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Interactions between small pelagic fish and young cod across the North Atlantic

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Abstract. Species interactions that play out over large spatial scales are difficult to observe, particularly in the oceans. The current lack of empirical evidence for biologically meaningful interaction parameters likely delays the application of holistic management procedures. Here we estimate interactions during the early life history of fish across regions. We present separate and hierarchical Bayesian models that estimate the direction and strength of interactions between Atlantic cod and dominant pelagic fishes across much of their range in the North Atlantic. We test the hypothesis that small pelagic fish may reduce survival of cod at early life stages, and thereby contribute to the delayed recovery of depleted cod populations.

Significant regional variation exists between cod recruitment and Atlantic herring abundance with eight of 14 regions displaying a negative relationship, four regions displaying no relationship, and a positive relationship observed in two regions. In contrast, most regions where Atlantic mackerel co-occurs showed no relationship with cod recruitment, with the possible exception of Gulf of St. Lawrence and Celtic Sea regions. Regions with sprat or capelin as dominant pelagics also displayed weak or no relationship, although the probability of a negative interaction with sprat increased when time series autocorrelation was accounted for. Overall, the interaction between herring and young cod was found to be negative with 94% probability, while the probability of negative interactions with mackerel was only 68%. Our findings suggest that the strength of predation or competition effects on young cod varies among small pelagic species but appears consistently for Atlantic herring; this effect may need to be considered in recovery trajectories for depleted cod populations. The methods introduced here are applicable in the investigation of species interactions from time series data collected across different study systems.

Key words: competition; cultivation–depensation; ecosystem-based management; hierarchical Bayesian; marine fish; measurement error; parameter standardization; population dynamics; predation; trophic triangle.

INTRODUCTION

Fished populations are often depleted past the region of maximum productivity, occasionally to very low biomass levels (Hutchings and Myers 1994, Myers et al. 1997*a*, 2001, Rosenberg et al. 2005). Of particular ecological concern is how such large-scale perturbations to the abundance of interacting species may reconfigure the community to an alternative state (Lewontin 1969, May 1977, Scheffer et al. 2001, Frank et al. 2005, Casini et al. 2009). An important implication would be that the ability of a fish population to recover from depletion may depend not only on the relaxation of fishing mortality, but also upon the capacity of an altered system to allow for recovery (Scheffer et al. 2001).

Such alternative states have been discussed for the North Atlantic, particularly regarding the slow recovery of depleted Atlantic cod (*Gadus morhua*, in the following simply referred to as cod) populations (Walters and Kitchell 2001, Frank et al. 2005, Shelton et al. 2006, Swain and Chouinard 2008). While continued directed and discard fishing mortality have been implicated in prolonging recovery (Horwood et al. 2006, Kelly et al. 2006, Shelton et al. 2006), so too have changes in productivity (Myers et al. 1997*a*, Shelton et al. 2006). Productivity of a fish population arises from adult survival, somatic growth and the influx of new individuals termed recruits (fish of the youngest age considered in a fishery).

Given that the strength of a cohort, upon which recovery often depends, is typically determined at a young age (Myers and Cadigan 1993), attention must focus on processes affecting this vulnerable period (Cushing 1975). Species interactions, density dependence, and environmental drivers often result in extraordinarily high levels of natural mortality that may approach 50% loss per day during the egg and larval stages (Harding and Talbot 1973, Cushing 1975, Houde 2008). This results in a classic type III survivorship curve (Pearl 1928), where mortality is initially very high and declines as the fish grow. The ability to survive these critical early life stages ultimately

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determines how many fish recruit into the adult population (Cushing 1975, 1996, Mace and Sissenwine 1993, Mertz and Myers 1995, Myers 2001).

Theoretical advances on the dynamics of early life history of fish emphasize the importance of competition and predation (Walters and Korman 1999). A prominent hypothesis in this regard is the cultivation-depensation hypothesis (Walters and Kitchell 2001), which predicts that predation and competition by smaller prey fish can limit the survival of larger predatory fish at the egg and larval stages. Hence the larger predator may 'cultivate' the ecosystem for its own young by cropping juvenile predators or competitors to low levels. Conversely, where the large predator population is substantially reduced, small- or medium-sized fish may increase in abundance and begin to inhibit recovery of the large predatory fish at early life stages. This may result in inversely density-dependent (or "depensatory") dynamics at low population levels (Walters and Kitchell 2001).

Although the dominant food of many small pelagic fish species is crustacean zooplankton such as copepods and mysids, field studies of predation by Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*) in the Baltic Sea indicate that these species can also contribute significantly toward pre-recruit mortality of cod (Köster and Möllmann 2000). Predation by herring on the eggs of European plaice (*Pleuronectes platessa*) and cod has been observed in the North Sea (Daan et al. 1985, Segers et al. 2007) and by herring and sprat on plaice in the Irish Sea (Ellis and Nash 1997). Observations of pelagic fish predation on spawning grounds of cod were reported off Norway (Melle 1985), and capelin (*Mallotus villosus*) predation on cod eggs has been documented in northeastern Newfoundland (Pepin 2006). Significant spatial overlap between cod larvae and pelagic species has been observed, during specifically designed surveys, on the southern flank of Georges Bank (Garrison et al. 2002) and between the eggs of the gadid Norway pout (*Trisopterus esmarkii*) and feeding herring in the North Sea (Huse et al. 2008). Predation by herring and Atlantic mackerel (*Scomber scombrus*) upon the early life history stages of cod may also be inhibiting the recovery of cod in the Gulf of St. Lawrence (Swain and Sinclair 2000) and the nascent recovery of cod and haddock on the Scotian Shelf was linked to the concomitant decline in forage fish there (Frank et al. 2011).

In turn, cod are important piscivores on clupeid species in most regions, e.g., the Baltic Sea, North Sea, off Norway, the Gulf of St. Lawrence, Scotian Shelf and Bay of Fundy, and Georges Bank (Daan 1973, Hanson and Chouinard 2002, Link and Garrison 2002, Harvey et al. 2003, Michalsen et al. 2008), although, in the Celtic Sea, clupeids and mackerel were relatively insignificant in the diet of adult cod (Trenkel et al. 2003).

Considering observed increases in small pelagic fish abundance (Worm et al. 2009), these observations motivate a more general analysis of the effects of small pelagic fish on young cod survival. To this end, Myers (2002) highlighted the importance of extending meta-analytic applications to the study of species interactions affecting fish recruitment. Worm and Myers (2003) first proposed a meta-analytic framework for analyzing species interactions from time series of fisheries stock assessments (in fisheries terminology a *stock* is a management unit of a population; where the stock consists of more than one population or a given population straddles two or more stocks, the terms *population* and *stock* are not equivalent). Here we modify and extend this approach by focusing on interactions during the early life history. We evaluate both the effects of interspecific as well as intraspecific processes on the recruitment of cod across much of its range in the North Atlantic. Our focus is primarily on the effect of dominant planktivorous pelagic species on the survival of cod, while accounting for the effects of changes in adult spawning abundance (Cardinale and Hjelm 2006) and density-dependence. To answer these questions more generally, we develop hierarchical methods that combine standardized estimates of the strength of the interaction across multiple regions. Such an approach allows estimates from any given population to maintain their region-specific interpretation while also borrowing strength from other regions (Hilborn and Liermann 1998).

METHODS

Data

Recent estimates of cod spawning stock biomass, recruitment, and total or spawning stock biomass for pelagic species were compiled from 16 regions across the North Atlantic (Table 1, Fig. 1). The pelagic populations are composed of herring (12 stocks; 14 regions), Atlantic mackerel (2 stocks; 10 regions), capelin (2 stocks, 3 regions), and sprat (1 stock, 2 regions). Overlapping species to be included per region were determined from a review of the literature presented in Appendix A and summarized in the *Discussion*. Where available and corresponding with the latest assessment, older assessment results, either from the original Myers' stock-recruitment database (Myers et al. 1995) or the literature, were spliced together with the recent assessments (at the earliest time of the most recent assessment) to create the longest possible time series. Most of the assessments use sequential cohort analyses, e.g., virtual population analysis (VPA), with the exception of the west coast of Scotland cod, which is assessed using a state space model. Full details are provided in Appendices A and D, including a description of omitted regions where cod and small pelagics co-occur. Note that a single pelagic stock, particularly mackerel, often overlaps with more than one cod stock owing to the wide dispersal of the pelagic species.

TABLE 1. Details of cod and pelagic populations investigated.

Region name	Region ID	$\mathrm{SPR}_{F=0}$ (kg)	Pelagic species	Area, 0–300 m (km^2)	Area, 0–200 m (km^2)
Georges Bank	GB	23.8	H, M	94 765	85 216
Gulf of Maine	GOM	27.9	H, M	53 078	34 485
Southern Scotian Shelf and Bay of Fundy	4X	14.7	M	68 744	56 704
Eastern Scotian Shelf	4VsW	11.7	M	97 460	90 749
Southern Gulf of St. Lawrence	SGOSL	7.0	H, M	110 863	100 134
Northern Gulf of St. Lawrence	NGOSL	4.1	H, M	101 418	70 387
Northeast Arctic	NEAR	12.1	H, C	969 737	784 495
Norwegian Coastal	NORCOAST	6.2	H, C	162 857	83 759
Iceland	ICE	18.9	H, C	236 408	141 751
West of Scotland	WSCOT	12.9	H, M	111 336	105 848
Irish Sea	IS	12.7	H, M	47 552	47 504
Celtic Sea	CS	19.9	H, M	236 522	230 764
North Sea	NS	18.2	H, M	616 382	579 062
Kattegat	KAT	7.8	H	21 788	21 788
Western Baltic	BA2224	5.3	H, S	44 049	44 049
Eastern Baltic	BA2532	3.3	H, S	214 916	213 016

Notes: $\mathrm{SPR}_{F=0}$ is the mass of cod spawners produced per cod recruit. Pelagic species investigated by region comprise Atlantic herring (H), Atlantic mackerel (M), European sprat (S), and capelin (C). Area is the area of the ocean floor between the contours of 0–300 m (used in cod standardization) and between the contours of 0–200 m (used in pelagic species standardization). Note that where a pelagic species covers more than one region, the sum of the areas was used in standardizing.

THEORY

Extended Ricker model

Assuming Ricker dynamics for the cohort in the absence of predators P (other than cannibals) and letting $f(N, P)$ be the predation mortality (a function of the abundance of prey and predators), the rate of change for the cohort can then be written as follows (Turchin 2003):

$$\frac{dN}{dt} = -(q + pS_0)N - f(N, P_0) \tag{1}$$

where N is the cohort abundance and q and pS_0 are the density-independent and stock-dependent (stock density-dependent) mortality rates, respectively (Hilborn and Walters 1992). Note that (1) the density-dependent mortality rate is here a function of the initial spawning stock size S_0 where the assumed biological mechanism is the presence of intraspecific compensatory predation mortality, e.g., cannibalism (Ricker 1954); and (2) the predation mortality is a function of the initial predator abundance P_0. Functional forms for $f(N, P_0)$ include linear, hyperbolic and ratio-dependent predation mortality rates, among others (Skalski and Gilliam 2001, Turchin 2003). We focus on the linear predation mortality rate (Volterra 1931):

$$\begin{aligned}\frac{dN}{dt} &= -(q + pS_0)N - uNP_0,\\ &= -(q + pS_0 + uP_0)N \end{aligned}\tag{2}$$

where u is the instantaneous predation rate per predator. We recognize that the assumption of a linear increase in predation mortality over all predator abundances is restrictive. Preliminary investigations showed that hyperbolic and sigmoid predation mortality alternatives for $f(N, P)$ were found to have complex or non-closed solutions but were also noteworthy in that they readily produced depensatory dynamics. A ratio-dependent predation mortality rate also induced depensatory dynamics.

Solving Eq. 2 with respect to time provides

$$N_t = N_0 e^{-(q+pS_0+uP_0)t}. \tag{3}$$

N_0 is the initial number of eggs, which is the product of initial spawner abundance S_0 and fecundity F (number of eggs per spawner), so Eq. 3 can be written as

$$N_t = S_0 F e^{-(q+pS_0+uP_0)t}. \tag{4}$$

Setting t at the age of recruitment τ,

$$N_\tau = S_0 F e^{-(q+pS_0+uP_0)\tau} \tag{5}$$

and letting recruitment $R = N_\tau$, $\alpha = e^{-q\tau}F$, $\beta = p\tau$, and $\gamma = u\tau$, the extended Ricker spawner–recruit relationship is given by

$$R = \alpha S e^{-(\beta S_0 + \gamma P_0)}. \tag{6}$$

Eq. 6 thus relates recruitment to spawner and pelagic species abundance via the parameters: α the rate at which recruits are produced per spawner at low spawner abundances (slope at the origin); β the density-dependent mortality; and γ the predation rate (hereafter termed the interaction coefficient). Thus a key assumption in the solution is that the predator abundance is constant over time τ.

Eq. 6, or a re-parameterized variant, is a common form used for general extensions to the Ricker (Quinn and Deriso 1999), e.g., including additional sources of mortality such as abiotic forcing (Brander and Mohn 2004). The estimation of the parameters of Eq. 6 will be the focus of this paper.

Standardization across stocks

To be comparable across stocks, the variables of Eq. 6 need to be standardized in two ways: (1) to convert the

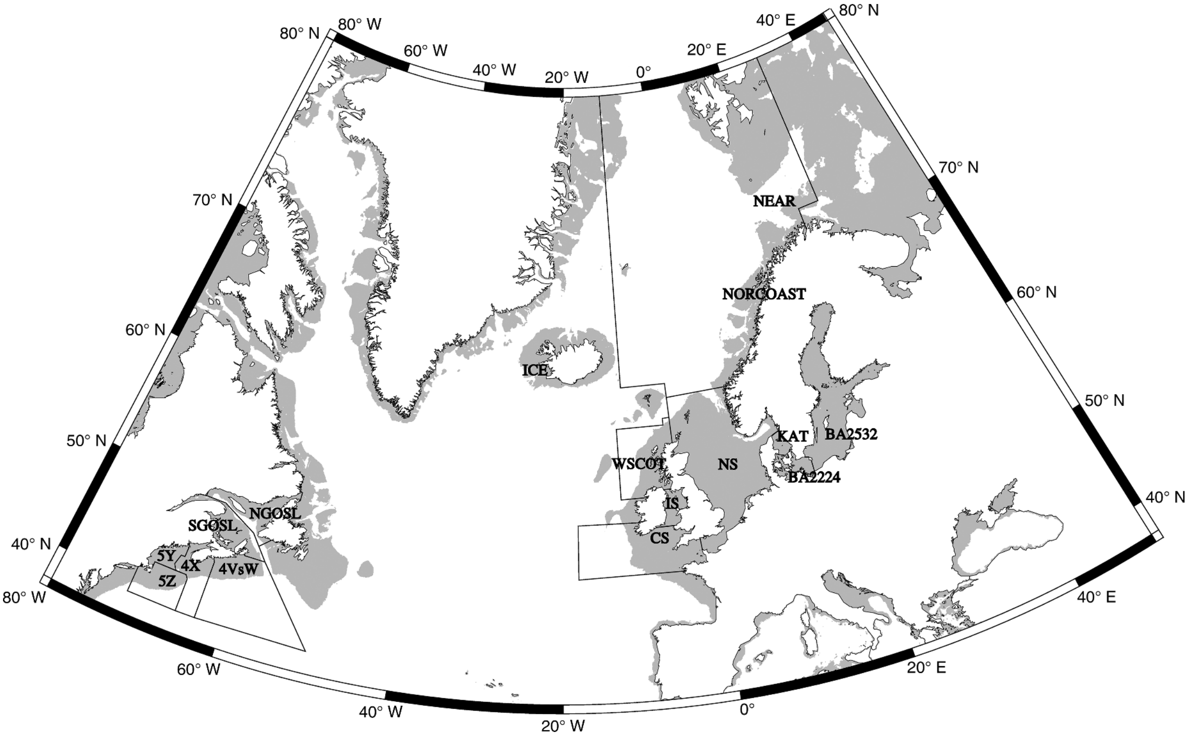

FIG. 1. Regions of the North Atlantic investigated. Major management areas are represented by solid black polygons. The 0–300 m contour line representing the preferred habitat of juvenile cod is shaded in gray. Note that the NEAR stock covers ICES regions I and II, east and west of the 30° meridian. Region IDs are identified and regions described in Table 1.

recruits into the same units as spawners (Myers et al. 1996, 2001) and (2) to account for differences in the areas occupied by the populations (Myers et al. 2001).

Owing to differences in growth rates and gear selectivity, the age at recruitment, when fish first enter the fishery, varies by region. For example, in the North Sea, cod recruit at age 1, in the Northeast Arctic at age 3. Not standardizing for this difference creates the risk of concluding that the recruitment productivity is lower in the Northeast Arctic whereas the age groups being different would obscure such a conclusion. Myers et al. (1996) achieved a method of comparing the relationships across regions by multiplying the recruits (in numbers) by the predicted spawner biomass per recruit assuming zero fishing mortality $\mathrm{SPR}_{F=0}$ (Table 1, see also Mace and Sissenwine 1993). This is a region-specific constant metric of the weight of spawners produced per recruit and accounts explicitly for the age at recruitment. It allows for the estimates of the maximum reproductive rate (a parameter of most stock–recruit relationships) to be compared across stocks (Myers et al. 1999).

Stock-recruit relationships also typically include a density-dependent term. Comparing density-dependent parameters across regions requires that the data are standardized to the area available for the juveniles. Myers et al. (2001) and Mantzouni et al. (2010) achieved this by dividing cod recruitment by the area occupied by the juveniles between 0–300 m and 40–300 m, respectively, by study. We use the 0–300 m definition here (Table 1). Similarly, an important issue arises when comparing interaction coefficients across regions, as the area occupied by interacting species is a dynamic region in time and space. This may be exacerbated with most small pelagic species where stock boundaries are difficult to establish. The approach we take is to define bottom depths between 0-200 m as suitable small pelagic species habitat. We extracted the bottom area (Table 1) between depth contours within each polygon (management area) using the GRDVOLUME function in the Generic Mapping Tools (Wessel and Smith 1991) and the GEBCO 1-minute bathymetry grid (IOC et al. 2003). The units of all variables are thus standardized to density (Mg/km^2). Time series of the standardized cod recruitment and pelagic species biomasses are shown in Fig. 2.

These standardizations affect the scale and not the relative ranking of the data (Myers 2002).

STATISTICAL ANALYSES

Analysis of extended recruitment functions for each region are treated separately (unpooled) and hierarchically.

Unpooled analyses

By assuming a lognormal residual error distribution and $j = 1, \ldots, M$ regions or stocks, the extended Ricker

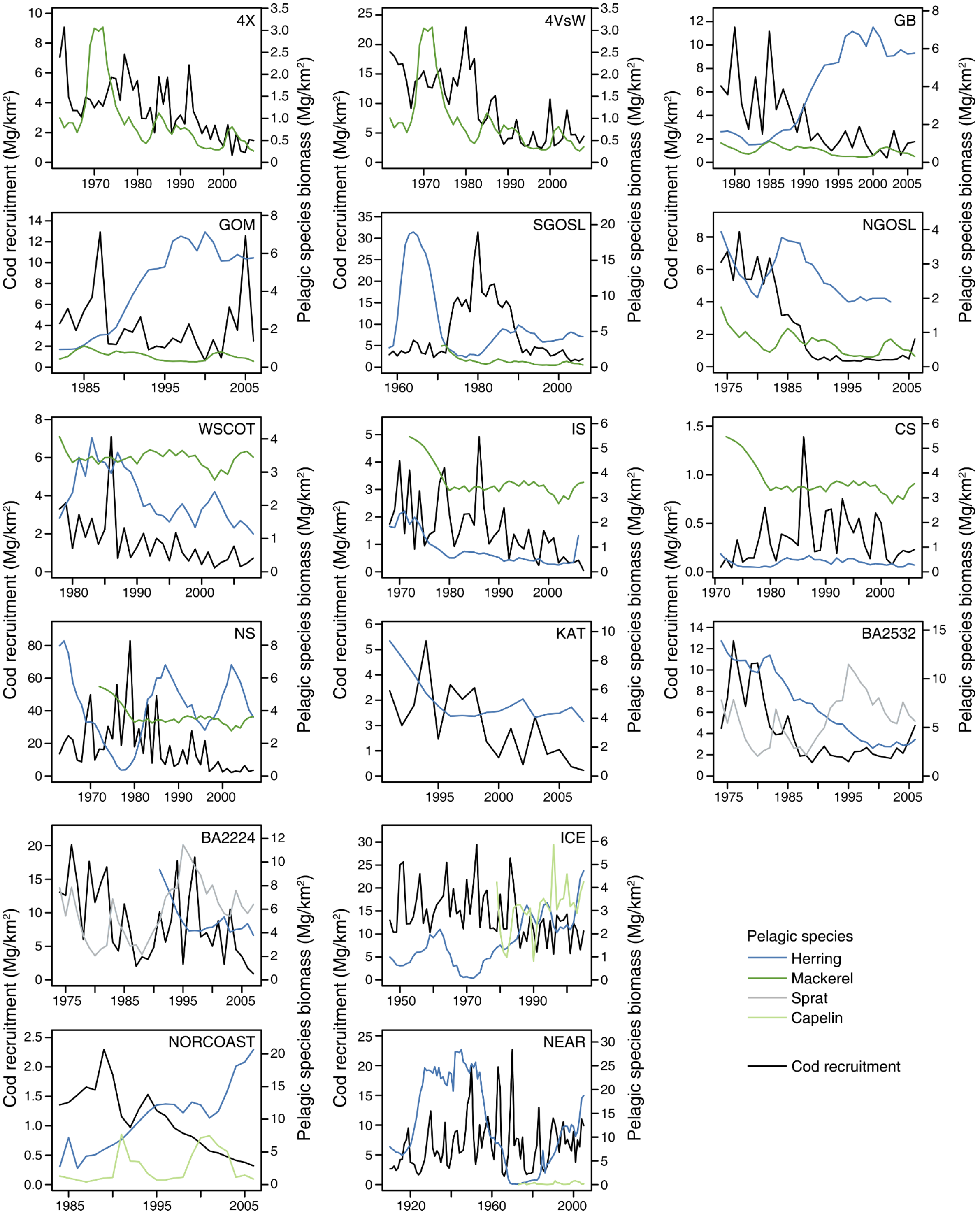

FIG. 2. Standardized cod recruitment and pelagic species biomasses by region across years. Cod recruitment is shown by the solid black line; pelagic species line colors are: herring (blue); mackerel (dark green); sprat (gray); and capelin (light green). Note that where a pelagic stock covers many regions the biomass per unit area refers to the total pelagic stock area. Region IDs are identified and regions described in Table 1.

recruitment relationship is written as follows:

$$R^*_{t,j} = \alpha_j S^*_{t-\tau_j,j} e^{-(\beta_j S^*_{t-\tau_j,j} + \gamma_j P^*_{t-\tau_j,j})} e^{\varepsilon_{t,j}} \tag{7}$$

where τ_j is the stock-specific age at recruitment, $\varepsilon_{t,j}$ are the residuals, which are discussed in the next paragraph, and an asterisk denotes the variables in units of density. The parameters are different from Eq. 6, with units for α, dimensionless; β, 1/(Mg adult cod/km^2); and γ, 1/(Mg predator/km^2). The Ricker curve may be linearized by taking logarithms:

$$\ln(R^*_{t,j}) = \ln(\alpha_j) + \ln(S^*_{t-\tau_j,j}) + \beta^*_j S^*_{t-\tau_j,j} + \gamma^*_j P^*_{t-\tau_j,j} + \varepsilon_{t,j}. \tag{8}$$

This model is often written with the logarithm of spawner abundance divided through, we have chosen to write the linearized Ricker with the log of spawner abundance as an offset, as this will assist in an exposition of the treatment of measurement error below. To ease interpretation the signs of the density-dependent and interaction terms have been changed such that $\beta^* = -\beta$ and $\gamma^* = -\gamma$.

The form of the residuals can affect parameter inference (Pyper and Peterman 1998), we therefore investigated four residual structures: (1) independent residuals with a common variance across stocks $\varepsilon_{t,j} \sim \mathcal{N}(0, \sigma^2_\varepsilon)$; (2) independent residuals with separate error variances by stock $\varepsilon_{t,j} \sim \mathcal{N}(0, \sigma^2_{\varepsilon,j})$; (3) common AR(1) autocorrelated structure across stocks $\varepsilon_{t,j} \sim \mathcal{N}(\phi\, \varepsilon_{t-1,j}, \sigma^2_\varepsilon)$; and (4) separate AR(1) autocorrelated structures by stock $\varepsilon_{t,j} \sim \mathcal{N}(\phi_j \varepsilon_{t-1,j}, \sigma^2_{\varepsilon,j})$.

Partial regressions were used to visualize the effect of the pelagic species abundance on cod recruitment having accounted for the effect of adult cod abundance and density-dependence. The partial regressions per region were between (1) the residuals of a regression between scaled cod recruitment and scaled cod spawner biomass (i.e., omitting the pelagic species from Eq. 8) and (2) the residuals of a regression between the scaled abundance of the interacting species and scaled cod spawner biomass. The slope of the regression between these residuals estimates γ^*_j in Eq. 8 (Montgomery et al. 2001). We plot the partial regressions as connected points to graphically investigate time-dependent dynamics.

Hierarchical analysis

A hierarchical implementation of Eq. 8 can be written

$$\ln(R^*_{t,j}) = \ln(a_j) + \ln(S^*_{t-\tau_j,j}) + b_j S^*_{t-\tau_j,j} + g_j P^*_{t-\tau_j,j} + \varepsilon_{t,j} \tag{9}$$

with the same assumptions on the residual error variances as in the unpooled analysis. The region-level parameters are now assumed to be distributed according to a multivariate normal distribution

$$\begin{pmatrix} \ln(a_j) \\ b_j \\ g_j \end{pmatrix} \sim \mathcal{N}\left(\begin{bmatrix} \mu_\alpha \\ \mu_\beta \\ \mu_\gamma \end{bmatrix}, \begin{bmatrix} \sigma^2_a & \sigma_{a,b} & \sigma_{a,g} \\ \sigma_{a,b} & \sigma^2_b & \sigma_{b,g} \\ \sigma_{a,g} & \sigma_{b,g} & \sigma^2_g \end{bmatrix} \right) \tag{10}$$

where $\{\mu_\alpha, \mu_\beta, \mu_\gamma\}$ are the overall hierarchical means and a, b, and g are the hierarchical slope at the origin, density-dependent mortality, and interaction coefficients, respectively. Note that a key assumption of Eq. 10 is that of exchangeability (Gelman et al. 2004), i.e., commensurate with the model being an accurate depiction of the system, the region-specific parameters are randomly distributed around the hierarchical mean. Additional structure between the estimated hierarchical interaction coefficients g_j and other gradients, such as mean annual shelf temperature (Myers et al. 2001), mean spring surface temperature (Mantzouni et al. 2010), latitude and longitude were investigated using linear regression post-estimation (Appendix B).

Parameter priors

For the unpooled analysis, we chose noninformative normal priors on $\{\ln(\alpha_j), \beta_j, \gamma_j\} \sim \mathcal{N}(0, 1/0.0001)$ and a uniform distribution on the standard error of the residual variance $\{\sigma_y, \sigma_{y,j}\} \sim U(0, 100)$. Autocorrelation terms had priors $\{\phi, \phi_j\} \sim U(-0.9999, 0.9999)$. The hierarchical analysis required specification of prior distributions on the overall means $\{\ln(\mu_\alpha), \mu_\beta, \mu_\gamma\} \sim \mathcal{N}(0, 1/0.0001)$ and region-level variances, which were constructed via a Cholesky decomposition with the lower triangular matrix priors distributed normally $\mathcal{N}(0, 1/0.0001)$. Common, separate or autocorrelated residual error variances were modeled as in the unpooled analysis.

Samples were drawn from the posterior distribution of all parameters using WinBUGS (Lunn et al. 2000). Initially, three Markov Chain Monte Carlo (MCMC) chains were run for 25 000 iterations from dispersed starting values for all models. All models were then compared using deviance information criterion (DIC; Spiegelhalter et al. 2002). Following model selection, final runs consisted of 100 000 MCMC iterations. The first half of each chain was conservatively discarded (Gelman et al. 2004) and the second half sampled every 50 iterations to provide 3000 posterior samples per parameter. Chain convergence was assessed via autocorrelation and the Raftery and Lewis diagnostic within each chain, and the Gelman and Rubin diagnostic between chains (Gelman et al. 2004).

Measurement error

The data used in the analysis are not raw data but estimates of absolute abundances from complex population dynamics models. These model outputs are not typically presented with uncertainty estimates. It is known, however, that the presence of measurement errors can bias the coefficients of the Ricker model, contingent on the range of spawner values observed (Walters and Ludwig 1981, Kehler et al. 2002). The extent of the measurement error likely decreases further back in the time series where cohorts have completely passed through the fishery but recent estimates are likely to contain higher levels of measurement error. We

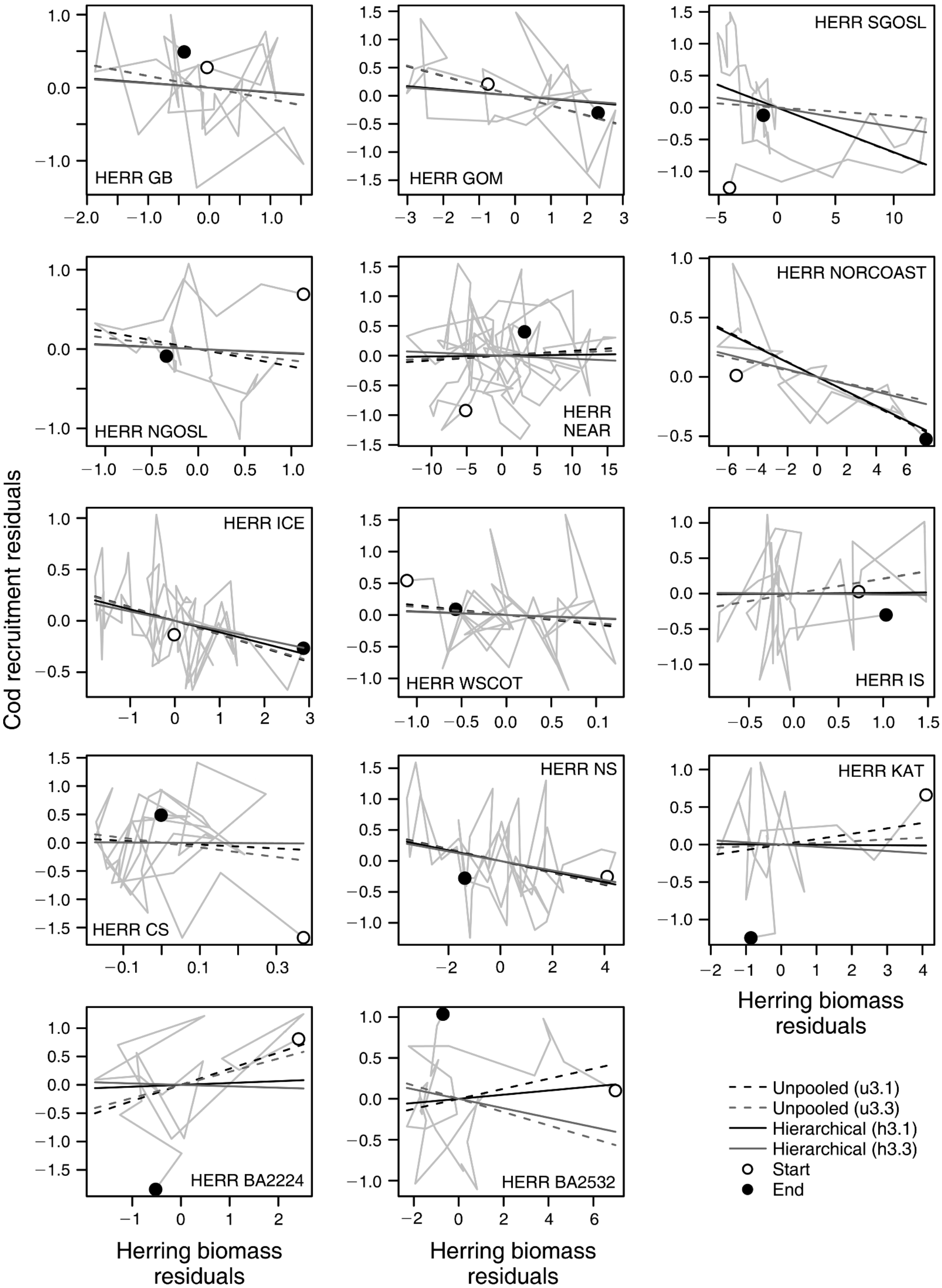

FIG. 3. Partial regression plots of the relationship between standardized cod recruitment and herring total biomass by region. The effect of cod spawning stock biomass is removed prior to plotting, making the slope of the relationship interpretable as the interaction coefficient. Observations are displayed as gray lines with the first and last time point indicated by a white and black point, respectively. Dashed black and dark gray lines are interaction estimates from the unpooled independent (u3.1) and autocorrelated (u3.3) models, respectively; Solid black and dark gray lines are the interaction estimates from the hierarchical independent (h3.1) and autocorrelated (h3.3) models, respectively (Table 2).

Table 2. Cod and pelagic model comparison table.

			Herring			Mackerel		
ID	Terms	Residual structure	$\bar{D}$	p_D	ΔDIC	$\bar{D}$	p_D	ΔDIC
Unpooled								
u1.0	α_j	$\mathcal{N}(0, \sigma_\varepsilon^2)$	1119.32	14.97	286.95	706.09	10.91	93.92
u1.1	α_j	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	1104.97	26.84	284.47	696.77	19.60	93.29
u1.2	α_j	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	1006.79	16.05	175.51	678.59	11.98	67.49
u1.3	α_j	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	872.84	41.2	66.69	605.42	29.74	12.08
u2.0	$\alpha_j + \beta_j S$	$\mathcal{N}(0, \sigma_\varepsilon^2)$	1005.3	28.77	186.74	656.17	21.06	54.14
u2.1	$\alpha_j + \beta_j S$	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	975.7	40.88	169.23	653.87	29.30	60.09
u2.2	$\alpha_j + \beta_j S$	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	950.08	30.19	132.93	647.42	22.05	46.39
u2.3	$\alpha_j + \beta_j S$	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	807.03	54.12	13.81	590.99	39.31	7.21
u3.0	$\alpha_j + \beta_j S + \gamma_j P$	$\mathcal{N}(0, \sigma_\varepsilon^2)$	972.46	43.33	168.45	657.33	31.01	65.25
u3.1	$\alpha_j + \beta_j S + \gamma_j P$	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	928.66	54.29	135.6	657.08	39.30	73.30
u3.2	$\alpha_j + \beta_j S + \gamma_j P$	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	938.85	43.9	135.41	651.82	31.97	60.71
u3.3	$\alpha_j + \beta_j S + \gamma_j P$	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	801.09	67.15	20.9	586.43	47.97	11.33
Hierarchical								
h1.0	a_j	$\mathcal{N}(0, \sigma_\varepsilon^2)$	1119.53	14.96	287.15	705.95	10.71	93.58
h1.1	a_j	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	1105.31	26.88	284.86	696.54	19.27	92.73
h1.2	a_j	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	1006.9	15.56	175.12	678.77	11.98	67.66
h1.3	a_j	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	871.5	38.09	62.24	605.21	28.16	10.29
h2.0	$a_j + b_j S$	$\mathcal{N}(0, \sigma_\varepsilon^2)$	1007.51	23.03	183.2	658.77	17.37	53.06
h2.1	$a_j + b_j S$	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	976.25	34.63	163.55	655.24	25.20	57.35
h2.2	$a_j + b_j S$	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	952.38	23.05	128.1	649.74	17.82	44.47
h2.3	$a_j + b_j S$	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	807.07	43.85	3.57	591.91	32.14	0.97
h3.0	$a_j + b_j S + g_j P$	$\mathcal{N}(0, \sigma_\varepsilon^2)$	978.62	31.89	163.17	660.04	21.94	58.90
h3.1	$a_j + b_j S + g_j P$	$\mathcal{N}(0, \sigma_{\varepsilon,j}^2)$	932.05	42.42	127.13	656.53	29.23	62.68
h3.2	$a_j + b_j S + g_j P$	$\mathcal{N}(\phi\varepsilon_{j,t-1}, \sigma_\varepsilon^2)$	944.49	29.46	126.61	651.23	21.76	49.90
h3.3	$a_j + b_j S + g_j P$	$\mathcal{N}(\phi_j\varepsilon_{j,t-1}, \sigma_{\varepsilon,j}^2)$	799.58	47.76	0	587.12	35.96	0

Notes: Each model has an ID referred to in the text. Terms for each model also include an offset (ln[S]); time and region subscripts are omitted from the model terms but are provided in *Results* and *Discussion*. Unpooled and hierarchical refer to models with separate or hierarchical parameterizations. The residual variance structure is either independent or autocorrelated with combined or separate parameters by region. The effective number of parameters is given by p_D, DIC is the sum of the mean deviance $\bar{D}$ and p_D, and ΔDIC is the difference in the DIC values between the model in that row and the best model of those investigated per hypothesized interacting species. Other model terms are: j, stock index; α, unpooled slope at the origin; β, unpooled density-dependent term; γ, unpooled interaction term; a, hierarchical slope at the origin; b, hierarchical density-dependent term; g, hierarchical interaction term; $\varepsilon_{j,t}$, residual of stock j at time t; σ_ε^2, constant residual variance; $\sigma_{\varepsilon,j}^2$, separate residual variance by stock; ϕ, constant autocorrelation coefficient; and ϕ_j, separate autocorrelation coefficient by stock. $\mathcal{N}$ stands for normally distributed. Empty cells represent instances where hierarchical modeling was not possible.

investigated the sensitivity of the results to measurement error by assigning each predictor variable data point a distribution of known error variance and comparing the estimated parameters (Appendix C).

Results

Time series trends

Time series of cod recruitment typically displayed high interannual variability with overall declining trends observed in many regions (Fig. 2). Pelagic total biomass series are generally smoother, as would be expected from a summed biomass across many age groups. Importantly, periods of relatively high and low pelagic species biomass occur in most regions with some (e.g., North Sea herring) exhibiting multiple peaks and troughs. Many pelagic species display increasing trends over time, although northwest Atlantic mackerel and Baltic stocks of herring are decreasing (Fig. 2). In some regions, periods of high pelagic abundance coincide with decreased recruitment of cod, e.g., Southern Gulf of St. Lawrence, Georges Bank; in others, this varies over the course of the series, e.g., early and late periods in the North Sea.

Model convergence

All MCMC chains mixed well and appeared to converge, as indicated by low within-chain autocorrelation, Gelman and Rubin diagnostics of 1 and Raftery and Lewis diagnostics of 1 also.

Effect of herring

Visually inspecting the partial regression plots of the relationship between herring abundance and cod re-

Table 2. Extended.

Sprat			Capelin		
$\bar{D}$	p_D	ΔDIC	$\bar{D}$	p_D	ΔDIC
144.1	2.98	34.76	91.74	3.9	19.62
144.24	3.93	35.86	91.15	5.6	20.72
118.81	4.23	10.72	88.83	5.04	17.85
106.45	5.86	0	82.82	8.81	15.6
138.57	4.91	31.16	77.71	6.87	8.54
136.65	5.78	30.12	79.7	8.67	12.34
118.29	6.03	12	77.78	8.05	9.8
104.96	7.82	0.47	64.82	11.21	0
140.38	6.93	34.99	78.88	9.78	12.63
138.78	7.87	34.34	80.9	11.41	16.29
119.09	8.22	14.99	79.4	10.81	14.19
105.78	9.63	3.1	65.96	14.02	3.95

cruitment shows a negative relationship in eight regions, no relationship in two regions, and a positive relationship in four regions (Fig. 3). For a given residual error structure, the hierarchical model typically fit better (lower DIC) than the unpooled counterpart (Table 2). For a given residual error structure in the hierarchical fits, those models including herring (models h3.0–h3.3, Table 2) fit better than those excluding herring (models h1.0–h2.3). The overall best-fitting model was hierarchical, included herring, and had separate autocorrelated residual structures by stock (model h3.3, Table 2). The closest model, separated by only 3.57 DIC units, had the same residual structure but omitted herring (model h2.3, Table 2). Of the unpooled analysis, the simpler model omitting herring fit best (model u2.3, Table 2).

The overall mean interaction coefficient from the best fitting model (hierarchical with separate autocorrelated errors by region: model h3.3 in Table 2) was −0.043 with a 94% probability of being negative. The non-autocorrelated version (model h3.1 in Table 2) had a mean interaction of −0.038 with 88% probability of being negative.

At the region level, we compare the results of the unpooled and hierarchical analyses under the assumptions of separate independent errors and separate autocorrelated errors (models u3.1, u3.3 and h3.1, h3.3, Table 2). The number of regions with $\geq$90% ($\geq$80% in parentheses) probability of a negative interaction by model was: unpooled independent errors, 5 (7); unpooled autocorrelated errors, 3 (6); hierarchical independent errors, 5 (6); and hierarchical autocorrelated errors, 3 (8) (Table 3). The hierarchical models showed increased probability of a negative interaction in 7 and 10 regions for the independent and autocorrelated implementations, respectively. There was evidence of shrinkage of both strongly positive and negative separate estimates toward the overall mean in the hierarchical analyses (Fig. 5). Regions with a positive relationship in the unpooled analysis generally became flat or weakly negative in the hierarchical analyses (Table 3, Fig. 3). For example, the western Baltic region displayed a positive relationship between herring abundance and juvenile cod recruitment in the separate analysis (Table 3, Figs. 4 and 5). This became flat in the hierarchical and hierarchical autocorrelated models (Figs. 4 and 5).

Effect of other pelagics

Most regions displayed no relationship between cod recruitment and mackerel biomass with the exceptions of the Gulf of St. Lawrence and Celtic Sea (Fig. 4). For a given error structure, models excluding mackerel typically fit best (Table 2). Although the best fitting model included mackerel (model, h3.3, Table 2), it was separated by less than 1 DIC unit (0.97) from the next best fitting model (model h2.3, Table 2), which excluded mackerel.

The overall mean interaction coefficient from the best fitting model (hierarchical with separate autocorrelated errors by region: model h3.3 in Table 2) was −0.077 with a comparatively low (68%) probability of being negative. The non-autocorrelated version (model h3.1, Table 2) had a positive interaction of 0.044 with only a 34% probability of being negative.

Once autocorrelation was accounted for, the southern Gulf of St. Lawrence recruitment displayed a negative relationship with mackerel with high probability (99%) (Table 3). The Celtic Sea and Northern Gulf of St. Lawrence regions also displayed relatively high probabilities of a negative relationship (91% and 87%, respectively). Other regions displayed consistently low probabilities of a negative relationship across models.

The relationship between cod recruitment and sprat in the Baltic regions had low probabilities of being negative when analyzed with independent residual error structures (Western Baltic, 29%; Eastern Baltic, 59%). However the probability of a negative relationship was greater when autocorrelation was accounted for (Western Baltic, 0.79; Eastern Baltic, 0.83) (Figs. 4 and 5, Table 3). Of the three regions with capelin, one showed

TABLE 3. Posterior means of the interaction coefficients by region.

	Herring				Other species		
	Unpooled		Hierarchical			Unpooled	
Region	Independent	Autocorrelated	Independent	Autocorrelated	Species	Independent	Autocorrelated
GB	−0.16 (0.88)	−0.16 (0.88)	−0.06 (0.91)	−0.06 (0.94)	mackerel	−0.07 (0.55)	−0.05 (0.53)
GOM	−0.17 (0.99)	−0.18 (0.97)	−0.06 (0.88)	−0.05 (0.87)	mackerel	0.82 (0.13)	0.8 (0.16)
4X					mackerel	0.05 (0.3)	0.06 (0.33)
4VsW					mackerel	0.05 (0.35)	−0.1 (0.68)
SGOSL	−0.07 (1)	−0.01 (0.64)	−0.07 (1)	−0.03 (0.84)	mackerel	0.02 (0.44)	−0.71 (1)
NGOSL	−0.22 (0.86)	−0.14 (0.69)	−0.05 (0.76)	−0.05 (0.79)	mackerel	0.14 (0.34)	−0.47 (0.84)
NEAR	0.01 (0.22)	0.01 (0.38)	0 (0.44)	−0.01 (0.61)	capelin	−0.03 (0.53)	0 (0.5)
NORCOAST	−0.06 (1)	−0.03 (0.85)	−0.06 (1)	−0.03 (0.89)	capelin	−0.02 (0.71)	−0.02 (0.82)
ICE	−0.13 (1)	−0.13 (0.99)	−0.11 (1)	−0.09 (0.99)	capelin	−0.1 (0.9)	−0.09 (0.88)
WSCOT	−0.15 (0.77)	−0.13 (0.74)	−0.05 (0.77)	−0.05 (0.82)	mackerel	0.73 (0.06)	0.66 (0.07)
IS	0.21 (0.15)	0.21 (0.18)	0.01 (0.49)	−0.01 (0.62)	mackerel	0.02 (0.46)	0.28 (0.26)
CS	−0.34 (0.63)	−0.84 (0.75)	−0.03 (0.67)	−0.04 (0.73)	mackerel	−0.32 (0.96)	−0.33 (0.93)
NS	−0.1 (0.97)	−0.09 (0.95)	−0.09 (0.97)	−0.08 (0.96)	mackerel	−0.09 (0.64)	−0.09 (0.66)
KAT	0.07 (0.29)	0.02 (0.4)	0 (0.56)	−0.03 (0.71)			
BA2224	0.28 (0.07)	0.23 (0.17)	0.03 (0.4)	−0.03 (0.7)	sprat	0.03 (0.29)	−0.08 (0.79)
BA2532	0.06 (0.09)	−0.08 (0.82)	0.03 (0.3)	−0.06 (0.89)	sprat	−0.01 (0.59)	−0.04 (0.83)

Notes: Estimates derive from models: unpooled independent residuals u3.1, unpooled autocorrelated residuals u3.3, hierarchical independent residuals h3.1, and hierarchical autocorrelated residuals h3.3 in Table 2. Probability of the interaction coefficient being negative is given in parentheses. Empty cells represent species–area combinations for which no analyses where conducted.

no relationship and two showed relatively high probabilities (≥80%) of a negative relationship (Figs. 4 and 5, Table 3).

Post-estimation relationships

No relationships were found between the strength of the interaction terms and temperature, latitude or longitude in the herring or mackerel analyses (Appendix B).

DISCUSSION

Our analyses of species interactions documented regional and by-species variation in the strength of the relationship between cod recruitment success and small pelagic fish abundance over the North Atlantic (Figs. 3–5). Consistently negative relationships detected between Atlantic herring and young cod, illustrating the importance of considering predation as a driving factor in recruitment relationships. Our findings consolidate results from a number of disparate investigations at the regional level and suggest an ecological link between pelagic and demersal communities via interactions occurring during the early life stages. A Bayesian approach allowed for probabilistic assertions on the direction, strength, and uncertainty associated with these relationships within and across regions.

Regional variation and interpretation

All Northwest Atlantic regions where Atlantic herring assessments were available displayed negative relationships with recruitment success of cod (Table 3, Figs. 3–5), with the Northeast Atlantic displaying more variability in the direction and strength of the relationship (Table 3, Figs. 3–5). This may reflect historical differences in exploitation between the Northwest and Northeast Atlantic, with intense fisheries for both species in the Northeast Atlantic preventing the dominance of herring but lower fishing pressure on herring in the Northwest Atlantic. An alternative hypothesis is that fish communities in the Northwest Atlantic are less species rich (excluding the most northern Northeast Atlantic regions), which may increase the likelihood of strong interactions between given subsets of species.

In the Baltic and Kattegat regions, flat or positive relationships with both herring and sprat were observed, although these became weakly negative when autocorrelation was accounted for (Table 3). Paradoxically, the Baltic region is where predation by herring on cod eggs was directly observed (Köster and Möllmann 2000) and a negative recruitment relationship with sprat has been previously elucidated (Sparholt 1996). Potential reasons for this disparity include confounding environmental variables, particularly changes in salinity and oxygen levels. These may override or mask the effects of species interactions on cod recruitment. The time period used to investigate the sprat relation also differed from previous investigations (Sparholt 1996). The series used for herring for the western Baltic and Kattegat is the shortest series used with comparatively little contrast over the 17 years of abundance data (Appendix D: Fig. D8). Similarly, no relationship existed between herring abundance and cod recruitment in the longest time series available, the Northeast Arctic. Hjermann et al. (2007) concluded that the effect of herring on the recruitment of cod in that region is likely an indirect effect mediated via exclusion of capelin and increased cannibalism in cod, which is in turn dependent on the stock size. So in the case of the Northeast Arctic cod, it is unlikely that a direct effect of herring would be detected in our models.

Table 3. Extended.

Other species	
Hierarchical	
Independent	Autocorrelated
0.04 (0.39)	−0.1 (0.64)
0.09 (0.35)	0.1 (0.41)
0.04 (0.34)	0.01 (0.45)
0.06 (0.32)	−0.06 (0.6)
0.03 (0.42)	−0.49 (0.99)
0.02 (0.46)	−0.33 (0.87)
0.1 (0.29)	0.05 (0.43)
−0.03 (0.61)	−0.09 (0.77)
−0.12 (0.8)	−0.18 (0.91)
0.21 (0.08)	0.31 (0.05)

Caveats

While the present study attempted to use all available stock assessment information to investigate the hypothesis, ultimately our approach remains correlative. Yet, the analysis goes beyond other observational studies, in that it is essentially replicated across regions with differing historical trajectories, particularly for herring. As potentially confounding factors remain uncontrolled for, however, our conclusions must be interpreted with caution (Montgomery et al. 2001).

The rationale behind the hierarchical approach is that we effectively treat each population as a realization of a natural experiment (Myers and Mertz 1998). An underlying assumption is that the same processes operate in all populations. The validity of this assumption may be critically questioned for investigating species interactions where assemblages of prey, predators, and competitors vary in their composition between regions and indeed we found that the strength of the interaction varies widely between regions. Yet, the overall effect of herring across populations was negative (Fig. 5). In adherence with the ecosystem-based management approach (Larkin 1996), there remains a requirement to understand pertinent interactions over the large scales at which these populations are managed. This requirement is all the more important when considering the effects of trophic cascades (Pace et al. 1999, Frank et al. 2005, Myers et al. 2007) and alternative stable states (Scheffer et al. 2001, Beisner et al. 2003) in determining population persistence and recovery at low population levels.

By assembling the longest available time series and visualizing the partial regressions, the time dynamic of the relationship between pelagic fish abundance and cod recruitment can be inspected. Ideally multiple historical peaks and troughs in the abundance of the interacting pelagic species would ensure that the hypothesized effect on recruitment does not appear unidirectional in Figs. 3 and 4.

It is also important to note that the dominant small pelagic species within a region are treated separately whereas their combined effect as a functional group may be more relevant (Petrie et al. 2009). Given that some small pelagic species such as mackerel are widely ranging, we did not attempt to combine their abundance with that of more localized stocks. Index combination methods may be useful in this regard.

Spatial overlap in spawning and feeding areas

Given the relatively small gape size of small pelagic species, the inferred predation or competition for the same food source (early stage copepods) must concern eggs and small larvae, either prior to or shortly after settling. Cod spend up to 10 weeks in the planktonic phase before metamorphosis. The overlap between feeding pelagic fish and cod larvae during this stage is critical in determining the strength of this source of potential mortality (Huse et al. 2008). Interannual variability in temporal and spatial dynamics make it difficult to obtain accurate estimates of spatial overlap. The approach used here was to review literature on the general spawning areas for cod and feeding areas of pelagic species (Appendix A). Broadly, there appears to be sufficient evidence for the potential overlap of feeding herring and the spatial distribution of cod eggs and larvae. The picture is less clear for mackerel stocks, which are typically highly migratory. This may be reflected in the lack of evidence for a negative relationship between Atlantic mackerel and cod recruitment (Figs. 4 and 5). An a priori decision was made to analyze only those regions presented in the stock assessment report but it is noteworthy that mackerel are increasingly caught in other regions, e.g., off the Faroe Islands and Iceland. However, these did not appear in the dominant migratory patterns and were thus excluded. It is also questionable how much mackerel foray into the North Sea, especially since this historic component was virtually extirpated and has not recovered. The results from the North Sea were in agreement in that no relationship was observed between cod recruitment and mackerel abundance there (Table 3).

Other potential covariates

Much attention has focused on the important effects of temperature anomalies and climatic trends (Planque and Fredou 1999, O'Brien et al. 2000, Brander and Mohn 2004, Mantzouni et al. 2010) on cod recruitment. With the effect of temperature varying according to the geographical position, for example, higher temperatures favor strong recruitment in more northern areas but lower temperatures favor recruitment in more southern stocks. There have also been studies into the effects of larval prey availability and subsequent recruitment, e.g., match-mismatch between young cod and zooplankton in the North Sea cod (Beaugrand et al. 2003). Recently, a detailed study of the North Sea by Fauchald (2010)

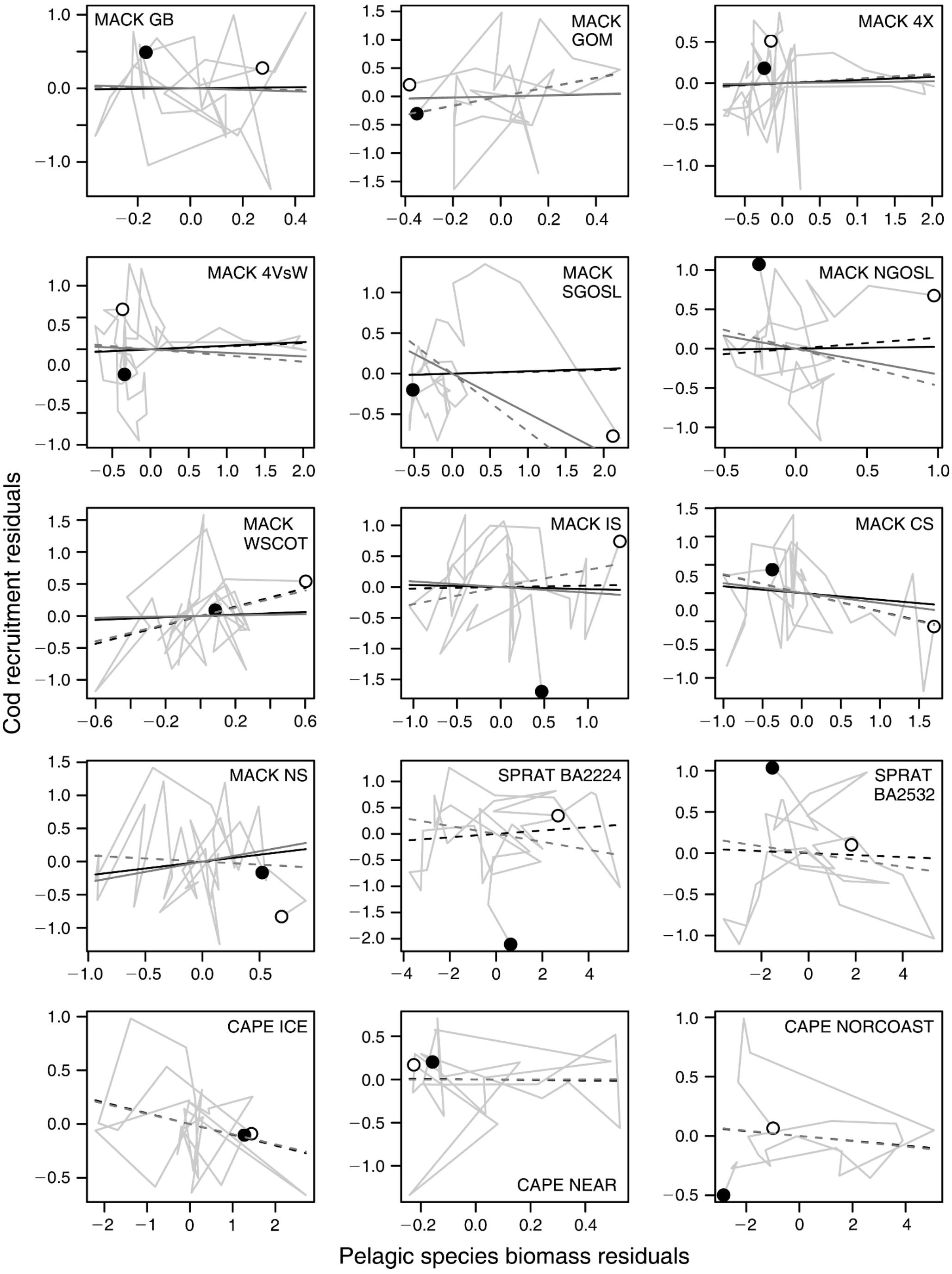

FIG. 4. Partial regression plots of the relationship between standardized cod recruitment and other pelagic species total biomass by region. Details are as in Fig. 3.

investigated the effect of sea surface temperature, copepod (*Calanus finmarchicus*) abundance, adult herring abundance and a competitive effect of herring predation on *C. finmarchicus*. The effect of herring on cod recruitment remained significant after having accounted for the effects of a nonlinear function of adult cod abundance and the abundance of *C. finmarchicus* in the best fitting model. Although the present study ignored such covariates, it is the first to investigate this potential ecological interaction across the north Atlantic region. It is also worth noting that allowing an autocorrelated structure on the residuals may absorb error associated with unobserved autocorrelated environmental covariates. Ultimately, a multiple-hypothesis

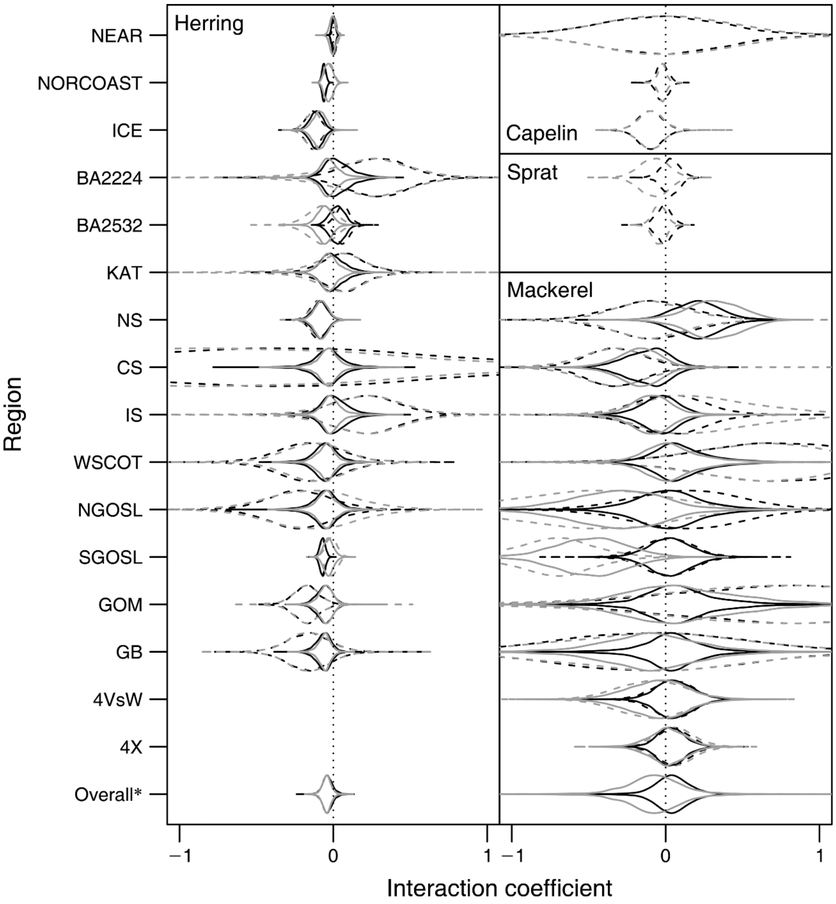

FIG. 5. Posterior densities of the interaction coefficient between standardized cod recruitment and small pelagic fish biomass by region. Densities by model are delineated by line type and color: unpooled independent residuals (u3.1, dashed black lines); unpooled autocorrelated residuals (u3.3 dashed dark gray lines); hierarchical independent residuals (h3.1 solid black lines); hierarchical autocorrelated residuals (h3.3 solid gray lines) (Table 3). Each density arises from 3000 Markov chain Monte Carlo thinned samples from the posterior density.

* The overall effect in the best-fitting herring and mackerel hierarchical analyses.

testing framework or hierarchical implementation of the approach adopted in Fauchald (2010), including the methods developed in Mantzouni et al. (2010), may best determine the proximal relationships. Deriso et al. (2008) present promising generalized methods at the stock assessment stage that allow for the investigation of multiple factors through a combination of multiple factor and randomization tests. Such an approach is beyond the scope of the present analysis.

Modeling assumptions

The key modeling assumptions are that the strength of density dependence is a function of the initial stock density and that the predation mortality term is linear in predator abundance; hence the extended Ricker formulation. Cannibalism has been observed for many cod stocks so the first choice appears appropriate. Given that eggs are likely only a small proportion of the pelagic species diet, satiation is unlikely to occur so that the linear functional form may also be a suitable choice (Sparholt 1996). From a purely practical perspective, the extended Ricker model also lends itself to relatively straightforward visualization, including the partial regression plots we present.

Using a standard definition for depensation: "… the per-capita rate of growth decreases as the density or abundance decreases to low levels" (Liermann and Hilborn 2001), the linear predation mortality term we have used does not give rise to a depensatory model. The per-capita rate of growth is monotonic decreasing over adult abundance at a given predator abundance. Rather, we have addressed is a simpler question of whether the per-capita growth rate is depressed with increasing predator abundance.

Implications

Our extension of the Ricker model is basic and provides a surface with no discontinuities, thresholds or inherent depensatory dynamics. Therefore, we cannot say conclusively whether the systems under investigation have entered new regimes or stable states. Petraitis and Dudgeon (2004) set out conditions for the detection of alternative stable states in the marine environment, including that the alternate states occur in the same habitat, the perturbation must occur quickly, and the system observed for long enough to ensure the stability of the alternate state. In comparison, our observational data are gathered over dynamic environmental conditions where fishing has been relatively protracted over modest time periods. Therefore the ability to detect true alternate states may be limited. From the time-dynamic of Figs. 3 and 4, the relationships are noisy but do not display any sharp transitions to indicate alternate states.

Given the finding that recruitment success of cod often covaries inversely with Atlantic herring abundance, an applied utility is in adjusting the recovery time for populations at severely reduced abundances. Myers et al. (1997*b*) estimated recovery times from maximum population growth rates based on past data. The inherent assumption that the environment remains constant may not be realistic, given the large changes in prey abundance, and the potential feedback on predator recruitment discussed here. Incorporating changes in the abundance of potential egg and larval predators will modify the realized population growth rates. Time series alternatives that don't include specific drivers but allow the population growth rates to evolve in time (Peterman et al. 2003) should also merit further investigation in predicting recovery times given contemporaneous environmental conditions.

From a management advice perspective, the question must ultimately be posed whether negatively interacting species should be fished down or cropped to enhance the prospect of recovery of the depleted population. Given the correlative nature of the present study, to advocate such an action without taking into account secondary interactions of importance (Bax 1998) would be ill advised. For example, were the small pelagics in a region to be fished down, predators of those species and cod, e.g., grey seals (*Halichoerus grypus*), could increase the per-capita predation rate on cod. We anticipate that further investigation of these secondary interactions, including fishing fleet dynamics, will provide important insights into the possible indirect effects of intervening management options. Such an approach generalizes to holistic ecosystem models. These models are far more general than those presented here but they also carry many assumptions and largely ignore uncertainties (Whipple et al. 2000). The hierarchical posterior distributions we have estimated could contribute to the propagation of these uncertainties.

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Supplemental Material

Appendix A

Review of cod spawning and small pelagic fish feeding overlap (*Ecological Archives* E093-203-A1).

Appendix B

Post-estimation interaction coefficient relationships with environmental gradients (*Ecological Archives* E093-203-A2).

Appendix C

Sensitivity analyses to assumed levels of measurement error (*Ecological Archives* E093-203-A3).

Appendix D

Description of data sources and references (*Ecological Archives* E093-203-A4).