Atlantic Bight region were computed as a weighted average of northern (54%) and southern (46%) Mid-Atlantic Bight anomaly series.

Temperature anomaly values were missing for Georges Bank (GB) in autumn 1990 and for the Gulf of Maine (GM) in autumn 1999. Given the high positive correlations between spring and autumn bottom and surface temperature anomalies among and within regions, we used linear models to predict the missing temperature anomaly values. The model selection criterion for the linear models was that each factor had to be significant at the $\alpha = 0.1$ significance level. The initial model consisted of one of the four series with missing values (GB or GM autumn surface or bottom temperature anomalies) using all remaining series with non-missing data as predictors. Factors were deleted until all factors were significant at the $\alpha = 0.1$ level. This process produced one predictive linear model for each series with missing values. Each of the four selected models was highly significant ($p < 0.0001$). Coefficients of the selected model were then used to predict the missing temperature anomalies for GB in autumn 1990 and GM in autumn 1999.

Principal components analyses were conducted on the temperature anomaly series (spring or autumn and surface or bottom temperature) within each region (Figure 2b and c). Temperature anomaly series generally exhibited a significant positive correlation within each region. The first two principal components explained the vast majority of variability in each region: Gulf of Maine (78%), Georges Bank (92%), Mid-Atlantic Bight (88%). The first two principal components were then used as independent orthogonal predictors of the overall temperature anomaly in each region.

Measurements of windstress and direction were used (Bakun, 1975; Norton *et al.*, 2002) to compute an index of shoreward geostrophic currents that might retain larvae in continental shelf waters. Data were obtained from a total of six NOAA buoys in the study area: Gulf of Maine, Massachusetts Bay, Nantucket Sound, Georges Bank, Long Island, and Virginia Beach. One buoy was assigned to each stock based on the spatial overlap of larval and egg distributions (Berrien and Sibunka, 1999) with the buoy site. For each stock, monthly windstress and direction (Manning and Strout, 2001) were averaged from the first month of peak spawning (O'Brien *et al.*, 1993) through the expected number of months required for settlement (Kelly and Barker, 1961; Fahay, 1983; Bolz and Lough, 1988; Miller *et al.*, 1991). For each buoy, the optimal direction of surface wind-driven currents was perpendicular to the shelf isobaths. This direction was offset 90E (90 degrees) from the optimal wind direction owing to Coriolis deflection. Here, it was assumed owing flow throughout the water column was important for transport prior to settlement. Given the optimal wind direction θ, a directional index of the signed magnitude of favourable geostrophic flow was calculated as $D = \mathrm{Cos}(\theta \pm 90°)$. For each stock, an index of shoreward geostrophic currents (W) was computed as windstress (S) times the directional index (Figure 2d). Thus, the wind index depended on both the windstress and direction.

Randomization tests

Randomization methods (Manly, 1997) were used to test whether the distribution of recruits per spawner anomalies across stocks was extreme in any given year. These methods are valid even when samples are not collected randomly, and are also flexible enough to compute non-standard test statistics. The null hypothesis was that there was no year effect for the RS anomalies.

Randomization distributions were computed for the average recruits per spawner anomalies across stocks by region ($E[RS_j]$), and two measures of dispersion ($Var[RS_j]$ and $D[RS_j]$) were derived. The average RS anomalies measured whether there was a synchronous positive or negative environmental impact on juvenile survival in a given year, while the two measures of dispersion indicated whether there was more or less annual variation across stocks. The randomization distributions (F) were constructed by randomly selecting a year index k^* for each stock in a region and then computing the randomized statistic. For example, a single value (F_b) in the randomization distribution of $E[RS_j]$ would be

$$F_b\left(E\left[RS_j\right]\right) = \frac{1}{n}\sum_{k^* \in K} RS_{j,k^*} \quad (5)$$

where K is a random vector of stock indices k*, and n is the number of stocks in the area.

Approximate p-values were computed by comparing observed test statistics for each year with the randomization distribution. A total of $b = 1000$ randomizations was used to compute each p-value. The p-value is interpreted as the probability of observing a more extreme value of the test statistic by random chance alone. A significance level of $\alpha = 0.2$ was used to judge whether a given year was anomalous for each region and for all stocks combined.

Generalized additive model analyses

Generalized additive models (Hastie and Tibshirani, 1990) were fitted to the standardized RS anomalies for each stock to identify potential nonlinear effects of environmental factors. These models allow additive effects to be modelled without specifying a single equation for each environmental effect. We viewed this as an essential component of investigating the impacts of environmental factors on RS anomalies. Potential predictor variables for the generalized additive models (GAMs) included the contemporaneous (NAO), and the forward-lagged 1- and 2-year (NAO_1 and NAO_2) North Atlantic Oscillation index values. The forward-lagged NAO index values preceded the RS anomalies in time so that a 1-year lag would imply that an anomaly in year t was some unknown function of the NAO index in year $t-1$. That is, $RS(t) = f(NAO(t-1))$. Both the lagged and contemporaneous NAO variables were investigated because the NAO can produce both local and time-lagged physical changes in oceanographic and atmospheric conditions that could affect groundfish recruitment success. Potential predictor variables also included the first two principal components of regional water temperature anomalies (P_1 and P_2), the modelled windstress index (WS) by region, and the shelf water volume anomaly (V) for stocks in the Mid-Atlantic Bight (Figure 1). In addition to the GAMs analyses, correlations among the predictor variables were computed to evaluate the degree of collinearity among potential predictor variables. Correlation coefficients (ρ) with magnitude $|\rho| > 0.35$ were judged to be potentially important, since such values would be considered significant at the $\alpha = 0.05$ level assuming $n = 35$, the typical length of the environmental time-series. Autocorrelations of individual environmental time-series were also evaluated to examine whether low-frequency forcing was important. In this case, autocorrelations with lags less than one-fourth of the time-series length that were significant at the $\alpha = 0.05$ level were judged to be important.

We fitted generalized additive models to the RS anomalies using a stepwise model-selection approach beginning with all variables as the null model and also using the three NAO series in isolation to examine the potential effects of this broad-scale forcing mechanism. Each generalized additive model had the form

$$E[RS|\underline{X}] = \alpha + \sum_j s_j\left(X_j\right) + \varepsilon \quad (6)$$

where α is a constant, $\underline{X}$ is the vector of predictor variables, the s_j are arbitrary smooth univariate functions, and the errors are independent of the X_j with zero mean and constant variance. Individual additive models were fitted to the RS anomalies using smoothing splines with 3 degrees of freedom for each factor and a standard backfitting algorithm (Hastie, 1993).

We used a stepwise approach to select a generalized additive model for each stock. The initial null model included all potential predictors. In each step of the selection process, predictor variables were eliminated from the subsequent additive model fit if they had an associated p-value greater than 0.2. This step was repeated until all predictor variables had p-values of 0.2 or less. The significance level of $\alpha = 0.2$ was chosen to allow for the possibility of multiple environmental effects on relatively short time-series of RS anomalies. In some cases, no model was selected. A pseudo-R^2 value (Swartzman *et al.*, 1992) was also computed to provide an indication of the overall goodness-of-fit of the selected model.

Results

Randomization tests

Among the time-series of standardized RS anomalies for all 12 stocks combined, the largest positive anomalies occurred in 1987, 1992, and 1996, while the most negative occurred in 1999 and 2000 (Figure 1a). Randomization test results using all stocks showed that 1975, 1987, 1992, and 1996 had significant positive average RS anomalies (Table 1) while 1999 through 2001 had significant negative anomalies. The variance of RS anomalies for all stocks was significantly higher in 1975, 1987, and 1992 and was significantly lower in 1984, 1988, 1994, and 1999. The absolute deviation of RS anomalies for all stocks had a similar pattern to the variance with the exception of 1999.

Within the Gulf of Maine, RS anomalies appeared to be atypical in at least 3 years: 1987, 1992, and 2000 (Figure 1b). In 1987, RS anomalies were positive and dominated by witch flounder and yellowtail flounder; in 1992 RS anomalies were positive and dominated by redfish; and in 2000 RS anomalies were negative and dominated by American plaice and Atlantic cod (Figure 1b). Spatial randomization tests indicated that the average RS anomaly for the six Gulf of Maine stocks was significantly positive in 1987 and 1998 (Table 1) and was significantly negative in 1980 and 2000. Randomization tests on the variance of the RS anomalies indicated significantly higher variance in 1987 and 1992 (Table 1). Similarly, tests on the absolute deviation of RS anomalies showed that 1987 and 1992 had significantly larger absolute deviations while those in 2001 were significantly lower. Significant year effects were detected in 1987 and 1992 in all three randomization tests for the Gulf of Maine stocks.

For the three Georges Bank stocks, RS anomalies appeared unusually positive in 3 years: 1975, 1985, and 1996 (Figure 1c). Of these years, the positive RS anomaly for haddock dominated in 1975, the positive cod RS anomaly dominated in 1985, while positive cod and yellowtail flounder RS anomalies dominated in 1996. Spatial randomization tests on the average RS anomaly for Georges Bank stocks indicated significant positive effects in 1975, 1985, 1987, and 1996 and significant negative effects in 1982, 1989, and 2001 (Table 1). Randomization tests on the variance of RS anomalies indicated significantly higher variances in 1975, 1985, and 1997, and significantly lower variances in 1989, 1991, and 1999. Randomization tests on the absolute deviations of the RS anomalies indicated significant year effects in 1975, 1985, 1988, and 1991. For Georges Bank stocks, all three randomization tests indicated significant year effects in 1975 and 1985.

In the Southern New England region, RS anomalies were unusually positive in 1987, dominated by yellowtail flounder (Figure 1d). Spatial randomization tests performed using the average RS anomaly indicated significant positive year effects in 1981, 1982, and 1987, and significant negative effects in 1999, 2000, and 2001 (Table 1). Randomization tests on the variance of the RS anomalies indicated significantly higher variances in 1987 and 1996, and significantly lower variances in 1984, 1986, 1989, 1991, 1994, and 1999. Tests on the absolute deviations showed significantly higher deviations in 1987, 1991, and 2001, with significantly lower deviations in 1984, 1986, and 1994. Significant year effects were detected in 1987 in all three randomization tests for the three Southern New England stocks.

Several general patterns emerged from the application of randomization tests to detect year effects. First, the randomization tests consistently showed that 1987 was an unusual year. In particular, there was a significant positive average RS anomaly in all three regions during 1987. Similarly, variances and absolute deviations were significantly higher in two of three regions and for all stocks combined. This pattern suggested that broad-scale forcing had a synchronous positive impact on recruits per spawner across the entire continental shelf ecosystem. Second, average RS anomalies appeared to be more positive during 1981−1998 than during 1999−2001. In particular, 12 out of 14 significant year effects (86%) for each region and all stocks combined were positive during 1981−1998 compared with eight out of eight significant negative year effects (100%) during 1999−2001. This suggests that environmental conditions shifted from having a positive to a negative impact on juvenile survival in recent years across regions. Third, regional differences in RS anomalies are apparent. In particular, the Southern New England region had the highest percentages of significant year effects on the average (29%), variance (38%), and absolute deviation (29%) of RS anomalies than either Georges Bank or the Gulf of Maine. In contrast, the Gulf of Maine had the lowest percentages of significant year effects on the average (23%), variance (9%), and absolute deviation (14%) of RS anomalies. This suggests that latitudinal differences among regions probably affect the variability of RS anomalies.

Generalized additive model analyses

Results of the correlation analyses indicated that some collinearity existed among the potential predictive variables for the GAMs analyses. About 17% of the possible correlations between NAO and other environmental factors appeared to be important. Similarly, 16%, 19%, and 20% of the possible correlations between temperature, volume anomaly, and windstress, respectively, and other environmental factors were important. Overall, the correlation

Table 1. Results of randomization tests of whether a significant year effect ($\alpha = 0.2$) was detected for the average, variance, and sum of absolute deviations of recruits per spawner (RS) anomalies for stocks in the Gulf of Maine (1980−2001), Georges Bank (1973−2001), Southern New England (1981−2001) regions, and all regions combined (1973−2001). Test statistics with a positive deviation from the randomized mean and a p-value greater than 0.9 are denoted by P. Test statistics with a negative deviation from the randomized mean and a p-value less than 0.1 are denoted by N. Non-significant statistics are denoted with a blank.

	2-Digit year																												
Region	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01
Average																													
Gulf of Maine								N							P					P						P		P	
Georges Bank			P							N			P		P		N							P					N
S. New England									P	P					P												N	N	N
All			P												P					P				P			N	N	N
Variance																													
Gulf of Maine															P					P									
Georges Bank			P										P				P		P						P		N		
S. New England												N		N	P		N		N			N		P			N		
All			P									N			P	N				P		N					N		
Sum of absolute deviations																													
Gulf of Maine															P					P									N
Georges Bank			P										P			N			N										
S. New England												N		N	P				P			N							P
All			P									N			P	N				P		N							

analyses indicated that linear associations between some of the environmental factors were apparent, as might be expected. In contrast, the autocorrelation analyses showed that there was a limited degree of serial correlation in the environmental factors, since only 3 out of 22 series exhibited substantial serial correlation. Windstress time-series for American plaice, witch, and Gulf of Maine yellowtail flounder each had significant lag-4 autocorrelations, which is not surprising since these series were derived using data from the same buoy.

Results of the generalized additive model analyses using all potential predictor variables show that the NAO predictor variables are important for many stocks (Table 2). In particular, at least one NAO variable was significant for 11 of the 12 stocks. The NAO index forward-lagged by 2 years was significant at the $\alpha = 0.2$ level for 9 out of 12 stocks (75%). The next most important variable was the NAO index forward-lagged by 1 year, which was significant for 5 out of 12 stocks (42%). RS anomalies of both Atlantic cod stocks appeared to be affected by the lagged NAO variables. Of the remaining variables, the NAO index was significant for 3 out of 12 stocks, while the temperature and windstress variables were significant for 2 out of 12 stocks. In contrast, shelf water volume was not significant for any of the Southern New England stocks.

The shape of the RS anomaly responses to the NAO predictor was nonlinear across stocks (Figure 3). RS anomalies of both American plaice and Southern New

Table 2. Generalized additive model selection results using all variables and only NAO variables for Gulf of Maine, Georges Bank, and Southern New England stocks. p-values for each significant predictor are listed including the North Atlantic Oscillation (NAO) index, the North Atlantic Oscillation index forward-lagged by 1 year (NAO_1), the North Atlantic Oscillation index forward-lagged by 2 years (NAO_2), the first (P_1) and second (P_2) principal components of water temperature anomalies, the stock-specific wind index (W), and the continental shelf water volume anomaly (V) as well as the number of years used to fit the model (N), the pseudo-R^2 value (R^2), and the degrees of freedom used in the smoothing spline for the GAM fitting (d.f.).

Using all variables

Region	Stock	N	R^2	d.f.	NAO	NAO_1	NAO_2	P_1	P_2	W	V
Gulf of Maine	Cod	19	0.69	6		0.10	0.09				
	Redfish	33	0.72	12		0.04	<0.01		0.05	<0.01	
	Winter flounder	20	0.55	3			<0.01				
	American plaice	21	0.68	9	0.13	0.16		0.09			
	Witch flounder	19	0.42	3			0.05				
	Yellowtail flounder	16	0.56	3			0.05				
Georges Bank	Haddock	35	0.53	9	0.04		0.15	0.12			
	Cod	24	0.46	6		0.13	0.11				
	Yellowtail flounder	28	0.68	9		<0.01	0.11		0.18		
S. New England	Winter flounder	21	0.60	6	0.09					0.07	
	Summer flounder	20	0.42	3			0.07				
	Yellowtail flounder	28									

Using only NAO variables

Region	Stock	N	R^2	d.f.	NAO	NAO_1	NAO_2
Gulf of Maine	Cod	19	0.69	6		0.10	0.09
	Redfish	48	0.31	6		0.19	0.02
	Winter flounder	20	0.80	6		0.02	<0.01
	American plaice	21	0.27	3		0.14	
	Witch flounder	19	0.94	9	0.03	<0.01	0.02
	Yellowtail flounder	16	0.86	6		0.11	0.03
Georges Bank	Haddock	71	0.29	3	0.03		
	Cod	24	0.46	6		0.13	<0.01
	Yellowtail flounder	28	0.56	6		0.01	0.07
S. New England	Winter flounder	21	0.60	6	0.13		0.09
	Summer flounder	20	0.42	3			0.07
	Yellowtail flounder	28					

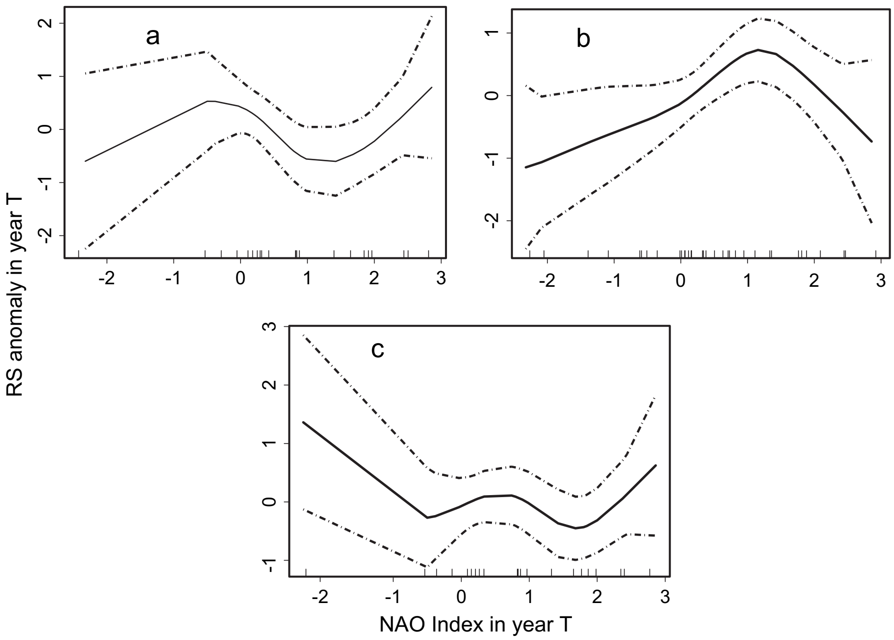

Figure 3. Estimated effects of the North Atlantic Oscillation (NAO) index on recruits per spawner (RS) anomalies of American plaice (a), Georges Bank haddock (b), and Southern New England winter flounder (c).

England winter flounder had a convex response to increasing NAO values. In contrast, Georges Bank haddock RS anomalies had a concave response to increasing NAO values. In this case, positive NAO values had a positive effect on haddock recruitment strength. Overall, the RS anomaly responses to NAO differed in shape among the three stocks.

For the NAO_1 variable, the response of the RS anomalies was also nonlinear and more varied than for the NAO variable (Figure 4). The shapes of the RS anomalies for Georges Bank and Gulf of Maine cod were similar with an alternating concave then convex response to increasing NAO_1 values. A positive NAO_1 value was associated with negative RS anomalies for these stocks. The shapes of the RS anomaly response for Georges Bank yellowtail flounder and American plaice were also similar; both stocks had positive RS anomalies when the NAO_1 was positive. The shape of the RS anomaly response for redfish was concave and decreasing with increasing NAO_1 values. As with the NAO, the shape of the RS anomaly response was nonlinear and differed among stocks.

The NAO_2 variable also produced a diverse set of nonlinear RS anomaly responses (Figure 5). The RS anomaly response was concave with increasing NAO_2 for five stocks: Gulf of Maine winter flounder, witch flounder, and Georges Bank cod, haddock, and yellowtail flounder. For those stocks, positive NAO_2 values were associated with positive RS anomalies. In contrast, three stocks had negative RS anomalies associated with a positive NAO_2 index; Gulf of Maine cod and yellowtail flounder and summer flounder. For redfish, RS anomalies appeared to increase with increasing NAO_2 values. Overall, the shape of RS anomaly responses to the NAO_2 variable was nonlinear and differed among stocks.

The response of the RS anomalies to temperature variation also differed among stocks (Figure 6). For American plaice, the RS anomaly response was convex, with increasing values of the first principal component of temperature. In contrast, the shape of the RS anomaly for Georges Bank haddock to the first principal component of temperature was concave. For redfish, the RS anomaly response switched from concave to convex with increasing values of the second principal component of temperature. The shape of the RS anomaly response for Georges Bank yellowtail flounder was convex, with increasing second principal component of temperature. Thus, the RS anomaly responses to temperature differed among stocks and were divided between first and second principal components effects.

The response of the RS anomalies to variation in windstress was convex with increasing windstress for both redfish and Southern New England winter flounder (Figure 7). This suggests that there is an intermediate range of favourable windstress values for both stocks.

On a regional basis, results of the GAM analyses using all variables indicate that Georges Bank stocks had the highest percentage of significant predictor variables (44%). The region with the next highest percentage was the Gulf of Maine (33%). Southern New England stocks had the lowest percentage (17%) of significant predictor variables.

Almost all stocks had one or more significant predictor variables. Redfish had the most significant predictors (4), and is the only live-bearing fish in this study. Four stocks

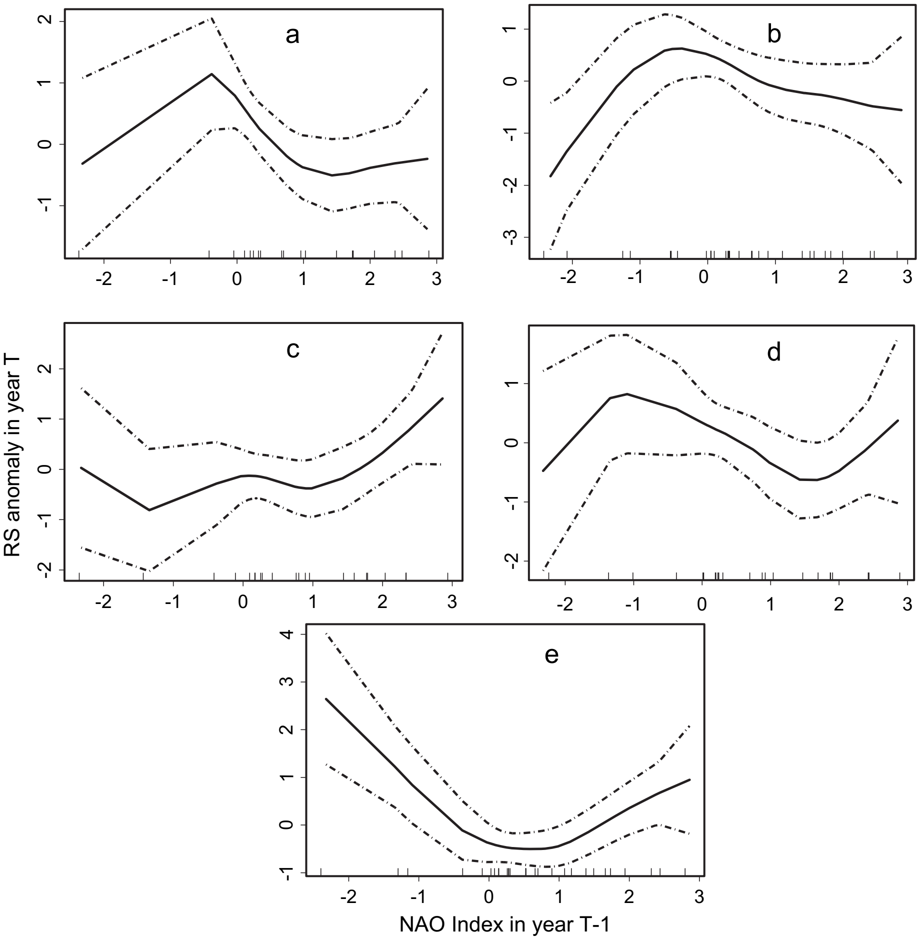

Figure 4. Estimated effects of the North Atlantic Oscillation (NAO) index forward-lagged by 1 year (NAO_1) on recruits per spawner (RS) anomalies of Gulf of Maine cod (a), redfish (b), American plaice (c), Georges Bank cod (d), and Georges Bank yellowtail flounder (e).

had three significant predictors: American plaice, Georges Bank haddock, yellowtail flounder, and Southern New England winter flounder. Of the remaining stocks, the only one without a significant predictor was Southern New England yellowtail flounder.

Results of the GAM analyses using only the three NAO variables showed that the NAO index forward-lagged by 2 years was significant for 9 out of 12 stocks and was the most important predictor of RS anomalies (Table 2). The NAO and NAO_1 variables were significant in three and eight stocks, respectively. Overall, the lagged NAO variables appeared to be more important than the NAO index itself.

Results of the GAM analyses using only NAO variables grouped by region indicate that the Gulf of Maine had the highest percentage of significant predictor variables (67%), followed by Georges Bank (55%). Southern New England stocks had the lowest percentage (33%) of significant predictor variables.

As in the analyses using all variables, almost all stocks had one or more significant predictor variables using only the NAO variables. Of the 12 stocks, Southern New England yellowtail flounder was the only stock with no significant predictor variables. All three NAO variables were significant for witch flounder. This species has the longest larval settlement time—up to 1 year. A majority of stocks had two significant NAO predictor variables (58%), while three had only one significant predictor.

Discussion

A key point of our analysis is that it is important to remove the influence of maternal factors on recruitment (to the extent possible) before attempting to evaluate the impacts of environmental factors. In general, recruitment depends on spawner abundance (Myers and Barrowman, 1996), although this relationship is often obscured by high inherent variation and observation errors. The approach of using recruits per spawner anomalies instead of absolute recruitment strength provides a straightforward way to

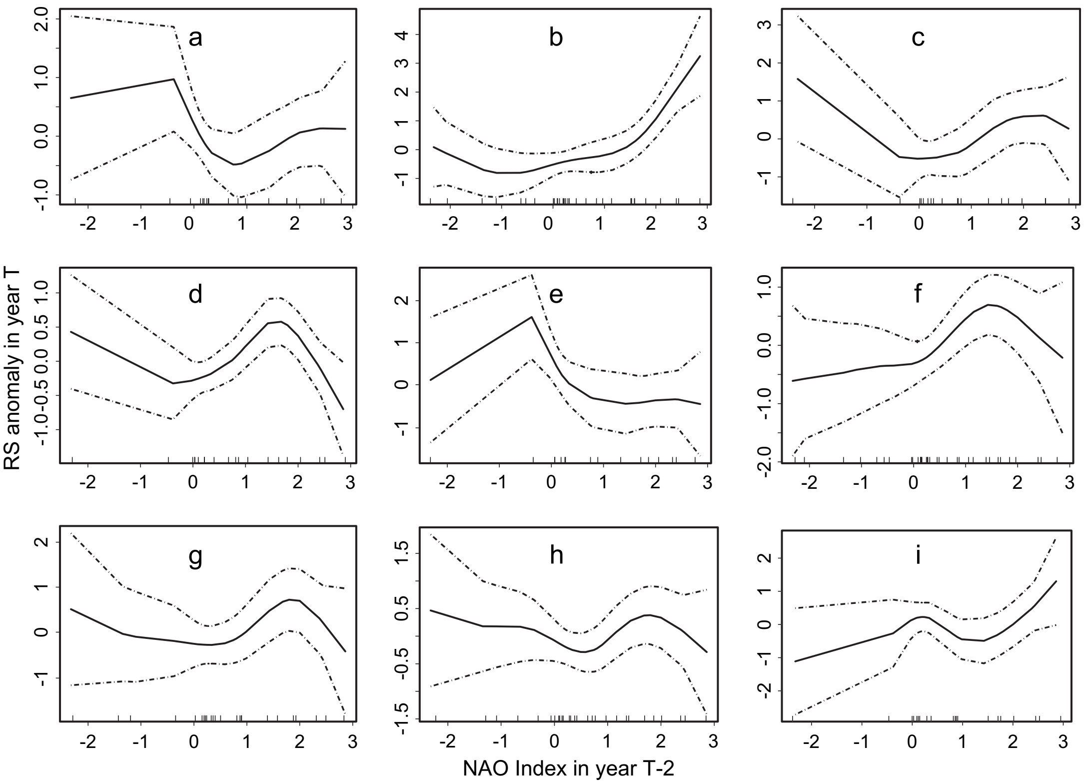

Figure 5. Estimated effects of the North Atlantic Oscillation (NAO) index forward-lagged by 2 years (NAO_2) on recruits per spawner (RS) anomalies of Gulf of Maine cod (a), redfish (b), Gulf of Maine winter flounder (c), witch flounder (d), Cape Cod−Gulf of Maine yellowtail flounder (e), Georges Bank haddock (f), Georges Bank cod (g), Georges Bank yellowtail flounder (h), and summer flounder (i).

separate the effects of two necessary causal mechanisms, positive maternal factors, and favourable environmental conditions.

The approach of evaluating the regional impact of year effects using nonparametric randomization tests is very general and could readily be applied to other ecosystems with extensive environmental and assessment data, such as the North Sea, for example. While the randomization approach provides no information on the mechanism of environmental influence, it does identify years that warrant further investigation. In this context, we found that 1987 was an anomalous year with positive recruits per spawner anomalies across all three regions. Polacheck *et al.* (1992) suggested that unusual geostrophic currents transported haddock larvae westward from Georges Bank to the Southern New England region in 1987 and had a positive impact on haddock recruits per spawner. In comparison, our results suggest that a broader-scale regional environmental factor was responsible for the positive and coherent effect on groundfish recruits per spawner anomalies in the Gulf of Maine through Southern New England. In this case, it seems more likely that enhanced vertical mixing and stratification under atypical wind conditions would have a positive effect on larval food supply and survival than favourable geostrophic currents.

In contrast, the finding that 1998 had a positive RS anomaly for Gulf of Maine stocks was likely related to the unusual intrusion of Labrador Subarctic Slope water into this region (Pershing *et al.*, 2001). In this case, the substantial change in the NAO index 2 years prior produced a lagged biological response owing to increased southerly transport of Labrador Subarctic Slope water. Last, the detection of negative impacts on recruits per spawner anomalies in 2000−2001 suggests that a broad-scale oceanographic or ecological change had a common negative impact on early life history stage survival of groundfish across regions. In this case, however, no mechanism has yet been identified. Overall, the finding that there were coherent positive or negative impacts on RS anomalies across regions and stocks in particular years suggests that models to predict recruitment need to account for atypical years. In this case, modelling environmental forcing as a mixture distribution with two or more component distributions to represent years with normal and atypical environmental variation may be a useful approach.

The nonparametric approach of using generalized additive models is especially appropriate when the functional form of the underlying model relating response, in this case RS anomalies, to one or more environmental factors is unknown. Since there are typically numerous factors that can

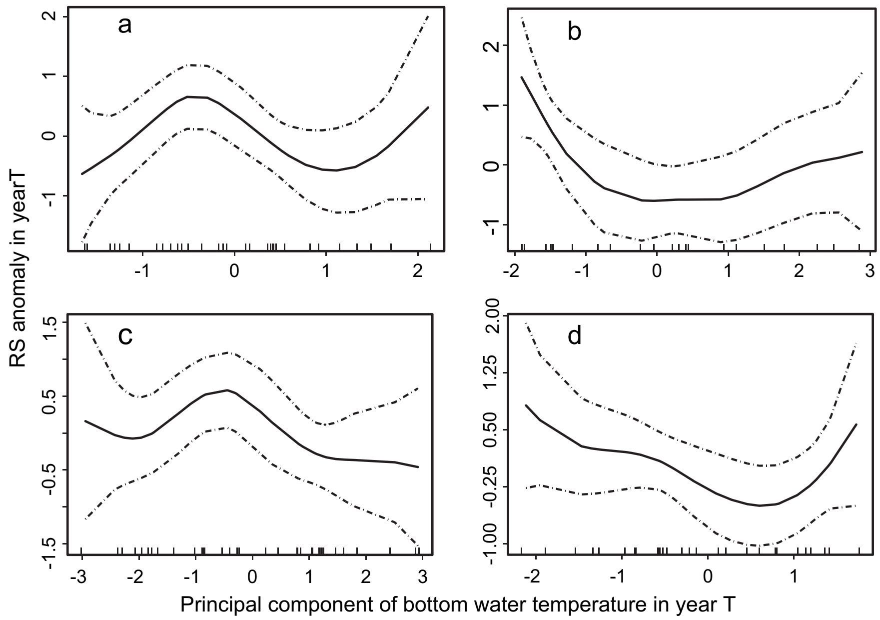

Figure 6. Estimated effects of the first principal component of water temperature anomalies on recruits per spawner anomalies of redfish (a), American plaice (b), and Georges Bank haddock (c), and estimated effects of the second principal component of water temperature anomalies on recruits per spawner anomalies of Georges Bank yellowtail flounder (d).

affect the recruitment process (e.g. see Shepherd *et al.*, 1984), we believe that this approach could have wider potential application in fisheries oceanography. In particular, GAM analyses provide a flexible approach for constructing a nonlinear predictor. This is clearly a positive feature when the focus is on empirical prediction. On the other hand, apparent correlations between recruitment and environmental factors may arise and later be found to be spurious or disappear over time (see, for example, Myers *et al.*, 1995). One potential cause for such changes is the attempt to use a linear correlation to model a nonlinear process.

Although the answer to the question, "Do environmental factors affect recruits per spawner anomalies of New England groundfish?" is a qualified "Yes", for most regions, the relative importance of the environmental factors differed among stocks. This is not surprising given differences in life history characteristics of the groundfish stocks. For Georges Bank haddock, recruitment strength had previously been found to be affected by autocorrelated error processes (Brodziak *et al.*, 2001), suggesting that low-frequency environmental forcing was important for this stock. However, for most stocks, the brevity of most of the available time-series and inherent variability of stock-recruitment data made it difficult to detect associations between RS anomalies and environmental factors. In general, one needs to observe several cycles of an oscillatory environmental factor to be able to discern whether it may have an important effect on the recruitment process. It is therefore not surprising that the NAO, which in our study had the longest time-series of any of the environmental factors, had a nonlinear effect on the RS anomalies of both haddock and redfish. These two stocks had the longest time-series of RS anomalies, and these larger sample sizes enhanced the ability to detect environmental effects. This also emphasizes the importance of maintaining long-term data sets and current monitoring programmes for future research.

It was somewhat surprising that the geostrophic current index was relatively unimportant for most stocks. Nonetheless, the dome-shaped pattern of the wind effect for redfish and Southern New England winter flounder was consistent with the optimal environmental window hypothesis of Cury and Roy (1989), which suggests that intermediate wind-stresses produce the best conditions for early life history stage survival under Ekman-type upwelling (Cury and Roy, 1989). The relative lack of detectable wind effects could also be due to aliasing of windstress with the NAO index, which affects the strength of westerly winds across the North Atlantic (Marshall *et al.*, 2001). While the methods used to construct the wind effect index may warrant further research, it may also be useful to evaluate the effects of windstress in isolation without attempting to model its impact on larval retention in continental shelf nursery waters. In this context, windstress may have a direct impact on larval survival through increased diatom production attributable to wind-induced vertical mixing (Mann, 1993). The wind-effect signal may have been masked by the calculation of a favourable direction for shoreward transport. The potential positive effect of wind-induced mixing and enhanced food availability might also explain the uniqueness of 1987 as a year in which overall groundfish RS anomalies were positive.

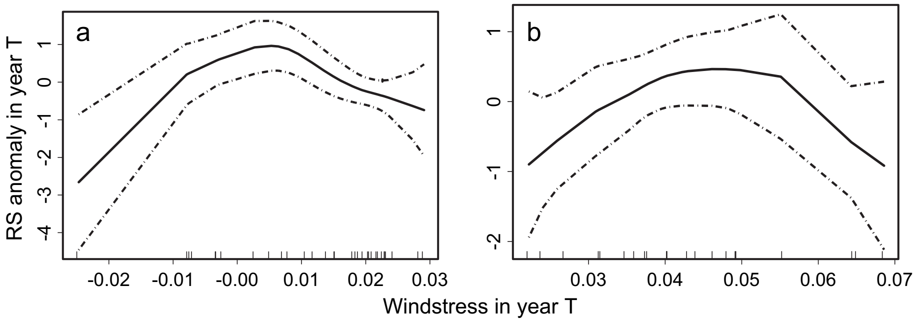

Figure 7. Estimated effects of windstress on recruits per spawner anomalies of redfish (a), and Southern New England winter flounder (b).

In the Southern New England region, there was some indication of a recent shift in the sign of RS anomalies in the randomization tests. Given that there were more years with positive average RS anomalies across regions in the 1980s through late-1990s, relative to the negative average, anomalies of more recent years suggest a potential regional effect. Although the hypothesis of regime shifts in oceanographic conditions has credible support in the Northeast Pacific (Francis *et al.*, 1998), it is unknown whether similar shifts occur in regions of the Northwest Atlantic. If such shifts do exist, it seems likely that they would be related to variations in the North Atlantic Oscillation.

The most important yet unsurprising finding in our analysis is that the NAO, a dominant climatic feature affecting the Northwest Atlantic (Marshall *et al.*, 2001), had the strongest detectable effect on RS anomalies. In particular, the NAO index and the NAO forward-lagged by 1 year both appeared to be important. For the NAO_1 effects, the 1-year lag may reflect autocorrelation in spatial processes induced by fluctuations in the NAO. While annual changes in the NAO and NAO_1 variables do affect wind patterns and storm frequency in a particular year, the NAO forward-lagged by two years had the most pronounced effect on RS anomalies in the region. In fact, the RS anomaly responses of 75% of the stocks were affected by the NAO_2 variable. This apparent effect is notable because it could provide a leading indicator of RS anomalies for some commercially exploited stocks. In particular, the three primary groundfish stocks on Georges Bank (cod, haddock, and yellowtail flounder) all exhibited positive RS anomalies when the NAO_2 variable was positive.

The relative importance of the NAO forward-lagged by 2 years suggests that an advective connection exists between the atmospheric forcing of the NAO and the biological response of recruits per spawner anomalies. The predominance of the NAO_2 is consistent with the hypothesis that hydrographic changes in the coupled slope water system in the Scotian Shelf and Gulf of Maine regions directly impact groundfish early life history stage survival. In particular, the 2-year lag in this apparent effect matches the lag between changes in regional slope water temperature and the NAO and also reflects the lagged association between the NAO and the position of the Gulf Stream. That is, there is generally a 2-year lag between changes in the NAO and associated changes in the position of the northern edge of the Gulf Stream (Taylor and Stephens, 1998). The position of the Gulf Stream influences the relative amount of warm, high-salinity Atlantic Temperate Slope Water and cool, low-salinity Scotian Shelf Water that enters the Gulf of Maine (Mountain, 2004). This, in turn, influences water mass properties, and also the shelf water volume of the entire northeast USA continental shelf ecosystem. Although decadal changes in the amount of shelf water volume were detected between the 1980s and the 1990s (Mountain, 2004), further research will be needed to identify and model the causal mechanisms affecting recruits per spawner anomalies of New England groundfish stocks.

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