

# Does spawning stock affect recruitment of New England groundfish?

Jon K.T. Brodziak, William J. Overholtz, and Paul J. Rago

**Abstract:** We evaluated the effects of spawning-stock size on the recruitment abundance of 11 groundfish stocks in waters off New England. Empirical patterns of association between spawning biomass and recruitment were investigated using nonparametric approaches. For most stocks, higher recruitment occurred at high stock sizes and lower recruitment at low stock sizes. Survival ratios, indexed by recruitment per unit of spawning biomass, were higher at low stock sizes and lower at high stock sizes—as expected under density dependence. To assess assumptions about recruitment dynamics, we analyzed constant-recruitment and compensatory and overcompensatory stock–recruitment models with uncorrelated and autocorrelated error structures, using Bayesian methods of statistical inference. Although no single model was adequate for all stocks, most groundfish had better than even odds of having density-dependent dynamics, and most had better than even odds of having dynamics with uncorrelated environmental variation. While some geographic and taxonomic differences in potential productivity were apparent, all stocks exhibited compensation in survival ratio at low stock sizes, albeit with substantial variation. These results indicate that conservation measures intended to increase the spawning biomass of New England groundfish will, on average, result in higher recruitment and, eventually, in increased and more stable fishery yields.

**Résumé :** Nous avons examiné les effets de la densité des reproducteurs sur l'importance du recrutement chez 11 stocks de poissons benthiques au large de la Nouvelle-Angleterre. Les patterns empiriques d'association entre la biomasse des reproducteurs et le recrutement ont été étudiés à l'aide de méthodes non-paramétriques. Pour la plupart des stocks, il y a un recrutement plus élevé lorsque la densité des reproducteurs est grande, et un recrutement faible lorsque la densité est faible. Les rapports de survie, exprimés comme le recrutement par unité de biomasse des reproducteurs, sont plus élevés lorsque la densité des reproducteurs est faible et plus bas lorsque la densité est élevée—comme cela arrive dans les cas de densité-dépendance. Pour évaluer diverses suppositions sur la dynamique du recrutement, nous avons analysé, à l'aide de méthodes bayésiennes d'inférence statistique, des modèles reliant la densité des reproducteurs et le recrutement, modèles de type constant, compensatoire et surcompensatoire, avec des structures d'erreur non-corrélées et autocorrélées. Bien qu'aucun modèle particulier ne se soit montré adéquat pour tous les stocks, la plupart des stocks ont une probabilité plus qu'aléatoire d'avoir une dynamique densité-dépendante et cette dynamique tend à n'être pas corrélée à l'environnement. Malgré certaines différences géographiques et taxonomiques dans la productivité potentielle, tous les stocks montrent de la compensation, bien qu'avec beaucoup de variation, dans le rapport de survie lorsque les densités des reproducteurs sont basses. Ces données indiquent que les mesures de conservation destinées à accroître la biomasse des reproducteurs chez les poissons benthiques de la Nouvelle-Angleterre résulteront, en moyenne, en un recrutement plus élevé et, éventuellement, en des rendements de pêche plus grands et plus stables.

[Traduit par la Rédaction]

## Introduction

Competing theories on whether climate, spawner abundance, or trophic interactions are the primary determinants of marine fish stock recruitment have been debated for decades. The mechanisms underlying recruitment variability have great practical significance for fishery management. Two dichotomous views are that either population-level

(density-dependent) processes or environmental (density-independent) processes primarily determine recruitment strength. While neither density-dependent nor density-independent regulation will explain recruitment variability in all cases, each has its proponents (Laevastu and Favorite 1988; Myers and Barrowman 1996 and references therein), and debate continues over which theory is best supported (Gilbert 1997; Hilborn 1997; Myers 1997). The relative importance of density-dependent versus density-independent processes is contingent upon species and ecosystem. In practice, quantifying the relative importance of each must be done on a case-by-case basis. In this context, we determined the relative importance of density-dependent and density-independent processes on recruitment of 11 commercially valuable groundfish stocks off the New England coast.

Many New England groundfish stocks have been overfished by distant-water and U.S. fleets over the past three decades (Murawski et al. 1997). Under provisions of the U.S.

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Sustainable Fisheries Act of 1996, rebuilding plans must be developed and implemented for all overfished resources within U.S. waters. The question of how rapidly stocks can be rebuilt depends, in large part, upon future recruitment. Because future recruitment will fluctuate, stochastic models of stock–recruitment relationships are essential to meaningfully evaluate rebuilding trajectories for depleted stocks. To this end, stock–recruitment data for 11 groundfish stocks in the Gulf of Maine, Georges Bank, and southern New England areas (Fig. 1) were used to analyze assumptions about stock–recruitment dynamics. These stocks included: Georges Bank haddock (*Melanogrammus aeglefinus*); Georges Bank and Gulf of Maine cod (*Gadus morhua*); Georges Bank, southern New England, and Gulf of Maine yellowtail flounder (*Limanda ferruginea*); Georges Bank and southern New England winter flounder (*Pseudopleuronectes americanus*); Gulf of Maine witch flounder (*Glyptocephalus cynoglossus*); Gulf of Maine American plaice (*Hippoglossoides platessoides*); and Gulf of Maine white hake (*Urophycis tenuis*).

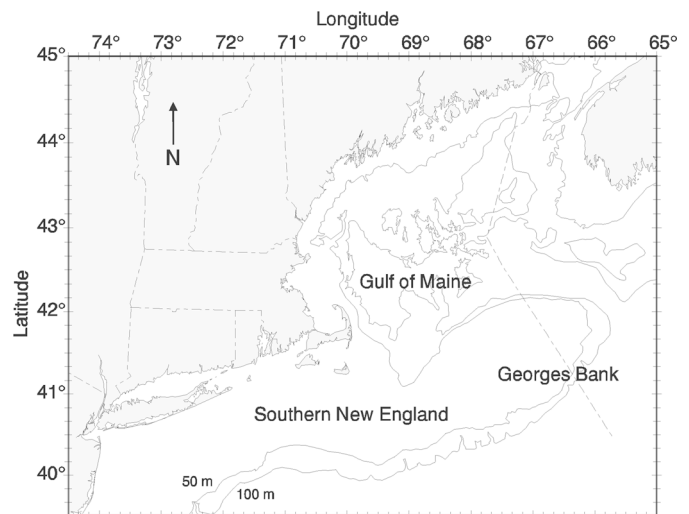
To analyze these data, we first enlarged our stock–recruitment data sets by extending the available time series backwards to include years not covered by sequential age-structured population analyses by relating absolute-population estimates to relative abundance indices from fishery-independent surveys. Empirical relationships in the enlarged data sets were analyzed to detect compensation (e.g., higher recruitment per spawner at low spawner abundance) and temporal trends in recruitment ( $R$ ), spawner abundance ( $S$ ), and recruitment per spawner ratios ( $R/S$ ). To assess assumptions about recruitment dynamics, we analyzed six compensatory stock–recruitment models: constant recruitment, compensatory, and overcompensatory (e.g., lower  $R$  at very high  $S$ ), with uncorrelated and serially correlated random variation. The appropriateness of stock–recruitment models was assessed using a small-sample form of Akaike's information criterion ( $AIC_C$ ; Burnham and Anderson 1998). We calculated the posterior probability of each stock–recruitment hypothesis from its relative  $AIC_C$ , using Bayes' theorem with an uninformative prior. These probabilities quantified the stock–recruitment model uncertainty for each of the 11 New England groundfish stocks. We also investigated variations in potential productivity by subarea and taxonomic group.

## Materials and methods

### Stock–recruitment data

For each of the 11 stocks, age-structured assessments were recently updated to assess stock status and provide management information (Northeast Fisheries Science Center 1999), using a sequential population analysis (SPA) model (ADAPT; Gavaris 1988; Conser and Powers 1990; National Research Council 1998). The ADAPT formulation uses age-specific abundance indices from research surveys to calibrate SPA estimates of stock size and fishing mortality. Estimates of population numbers at age from this SPA model were limited in time by the availability of catch-at-age estimates. As a result, each series of SPA-based stock-size estimates was much shorter than the full time series of fishery-independent abundance data available from the autumn groundfish bottom trawl survey conducted by the Northeast Fisheries Science Center (NEFSC; Azarovitz 1981) from 1963 onwards, except for Georges Bank haddock (Table 1). To extend and enlarge the time series of stock–recruitment data, we used the estimated catchability

**Fig. 1.** New England groundfish stock areas in the northwest Atlantic.



coefficients from the SPA,  $q = n \cdot N^{-1}$ , relating the survey abundance index  $n$  to the population size  $N$  estimated by SPA, to calculate recruitment and spawning-stock sizes from the 1960s to the present. This approach had been previously used to extend the time series of stock–recruitment data for Gulf of Maine cod (National Research Council 1998).

Estimates of catchability at age ( $q_a$ ) for the NEFSC autumn survey from the age-structured assessment were used to produce estimates of time series of recruitment for each stock, except for Georges Bank haddock. We defined the age of recruitment and its associated length range for each stock on the basis of age at capture in the commercial fishery. In some cases, this led to an older age of recruitment than was used in the assessment (typically, age-1 or age-2). Given the index of recruitment from the autumn survey during the  $y$ th year,  $I(y)$ , we computed recruitment in year  $y$  as the survey recruitment index divided by the age-specific catchability,  $R(y) = I(y) \cdot q_a^{-1}$ . Using survey data to measure recruitment may be less susceptible to errors in catch at age (owing to discarding or under-reporting of the catch) than SPA-based estimates (Myers 1998), but may also result in substantial measurement error, because less information is used to estimate stock size.

Estimates of survey catchability at age were also used to calculate spawning stock. The procedure that was used depended on the availability of survey age data. For the four stocks with age-specific survey time series for 1963–1998 (Georges Bank cod and yellowtail flounder; southern New England yellowtail flounder; and Gulf of Maine cod), age-specific catchabilities were directly applied to survey indices. Spawning biomass in year  $y$  ( $S(y)$ ), given the average weight of an age- $a$  spawner in year  $y$  ( $W_a(y)$ ), was

$$(1) \quad S(y) = \sum_a = \frac{I_a(y)W_a(y)}{q_a(y)}$$

For the six stocks lacking historical-survey age data (Gulf of Maine witch flounder, American plaice, white hake, and yellowtail flounder; and Georges Bank and southern New England winter flounder) but possessing length-composition data, a length cutoff representing the onset of full maturity at the time of survey was applied. Survey numbers at length were summed from the cutoff length to the maximum length and the mean length was calculated. Mean weights were converted from mean lengths using the length–weight equation for each stock. An estimate of average autumn survey catchability of fully mature age-classes ( $\bar{q}_s$ ) was computed as the average of survey catchabilities at age weighted by ADAPT

**Table 1.** Summary of stock–recruitment time series, Pearson correlation coefficients between estimated spawning biomass ( $S$ ) and recruitment ( $R$ ) with sequential population analysis (SPA) estimates, and maximum observed spawning biomass ( $S_{\text{MAX}}$ , millions of kilograms) for 11 New England groundfish stocks.

Stock	Scientific name	SPA series	Estimated series	Spawner ages	Recruitment age	Correlations		
						S	R	S <sub>MAX</sub>
Gulf of Maine	<i>Hippoglossoides platessoides</i>	1980–1996	1963–1994	Age-3+	Age-2	0.80***	0.87***	20.9
	<i>Glyptocephalus cynoglossus</i>	1982–1994	1963–1995	Age-4+	Age-3	0.69**	0.78***	128.4
	<i>Gadus morhua</i>	1982–1996	1963–1996	Age-2+	Age-2	0.66***	0.88***	85.7
	<i>Urophycis tenuis</i>	1985–1996	1963–1995	Age-3+	Age-2	0.70**	0.86***	34.0
	<i>Limanda ferruginea</i>	1985–1997	1979–1996	Age-2+	Age-2	0.48*	0.45*	2.4
Georges Bank	<i>Melanogrammus aeglefinus</i>	1931–1998	—	Age-2+	Age-1	—	—	199.5
	<i>Gadus morhua</i>	1978–1998	1963–1996	Age-2+	Age-2	0.48**	0.54**	233.8
	<i>Limanda ferruginea</i>	1973–1997	1963–1996	Age-2+	Age-2	0.85***	0.50**	46.4
	<i>Pseudopleuronectes americanus</i>	1982–1996	1963–1995	Age-3+	Age-2	0.63**	0.39*	18.5
Southern New England	<i>Pseudopleuronectes americanus</i>	1981–1997	1963–1996	Age-3+	Age-2	0.57**	0.64***	48.8
Winter flounder	<i>Pseudopleuronectes americanus</i>	1981–1997	1963–1996	Age-3+	Age-2	0.57**	0.64***	48.8
Yellowtail flounder	<i>Limanda ferruginea</i>	1973–1997	1963–1996	Age-2+	Age-2	0.76***	0.82***	122.9

Note: \*,  $0.20 \geq P > 0.05$ ; \*\*,  $0.05 \geq P > 0.01$ ; \*\*\*,  $P \leq 0.01$ .

estimates of numbers at age for the terminal year of the sequential population analysis ( $N_a$ ):

$$(2) \quad \bar{q}_s = \frac{\sum_a q_a N_a}{\sum_a N_a}$$

Spawning-stock biomass was the sum of fully mature age-classes of survey numbers at length ( $I_L(y)$ ) multiplied by the average autumn survey weight at length ( $W_L(y)$ ) divided by the average spawner catchability as

$$(3) \quad S(y) = \frac{\sum_L W_L(y) I_L(y)}{\bar{q}_s}$$

Length frequency information was inadequate to perform these calculations for one or two of the years for Gulf of Maine witch flounder (1984 and 1985), Georges Bank winter flounder (1989), and southern New England winter flounder (1966 and 1969).

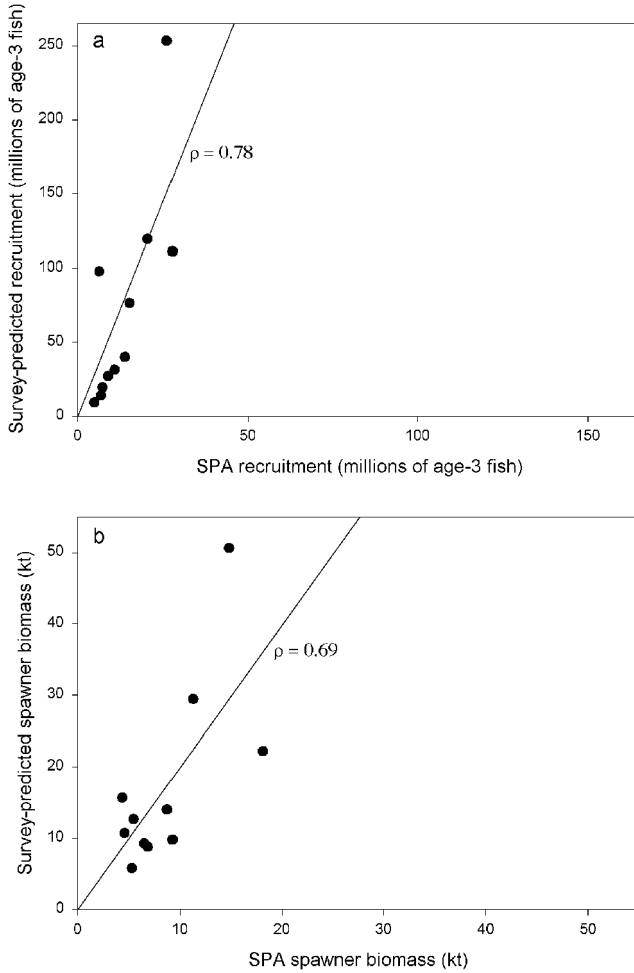
We compared estimated time series of spawning biomass and recruitment with the ADAPT time series where the two series overlapped (Table 1). The two time series of recruitments were positively correlated, with Pearson correlation coefficients ranging from 0.39 to 0.88 (Table 1): an example for recruitment of Gulf of Maine witch flounder shows a typical pattern (Fig. 2a). Similarly, the SPA and imputed series of spawning stock size estimates were highly positively correlated, with correlations ranging from 0.48 to 0.85: an example for spawning biomass of Gulf of Maine witch flounder shows a typical pattern (Fig. 2b). By using the catchability-based estimates, we added 141 stock–recruitment data points. With the exception of Gulf of Maine American plaice, these additional data provided greater contrast in recruitment and spawning-stock sizes.

### Empirical patterns

Empirical patterns of association between spawning biomass and recruitment were investigated using nonparametric approaches. The relative ranks of maximum and minimum recruitment ranked by the spawning biomass that produced them (see Myers and Barrowman 1996) were calculated, to show whether extreme values of  $R$  had been produced at relatively high (rank near 1) or low (rank near 0) spawning biomass. Similarly, the relative ranks of maximum- and minimum-survival ratios (recruitment per unit of spawner biomass ( $R/S$ )) ranked by spawning biomass and the ratios of expected  $R/S$  above median spawner abundance ( $E[(R/S)_{S > \text{med}(S)}]$ ) to expected  $R/S$  below median spawner abundance ( $E[(R/S)_{S < \text{med}(S)}]$ ) were calculated for each stock, to show whether survival ratios depended upon spawning-stock size. In theory,  $R/S$  values would be expected to decline as spawning stock increased and to increase as spawning stock declined, in the absence of depensation. To detect long-term trends in recruitment and spawning stock, linear regressions of  $R$  versus time and  $S$  versus time were computed. For comparison, temporal fluctuations in survival ratios were discerned using a locally weighted scatterplot smoother (Cleveland 1979) with a tension parameter of  $1/2$ . The significance of the relative rankings, ratios, and regression slopes were tested using randomization methods (Manly 1997). To do this, the randomization distribution was computed for each statistic (e.g., for the relative rank, ratio, or slope), using 5000 random permutations of the input data. The observed statistic was then compared with its randomized distribution, to assign probability values of obtaining a more extreme outcome by chance.

To detect association between recruitment and spawning-stock size, we applied log-linear models (e.g., Bishop et al. 1975) to compute the odds of increased recruitment given an increase in

**Fig. 2.** Comparisons of sequential population analysis (SPA) estimates and survey-based estimates of recruitment (*a*) and spawner biomass (*b*) for witch flounder along with estimated correlations ( $\rho$ ).



spawning biomass. Recruitment and spawning biomass time series were divided into groups (low, high) corresponding to observations below and above the median: an example for Georges Bank haddock shows the typical pattern of high variability in recruitment both above and below the median spawning biomass (Fig. 3). The association between recruitment and spawning biomass was summarized by a  $2 \times 2$  contingency table. The response variable ( $n_{S,R}$ ) was the number of observations (i.e., years) for each combination of the two levels of  $R$  and  $S$ , where index values of 1 and 2 indicated observations below and above the median, respectively. The odds that  $R$  and  $S$  coincided were determined from the  $2 \times 2$  contingency table. For example, the conditional probability of attaining a high  $R$  when  $S$  was high was  $n_{22}/(n_{21} + n_{22})^{-1}$ . Given the conditional probabilities, the odds ( $\Omega$ ) of attaining a high versus low  $R$  when  $S$  was above its median was

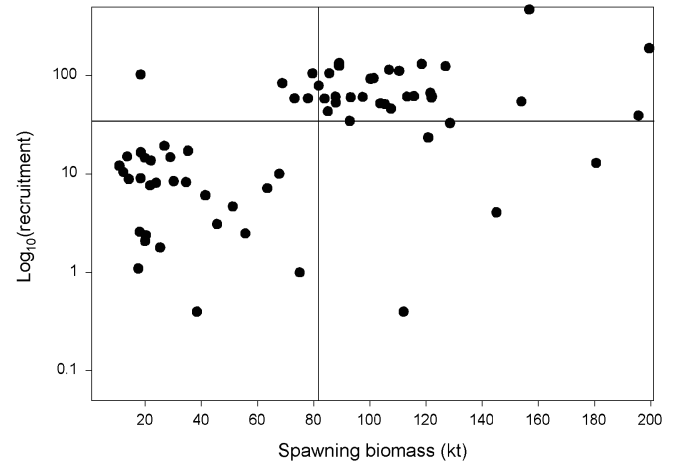
$$(4) \quad \Omega_{S_{\text{HIGH}}} = \frac{\Pr(R_{\text{HIGH}} | S_{\text{HIGH}})}{\Pr(R_{\text{LOW}} | S_{\text{HIGH}})} = \frac{n_{22}}{n_{21}}$$

while the odds of attaining a high  $R$  versus low  $R$  when  $S$  was below its median was

$$(5) \quad \Omega_{S_{\text{LOW}}} = \frac{\Pr(R_{\text{HIGH}} | S_{\text{LOW}})}{\Pr(R_{\text{LOW}} | S_{\text{LOW}})} = \frac{n_{12}}{n_{11}}$$

The odds ratio, denoted as  $O$ , was

**Fig. 3.** Scatterplot of Georges Bank haddock recruitment and spawning biomass in relation to median recruitment (horizontal line) and median spawning biomass (vertical line), 1931–1998.



$$(6) \quad O = \frac{\Omega_{S_{\text{HIGH}}}}{\Omega_{S_{\text{LOW}}}} = \frac{n_{11}n_{22}}{n_{12}n_{21}}$$

An odds ratio equal to  $Q$  indicated that the odds of obtaining  $R$  above the median when  $S$  was high was  $Q$  times greater than the odds of obtaining  $R$  above the median when  $S$  was low. By symmetry,  $O^{-1}$  was the odds ratio of obtaining  $R$  above the median when  $S$  was low. Statistical significance of the odds ratio was assessed using the standard  $\chi^2$  statistic (which is reasonable when the number of observations exceeds the number of cells by a factor of from four to five). The expected value of recruitment when  $S$  was above or below the median was estimated as the geometric mean of the recruitment. The ratio of the geometric mean  $R$  at high and low  $S$  (recruitment ratio) was used to measure the expected change in recruitment from low to high spawning-stock size.

### Stock–recruitment dynamics

We chose a set of models of stock–recruitment dynamics that was consistent with the empirical patterns. This indicated that spawning stock and recruitment were strongly correlated for some stocks, implying that modeling density dependence was important, and that recruitment variability was substantial across stocks; hence, modeling apparent random variation was important. Each model had a deterministic component accounting for compensation and a stochastic component accounting for environmental variability.

The deterministic component was either a density-independent, a compensatory, or an overcompensatory model. The density-independent model was  $R = \mu_R$ , where  $\mu_R$  was mean recruitment for the observed time series. The compensatory model was a modified Beverton–Holt curve (Mace and Doonan 1988), with  $R$  related to  $S$  as

$$(7) \quad R = \frac{4zR_{\text{MAX}}S}{S_{\text{MAX}}(1-z) + S(5z-1)}$$

where  $S_{\text{MAX}}$  is the maximum observed level in the stock–recruitment data;  $R_{\text{MAX}}$  is the maximum expected recruitment at a spawning-stock size of  $S_{\text{MAX}}$ ; and  $z$  is the steepness of the modified Beverton–Holt curve computed as the ratio of  $R$  at 20% of  $S_{\text{MAX}}$  to  $R_{\text{MAX}}$ . The overcompensatory model was a Ricker curve:

$$(8) \quad R = Se^{\alpha+\beta S}$$



where  $\alpha$  is the slope at the origin and  $\beta$  is the strength of density dependence in the relationship. The constant-recruitment model represented unbounded compensation as spawner abundance decreased, while the Beverton–Holt and Ricker curves represented the extremes of density-dependent behavior; recruitment either approaches an asymptote or decreases with spawning stock.

The stochastic component was represented by a multiplicative lognormal or an autoregressive multiplicative lognormal error structure with a lag of 1 year. The stochastic component was multiplied by the deterministic component, denoted as  $f(S_i)$  for the  $i$ th data point, to obtain the stock–recruitment model:

$$(9) \quad \hat{R}_i = f(S_i)e^{\varepsilon_i}$$

For uncorrelated errors, the  $\varepsilon_i$  were iid Gaussian random variables with zero mean and constant variance  $\sigma^2$ . In this case, the error variance ( $\sigma^2$ ) was a parameter to be estimated. For autoregressive lag-1 errors, the  $\varepsilon_i$  were distributed as

$$(10) \quad \varepsilon_i = \phi\varepsilon_{i-1} + w_i$$

where  $|\phi| < 1$ ,  $\text{Var}(\varepsilon) = \sigma^2$ ,  $w_i \sim N(0, \sigma_w^2)$ , and  $\sigma_w^2 = (1 - \phi^2)\sigma^2$  and the autoregressive coefficient and the error variance were additional model parameters to be estimated. We chose a multiplicative lognormal error term, because this positively skewed distribution arises naturally when groundfish survival rates during early life history are affected by numerous independent random events. The autoregressive error term was included to model serial correlation in random environmental variation. This choice of error structure allowed successive recruitments to be correlated when the effects of environmental forcing were strong—for example, periods of good recruitment followed by periods of poor recruitment—regardless of the deterministic component. Overall, this led to six possible models with a wide range of possible dynamical behavior.

The support functions, or loglikelihoods ( $\log L$ ), for a total of  $n$  stock–recruitment data points ( $R_i, S_i$ ) with uncorrelated lognormal errors (eq. 11) and autoregressive lag-1 correlated lognormal errors (eq. 12) (see Seber and Wild 1989) were

$$(11) \quad \log L(\theta, \sigma^2) = -\frac{n}{2} \log(2\pi) - n \log \sigma^2 - \sum_{i=1}^n \log R_i - \frac{1}{2\sigma^2} \sum_{i=1}^n (\log R_i - \log f(S_i))^2$$

$$(12) \quad \log L(\theta, \sigma^2, \phi) = -\frac{n}{2} \log(2\pi) - n \log \sigma_w^2 - \sum_{i=1}^n \log R_i - \frac{1}{2} \log(1 - \phi^2) - \frac{1}{2\sigma_w^2} \sum_{i=2}^n (\log R_i - \phi \log R_{i-1} - \log f(S_i))^2 + \phi \log f(S_{i-1})^2 - \frac{(1 - \phi^2)}{2\sigma_w^2} (\log R_1 - \log f(S_1))^2$$

Maximum likelihood estimates (MLEs) of model parameters were computed using these support functions and the estimated time series of stock–recruitment data (Table 1). For stocks with gaps in stock–recruitment data, we used the longest continuous time series, in order to fit the autoregressive models. In particular, time series for estimating stock–recruitment models for Gulf of Maine witch flounder, Georges Bank winter flounder, and southern New England winter flounder were limited to 1963–1983, 1963–1988, and 1970–1996, respectively.

Likelihood-based selection criteria were applied to evaluate candidate models using two approaches. In the standard approach, we

applied  $\text{AIC}_C$  (Burnham and Anderson 1998 and references therein), a bias-corrected form of AIC, to select a single best model. The value of  $\text{AIC}_C$  for a model fit to data set  $D$ , with  $K$  parameters,  $n$  data points, and likelihood value  $L(D|\Theta)$  at the MLE  $\Theta$ , equals

$$(13) \quad \text{AIC}_C = -2 \log L(D|\Theta) + 2K + \frac{2K(K+1)}{n-K-1}$$

The best model had the lowest  $\text{AIC}_C$  value. However, when  $\text{AIC}_C$  values were very similar among models, support for a single best model was clearly limited.

Alternatively, Bayes' theorem was applied to evaluate the relative performance of each model. We computed the probability that each candidate model was correct given the available data. Estimated  $\text{AIC}_C$  values were used to measure the relative likelihood of each model, with a penalty applied for the number of parameters that differed, according to the assumed error structure, viz., let  $\underline{M} = \{M_k\}$  denote the set of candidate models and let  $M_{\text{MAX}}$  denote the model with the maximum  $\text{AIC}_C$  value;  $M_{\text{MAX}}$  is the least likely model in  $\underline{M}$ . Thus, for a given set of stock–recruitment data  $D$  and model  $M$  with a corresponding  $\text{AIC}_C$  value of  $\text{AIC}_C(D|M)$ , the likelihood ratio of model  $M$  to the least likely model is  $\Lambda(D|M, M_{\text{MAX}})$  where

$$(14) \quad \Lambda(D|M, M_{\text{MAX}}) = \frac{L(D|\Theta_M)}{L(D|\Theta_{M_{\text{MAX}}})} \propto \frac{e^{-\frac{1}{2}\text{AIC}_C(D|M)}}{e^{-\frac{1}{2}\text{AIC}_C(D|M_{\text{MAX}})}}$$

The posterior distribution of relative model credibility was calculated from the likelihood ratio form of Bayes' theorem, using the model likelihood ratios relative to the least likely model and the prior distribution of each model,  $\text{Pr}(M_k)$ . The posterior probability of model  $M$ , denoted by  $\text{Pr}(M|D)$ , is the product of its likelihood ratio and prior probability divided by a normalizing constant:

$$(15) \quad \text{Pr}(M|D) = \frac{\Lambda(D|M, M_{\text{MAX}})\text{Pr}(M)}{\sum_{M_k \in \underline{M}} \Lambda(D|M_k, M_{\text{MAX}})\text{Pr}(M_k)}$$

In the absence of any prior information on the credibility of candidate models, we assumed equal prior probabilities for each of the six possible models. Given the posterior model probabilities, the expected value of the autoregressive parameter,  $E[\phi]$ , was computed for each stock, to show the strength of serial correlation in the stock–recruitment data. Similarly, the posterior odds ratio of density-dependent (Beverton–Holt or Ricker curves) to density-independent (constant-recruitment) models and the posterior odds ratio of uncorrelated to serially correlated environmental variation were computed for each stock.

To evaluate the strength of regional or taxonomic patterns in potential productivity, model results were compared among areas and related species. Regional comparisons were made by grouping stocks into two areas: (1) Georges Bank (haddock, cod, yellowtail flounder, and winter flounder) and southern New England (yellowtail flounder and winter flounder) and (2) the Gulf of Maine (cod, witch flounder, American plaice, yellowtail flounder, and white hake). Taxonomic groups included gadids (Georges Bank haddock and cod; and Gulf of Maine cod and white hake) and flounders (Georges Bank yellowtail and winter flounders; Gulf of Maine witch flounder, American plaice, and yellowtail flounder; and southern New England yellowtail and winter flounders). To contrast productivity of recruitment per unit area among groups, average group values were calculated for the expected ratio of recruitment at maximum observed spawning biomass to size of the mean area occupied by the stock ( $R(S_{\text{MAX}})/\text{Area}$ ). For each stock, the expected values of these ratios were computed, using the MLEs of  $R(S_{\text{MAX}})$  and the model probabilities  $\text{Pr}(M|D)$ .

## Results

### Empirical patterns

Recruitment variability was substantial for all 11 stocks. Coefficients of variation ( $CV = 100 \cdot SD \cdot \text{mean}^{-1}$ ) of  $R$  ranged from 59 to 133%. The relative rank of the  $S$  that produced the maximum recruitment ( $\max(R)$ ) in the spawning biomass time series was in the upper half of the data for 7 of the 11 stocks, and the relative rank of  $\max(R)$  for Georges Bank haddock was significant (Table 2). Similarly, the relative rank of the  $S$  in the spawning biomass time series that produced the minimum recruitment ( $\min(R)$ ) was in the lower half of the data for 7 of the 11 stocks. Thus, despite substantial variability, the highest recruitments were generally produced at higher spawning biomasses and vice versa.

Variability in survival ratios was even greater than for recruitment. Coefficients of variation of  $R/S$  ranged from 69 to 232%, with most CVs near or above 100%. For all 11 stocks, the relative rank of the spawning stock that produced the maximum  $R/S$  value was below the median (Table 2). Gulf of Maine witch flounder and southern New England yellowtail flounder had significant relative ranks of  $\max(R/S)$ . Thus, per capita production of recruits peaked when spawning biomass was below the median. Similarly, the minimum  $R/S$  value occurred when spawning stock was above the median for 9 of the 11 stocks, and the relative rank of  $\min(R/S)$  was significant for 6 of the 11 stocks. These patterns were consistent with expected compensation in stock–recruitment dynamics at higher stock sizes. The ratio of average  $R/S$  when  $S$  was above its median to the average  $R/S$  when  $S$  was below its median was less than unity for 10 of the 11 stocks and was significantly less than unity for 8 of the 11 stocks. Thus, survival ratios were, on average, lower at high spawning biomass and higher at low spawning biomass, as would be expected if density-dependent mechanisms were important.

Long-term declines in spawning stock and recruitment were detected for several stocks. Linear-regression analyses (Table 2) showed that 9 of the 11 stocks had a significant declining trend in spawning-stock biomass (e.g., Georges Bank haddock, cod, and yellowtail and winter flounders; Gulf of Maine cod, witch flounder, and American plaice; and southern New England yellowtail and winter flounders). The remaining two stocks, Gulf of Maine white hake and Gulf of Maine yellowtail flounder, had no time trend in spawning stock. Recruitment showed a significant declining trend for four stocks (Table 2): Georges Bank haddock and yellowtail flounder and southern New England yellowtail and winter flounders. One stock, Gulf of Maine witch flounder, had a significant increasing trend in recruitment. The remaining six stocks had no apparent trend in recruitment. Overall, the majority of stocks have experienced long-term declines in spawning stock, while long-term declines in recruitment were apparent in about one-third of the stocks.

Scatterplots of  $R/S$  values (with plot symbols proportional to annual recruitment) and locally weighted regression lines showed temporal changes in survival ratios for several stocks. In the Gulf of Maine, survival ratio ( $R/S$ ) and recruitment trends varied by stock. For Gulf of Maine American plaice (Fig. 4a),  $R/S$  generally increased from 1962 onwards, with recruitment markedly increasing in the late 1980s. For

Gulf of Maine witch flounder (Fig. 4b),  $R/S$  and recruitment were relatively stable during 1960–1980 but, subsequently, have substantially increased. In contrast, the survival ratio for Gulf of Maine cod (Fig. 4c) increased during 1963–1980 and has since declined. Recruitment for this stock was relatively high during the 1970s but has been much lower in recent years. For Gulf of Maine white hake (Fig. 4d),  $R/S$  values decreased during the period from 1960 to the mid-1970s, increased from the mid-1970s to the mid-1980s, and have since declined. Recruitment in this stock has increased since about 1980. For Gulf of Maine yellowtail flounder (Fig. 4e), survival ratios were relatively low and constant during 1980–1985 and 1990–1995 but were higher during the late 1980s. Recruitment was relatively high during the mid-1980s to early 1990s. Overall, survival ratios of the two Gulf of Maine gadid stocks have decreased in recent years, while survival ratios of two out of three flounder stocks have increased.

Within the continental shelf waters of Georges Bank and southern New England, haddock (Fig. 4f) had above-average  $R/S$  values, high spawning-stock sizes, and high recruitments during 1930–1960. Survival ratios then declined moderately from the mid-1960s to the mid-1970s, with marked declines in recruitment and spawning stock. Subsequently, both recruitment and  $R/S$  have moderately increased. By contrast, for Georges Bank cod (Fig. 4g),  $R/S$  has been increasing since roughly 1980, with high recruitment occurring intermittently throughout the time series. Georges Bank yellowtail flounder exhibits yet another pattern (Fig. 4h), with  $R/S$  relatively constant during 1960–1980, moderately decreasing during the 1980s, and then slightly increasing during the mid-1990s. Recruitment for this stock was high during the 1960s and 1970s and declined substantially after 1980. Georges Bank winter flounder has exhibited an increasing trend in  $R/S$  since 1970 (Fig. 4i), with a period of relatively high recruitment in the 1980s. Southern New England winter flounder show a cyclical pattern in  $R/S$  (Fig. 4j), with decreasing trends during the 1960s and late 1970s and increasing trends during the mid-1970s and from the 1980s onwards. Recruitment in this stock appeared to be higher during periods of decreasing  $R/S$ . Southern New England yellowtail flounder showed no trend in  $R/S$  during 1960–1990 (Fig. 4k), but have shown an increasing trend since 1990. Recruitment in this stock was relatively high during the 1960s and during 1980–1981, but has been low otherwise. Overall, the Georges Bank and southern New England stocks exhibited heterogeneous trends in  $R/S$  and recruitment.

Changes in  $R/S$  values were generally concordant with those predicted by stock–recruitment theory. For the nine stocks that exhibited significant long-term declines in spawning biomass, there was a tendency for  $R/S$  values to have increased in recent years. In contrast, the two stocks where spawning stock varied without trend, Gulf of Maine white hake and Gulf of Maine yellowtail flounder, did not have increasing trends in survival ratio in recent years. Thus, the expectation of stock–recruitment theory that  $R/S$  should increase as spawning stock decreases was evident across stocks and showed that stock–recruitment models need to reflect this compensatory behavior. In addition, temporal changes in the  $R/S$  values of some stocks showed that mod-

**Table 2.** Summary of relative rankings of maximum and minimum recruitment ( $\max(R)$  and  $\min(R)$ , respectively) ranked by spawner abundance, relative rankings of maximum and minimum recruitment per spawner ( $\max(R/S)$  and  $\min(R/S)$ , respectively) ranked by spawner abundance, ratios of expected  $R/S$  above median spawner abundance  $E[(R/S)_{S>\text{med}(S)}]$  to expected  $R/S$  below median spawner abundance  $E[(R/S)_{S<\text{med}(S)}]$  and their corresponding one-tailed probability values based on randomization tests for 11 New England groundfish stocks, along with slopes of linear regressions of recruitment versus time and spawning biomass versus time and their two-sided probability values of estimated slopes based on randomization tests.

	Relative ranking of $S$				$E[(R/S)_{S>\text{med}(S)}]/$	Regression slope	
Stock	Max( $R$ )	Min( $R$ )	Max( $R/S$ )	Min( $R/S$ )	$E[(R/S)_{S<\text{med}(S)}]$	$R$	$S$
<b>Gulf of Maine</b>							
Americian plaice	0.13	0.71	0.13*	0.97**	0.39***	1.34*	-0.19**
Witch flounder	0.23	0.97	0.00***	0.97**	0.09***	2.53***	-2.95***
Cod	0.94*	0.15*	0.12*	0.88*	0.57*	-0.03	-0.74**
White hake	0.28	1.00	0.06*	1.00***	0.48***	0.19*	0.19*
Yellowtail flounder	0.76	0.35	0.06*	0.82*	0.20**	0.14	0.01
<b>Georges Bank</b>							
Haddock	0.95**	0.77	0.09*	0.77*	1.14	-1.36***	-1.57***
Cod	0.64	0.27	0.12*	1.00***	0.50**	-0.44*	-2.63***
Yellowtail flounder	0.67	0.21	0.06*	0.21	0.70*	-2.83***	-0.96***
Winter flounder	0.32	0.06*	0.32	1.00***	0.36***	0.05	-0.19***
<b>Southern New England</b>							
Winter flounder	0.94*	0.13*	0.06*	0.97**	0.62**	-6.80***	-0.87***
Yellowtail flounder	0.73	0.30	0.00***	0.30	0.17**	-2.91***	-1.99***

Note: \*,  $0.20 \geq P > 0.05$ ; \*\*,  $0.05 \geq P > 0.01$ ; \*\*\*,  $P \leq 0.01$ .

els with correlated error structures might be needed to account for environmental forcing.

The chances of obtaining high recruitment generally improved when spawning-stock size was high (Fig. 5a). Odds ratios were significantly greater than unity for five stocks: Georges Bank haddock and yellowtail and winter flounders and Southern New England yellowtail and winter flounders. Further, the odds ratio was greater than unity for 8 of 11 stocks, the exceptions being Gulf of Maine cod, American plaice, and witch flounder. For two of these three stocks, the odds ratio was less than unity, suggesting the possibility of overcompensatory stock-recruitment dynamics. The recruitment ratio was also above unity for 8 of the 11 stocks (Fig. 5b). This implies that there was little risk of reduced recruitment if high spawning stocks were maintained. For many of the 11 stocks, substantial gains in productivity were obvious when  $S$  was high. For example, the odds of obtaining high recruitment were over 20 times greater when  $S$  was high for the Georges Bank haddock and yellowtail flounder stocks. Conversely, the odds of obtaining high  $R$  at low  $S$  were less than 1 in 20. Further, the expected year-class size would be over five times greater at high  $S$  for these two productive stocks. Overall, the odds ratio analyses indicated that density-dependent factors influence recruitment in most New England groundfish.

Two important patterns emerged from the empirical analyses. First, the stock-recruitment data were highly variable for all stocks. Any model of stock-recruitment dynamics would need to reflect this variability. Second, the 11 stocks exhibited different degrees of density dependence. Hence, no single model could be expected to be suitable for all stocks.

### Stock-recruitment dynamics

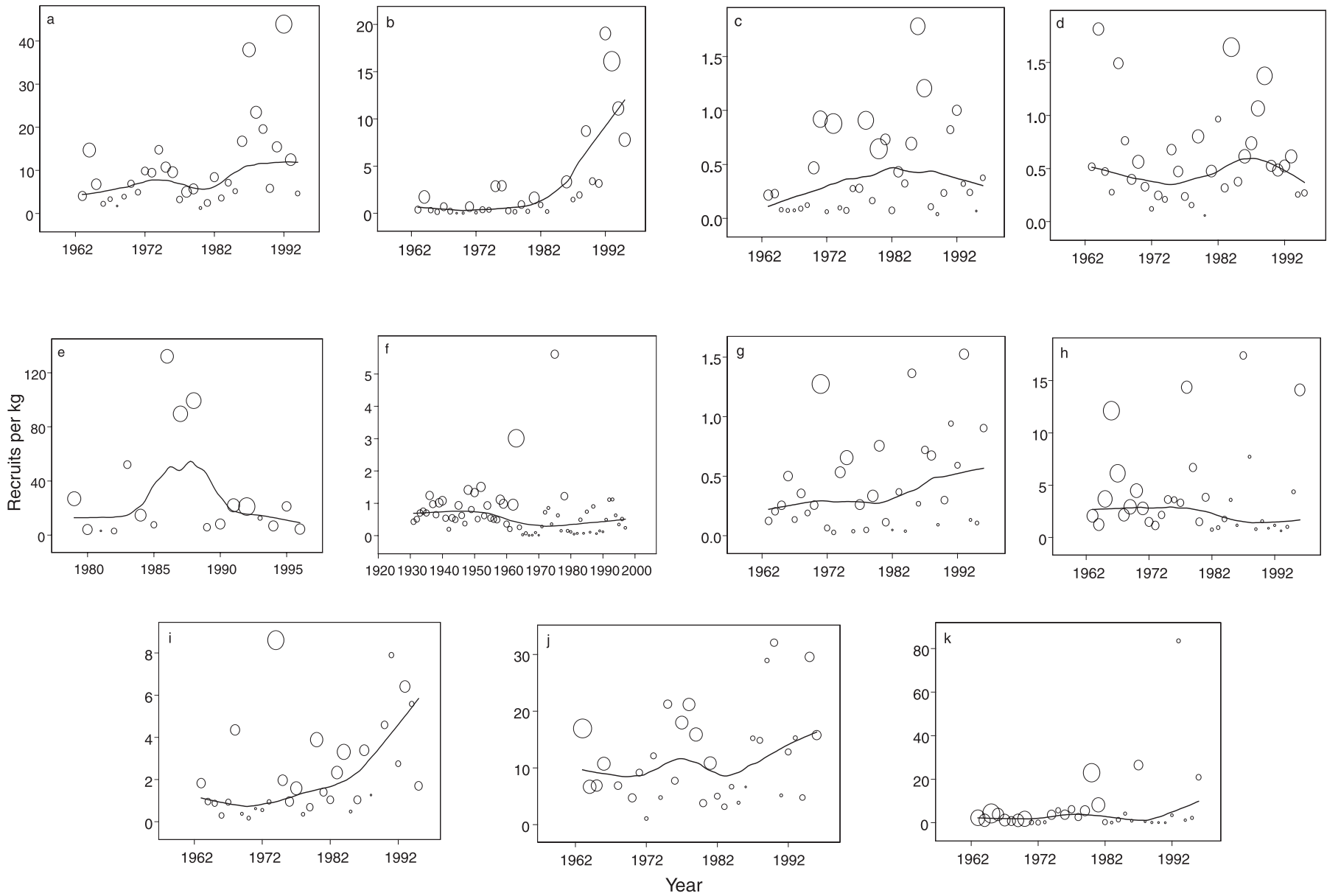
Selection of a single best model based on  $AIC_C$  values led to four models being chosen (Table 3). The constant recruitment with uncorrelated errors model had the minimum  $AIC_C$

value for Gulf of Maine cod and yellowtail flounder and Georges Bank cod. The constant recruitment with correlated errors model provided the best fit for southern New England winter and yellowtail flounders. The serially correlated Beverton-Holt model was chosen for three stocks: Gulf of Maine American plaice and Georges Bank haddock and yellowtail flounder. The uncorrelated Ricker model was selected for three stocks: Gulf of Maine witch flounder and white hake and Georges Bank winter flounder. Selected models for some stocks, for example, Gulf of Maine American plaice, Georges Bank haddock, and southern New England winter flounder, had only modest differences in  $AIC_C$ , indicating that these selections were not robust.

In contrast, the posterior probabilities explicitly quantified the relative probability of each dynamic model (Table 4), given the available data. For Gulf of Maine American plaice and Georges Bank haddock, there was considerable uncertainty as to the best model, because the odds ratio of the highest posterior probability model to the next most-likely model was roughly one. In contrast, for Gulf of Maine cod, witch flounder, and yellowtail flounder and southern New England yellowtail flounder, there was a high degree of certainty about a stock-recruitment model, with an odds ratio of the most likely model to the next most-likely model of greater than two. There were five other stocks that exhibited a moderate degree of certainty about a stock-recruitment model: Gulf of Maine white hake; Georges Bank cod and yellowtail and winter flounders; and southern New England winter flounder. Odds ratios for these stocks were between roughly 1.4 and 1.8. Thus, stock-recruitment models were well determined for some stocks but relatively uncertain for others.

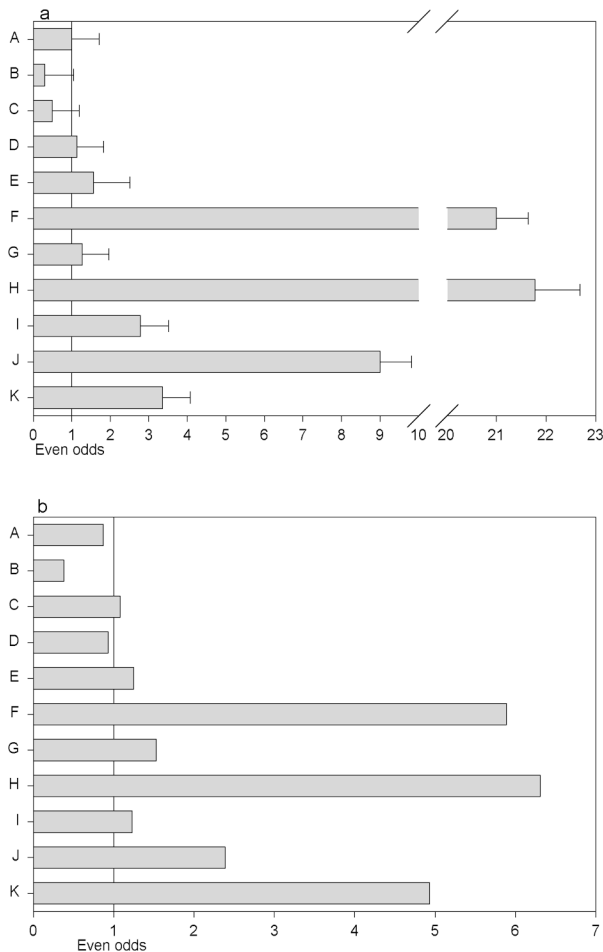
Eight of the 11 stocks had higher odds of having density-dependent versus density-independent dynamics, based on the posterior model probabilities (Table 4; Fig. 6a): Gulf of Maine American plaice, witch flounder, and white hake;

**Fig. 4.** Trends in survival ratios (recruitment per spawner), with circle size scaled relative to the magnitude of recruitment by stock, for Gulf of Maine American plaice (*a*), witch flounder (*b*), cod (*c*), white hake (*d*), and yellowtail flounder (*e*); Georges Bank haddock (*f*), cod (*g*), yellowtail flounder (*h*), and winter flounder (*i*); and southern New England winter flounder (*j*) and yellowtail flounder (*k*).





**Fig. 5.** Odds ratio of obtaining recruitment above the median when spawning-stock size was above its median versus when spawning-stock size was below its median (*a*) and recruitment ratio of geometric mean recruitment above median spawning-stock size to geometric mean recruitment below median spawning-stock size (*b*) for Gulf of Maine American plaice (A), witch flounder (B), cod (C), white hake (D), and yellowtail flounder (E); Georges Bank haddock (F), cod (G), yellowtail flounder (H), and winter flounder (I); and southern New England winter flounder (J) and yellowtail flounder (K).



Georges Bank haddock, cod, and yellowtail and winter flounders; and southern New England winter flounder. Density-independent dynamics were more likely over the range of observed stock–recruitment data for Gulf of Maine cod and yellowtail flounder and southern New England yellowtail flounder (Fig. 6a). For most stocks, the stock–recruitment data were relatively informative about whether density-dependent or density-independent dynamics were more likely over the range of observed data.

Similarly, 6 of the 11 stocks had high odds of having uncorrelated versus serially correlated environmental variation, based on the posterior model probabilities (Table 4; Fig. 6b). Gulf of Maine witch flounder, cod, white hake, and yellowtail flounder and Georges Bank cod and winter flounder had high odds of having uncorrelated errors. In contrast, four of the remaining five stocks had higher odds of having correlated errors: Gulf of Maine American plaice; Georges

Bank haddock and yellowtail flounder; and southern New England yellowtail flounder. For southern New England winter flounder, the odds of serially correlated errors were less than two to one. Thus, for most stocks, it was relatively clear whether uncorrelated or serially correlated environmental variation was more appropriate.

The strength of serially correlated environmental variation differed among stocks (Table 4). Three stocks, Georges Bank haddock and yellowtail flounder and southern New England yellowtail flounder, exhibited strong serial correlation, with values of  $E[\phi]$  of roughly  $\frac{1}{2}$  or greater. Serial correlation in the stock–recruitment data was moderate for two flounder stocks, Gulf of Maine American plaice and southern New England winter flounder, while serial correlation was negligible for the remaining six stocks. On average, flounders had stronger serial correlation (0.27) than gadids (0.12). Similarly, serial correlation was stronger, on average, for Georges Bank and southern New England stocks (0.34) than for Gulf of Maine stocks (0.07). Thus, taxonomic and geographic differences in serial correlation were apparent.

The expected recruitment at maximum observed spawning biomass per unit area was highest for Georges Bank haddock and lowest for Gulf of Maine white hake. Georges Bank and southern New England stocks had much higher expected recruitments at maximum observed spawning biomass per unit area (Table 4), averaging two and a half times more recruits per area (1281) than Gulf of Maine stocks (508). Similarly, four of the five stocks with expected recruitment at maximum observed spawning biomass per unit area above 1000 were from the continental shelf waters of Georges Bank or southern New England. Thus, geographic differences in potential productivities per unit area were apparent, with Gulf of Maine stocks having the lowest expected values.

There were also consistent differences in expected recruitment at maximum observed spawning biomass per unit area between flounders and gadids (Table 4). Flounders had a higher production of recruits per area at high spawning-stock size, on average (994), than gadids (817). Of the flounders, yellowtail flounder stocks had the highest production of recruits per area at high spawning-stock size, while Gulf of Maine witch flounder had the lowest. Among the gadids, Georges Bank haddock had an order of magnitude greater production of recruits per area at high spawning-stock size than did Georges Bank cod or Gulf of Maine cod or white hake. This suggested that taxonomic and evolutionary traits accounted for some of the differences in recruitment dynamics among stocks.

## Discussion

Our results provide strong evidence that spawning-stock size affects recruitment of New England groundfish. Maximum  $R$  occurred at relatively high spawner abundance and minimum  $R$  occurred at relatively low spawner abundance for the majority of stocks. The stock–recruitment data showed that the maximum survival ratio occurred at low spawner abundance for all stocks, and that survival ratios tended to increase with decreasing spawning-stock sizes. Similarly, the minimum survival ratio occurred at high

**Table 3.** Summary of differences ( $\Delta AIC_C$ ) between the bias-corrected Akaike's information criterion ( $AIC_C$ ) of the best model and the  $AIC_C$  values of alternative stock–recruitment models for 11 New England groundfish stocks.

Stock	$\Delta AIC_C$					
	Constant recruitment		Beverton–Holt		Ricker	
	Uncorrelated errors	Correlated errors	Uncorrelated errors	Correlated errors	Uncorrelated errors	Correlated errors
<b>Gulf of Maine</b>						
Americian plaice	4.05	0.34	1.57	—	8.04	2.70
Witch flounder	2.05	4.63	2.71	5.79	—	2.72
Cod	—	1.54	2.08	3.76	2.76	4.34
White hake	1.16	3.58	3.39	5.99	—	5.99
Yellowtail flounder	—	2.70	2.82	6.04	8.63	11.90
<b>Georges Bank</b>						
Haddock	36.02	3.36	16.04	—	16.03	0.02
Cod	—	1.72	1.73	2.69	0.95	1.93
Yellowtail flounder	30.89	0.73	5.70	—	5.66	1.12
Winter flounder	1.07	3.24	1.97	4.44	—	2.80
<b>Southern New England</b>						
Winter flounder	4.09	—	1.83	1.78	0.66	1.42
Yellowtail flounder	14.51	—	10.76	1.97	10.79	9.35

Note: The best model is denoted by “—.”

**Table 4.** Posterior probabilities of alternative stock–recruitment models (rounded to the nearest whole percentage), as well as expected values of the autoregressive parameter ( $E[\phi]$ ) and the recruitment (numbers of fish) at maximum observed spawning-stock size per unit area,  $E[R(S_{\max})]\cdot\text{km}^{-2}$ , for 11 New England groundfish stocks.

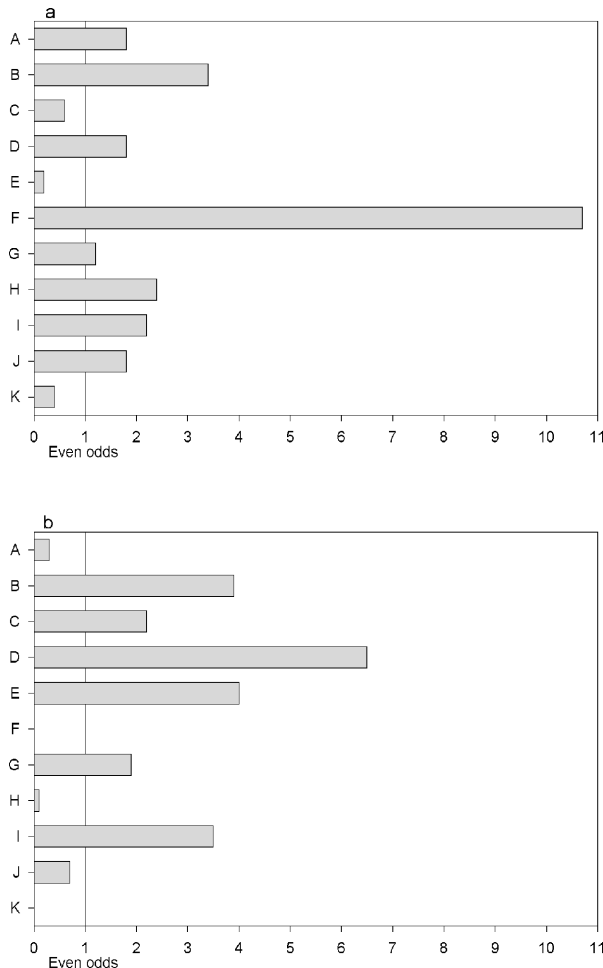
Stock	Posterior probability (%)						$E[\phi]$	$E[R(S_{\max})]\cdot\text{km}^{-2}$
	Constant recruitment		Beverton–Holt		Ricker			
	Uncorrelated errors	Correlated errors	Uncorrelated errors	Correlated errors	Uncorrelated errors	Correlated errors		
<b>Gulf of Maine</b>								
Americian plaice	5	31	17	37	1	10	0.32	547
Witch flounder	18	5	13	3	49	13	−0.01	272
Cod	43	20	15	7	11	5	0.05	217
White hake	28	8	9	2	50	2	0.00	96
Yellowtail flounder	64	17	16	3	1	0	0.02	1410
<b>Georges Bank</b>								
Haddock	0	9	0	46	0	45	0.50	2633
Cod	32	14	14	8	20	12	−0.07	323
Yellowtail flounder	0	29	2	42	2	24	0.70	1399
Winter flounder	23	8	15	4	40	10	0.02	239
<b>Southern New England</b>								
Winter flounder	4	32	13	13	23	16	0.25	1190
Yellowtail flounder	0	72	0	27	0	1	0.64	1900

Note:  $R$ , recruitment;  $S$ , spawner abundance.

spawning-stock size for 9 of the 11 stocks and the ratio of the expected survival ratio above median spawning stock to that below median spawning stock was less than unity for 10 of the 11 stocks. Thus, for most stocks, spawning stock affected the survival ratios and extreme values of recruitment, as one would expect if compensatory processes were important determinants of recruitment. Furthermore, the odds of higher  $R$  at higher  $S$  was above unity in 8 of the 11 stocks, showing that higher recruitment was more likely at high spawner abundance and, conversely, that lower recruitment was more likely at low spawner abundance, for most stocks.

Of these eight stocks, five showed strong evidence of dependence of recruitment on spawning stock based on the results of the log-linear model: Georges Bank haddock and yellowtail and winter flounders; and southern New England yellowtail and winter flounders. Association between recruitment strength and spawning-stock size in the other stocks was not detected. This is not surprising, given the variability and measurement error in our stock–recruitment data and the short time series in some cases. However, the absence of a statistically significant model does not imply that recruitment is independent of spawning-stock size over

**Fig. 6.** Odds of density-dependent dynamics versus density-independent dynamics (*a*) and odds of uncorrelated versus serially correlated environmental variation (*b*) for Gulf of Maine American plaice (A), witch flounder (B), cod (C), white hake (D), and yellowtail flounder (E); Georges Bank haddock (F), cod (G), yellowtail flounder (H), and winter flounder (I); and southern New England winter flounder (J) and yellowtail flounder (K).



all ranges of  $S$ , and recruitment must eventually decline as spawning stock declines. Although environmental variation undoubtedly influences recruitment strength, in this context the results of Myers and Barrowman (1996) are very important, because they show that, when a large number of stocks ( $n = 364$ ) is examined, the relationship between spawning stock and recruitment becomes readily apparent.

One important consequence of our results is that the benefit of maintaining higher spawning-stock sizes of New England groundfish is likely to be great. Results suggest that the odds of obtaining higher recruitment are increased when a stock is kept above the median level of spawning biomass. In a majority of cases, odds ratios were greater than one, indicating a better than 50% chance that recruitment would improve if spawning stock was kept above its observed median. Furthermore, recruitment ratios were greater than one for a majority of stocks, indicating that average recruitment was higher when spawning stock was above its median. For some stocks, recruitment can be expected to be markedly

higher if spawning stock is increased. For example, when the spawning biomass is kept above the median spawning biomass, the average year-class of haddock is expected to be about six times larger and the odds of above-average recruitment are 21 times greater than when spawning stock is below the median. This would result in larger fishery yields and revenues, more stable stock conditions, and enhanced net benefits (Edwards and Murawski 1993; Overholtz et al. 1995).

The Bayesian approach to depicting uncertainty about stock–recruitment models allows the quantification of the relative importance of density dependence and error structure in evaluating alternative stock–recruitment hypotheses. While the use of a suite of stock–recruitment models complicated our analyses, it provided a more robust and accurate depiction of our knowledge of the stock–recruitment dynamics of New England groundfish over the range of observed data, and represented a technical improvement over the assumption that a particular model would be adequate for all stocks based on theoretical grounds (National Research Council 1998). Undoubtedly, further refinements will occur in the understanding of stock–recruitment dynamics of New England groundfish by investigating nonstationarity in stock–recruitment relationships (Sainsbury 1998). For example, recent increases in the abundance of herring and mackerel may have impacted groundfish survival ratios (see, for example, Fogarty and Murawski 1998), and this may be an important trophic interaction to investigate.

The Bayesian analysis also provides the information needed to incorporate stock–recruitment model uncertainty into short-term projections of stock dynamics under alternative rebuilding plans. Given a set of harvest strategies, the probable consequence of applying each strategy can be evaluated by randomly selecting a stock–recruitment model for each simulation of the stock through the rebuilding time horizon. Stock–recruitment dynamics are then simulated according to the deterministic component related to spawning stock and the stochastic lognormal error term that may be correlated or uncorrelated. Simulation results can then be summarized in a decision table (Francis and Shotton 1997) depicting the expected consequences of each harvest strategy under the alternative stock–recruitment models, along with the probabilities that each model represents the true state of nature. While uncertainty in initial population size or other factors may also be incorporated into such projections, explicitly accounting for uncertainty in stock–recruitment dynamics will be a key feature for realistically characterizing the uncertainty in stock rebuilding plans (Brodziak et al. 1998), especially when small differences in goodness-of-fit measures exist between models.

The eight stocks that had better than even odds of having a density-dependent stock–recruitment model (Gulf of Maine American plaice, witch flounder, and white hake; Georges Bank haddock, cod, and yellowtail and winter flounders; and southern New England winter flounder) showed a variety of stock–recruitment dynamics, as indicated by the most likely model. However, model uncertainty was substantial for all of these stocks. The most likely models had probabilities ranging from 32 to 50%, with odds ratios of less than three for the most probable to the next most probable stock–recruitment

hypothesis. Thus, while most New England groundfish show evidence that recruitment is dependent on spawner abundance, the functional form of this density dependence is uncertain.

In contrast, environmental variation may be an important determinant of recruitment in the three New England groundfish stocks that had less than even odds of having a density-dependent model (Gulf of Maine cod and yellowtail flounder and southern New England yellowtail flounder). Of these, the best model was relatively certain for Gulf of Maine yellowtail flounder (64%) and southern New England yellowtail flounder (72%). Nonetheless, dependence of survival ratio on spawner abundance was generally indicated in these three stocks, as survival ratios declined when spawner abundance was high and minimum and maximum values occurred at high and low spawner abundances, respectively. Although constant-recruitment models may be useful for simulating recruitment in these stocks, it is risky to extrapolate these relationships below the observed range of spawning stock, given the long-term declines in spawning stock for Gulf of Maine cod and yellowtail flounder and Georges Bank cod.

While all stocks exhibited density dependence in survival ratio, only five had better than even odds of having serially correlated environmental variation: Gulf of Maine American plaice; Georges Bank haddock and yellowtail flounder; and southern New England winter and yellowtail flounders. Of these, Georges Bank haddock and yellowtail flounder and southern New England yellowtail flounder had very high probabilities (>95%) of having a stock-recruitment model with autoregressive errors. Although recruitment overfishing is generally believed to be the primary cause of New England groundfish depletion (Sinclair and Murawski 1997), environmental conditions can affect recruitment strength and will likely influence how rapidly some stocks can be rebuilt. Regardless, longer time series of stock-recruitment data will be needed to accurately measure the relative strengths of environmental-forcing versus density-dependent effects over decadal time scales.

Most New England groundfish did not appear to require serial correlation to model stock-recruitment dynamics. Of the six stocks that had less than even odds of having autoregressive errors (Gulf of Maine cod, witch flounder, white hake, and yellowtail flounder; Georges Bank cod and winter flounder), most were from the Gulf of Maine. Because these six stocks had high probabilities of having independent errors (range 66–87%), it was relatively certain that serial correlation was either unimportant or not detectable for these stocks.

Potential recruitment strengths of New England groundfish stocks appeared to differ by region. The continental shelf waters of southern New England and Georges Bank generally have higher primary productivity than Gulf of Maine waters (O'Reilly et al. 1987). The expectation that this productivity funnels upward through the food chain and leads to greater fish production was consistent with our findings. Recent survival ratios of the two most productive Georges Bank stocks (haddock and yellowtail flounder) and the two most productive southern New England stocks (yellowtail and winter flounders) have increased. The causes of

these trends are unknown, but may result from regional similarities in environmental forcing that are reflected in the strength of serial correlation in stock-recruitment models for the Georges Bank and southern New England stocks versus Gulf of Maine stocks.

Although environmental forcing can be expected to affect recruitment (e.g., variation in wind stress or water temperature) on a broad scale, we did not attempt to model recruitment synchrony among New England groundfish stocks. Nonetheless, we did observe that recruitment time series of Georges Bank and southern New England yellowtail flounder were highly correlated. Recruitment strengths of these yellowtail flounder stocks may be linked in some years when larvae are advected from Georges Bank to southern New England in water flows through Nantucket Shoals (Mountain and Schlitz 1987). The fact that these stocks exhibited similar empirical patterns of density dependence and serial correlation suggests that further investigation into the recruitment mechanisms for these stocks is warranted.

The strong density dependence of Georges Bank haddock and yellowtail flounder was consistent with previous analyses of these stocks (Overholtz et al. 1986; Brodziak et al. 1998). The rebuilding of these productive stocks to historic abundance levels will require reduced fishing effort but is expected to generate substantial benefits (Overholtz et al. 1995). Our analyses show that, over the long term, survival ratios of these stocks have varied with little or no trend; this implies that higher average recruitment can be expected when spawner abundance is increased. Our analyses also show that these stocks exhibit serial correlation in recruitment dynamics. This is an important feature to model in forecasting the rebuilding of these stocks, although the causes of these correlations (e.g., due to environmental effects or other factors) are unknown.

Some believe that it is not necessary to manage groundfish stocks to maintain spawner abundance and that fisheries exhibit "chaotic" unpredictable behavior making quota-based management infeasible (Wilson et al. 1994). While these notions have been challenged (Fogarty 1995; Hilborn and Gunderson 1996), the pragmatic issue of how best to predict the consequences of alternative management measures remains. Quantitative prediction is model dependent, and different modeling approaches can yield different outcomes. Clearly, our results show that stochastic models are necessary to describe the stock-recruitment dynamics of New England groundfish. While both randomness and chaos imply a lack of system predictability in the absence of perfect information on system state, it is clear that the use of stochastic models to describe recruitment fluctuations is both parsimonious and consistent with the available data. Further, our approach to quantifying the uncertainty in stock-recruitment dynamics provides an objective basis for evaluating the impacts of future harvests on rebuilding plans for depleted stocks.

Three key implications of our findings for rebuilding New England groundfish stocks are: (1) time horizons for stock rebuilding will be uncertain, owing to recruitment variability, (2) some productive stocks (haddock, yellowtail flounder) have serial correlation in recruitment and this may either enhance or diminish chances for rapid stock recovery,



(3) effective management of New England groundfish will require information on stock dynamics at higher spawning-stock sizes and this, in turn, will require adaptive harvest policies that rebuild spawner abundance.

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## References

- Azarovitz, T.R. 1981. A brief historical review of the Woods Hole laboratory trawl survey time series. *In* Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. **58**: 62–67.
- Bishop, Y.M., Fienberg, S.E., and Holland, P.W. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Mass.
- Brodziak, J., Rago, P., and Conser, R. 1998. A general approach for making short-term stochastic projections from an age-structured fisheries assessment model. *In* Fishery stock assessment models. Edited by F. Funk, T.J. Quinn II, J. Heifitz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and C.-I. Zhang. Publ. No. AK-SG-98-01 of the University of Alaska Sea Grant College, Anchorage. pp. 933–954.
- Burnham, K.P., and Anderson, D.A. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York.
- Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* **74**: 829–836.
- Conser, R.J., and Powers, J.E. 1990. Extension of the ADAPT VPA tuning method designed to facilitate work on tuna and swordfish stocks. *Int. Comm. Cons. Atl. Tunas, Coll. Vol. Sci. Pap.* **32**: 461–467.
- Edwards, S.F., and Murawski, S.A. 1993. Potential economic benefits from efficient harvest of New England groundfish. *N. Am. J. Fish. Manag.* **13**: 437–449.
- Fogarty, M. 1995. Chaos, complexity, and community management of fisheries: an appraisal. *Marine Policy*, **19**: 437–444.
- Fogarty, M., and Murawski, S. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* **8**(Suppl. 1): S6–S22.
- Francis, R.I.C.C., and Shotton, R. 1997. "Risk" in fisheries management: a review. *Can. J. Fish. Aquat. Sci.* **54**: 1699–1715.
- Gavaris, S. 1988. An adaptive framework for estimation of population size. Res. Doc. No. 88/29 of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC). Available from the Library, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, N.S.
- Gilbert, D.J. 1997. Towards a new recruitment paradigm for fish stocks. *Can. J. Fish. Aquat. Sci.* **54**: 969–977.
- Hilborn, R. 1997. Comment: recruitment paradigms for fish stocks. *Can. J. Fish. Aquat. Sci.* **54**: 984–985.
- Hilborn, R., and Gunderson, D. 1996. Chaos and paradigms for fisheries management. *Marine Policy*, **20**: 87–89.
- Laevastu, T., and Favorite, F. 1988. Fishing and stock fluctuations. Fishing News Books Ltd., Farnham Surrey, U.K.
- Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish population dynamics. Res. Doc. No. 88/4 of the New Zealand Fisheries Association. Ministry of Fisheries, Wellington, New Zealand.
- Manly, B.F.J. 1997. Randomization, bootstrap, and Monte Carlo methods in biology. 2nd ed. Chapman & Hall, New York.
- Mountain, D.G., and Schlitz, R.J. 1987. Some biological implications of the circulation. *In* Georges Bank. Edited by R. Backus, R. Price, and D. Bourne. MIT Press, Cambridge, Mass. pp. 392–394.
- Murawski, S.A., Maguire, J.-J., Mayo, R.K., and Serchuk, F.M. 1997. Groundfish stocks and the fishing industry. *In* Northwest Atlantic groundfish: perspectives on a fishery collapse. Edited by J. Boreman, B. Nakashima, J. Wilson, and R. Kendall. American Fisheries Society, Bethesda, Md. pp. 27–70.
- Myers, R.A. 1997. Comment and reanalysis: paradigms for recruitment studies. *Can. J. Fish. Aquat. Sci.* **54**: 978–981.
- Myers, R.A. 1998. When do environment–recruitment correlations work? *Rev. Fish. Biol. Fish.* **8**: 285–305.
- Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? *Fish. Bull.* **94**: 707–724.
- National Research Council. 1998. Review of northeast fishery stock assessments. National Academy Press, Washington, D.C.
- Northeast Fisheries Science Center. 1999. Assessment of 11 Northeast groundfish stocks through 1999: a report to the New England Fishery Management Council Multi-species Monitoring Committee. Northeast Fisheries Science Center, Woods Hole, Mass.
- O'Reilly, J., Evans-Zetlin, C., and Busch, D. 1987. Primary production. *In* Georges Bank. Edited by R. Backus, R. Price, and D. Bourne. MIT Press, Cambridge, Mass. pp. 220–233.
- Overholtz, W., Sissenwine, P., and Clark, S. 1986. Recruitment variability and its implication for managing and rebuilding the Georges Bank haddock (*Melanogrammus aeglefinus*) stock. *Can. J. Fish. Aquat. Sci.* **43**: 748–753.
- Overholtz, W., Edwards, S., and Brodziak, J. 1995. Effort control in the New England groundfish fishery: a bioeconomic perspective. *Can. J. Fish. Aquat. Sci.* **52**: 1944–1957.
- Sainsbury, K. 1998. Living marine resource assessments for the 21st century: what will be needed and how will it be provided? *In* Fishery stock assessment models. Edited by F. Funk, T.J. Quinn II, J. Heifitz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and C.-I. Zhang. Publ. No. AK-SG-98-01 of the University of Alaska Sea Grant College, Anchorage. pp. 1–40.
- Seber, G.A.F., and Wild, C.J. 1989. Nonlinear regression. Wiley & Sons, New York.
- Sinclair, A.F., and Murawski, S.A. 1997. Why have groundfish stocks declined? *In* Northwest Atlantic groundfish: perspectives on a fishery collapse. Edited by J. Boreman, B. Nakashima, J. Wilson, and R. Kendall. American Fisheries Society, Bethesda, Md. pp. 71–93.
- Wilson, J., Acheson, J., Metcalfe, M., and Kleban, P. 1994. Chaos, complexity, and community management of fisheries. *Marine Policy*, **18**: 291–305.