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A cross-ecosystem comparison of spatial and temporal patterns of covariation in the recruitment of functionally analogous fish stocks

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ABSTRACT

Temporal and spatial patterns of recruitment (R) and spawning stock biomass (*S*) variability were compared among functionally analogous species and similar feeding guilds from six marine ecosystems. Data were aggregated into four regions including the Gulf of Maine/Georges Bank, the Norwegian/Barents Seas, the eastern Bering Sea, and the Gulf of Alaska. Variability was characterized by calculating coefficients of variation and anomalies for three response variables: ln(R), ln(*R*/*S*), and stock–recruit model residuals. Patterns of synchrony and asynchrony in the response variables were examined among and between ecosystems, between- and within-ocean basins and among functionally analogous species groups using pairwise correlation analysis corrected for within-time series autocorrelation, multivariate cross-correlation analyses and regime shift detectors. Time series trends in response variables showed consistent within basin similarities and consistent and coherent differences between the Atlantic and Pacific basin ecosystems. Regime shift detection algorithms identified two broad-scale regime shift time periods for the pelagic feeding guild (1972–1976 and 1999–2002) and possibly one for the benthic feeding guild (1999–2002). No spatial patterns in response variable coefficients of variation were observed. Results from multivariate cross-correlation analysis showed similar trends. The data suggest common external factors act in synchrony on stocks within ocean basins but temporal stock patterns, often of the same species or functional group, between basins change in opposition to each other. Basin-scale results (similar within but different between) suggest that the two geographically broad areas are connected by unknown mechanisms that, depending on the year, may influence the two basins in opposite ways. This work demonstrates that commonalities and synchronies in recruitment fluctuations can be found across geographically distant ecosystems but biophysical causes of the fluctuations remain difficult to identify.

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1. Introduction

A necessary first step toward understanding any ecosystem is to determine its community structure, function, and variability. Obtaining such understanding has proved difficult for marine ecosystems because of their complexity and the many interacting nonlinear relationships that define them. Spatially, marine ecosystems are usually embedded within large oceanic basins, often with dynamic ecosystem boundaries. More times than not, marine ecosystem boundaries do not conform to established political or management areas which often dictate or constrain data collection opportunities. Also, ecosystems respond simultaneously to multiple spatial scales including large basin-scale influences, as well as intermediate and regional forcing that control local conditions. Temporally marine ecosystems are impacted by annual, interannual, and multi-decadal scale influences that introduce significant variability in features such as sea surface temperature (SST), storm intensity, large-scale atmospheric forcing, advective processes, mixed layer depth, horizontal and vertical transport, and ecological dynamics. Trophodynamically, marine ecosystem food webs are dynamic and nonlinearly respond to climatic, anthropogenic, and ecological influences (Link, 2002).

The comparative approach is one method that has provided significant insights into ecosystem structure, function, and variability. Comparative analysis is a valuable scientific activity since the size and complexity of marine ecosystems precludes conducting controlled in situ experiments. Comparisons among and between

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ecosystems are powerful because they can take advantage of "natural experiments" that otherwise would not be feasible and can identify important similarities and differences between and among ecosystems. Scientific literature shows that comparative analysis can be used successfully in the study of marine ecosystems (Hunt and Megrey, 2005; Moloney et al., 2005; Megrey and Aydin, 2009; Sakshaug and Walsh, 2000) and the dynamics of individual species between ecosystems (e.g. cod, through the ICES/GLOBEC Cod and Climate program, Brander, 1994, 1995; Planque and Frédou, 1999; Dutil and Brander, 2003; Rätz and Lloret, 2003; Drinkwater, 2005). Comparisons afford the benefit of a broad perspective and offer the opportunity to draw generalizations about fundamental aspects of marine ecosystems and unique aspects of specific ecosystems. Such generalizations are important for successful application of the ecosystem approach to fisheries and may hold promise in determining the response of marine ecosystems to global warming and climate change.

The objectives of this study are to compare variability in temporal and spatial patterns of various measures of recruitment among functionally analogous species, similar feeding guilds, and from six Northern Hemisphere marine systems including the Gulf of Maine (GOM)/Georges Bank (GB), the Norwegian Sea (NS)/Barents Sea (BS), the eastern Bering Sea (EBS), and the Gulf of Alaska (GOA). Recruitment was chosen as the comparative index because it is one of the primary factors (along with growth and mortality) influencing changes in species biomass. Moreover, in ecosystems that contain managed commercially exploited fish stocks, estimates of recruitment and spawning biomass are always available from annual stock assessment models. Finally, recruitment is a good integrator of ecosystem productivity and is affected by ecosystem variability.

The close physical proximity of three pairs of adjacent ecosystems (EBS versus GOA; GOM versus GB; and NS versus BS), added to their similarities and differences make for a unique and interesting comparison of ecosystem properties. Potential comparisons can include: (1) large differences in latitudinal and longitudinal ecosystem location, (2) coastal shallow shelf ecosystems (GB, GOM, GOA, EBS) versus open deep basin ecosystems (NS, BS), (3) Pacific basin (EBS, GOA) versus Atlantic basin (GOM, GB, NS, BS), (4) western (GOM, GB) and eastern (NS, BS) ecosystems within the Atlantic basin, (5) functional groups and feeding guilds within and between ecosystems, (6) ecosystems that are ice-covered (EBS/BS) compared with those with no ice (GOAGB/GOM/NS), and (7) ecosystems influenced by warm water (northward) transport into their region (EBS/GOA/NS/BS) versus cold water (southward) transport (GOM/GB). Since many of the species included in this study are common to all ecosystems, we can investigate ecosystem responses between common species among ecosystems (e.g. cod).

Species were combined into functionally analogous groups by life history characteristics and feeding ecology to provide additional comparative opportunities. The various ecosystem, species, and functional group comparisons were used to examine temporal and spatial patterns of covariation, to look for synchronies in large-scale versus multi-decadal changes in the ecosystems both within and between ocean basins, to identify patterns of synchrony and asynchrony in recruitment and spawning stock indices, to evaluate links between recruitment time series and available physical time series, and finally to identify key areas of differences and similarities.

This study and several companion papers (Drinkwater et al., in this issue; Gaichas et al., in this issue; Link et al., in this issue; Mueter et al., in this issue) are part of the international Marine Ecosystems of Norway and the US (MENU) collaboration.

2. Materials and methods

2.1. Data

We used estimates of spawning stock biomass (*S*, 1000 metric tons (t)) and annual numbers of recruits (*R*, millions) from single species stock assessments based on commercial fisheries data for 23 exploited stocks spanning six northern hemisphere marine ecosystems. Ecosystems were aggregated into four groups including Gulf of Main/Georges Bank (GB), eastern Bering Sea (EBS), Gulf of Alaska (GOA), and the Norwegian/Barents Sea (BNS) (see Fig. 1). The common name (and species abbreviation), family name, scientific names, functional groups, and ecosystem for the species of fishes used in this study are summarized in Table 1.

Species data, which were classified according to life histories and ecological functionality, were then organized into pelagic

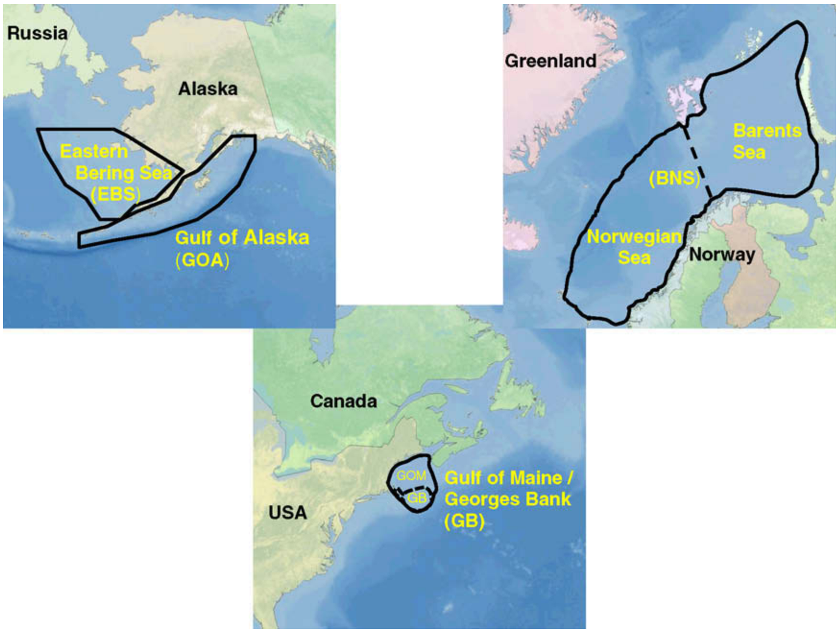

Fig. 1. Location of the four ecosystems used in this study.

Table 1
Common (with species abbreviation), family, scientific name, ecosystem and functional groups for the species of fishes used in this study.

Common name	Family	Scientific name	Ecosystem(s)	Feeding guild	Functional group
Pacific herring	Clupeidae	*Clupea harengus pallasi*	EBS, GOA	Pelagic	Herring
Atlantic herring	Clupeidae	*Clupea harengus harengus*	GB	Pelagic	Herring
Norwegian spring spawning herring	Clupeidae	*Clupea harengus harengus*	BNS	Pelagic	Herring
Atlantic mackerel	Scombridae	*Scomber scombrus*	GB	Pelagic	Mackerel
NE Atlantic mackerel	Scombridae	*Scomber scombrus*	BNS	Pelagic	Mackerel
Pacific cod	Gadidae	*Gadus macrocephalus*	EBS, GOA	Pelagic	Cod
NW Atlantic cod	Gadidae	*Gadus morhua*	GB	Pelagic	Cod
NE Arctic cod	Gadidae	*Gadus morhua*	BNS	Pelagic	Cod
Haddock	Gadidae	*Melanogrammus aeglefinus*	GB	Benthic	Haddock
NE Arctic haddock	Gadidae	*Melanogrammus aeglefinus*	BNS	Pelagic	Haddock
Walleye pollock	Gadidae	*Theragra chalcogramma*	EBS, GOA	Pelagic	Pollock
Blue whiting (BW)	Gadidae	*Micromesistius poutassou*	BNS	Pelagic	Pollock
Greenland turbot (GT)	Pleuronectidae	*Reinhardtius hippoglossoides*	EBS	Benthic	Flatfish
Pacific halibut	Pleuronectidae	*Hippoglossus stenolepis*	GOA	Benthic	Flatfish
Yellowtail flounder (YF)	Pleuronectidae	*Limanda ferruginea*	GB	Benthic	Flatfish
Greenland halibut (GH)	Pleuronectidae	*Reinhardtius hippoglossoides*	BNS	Benthic	Flatfish
Rockfish	Sebastidae	*Sebastes* spp.	EBS, GOA, GB	Benthic	Rockfish
Redfish	Sebastidae	*Sebastes marinus*	BNS	Benthic	Rockfish

EBS, eastern Bering Sea; GB, Georges Bank/Gulf of Maine; GOA, Gulf of Alaska; BNS, Barents/Norwegian Sea.

and benthic feeding guilds and functionally analogous groups (Table 1) to facilitate cross-ecosystem comparisons. Feeding guild assignments, made for statistical convenience, were based on the main prey groups of the species. However, we recognize that this classification is not absolute and that the fish will likely feed on other portions of the pelagia/benthos. The 23 species/ecosystem groups were organized into seven functionally analogous species groups, namely: Cod, gadid cods; Pollock, gadids (excluding cod and haddock); Haddock, gadids (excluding cod and pollock); Herring, clupeids; Mackerel, scombrids; Flatfish, pleuronectids; and Rockfish, *sebastes* spp. The recruitment and spawning biomass time series data are given in Appendix A.

In some ecosystems, species were combined into functional groups based on similar life histories, ecological functionality, or feeding characteristics. For example, in the eastern Bering Sea the Rockfish functional group was computed by summing the recruitment time series of northern rockfish and Pacific ocean perch (Table A1 – original time series not shown). Similarly, the Rockfish functional group in the Gulf of Alaska consisted of recruitment values from northern rockfish, dusky rockfish, rougheye rockfish, and Pacific ocean perch (Table A2 – original time series not shown). In the BNS ecosystem, the Cod functional group was made up of northeast Atlantic cod and coastal cod time series (Table A4 – original time series not shown). Similar data combinations were performed for the spawning biomass time series (Tables A5–A8).

Haddock were classified to the benthic and pelagic feeding guild in the GB and BNS ecosystems, respectively. Even though haddock are the same species in both systems, BNS haddock feed pelagically owing to the deeper waters located in the BNS ecosystem compared to the shallower GB ecosystem where they are benthivorous.

Three environmental data series from each ecosystem were also used in the study. Data were extracted on predefined grids that best represented the ecosystem boundaries (see Fig. 1, Mueter et al., in this issue). Sea surface temperature was derived from the Extended Reconstructed Sea Surface Temperature (ERSST, version 2) dataset. This dataset is based on the temperature compilation of the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) SST dataset and represents interpolation procedures that reconstruct SST fields in regions with sparse data (Smith and Reynolds, 2003, 2004). The data series begins in January 1854, but the signal is heavily damped before 1880 since the early data are more limited; SST estimates are more consistent after 1880. Spatial resolution of the data is 2° longitude by 2° latitude bins and the temporal resolution is monthly.

Chlorophyll a concentrations were derived from the sea-viewing wide field of view sensor (SeaWiFS) onboard the SeaStar spacecraft. We used the level-3 processed data at a temporal resolution of 1 month (available at the National Aeronautics and Space Administration Ocean Color website: http://www.oceancolor.gsfc.nasa.gov/) and we confined our spatial sampling to the domains prescribed in Fig. 1 of Mueter et al. (in this issue). Error estimates on the chlorophyll concentrations are 95% confidence intervals based on the monthly observations over the period 1998–2006. Estimates of net primary production are based on the vertically generalized production model (VGPM) of Behrenfeld and Falkowski (1997). This chlorophyll-based model uses a temperature-dependant relationship for photosynthetic efficiency.

Primary productivity data were available via the Ocean Productivity website and were also sampled at a temporal frequency of 1 month (http://www.web.science.oregonstate.edu/ocean.productivity/index.php). Error estimates for the net primary productivities are 95% confidence intervals based on the monthly observations over the period 1998–2006.

2.2. Response variables

We used three different response variables in our analysis (1) log-transformed recruitment (ln(R), log R using natural logarithms), (2) log-transformed ratio of recruitment to spawner biomass (ln(R/S), using natural logarithms) as an index of survival, and (3) stock–recruit residuals (SR residuals) from the best-fit stock–recruitment model as defined below. The SR residuals were obtained for each of the stocks listed in Table 1 by computing residuals from a stock–recruitment model that was fit to time series of recruits (R) that resulted from parental spawning biomass (S) occurring in the same year. Using SR residuals as an index has the effect of removing the presumed density-dependent effect of spawner abundance. Thus, the SR residual response variable reflects the unexplained variability in recruitment arising from environmental fluctuations and/or measurement errors (Peterman et al., 1998). Because we assume that the form of the stock–recruitment relationship is rarely known and that they likely vary among stocks, we fit two models to each spawner–recruit time series, including the Ricker and Beverton-Holt models. Models were fit using nonlinear least-squares regression. Parameter starting values were estimated by applying linear regression to the linearized form of the models. Functional forms for the linear and nonlinear forms and parameter estimation routines are described in Quinn and

Deriso (1999). The statistically "best-fit" model for each stock was selected based on the small-sample Akaike Information Criterion (AIC, Akaike, 1974; Hurvich and Tsai, 1989). We used residuals from the model with the lowest AIC score as our final SR residual response variable in further analyses. In some cases a nonlinear model would not converge. In these situations, the model was fit iteratively by hand in two steps. First we constrained one parameter (set to the linear regression estimate) and estimated the second parameter with nonlinear regression. Then, after the second parameter was estimated, it was constrained to the previous nonlinear regression estimate and the first parameter was free to be estimated by nonlinear regression. This process was repeated until the objective function stabilized.

To facilitate comparisons between ecosystems and response variable time series, variability in the response variables were characterized by calculating the time series anomalies (to put variables on the same scale and to minimize differences due to absolute magnitude of abundance) and coefficient of variation (a relative measure of variation) according to the following calculation. If x is a time series, then the anomaly was calculated as $(x - \mu_x)/\sigma_x$ and the coefficient of variation was calculated as σ_x/μ_x.

2.3. Analysis methods

Exploratory analyses (between and within functional groups, feeding guilds and ecosystems) were performed looking at temporal trends in time series anomalies, trends in the coefficient of variation (CV) with latitude, multivariate cross-correlation analyses (Dynamic Factor Analysis), and coherence in low frequency regime shifts or change-point analysis.

2.3.1. Trends in aggregate response variable time series anomalies

We compared response variables between functional groups, feeding guilds, within ecosystems, and between ecosystems. To estimate the magnitude of covariation, we aligned all response variable anomalies (ln(R), ln(R/S), and SR residuals) by year class and pooled anomalies for each year by calculating the average anomaly per year based on the available data for that year, in a manner similar to Mueter et al. (2007). This aggregation method was also used to calculate the average anomaly for each ecosystem by pooling anomalies for all species within an ecosystem. Mueter et al. (2007) points out that this particular aggregation method has the advantage of giving equal weight to each stock rather than weighting by abundance, which would give the most abundant species undue influence. Finally, a 10-year moving average was applied to the annual average anomaly over years to smooth interannual variability and to facilitate identifying within- and cross-ecosystem temporal patterns. The degree of smoothing was chosen to roughly correspond to the decadal-scale variability that is dominant in many biological and physical time series in the Northeast Pacific (Hare and Mantua, 2000) and the Northeast and Northwest Atlantic (Hurrell, 1995).

Correspondence and opposing associations were determined by calculating a two-tailed Pearson's product–moment correlation coefficient between pairs of smoothed time series. Correlations were corrected for autocorrelation introduced by applying the moving average smoother by adjusting the effective degrees of freedom of each test according to the procedure suggested by Pyper and Peterman (1998), under the null hypothesis that the two time series were mutually uncorrelated (i.e. H_o: the correlation coefficient was equal to zero; H_a: the correlation coefficient was not equal to zero). Only statistically significant correlations will be described.

2.3.2. Latitudinal patterns in response variable CV

High latitude ecosystems, three of which are included in this study (EBS, GOA, BNS), are especially sensitive to climate change as they bridge the transition region between Arctic and North Temperate ecosystems (Hunt and Megrey, 2005). The last few decades of modern ocean observation confirm significant annual and interannual variations in features such as ice cover, insolation, SST, storm intensity, large-scale atmospheric forcing, advective processes, and trophodynamic interactions. We felt the wide latitudinal range between the six ecosystems used in this study would provide sufficient contrast to test whether latitudinal patterns in recruitment variability, as expressed by the response variables CV, provide evidence for the existence of spatial patterns in the variability of the biological time series. Our working null hypothesis is that higher latitude ecosystems are more variable than lower latitude ecosystems because the response of upper trophic levels may be more direct in higher latitude systems where food webs and trophic interactions are simpler and where zooplankton and fish species are often limited by cold temperatures. We expect that recruitment time series of species from higher latitude ecosystems will have higher response variable CVs and we expect to find a positive relationship between the recruitment time series response variable CV and latitude.

To examine this hypothesis, we first calculated the CV of the response variables (ln(R), ln(R/S), and SR residuals) for each ecosystem/species time series and calculated the mean latitude of each ecosystem given its range in latitude (see Fig. 2 in Gaichas et al., in this issue). Mean latitudes were assigned to ecosystems as EBS = 58.75°N, GOA = 56.5°N, GB = 42.5°N and BNS = 72.5°N. CVs for all ecosystem/species groups for each response variable were ranked, and the CVs of the response variables were calculated by functional groups and feeding guild and ecosystem. We then looked for relationships between the CV for each data group and the mean latitude of the ecosystem using linear regression.

We also calculated the CV of each environmental time series by first calculating the annual mean from monthly values per year, then calculating the mean and standard deviation using all the available years. The value of the environmental time series CV was then matched with the mean latitude value for the respective ecosystem given above. The CV for the BNS ecosystem represented the mean CV from each of the three Barents Sea subareas and the Norwegian Sea area used to extract environmental data. (see Fig. 1 in Mueter et al., in this issue).

2.3.3. Dynamic Factor Analysis

Quantitative exploratory analyses were conducted on the time series of recruitment within and among functional groups and ecosystems using Dynamic Factor Analysis (DFA), a multivariate dimension-reduction technique especially designed for time series. Limited application to fisheries data exist (Addis et al., 2008; Zuur et al., 2003) and some applications to physical data have been (Friedland and Hare, 2007). Zuur et al. (2003) explains that DFA can indicate whether there are any underlying common patterns in a collection of time series, whether there are interactions between the response variables, and the effects of explanatory variables. Patterns can be common trends, common seasonal effects, or common cycles (Zuur et al., 2003).

The three recruitment response variable time series in this study were analyzed separately: log(R) anomaly, log(R/S) anomaly, and residuals from stock–recruitment relationships. DFA is limited in the number of time series that can be analyzed simultaneously, thus DFA was applied separately to all species in an ecosystem and separately to each functional group (benthic and pelagic) across ecosystems, and by ecosystem. These preliminary analyses lead to more explicit exploratory analyses examining common trends among ecosystems and functional groups. The DFA model fits of these explicit analyses indicated that two common trends were typically, but not always, the most appropriate (smallest AIC value). To keep the analyses similar across ecosystems and functional groups, all DFA

Table 2
Parameter estimates from fitting Ricker and Beverton-Holt spawner–recruit models to the recruitment and spawning biomass time series. AIC is the Akaike Information Criterion (Akaike, 1974).

Common name	Year classes	Ecosystem	Ricker			Beverton-Holt		
			α	β	AIC	α	β	AIC
Pacific herring	69–02	EBS	***29.31***	***−0.02***	*−349.20*	*234.52*	*48.91*	*−358.28*
	77–03	GOA	**5.30**	**−0.005**	−334.56	700.76	126.49	−334.57
Atlantic herring	67–03	GB	**9.80**	**−0.001**	−677.37	3395.56	206.02	−677.49
Norwegian spring spawning herring	50–05	BNS	19.63	−5.72e−06	−1540.25	**297880.36**	**6312.13**	−1539.99
Atlantic mackerel	62–03	GB	2.03	−0.0006	−750.92	**1244.72**	**70.31**	−749.28
NE Atlantic mackerel	72–05	BNS	**4.40**	**−0.0004**	−626.54	*7765.32*	*2443.65*	*−628.80*
Pacific cod	64–05	EBS	4.72	−0.002	−674.39	***807.82***	***38.33***	*−670.73*
	64–04	GOA	**2.03**	**0.00**	−522.39	1932.70	941.80	−522.38
NW Atlantic cod	78–04	GB	**0.53**	**−0.007**	−217.92	53.52	95.25	−218.12
NE Arctic cod	43–04	BNS	3.41	−0.002	−937.54	**740.31**	**69.89**	−934.68
Haddock	63–04	GB	**0.47**	**0.006**	−557.54	*463.20*	*379.96*	*−559.77*
NE Arctic haddock	47–03	BNS	**3.31**	**−0.005**	−799.33	381.49	89.11	−799.47
Walleye pollock	63–05	EBS	**45.05**	**−0.0006**	−949.76	*27197.46*	*200.93*	*−954.33*
	59–04	GOA	**4.09**	**−0.001**	−769.26	2273.12	490.10	−769.31
Blue whiting	80–04	BNS	**9.40**	**−7.09e−05**	−528.18	111243.25	11873.87	−528.38
Greenland turbot	75–05	EBS	**0.0011**	**0.011**	−239.73	*25.16*	*145.81*	*−268.23*
Pacific halibut	68–99	GOA	**0.32**	**−0.02**	−140.59	9.14	16.40	−143.04
Yellowtail flounder	73–04	GB	4.57	−0.05	−267.35	**63.53**	**12.38**	−267.27
Greenland halibut	59–01	BNS	1.05	−0.01	−292.39	**30.05**	**13.20**	−291.53
Rockfish	57–96	EBS	1.61	−0.004	−464.64	**189.66**	**83.53**	−464.32
	59–04	GOA	0.82	−0.001	−524.87	**440.86**	**501.70**	−524.83
	40–03	GB	0.88	−0.006	−763.86	**48.20**	**5.12**	−762.48
Redfish	87–03	BNS	1.67	−0.03	−88.42	***12.48***	***17.59***	*−82.33*

Italic and bolditalic: model did not converge; fit iteratively by hand.
Bold: model selected to calculate the residual.

analyses were subsequently preformed with two common trends. In reporting DFA results, factor loadings exceeding ±0.2 were considered important. DFA was implemented using the Brodgar 2.5.2 software package[1] (http://www.brodgar.com).

2.3.4. Regime shift identification

A "regime shift" can loosely be defined as an abrupt, high amplitude change from one relatively steady state to another (see Lees et al., 2006 and references therein). An ecosystem regime shift generally involves synchronized shifts in a number of indicator variables, both environmental (e.g. climatic, oceanographic) and ecological (e.g. species abundance, diversity). Regime shifts can also be characterized as occurring with low frequency (decadal and longer time scales) and at large spatial scales.

We applied change-point analysis using the "Sequential T-test Analysis of Regime Shifts" algorithm (STARS v3.2 http://www.beringclimate.noaa.gov/regimes/: Rodionov, 2004; Rodionov and Overland, 2005) to the response variables to investigate whether we could detect "regime shifts" in recruitment across the ecosystems and whether such shifts followed similar patterns in each ecosystem. We characterized changes in recruitment using the response variables described above and we performed separate change-point analyses for each response variable. Stocks within each ecosystem were grouped according to feeding guild (pelagic or benthic) and analyses were conducted separately for each guild.

STARS is one of several methods that have been developed to detect discontinuities ("change points" or "regime shifts") in time series (see reviews of other methods in Easterling and Peterson, 1995; Lanzante, 1996). STARS sequentially tests whether each subsequent data point in a time series differs significantly from the mean of previous data points belonging to the latest "regime". If the difference is significant, the point is identified as the potential start of a new regime. As more data points are added, the identification of a "regime shift" is statistically accepted or rejected. The identification of a regime shift is tested using the "regime shift index" (RSI), which represents the cumulative sum of normalized deviations from the hypothetical mean level for the "new" regime. The difference between this and the mean level for the current regime is tested using a *t*-statistic. A large average RSI may result from a pronounced shift in one or a few series or from small shifts in many individual series. The main advantage of STARS over other methods is its ability to identify potential shifts in real time and to measure the changing confidence in evidence for a shift as additional data arrive (Rodionov and Overland, 2005). Also, it can process data with multiple shifts and it does not require visual examination of a time series nor *a priori* hypotheses regarding the specific time when the shift occurs (i.e. via time series intervention analysis). Finally, evidence for regime shifts is integrated across multiple lines of evidence (i.e. different time series) by summing the RSI values from each time series for every year. As a statistical model, the STARS algorithm requires the prior specification of some model parameters and constants. These include a minimum value for the number of years in a regime, a *p*-value for significance testing, and a weighting parameter for data outliers.

Time series were subjected to the STARS algorithm for regime shift detection using a 10-year data window, a significance value of 0.1, and a Huber range of 3.0. Results from individual time series were then integrated within individual ecosystem and the pelagic versus benthic feeding guild by computing a summary RSI value for each year. Summary RSI values were then combined across ecosystems by feeding guild to highlight particularly broad scale or "energetic" regime shifts using a symmetric 5-point moving average filter (0.4, 0.9, 1.0, 0.9, 0.4) to combine evidence for shifts that differed by only a year or two. Results from the moving average were used to identify time periods with substantial evidence for regime shifts. Results from individual time series and summary plots by ecosystem/data category combinations were examined to identify potential synchronous regime shifts among the ecosystems, as well as asynchronous patterns suggesting similar dynamic responses among and within the six ecosystems.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

3. Results

3.1. Fitting spawner–recruit models to the spawning biomass and recruitment time series

The spawner–recruit data were generally noisy and often displayed patterns that were not approximated well by Ricker or Beverton-Holt spawner–recruit models. Which model described the data best varied between stocks (Table 2) and often the AIC value between the Ricker and Beverton-Holt models was very similar indicating that the fit of both models were similar. In several cases, we were unable to fit the spawner–recruit models using a least-squares or maximum likelihood approach because the models would not converge. Even in cases where the model was fit iteratively, the final AIC score was similar between recruitment models (i.e. BNS NE Atlantic mackerel, EBS Pacific cod, GB haddock, EBS walleye pollock, and BNS redfish).

3.2. Trends in aggregate response variable time series anomalies

In general, the within-basin temporal patterns showed coherent associations while between-basin patterns showed opposing associations (Table 3). All degrees of freedom values are reported adjusted for within-time series autocorrelation introduced by applying the moving average smoother.

3.2.1. Recruit [ln(R)] anomaly time series

The EBS and GOA and the GB and BNS time series covaried strongly together, with the EBS–GOA series demonstrating an opposing association with the GB–BNS time series (Fig. 2 and Table 3). For the benthic feeding guild, the EBS and GOA benthic series were positively correlated with each other while the EBS and GOA benthic series were both strongly negatively correlated with the BNS benthic series. For the pelagic feeding guild, the EBS and GOA pelagic series were both positively correlated, and the EBS and GOA pelagic series were negatively correlated with the GB pelagic series, the GOA pelagic series was negatively correlated with the BNS pelagic series and the GB and BNS pelagic series were positively correlated. At the ecosystem level, the EBS and

Table 3
Pair-wise Person's correlation coefficients (adjusted degrees of freedom) between response variable time series. Statistically significant correlations ($p < 0.01$) are in bold-face type. $|r| > 0.6$ (arbitrary) are italicized for purpose of comparison.

	ln(*R*) anomaly			
	EBS.benthic	GOA.benthic	GB.benthic	BNS.benthic
EBS.benthic	1.00	***0.55 (8.3)***	0.19	−***0.72 (10.5)***
GOA.benthic		1.00	0.25	−***0.81 (10.5)***
GB.benthic			1.00	−0.29
BNS.benthic				1.00
	EBS.pelagic	GOA.pelagic	GB.pelagic	BNS.pelagic
EBS.pelagic	1.00	***0.66 (10.4)***	−***0.62 (10.0)***	0.14
GOA.pelagic		1.00	−***0.70 (10.0)***	−***0.39 (8.3)***
GB.pelagic			1.00	***0.54 (10.9)***
BNS.pelagic				1.00
	EBS	GOA	GB	BNS
EBS	1.00‘	***0.85 (8.1)***	−0.23	−***0.39 (8.7)***
GOA		1.00	−0.27	−0.33
GB			1.00	***0.91 (5.7)***
BNS				1.00
	ln(*R*/*S*) anomaly			
	EBS benthic	GOA benthic	GB benthic	BNS benthic
EBS.benthic	1.00	0.23	−0.22	−0.19
GOA.benthic		1.00	0.21	***0.41 (8.1)***
GB.benthic			1.00	***0.86 (8.5)***
BNS.benthic				1.00
	EBS.pelagic	GOA.pelagic	GB.pelagic	BNS.pelagic
EBS.pelagic	1.00	***0.93 (10.1)***	−***0.51 (10.9)***	−***0.54 (9.5)***
GOA.pelagic		1.00	−***0.58 (9.8)***	−***0.69 (8.9)***
GB.pelagic			1.00	***0.50 (10.1)***
BNS.pelagic				1.00
	EBS	GOA	GB	BNS
EBS	1.00	***0.66 (7.4)***	−***0.62 (7.8)***	−***0.85 (7.9)***
GOA		1.00	−0.15	−***0.59 (8.0)***
GB			1.00	***0.59 (8.4)***
BNS				1.00
	SR residual anomaly			
	EBS.benthic	GOA.benthic	GB.benthic	BNS.benthic
EBS.benthic	1.00	0.36	0.13	0.13
GOA.benthic		1.00	−***0.44 (8.3)***	−***0.37 (11.2)***
GB.benthic			1.00	0.11
BNS.benthic				1.00
	EBS.pelagic	GOA.pelagic	GB.pelagic	BNS.pelagic
EBS.pelagic	1.00	0.31	−***0.65 (10.9)***	−0.32
GOA.pelagic		1.00	−***0.67 (10.4)***	−***0.61 (11.9)***
GB.pelagic			1.00	***0.59 (12.7)***
BNS.pelagic				1.00
	EBS	GOA	GB	BNS
EBS	1.00	***0.45 (8.8)***	−0.28	−***0.54 (9.8)***
GOA		1.00	−***0.82 (8.4)***	−***0.78 (9.5)***
GB			1.00	***0.43 (9.8)***
BNS				1.00

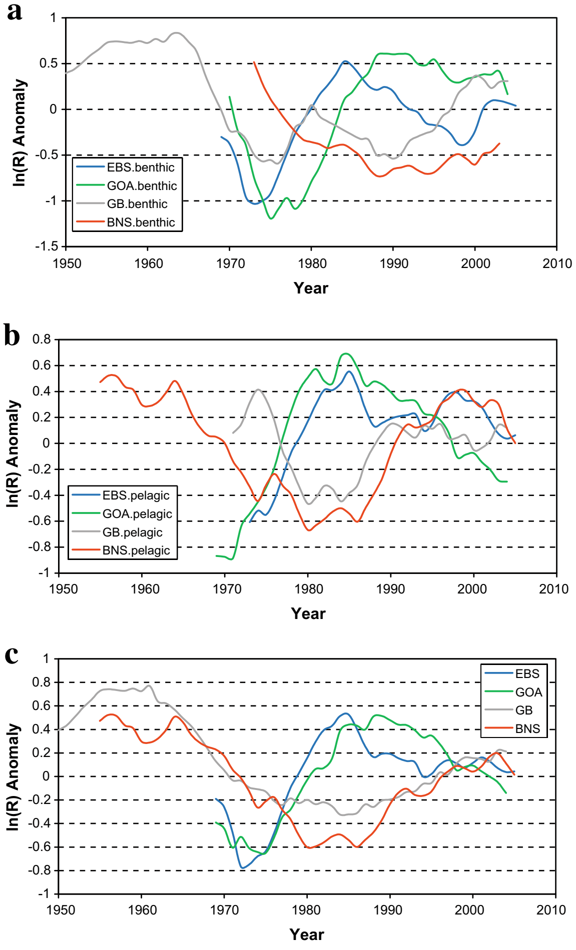


Fig. 2. Comparison of time series for the ln(*R*) response variable anomaly for the benthic (a), and pelagic (b) feeding guilds, and by ecosystem (c). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

GOA series were strongly positively correlated, the EBS series was weakly negatively correlated with BNS series, and the GB and BNS series were very strongly positively correlated.

3.2.2. Survival index [ln(R/S)] anomaly time series

Similar to patterns in ln(*R*), the survival index in the EBS and GOA and the GB and BNS covaried strongly together, and the EBS–GOA series demonstrated an opposing association with the GB–BNS time series (Fig. 3 and Table 3). The GOA benthic series was positively correlated with the BNS benthic series. The GB and BNS benthic series was very positively correlated. The EBS pelagic series was very positively correlated with the GOA pelagic series and negatively correlated with the GB pelagic and BNS pelagic series. The GOA pelagic series was negatively correlated with both the GB and BNS pelagic series and the GB and BNS pelagic series were positively correlated. The EBS series was positively correlated with the GOA series and negatively correlated with the GB and BNS series. The GOA series was negatively correlated with the BNS series, and the GB the BNS series were positively correlated.

3.2.3. SR residual anomaly time series

Again, the EBS/GOA and the GB/BNS time series covaried strongly together, however the EBS/GOA series demonstrated an opposing association with the GB/BNS time series (Fig. 4 and Table 3). The GOA benthic series was negatively correlated with the GB and BNS benthic series. The EBS and GB pelagic series were negatively correlated, and the GOA pelagic series was negatively correlated with both the GB and BNS pelagic series. The GB pelagic and BNS pelagic series were positively correlated. The EBS series was positively correlated with the GOA series and negatively correlated with the BNS series. The GOA series was negatively correlated with both the GB and BNS series. The GB series was positively correlated with the BNS series.

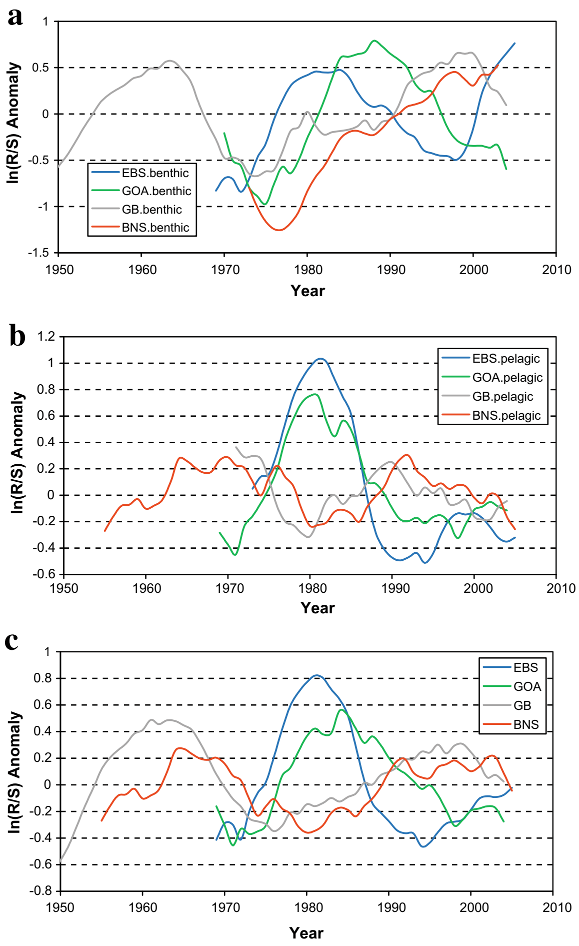


Fig. 3. Comparison of time series for the ln(*R*/*S*) response variable anomaly for the benthic (a), and pelagic (b) feeding guilds, and by ecosystem (c). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

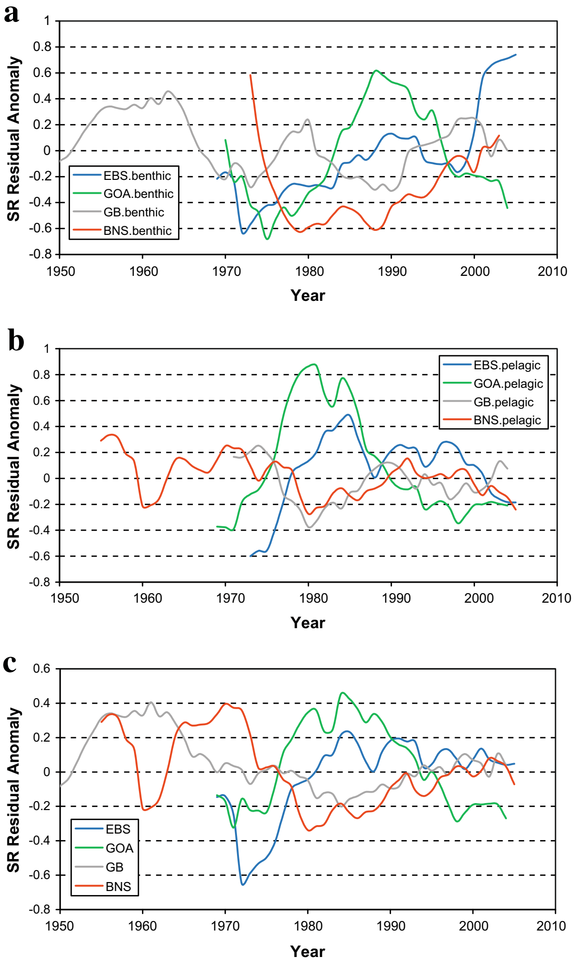


Fig. 4. Comparison of time series for the SR residual response variable anomaly for the benthic (a), and pelagic (b) feeding guilds, and by ecosystem (c). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

3.3. Latitudinal patterns in response variable CV

The ranked CV for the ln(R) response variable by ecosystem/species (Fig. 5a) show that GB haddock was the most variable and EBS pollock was the least variable. Other ecosystem/species groups fell intermediate between these two extremes in a rapid reduction in CV. The ranked CV for the ln(*R*/*S*) response variable (Fig. 5b) showed a large amount of uniformity approximately centered on zero. BNS haddock was the most variable and EBS Pacific herring was the least variable. The ranked CV for the SR residual response variable (Fig. 5c) also showed a large amount of uniformity approximately centered on zero. GB Yellowfin sole (YF) had the largest positive SR residual CV (i.e. a positive mean residual value) and GB mackerel had the largest negative SR residual CV (i.e. a negative mean residual value). Positive CV values included two benthic feeders (GB YF and BNS GH) and five pelagic feeders (BNS mackerel, EBS pollock, GOA pollock, GOA cod, and GB herring).

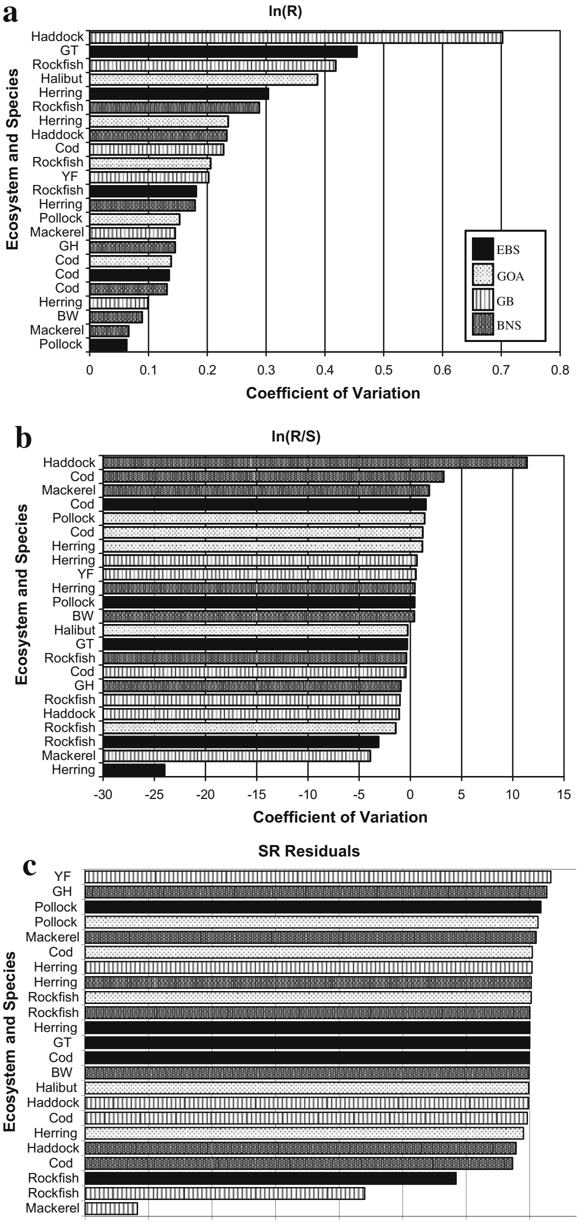


Fig. 5. Ranked trends in CV for ln(R) (a), ln(R/S) (b), and SR residual (c) response variables for each species and by ecosystem. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

Negative CV values included two benthic feeders (EBS rockfish and GB rockfish) and three pelagic feeders (BNS haddock, BNS cod, and GB mackerel). Haddock was the most variable species, with GB haddock having the largest ln(R) CV and BNS haddock having the largest ln(R/S) CV.

After calculating the response variable CV by ecosystem, species functional group and feeding guild (n = 23), there were no clear trends in CV with ecosystem mean latitude for any of the response variables. However, there were significant linear trends between CV and mean latitude (Fig. 6) for all the environmental variables (SST: slope = 225.96, $p < 0.01$; Chl a: slope = 57.04, $p < 0.01$; PP: slope = 78.77, $p < 0.01$). Examining the data by functional group and feeding guild did not show any clear relationship between CV and mean latitude among these variables (Table 4; graphical results not shown). While slope estimates varied between positive and negative, there were only two that were statistically significant (Table 4). For the ln(R/S) response variable, the Cod and Flatfish functional groups displayed statistically significant ($p < 0.01$) positive and negative slopes, respectively. Note that there were not enough data points to statistically estimate slopes for the Mackerel and Haddock functional groups as they only contained two observations. Qualitative observations for those two groups (not shown), indicate that in general, slopes were negative and positive for the ln(R) and ln(R/S) response variables, respectively. A more detailed analysis of associations between SST and recruitment can be found in Mueter et al. (in this issue).

3.4. Dynamic Factor Analysis

Patterns observed in the response variable anomaly trends were also seen in the DFA analyses. In all results, there are large amounts of uncertainty early in the trends owing to the limited number of time series extending prior to 1960. The two trends in the ln(R) response variable (Fig. 7) were: (1) rapid increase in the 1970s with variable but decreasing recruitment through the remainder of the series and (2) relatively moderate increase from 1970 to 1990 followed by a slow decrease from 1990 to the present. GB Cod and GOA Herring were positively associated with trend 1 and BNS Blue Whiting was negatively associated with trend 1. BNS Herring were positively associated with trend 2 and GOA Pollock and Herring were negatively associated with trend 2. The first trend for benthic species increased rapidly through the 1960s, was relatively stable through the mid-1990s, and then decreased slightly. The second trend decreased through the 1960s, increased from the mid-1970s to mid-1980s and then was relatively stable for the remainder of the series. BNS Rockfish were positively associated with trend 1 and BNS Greenland Halibut were negatively associated with trend 1. A number of species were positively associated with trend 2 (GB rockfish, GOA rockfish, EBS rockfish, and GOA halibut) and GB yellowtail flounder was negatively associated with this trend.

The two trends for the ln(R/S) response variable (Fig. 8) for pelagic species were: (1) increasing until about 1970 followed by a sharp decreased and then relative stability, and (2) sharply increasing during the 1970s then decreasing slightly over the remainder of the series. BNS Blue Whiting were negatively associated with trend 1 and EBS Cod, Pollock and Herring were positively associated with this trend. Herring in GOA and GB and Cod in GOA, GB, and EBS were positively associated with trend 2. For benthic species, the two trends were: (1) increasing to about the mid-1980s then decreasing and (2) increasing from the 1970s to 1990 and then relatively stable. EBS Greenland Turbot was negatively associated with trend 1 and GOA Rockfish and Halibut and EBS Rockfish were positively associated with trend 1. BNS Rockfish and Greenland Halibut and GB Rockfish were positively associated with trend 2.

The two trends in the SR residual response variable (Fig. 9) for pelagic species were similar. Trend 1 was stable until the late-1960s, decreasing through 1990, a rapid, moderate increase, and then stable through the remainder of the series. Trend 2 was stable until the late-1960s, rapidly increasing then decreasing through 1990, and stable through the remainder of the series. BNS Blue Whiting and EBS Herring were associated with trend 1 and GOA Pollock and EBS and GOA Cod and GOA Herring were associated with trend 2. For benthic species, the two trends were again similar: (1) a stable period beginning at about 1970 and (2) a slightly increasing trend from 1970 to mid-1980s and then slightly decreasing. BNS Rockfish and GB Yellowtail Flounder were negatively associated with trend 1 and EBS Greenland Turbot and GOA Halibut and Rockfish were positively associated with trend 1. BNS Greenland Halibut and EBS Greenland Turbot were positively associated with trend 2 and GB Yellowtail Flounder negatively.

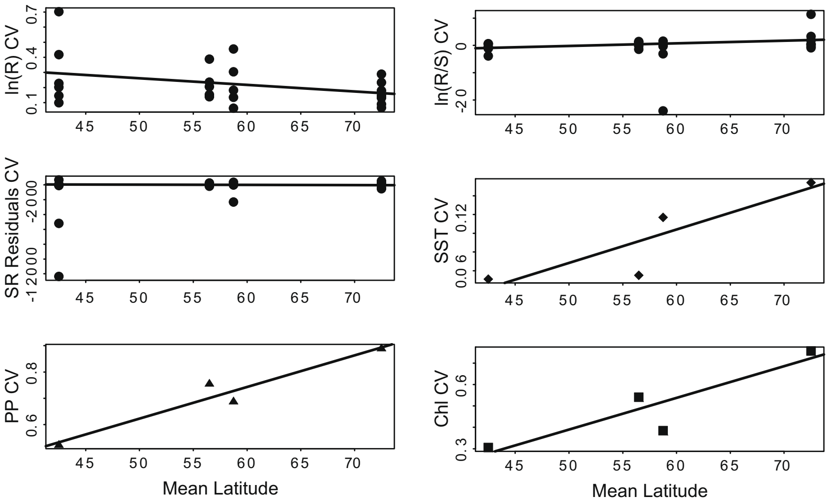


Fig. 6. Relationships between response variable and environmental variable CVs and mean latitude.

Table 4
Results from regressing CV on latitude for three response variables and two data groupings. Presented are the estimated slope (slope), the probability that the slope is not zero (p), and the percent of the variation explained by the regression (R^2). Slopes given as positive (pos) or negative (neg) indicate that there were not enough data points to statistically estimate the slope (i.e. $n = 2$, df = 0), but that visual inspection of the data indicated the slope was positive (pos) or negative (neg). Italicized rows show statistically significant slope estimates ($p < 0.05$).

Response variable	Group	Slope	p	R^2
ln(R)	Mackerel	neg	–	–
	Pollock	−0.002	0.760	0.130
	Rockfish	−0.004	0.490	0.260
	Cod	−0.003	0.150	0.720
	Flatfish	−0.002	0.860	0.020
	Haddock	neg	–	–
	Herring	0.003	0.590	0.160
	Pelagic	−0.001	0.680	0.020
	Benthic	−0.008	0.590	0.160
ln(R/S)	Mackerel	pos	–	–
	Pollock	−0.042	0.570	0.400
	Rockfish	0.016	0.830	0.030
	Cod	*0.124*	*0.001*	*0.990*
	Flatfish	*−0.049*	*0.004*	*0.990*
	Haddock	pos	–	–
	Herring	0.073	0.930	0.005
	Pelagic	−0.010	0.750	0.020
	Benthic	0.170	0.370	0.070
Residuals	Mackerel	pos	–	–
	Pollock	−21.198	0.230	0.870
	Rockfish	166.876	0.170	0.683
	Cod	−15.376	0.320	0.467
	Flatfish	−4.388	0.850	0.023
	Haddock	neg	–	–
	Herring	−0.395	0.960	0.002
	Pelagic	116.180	0.150	0.170
	Benthic	57.370	0.350	0.130

Analysis of the data by ecosystem for the ln(R) (Fig. 10), ln(R/S) (Fig. 11) and SR residual (Fig. 12) response variables show similarities in the temporal estimated trends between the EBS and GOA and between GB and BNS ecosystems. Individual species loadings onto the estimated trends did not reveal any consistent patterns. Generally, there were some consistent similarities between the EBS herring and walleye pollock and among the EBS benthic species.

The between ecosystem patterns described above for the functional groups were also observed in the DFA analyses of individual species. For benthic species, 64% of similar trends occurred within GOA and EBS or within GB and BNS. Similarly, 64% of dissimilar trends occurred between species in the GOA/EBS ecosystems and species in the BNS/GB ecosystems. For pelagic species, the patterns were not as strong; only 40% of similar trends occurred within GOA and EBS or within GB and BNS. However, 100% of dissimilar trends occurred between species in the GOA/EBS ecosystems and species in the BNS/GB ecosystems.

3.5. Regime shift analysis

3.5.1. Recruit [ln(R)] time series

Regime shift analysis of the ln(R) time series data (Fig. 13) detected 37 significant change points over all four ecosystems and feeding guilds. Twenty-two of these change points were detected among the pelagic feeding guild stocks, while 15 were detected among the benthic feeding guild stocks.

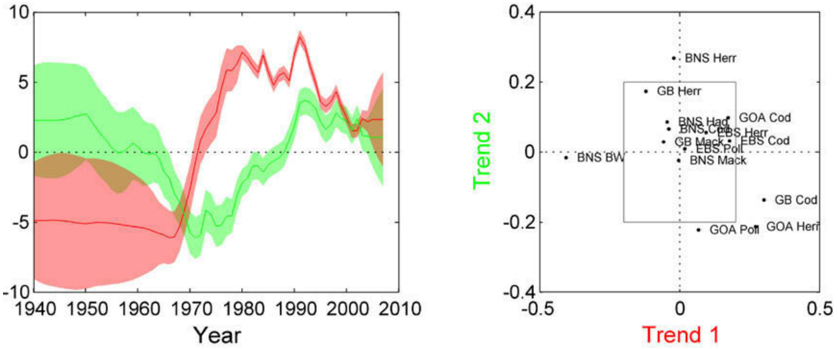
We identified two broad-scale regime shift periods for the pelagic stocks: 1972–1976 and 2000–2004. Change points were detected in all four ecosystems during both periods, although not necessarily in the same stocks. In the earlier period, change points were detected in cod stocks in three of the four ecosystems (GB being the exception), as well as mackerel in the GB. Although change points were detected in several stocks from 1980 to 1995, these were rather evenly distributed across the interval. Among the pelagic feeding guild stocks (Fig. 13a), the most change points (7) were detected for stocks in the GOA, although nearly as many (6) were detected in the GB and BNS; the fewest were detected in the EBS (3).

We identified two broad-scale regime shift periods for the benthic feeding guild stocks: 1966–1970 and 1981–1985. Flatfish in the BNS and rockfish in the GB exhibited the most change points (3 each), while BNS rockfish, EBS rockfish, and GOA flatfish exhibited the fewest (1 each). Among the benthic feeding guild stocks (Fig. 13b), a similar number of change points were detected for each ecosystem, with the most (5) detected in the GB while the least were detected in the EBS and GOA (3 each).

3.5.2. Survival index [ln(R/S)] time series

Regime shift analysis of the ln(R/S) response variable time series data detected 30 significant change points over all four ecosystems and both feeding guild categories (Fig. 14). These were nearly evenly split between the pelagic feeding and benthic feeding guild stocks, with pelagic feeding stocks exhibiting slightly more (16).

a) Pelagic Species



b) Benthic Species

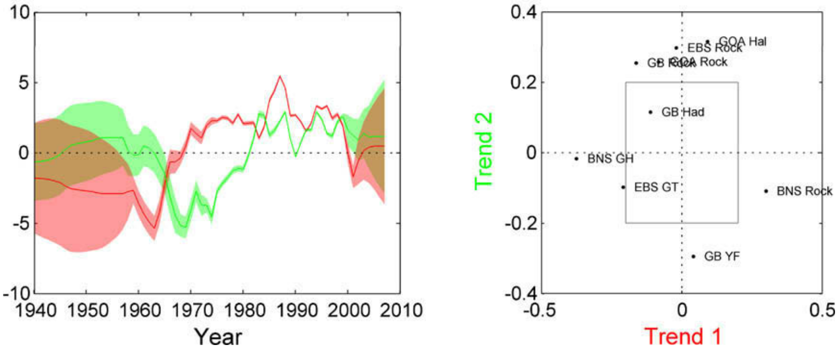
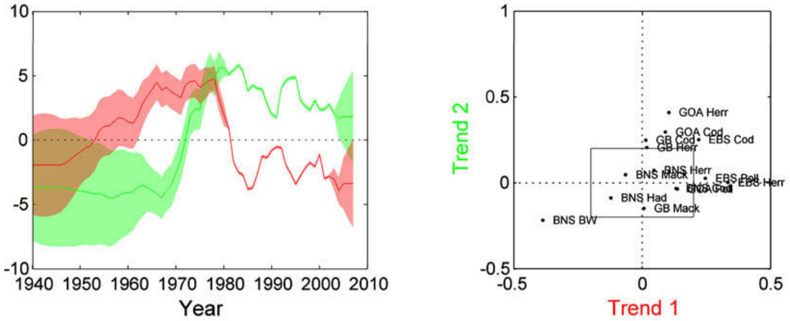


Fig. 7. Results of Dynamic Factor Analysis applied to the pelagic (a) and benthic (b) feeding guild ln(R) anomaly response variable time series pooled over ecosystems. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

a) Pelagic Species



b) Benthic Species

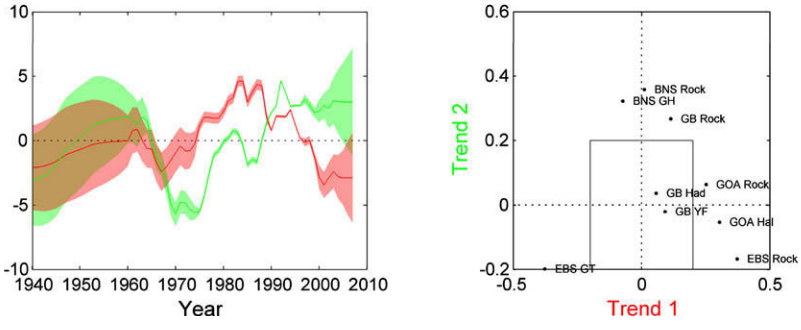
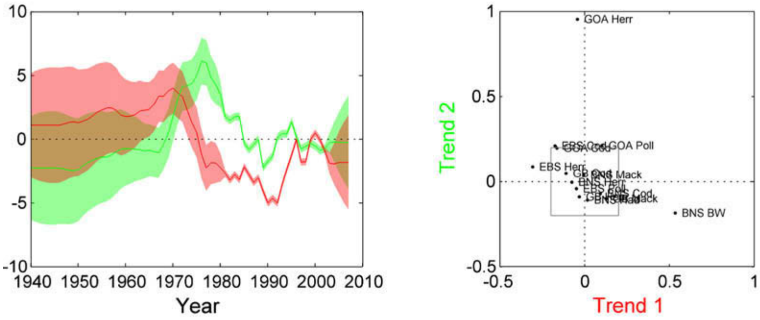


Fig. 8. Results of Dynamic Factor Analysis applied to the pelagic (a) and benthic (b) feeding guild ln(R/S) anomaly response variable time series pooled over ecosystems. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

a) Pelagic Species



b) Benthic Species

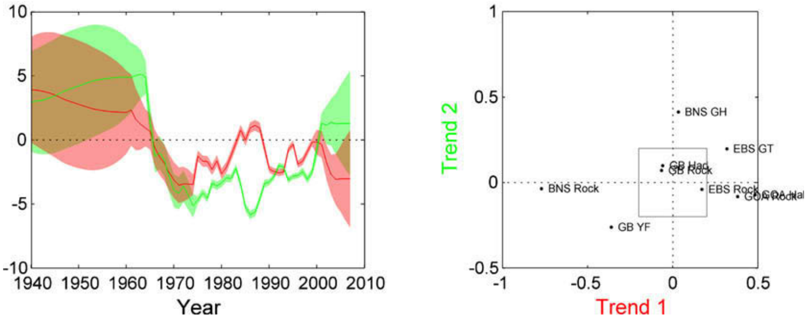


Fig. 9. Results of Dynamic Factor Analysis applied to the pelagic (a) and benthic (b) feeding guild SR residual anomaly response variable time series pooled over ecosystems. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

Among the pelagic feeders, we identified one broad-scale regime shift period: 1972–1976. This period corresponds roughly to the first period identified in the ln(*R*) time series. The BNS ecosystem exhibited the largest number of regime shifts (6) while the EBS and GOA ecosystems exhibited the least, with three change points each. In these latter ecosystems, herring stocks did not exhibit change points.

Few of the change points we identified in the survival time series corresponded directly to those found in the ln(R) time series. These included cod in the GOA (1972, 2001) and EBS (1973), mackerel in the GB (1975), GOA pollock (1980), and BNS Blue whiting (1995) among the pelagic feeders. Among the benthic feeding guild stocks, change points were detected for rockfish in the EBS and GOA in the mid-1970s in both data types, but the timing differed by a year or two.

The BNS also exhibited the largest number of change points for the benthic feeding guild (5), while the other three ecosystems exhibited fewer (3 each). Although fewer change points were detected among the benthic feeding stocks, as compared with the pelagic feeding stocks, these points were more closely grouped in time. Thus, we identified three broad-scale regime shift periods for the benthic feeding stocks: 1974–1978, 1988–1990, and 1999–2001. The first period overlaps the one identified for the pelagic feeding stocks, while the latter periods have no counterparts in the pelagic feeding stocks. In addition, none of the periods identified using the ln(R/*S*) dataset appear to correspond with those identified using the ln(*R*) dataset.

3.5.3. SR residual time series

The STARS analysis of the SR residual response variable time series identified the fewest change points of the three response variables we considered (Fig. 15). We found a total of 22 change points for this data type, with 13 from the pelagic feeding stocks and 9 from the benthic feeding stocks. Relatively few change points were detected at the same time (within a year or two) across all three data types. For the pelagic feeders, this occurred for five stocks: cod in the EBS (1973–1974), cod (1972, 2000) and pollock (1980) in the GOA, and Blue whiting (1995) and mackerel (2004) in the BNS. For the benthic feeders, this occurred for only three stocks: flatfish in the EBS (1999) and BNS (1999–2001) and rockfish in the BNS (2000–2001).

For the pelagic feeding stocks, we identified two broad-scale regime shift periods: 1972–1976 and 1999–2004. The first period corresponds to similar periods found in both the recruit abundance and recruit survival datasets. The latter period was also identified in the ln(R) dataset, but not in the ln(*R*/*S*) dataset.

For the benthic feeding stocks, we identified one broad-scale regime shift period: 1999–2001. A similar period was identified in the recruit survival dataset, but not in the ln(R) dataset. Conversely, earlier periods identified in the ln(*R*) and ln(R/*S*) datasets were not identified in this dataset.

4. Discussion

Among all of the analysis methods used in this study, we observed within- and between-ocean synchronies at the spatial scale of oceanic basins. It is unclear if our observed patterns were primarily a consequence of decadal-scale (regime-like) variability in bottom-up control of fish recruitment through low frequency changes in ocean productivity. It is impossible for fish populations so widely separated between oceanic basins to directly interact or affect each other, implying that broad large-scale signals are the driving force behind the observed synchronies. Basin-scale opposing associations from studies such as this or from whole system basin-scale numerical simulation experiments (Megrey et al., 2007) imply regime-like influences play a major role in shaping fish recruitment and may be interconnected between the Pacific and Atlantic Ocean basins.

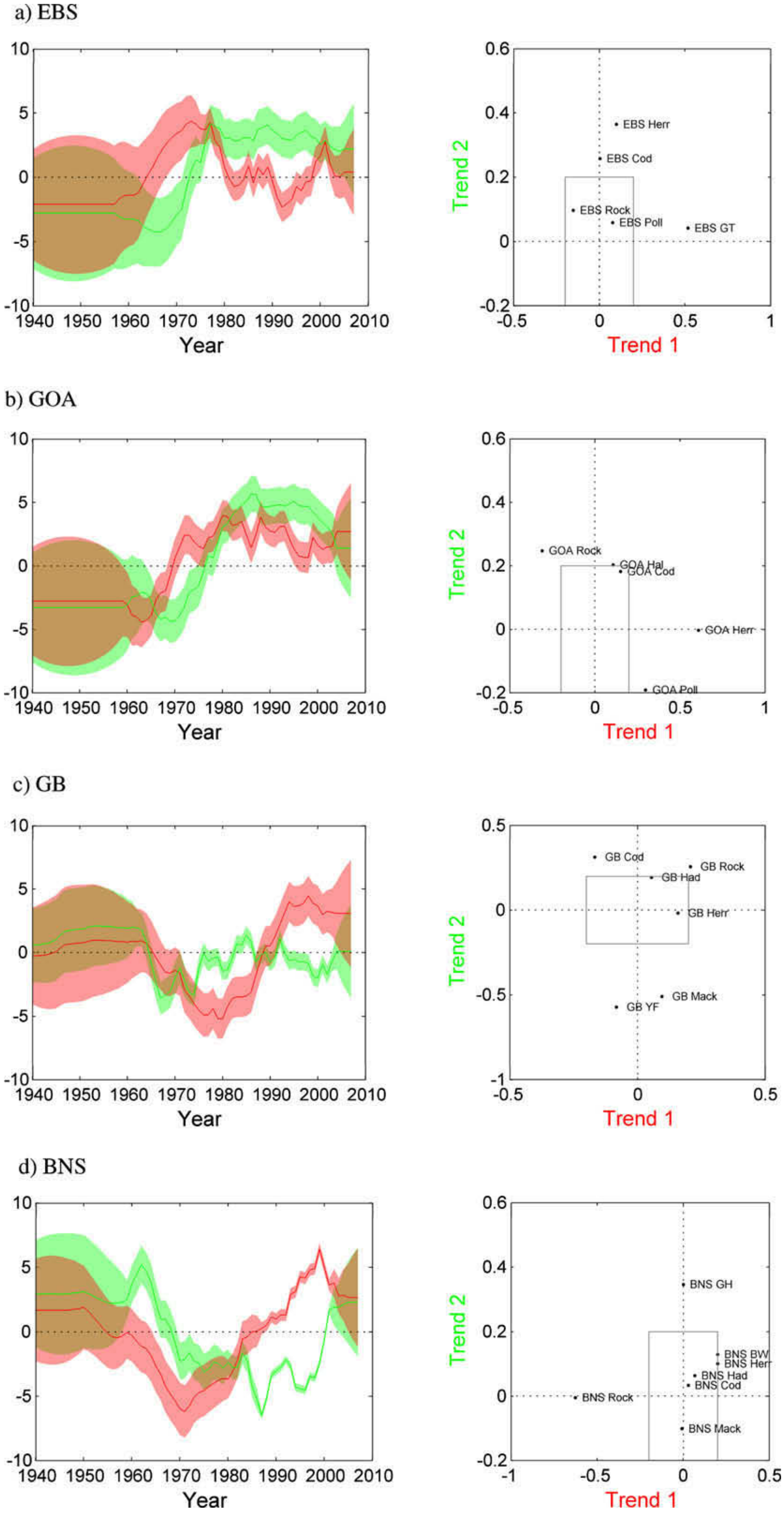


Fig. 10. Results of Dynamic Factor Analysis applied to the EBS (a), GOA (b), GB (c), and BNS (d) ln(R) anomaly response variable time series ecosystem data. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

Regime-like dynamics have been shown to affect fish production in many systems, but it was perhaps first observed in the alternation between different populations of sardines in the Pacific Ocean (Kawasaki, 1983) and soon after it was noticed that anchovy populations rose and fell directly out of phase with that of the Pacific sardine (Schwartzlose et al., 1999). Similar patterns have been observed for fish species in the Pacific basin. For example Pacific salmon populations (Beamish and Bouillon, 1993; Hare and Francis, 1995; Hare, 1996; Hare et al., 1999) and multiple groundfish taxa (Hollowed and Wooster, 1995; Francis et al., 1998; Hollowed et al., 2001) in the northeast Pacific have been shown to be affected by the Pacific Decadal Oscillation (PDO) (Hare and Mantua, 2000). Similar PDO

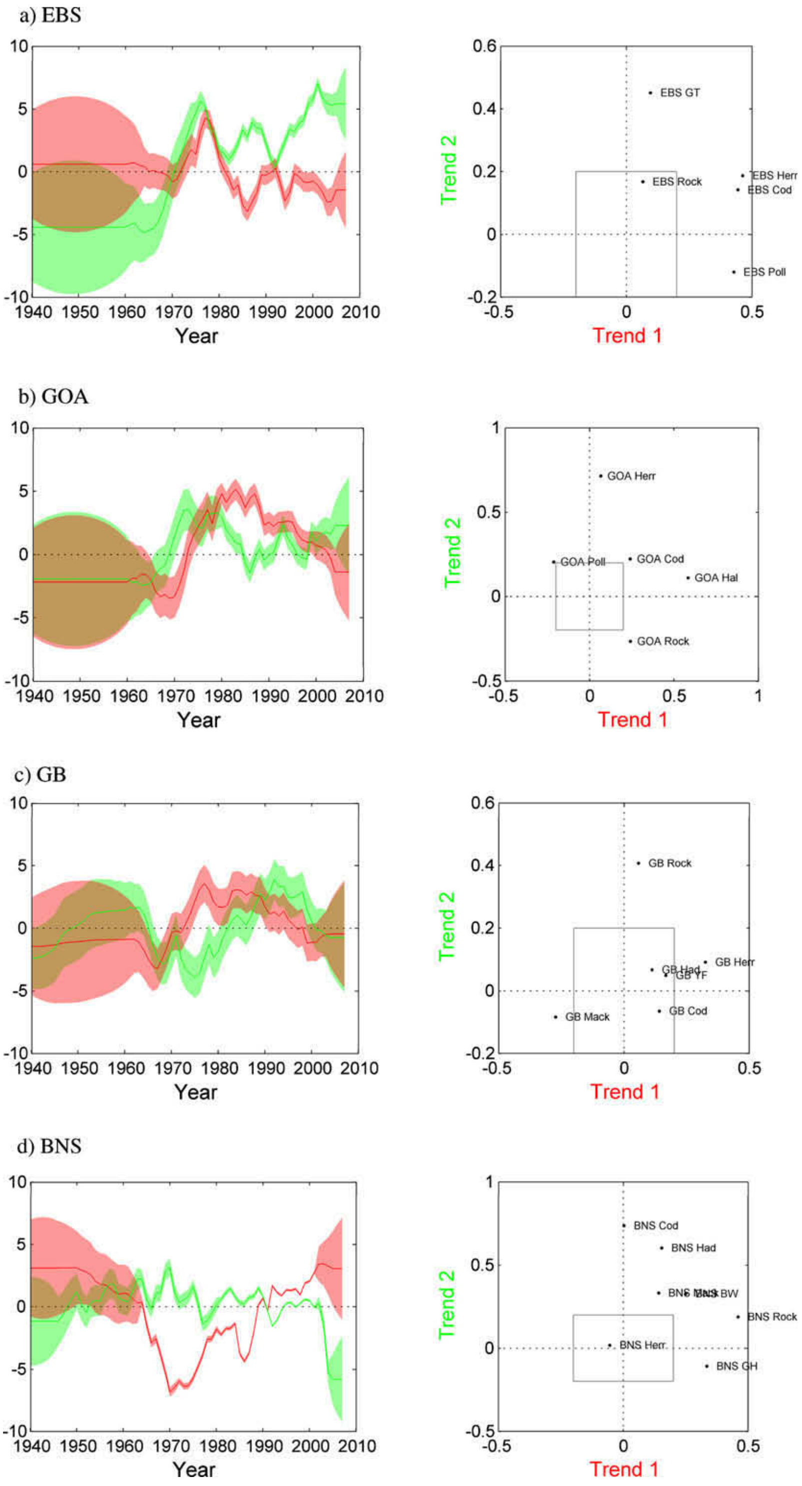
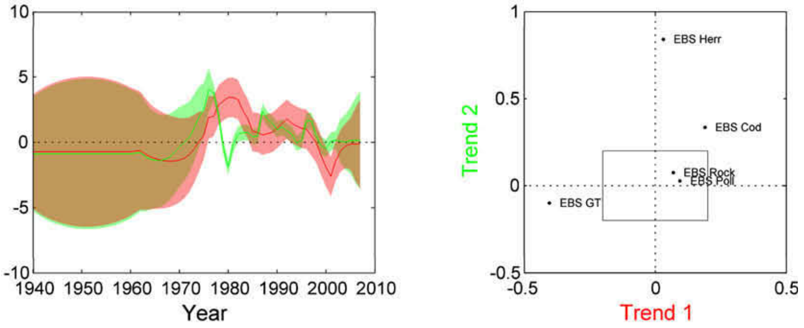


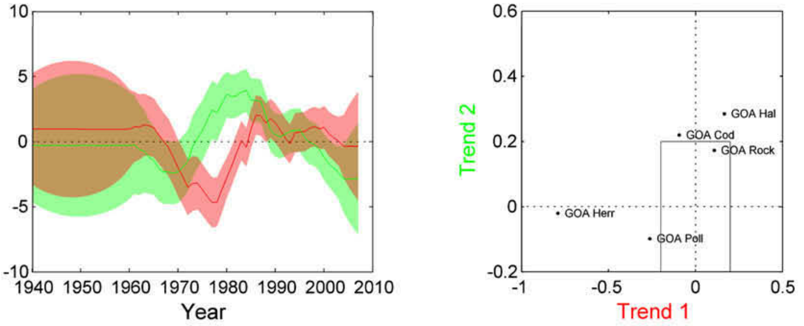
Fig. 11. Results of Dynamic Factor Analysis applied to the EBS (a), GOA (b), GB (c), and BNS (d) ln(R/S) anomaly response variable time series ecosystem data. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

affects have been demonstrated for the northwest Pacific (Zhang et al., 2007). In the Atlantic basin, several studies have related changes in fisheries recruitment or fish abundance to the North Atlantic Oscillation (NAO) (Hurrell, 1995). These include influences on cod recruitment (Solow, 2002; Stige et al., 2006; Solow and Beet, 2007) and growth (Brander, 2007), temperature influences on Barents Sea herring (Toresen and Østvedt, 2000; Fiksen and Slotte, 2002), with the presumption that NAO affects Kola line sea temperatures (Stige et al., 2006), changes in cod recruitment response to temperature (Drinkwater, 2005), unspecified influences on New England groundfish stocks (Brodziak and O'Brien, 2005), impacts on northeastern Atlantic stocks due to changes in the latitudinal excursion of the Gulf Stream system (de Fatima et al., 2002), and links between NAO, winter temperature, juvenile survival, and recruitment to estuarine species such as Atlantic croaker in the mid-Atlantic (Hare and Able, 2007).

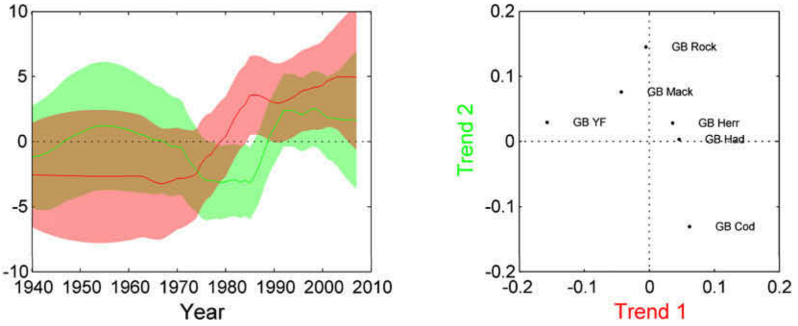
a) EBS



b) GOA



c) GB



d) BNS

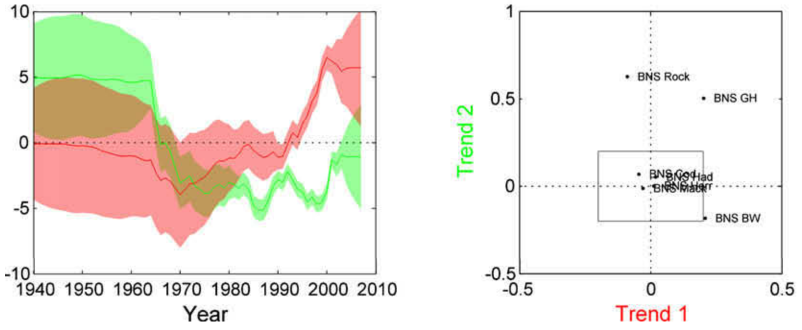


Fig. 12. Results of Dynamic Factor Analysis applied to the EBS (a), GOA (b), GB (c), and BNS (d) SR residuals anomaly response variable time series ecosystem data. The grey square on the ordination figure indicates ±0.2 loading values. EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

Klyashtorin (1998) reported on long-term fluctuations of several species included in this study including Alaska walleye pollock (EBS and GOA), Atlantic and Pacific herring, and Atlantic cod, noticing that these and other stocks exhibited long-term spectral periodicity (i.e. 54–58 years) that correlated well with the Atmospheric Circulation Index. Of interest, is the observation that the NAO and PDO have opposite expressions in the basins where they shape local or regional conditions. For example, in the positive phase, the NAO produces strong wind circulation in the North Atlantic, high atmospheric and sea temperatures in western Europe, and low temperatures on the east coast of Canada (Fromentin and Planque, 1996). When the PDO is in its warm positive phase, water temperatures are warm in

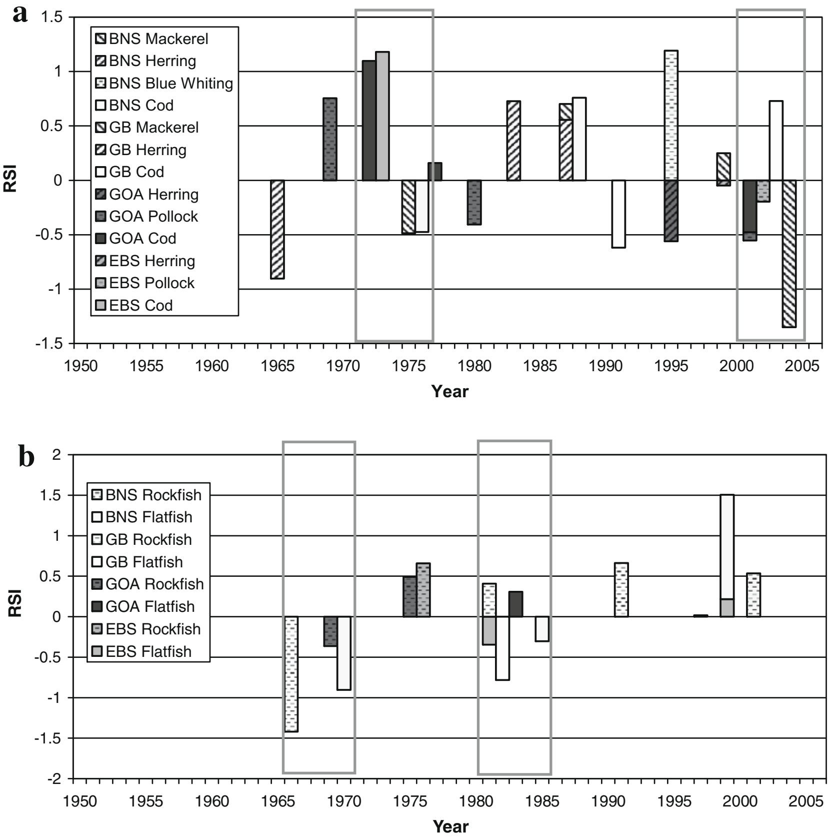


Fig. 13. Combined RSI from the STARS analysis versus year for the ln(R) anomaly response variable for the pelagic (a) and benthic (b) feeding guild. Grey boxes correspond to broad-scale regime shifts (pelagic feeding guild: 1972–1976, 2000–2004; benthic feeding guild: 1966–1970, 1981–1985). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

the eastern North Pacific close to North America and cold near Asia in the western North Pacific (Hare and Mantua, 2000). Localized conditions influence plankton production and fishes in the Atlantic (Drinkwater et al., 2003) and similar biological effects have been observed for the PDO in the Pacific.

A regime shift detection algorithm was applied to three fish stock–recruitment response variables to investigate whether the "regime shifts" identified by the algorithm occurred synchronously across the ecosystems and/or whether shifts occurred in similar patterns by response variable across ecosystems. Across the data types, more change points were detected in the pelagic feeding stocks (average = 17) than in the benthic feeding stocks (average = 12.7). This may reflect, in general, a greater sensitivity of the recruitment of pelagic feeding stocks to bottom-up environmental changes, although the actual mechanisms for this sensitivity are unknown and may, in fact, differ among the ecosystems. However, pelagic stocks are typically short lived and their recruitment is thought to be more closely linked to variability in lower trophic level production (Beaugrand et al., 2003). For the pelagic feeding stocks, we identified one time period of broad-scale regime shifts that were consistent across all three response variables: an early-to-mid-1970s period (Figs. 13–15). A late 1990s to early 2000s period was also identified in two of the three response variables. Although change points generally occurred in at least one stock from each ecosystem within these periods, the composition of stocks for which change points were detected was somewhat different across response variables. The shift in the early-to-mid-1970s was also apparent in the DFA analysis (Figs. 7a, 8a, and 9a). For the benthic feeding stocks, no broad-scale regime shift periods were evident across all three response variables. We did identify a late 1990s to early 2000s period in both the recruit survival and stock–recruit residuals datasets. However, none of the other periods identified in the recruit abundance and recruit survival datasets (two for each data type) were temporally synchronous across response variables. The late-1960s was a period of rapid change in trends from the DFA of all three responses for benthic species.

Numerous previous studies have identified a regime shift in the North Pacific Ocean during 1976–1977 in both environmental (climatic and oceanographic: e.g. Hare and Mantua, 2000; Mantua and Hare, 2002) and ecological indices (Mueter et al., 2007). It is not surprising, therefore, that we identified change points occurring near this time in fish stocks from the EBS and GOA. However, we also identified 1972–1976 as a period of broad-scale regime shift for the pelagic feeding stocks across all response variables, as well as a similar period (1974–1978) for the benthic feeding stocks using the ln(R/S) response variable. To our knowledge, a regime shift in the mid-1970s has not been previously identified in high latitude ecosystems in the North Atlantic, but Austin (2002) identified a regime shift in 1977 in Chesapeake Bay, which is south from the Georges Bank/Gulf of Maine systems considered here. Our identification of this time period as one coinciding with a broader-scale northern hemispheric shift suggests the existence of possible "teleconnections" among these high latitude ecosystems. Furthermore, given our results, these ecosystems appear to have collectively experienced another regime shift in the very recent past (i.e. late 1990s to early 2000s). Bond et al. (2003) suggested that winter climatic patterns in the North Pacific were much different than in previous years, providing some rationale for our results in the EBS and GOA. As a counterpoint to our results, though, we

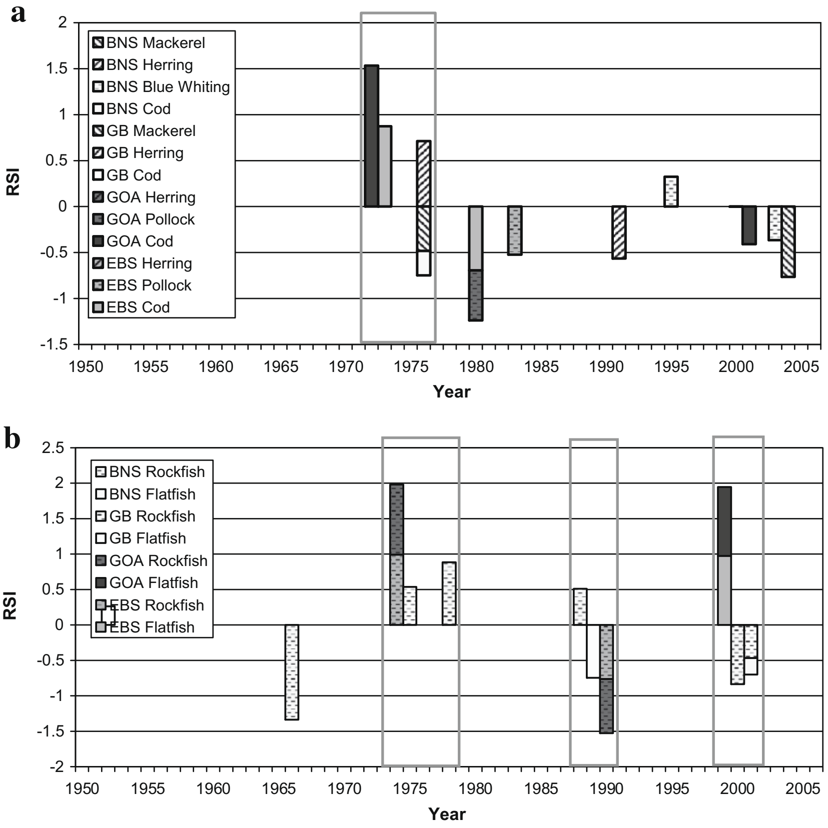


Fig. 14. Combined RSI from the STARS analysis versus year for the ln(*R*/*S*) anomaly response variable for the pelagic (a) and benthic (b) feeding guild. Grey boxes correspond to broad-scale regime shifts (pelagic feeding guild: 1972–1976; benthic feeding guild: 1974–1978, 1988–1990, 1999–2001). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

point out that a further regime shift identified as occurring in the North Pacific in 1989 (EBS: Rodionov and Overland, 2005; GOA: Mantua et al., 1997 and Litzow, 2006) was not detected in our analysis (except, perhaps, in the ln(*R*/*S*) response variable for benthic feeding stocks).

Our results show that the three types of response variables we considered do not yield completely consistent results among the different analysis methods. We were not surprised by this results since the response variables measure different quantities. While time series of ln(R) may, at first glance, appear to be the most straightforward data to use for this analysis, ln(*R*) is confounded with spawning stock size and decadal-scale shifts in mean recruitment may reflect shifts in spawning stock abundance (e.g. through fishing) rather than decadal-scale shifts in environmental conditions. Indices that reflect recruit survival, such as ln(R/*S*) or residuals from a fitted stock–recruit curve, may be more appropriate to use for detecting environmentally driven long-term shifts in recruitment.

There were some differences between the analyses of the three response variables. Fewer change points were detected using time series of stock–recruit residuals rather than ln(R/*S*). We suspect this may be due, in part, to the process of fitting a stock–recruit curve before performing the change-point analysis. Presumably, regime shifts can lead to changes in an underlying stock–recruit relationship (e.g. in parameter values) for a stock. However, fitting a single stock–recruit relationship to time series data that includes a regime shift would yield an “average” fit to the data which has the effect of minimizing residuals across the regime shift, thus making it more difficult to detect. Thus, we recommend using indices based on ln(R/*S*) in analyses of regime shifts on recruitment variability.

Dynamic Factor Analysis results were largely similar among the three recruitment response variables. Strong similarities were found between pelagic and benthic species in EBS and GOA and coherence across ecosystems and relatively weak similarities between species in GB and BNS ecosystems. There were more commonalities in the ln(*R*/*S*) time series than the ln(R) and SR residuals relationship. Perhaps ln(*R*/*S*) includes trends in stock size, but examination of biomass patterns (Link et al., this volume) does not support this hypothesis. Additionally, for the Georges Bank taxa there was greater similarity among taxa for the ln(R) series. The importance of this difference is unclear.

Other difficulties with drawing any firm conclusions from our analysis include the relatively small number of fish stocks we included in the analysis and the suitability of the three response variables considered. Ideally, dozens of fish stocks per ecosystem would have been included in the analysis to provide a higher level of confidence that the changes we detected actually reflected changes or “regime shifts” in the ecosystems considered (e.g. Mueter et al., 2007). However, our desire to include only stocks reflecting functionally equivalent species within each ecosystem limited our choices, as did the availability of time series data on recruitment. We also did not explore how noisy spawner–recruit data affected the analysis.

Similar to many previous studies (Myers and Barrowman, 1996; Myers, 1998; Planque and Frédou, 1999; Brander and Mohn, 2004; Stige et al., 2006) the approach taken in this study focused on comparative analysis: taking data from many ecosystems/stocks and performing a comparison in a unified analysis. We feel that comparative analysis proved effective at identifying between- and within-basin patterns of ocean-wide synchrony which only emerged when very broad patterns in the recruitment data were examined from the six ecosystems of the North Pacific and North Atlantic. Data suggest

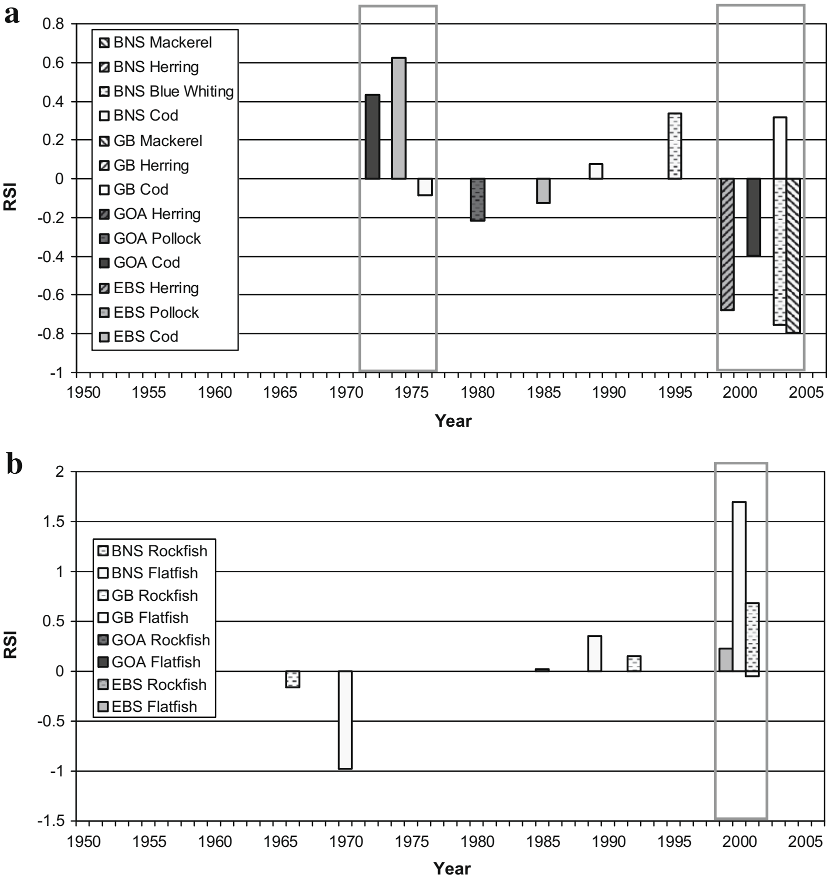


Fig. 15. Combined RSI from the STARS analysis versus year for the SR residual anomaly response variable for the pelagic (a) and benthic (b) feeding guild. Grey boxes correspond to broad-scale regime shifts (pelagic feeding guild: 1972–1976, 1999–2004; benthic feeding guild: 1999–2001). EBS: eastern Bering Sea; GOA: Gulf of Alaska; GB: Georges Bank/Gulf of Maine; and BNS: Barents/Norwegian Sea.

common external factors act in synchrony on stocks within ocean basins but temporal stock patterns, often of the same species or functional groups, between basins change in opposition to each other. Basin-scale results from our study (similar within but different between) suggest that the two broad areas are connected by unknown mechanisms, that depending on the year, may influence the two basins in opposite ways. In an analysis of 10 North Atlantic cod stocks, Rodionov (1995) concluded that an observed opposing pattern in cod year class strength (east–west versus north–south) within the North Atlantic basin was attributed to atmospheric teleconnections and periods of warming and cooling, respectively. Similarly, Krovnin (1995) also reported evidence for climatic effects on variations in the abundance of commercial fish stocks in the North Pacific and North Atlantic. He concluded fish abundance trends were influenced by spatial and temporal SST anomaly patterns with- and between-basins connected by well-known teleconnection patterns in the atmosphere. We did find it interesting that in our study there was no evidence of an east–west opposition in recruitment variable response trends within the Atlantic basin.

Remote synchronies triggered by a common external factor are impossible to prove and remain largely debatable. The data are just not available to make a firm determination. However, understanding the processes involved is commonly considered a key scientific task in terms of climate change, management, and prediction (Fréon et al., 2003). While the results of this study are intriguing, the underlying causes of the trends in recruitment and the large-scale climatic/atmospheric effects on recruitment, or the existence of teleconnections, are unresolved and certainly point to the need for further comparative studies as well as retrospective, process, and modeling studies to identify basin- and hemispheric-wide forcing that impact marine ecosystems.

Acknowledgments

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Appendix A. Recruitment and spawner biomass time series from the four ecosystems used in this study

See Tables A1–A8.

Table A1
Bering Sea ecosystem recruitment time series (millions of recruits).[a]

Recruitment age Year class	1 Walleye pollock	0 Pacific cod	1 Greenland turbot	4 Pacific herring	3 Rockfish[b]
1940					
1941					
1942					
1943					
1944					
1945					
1946					
1947					
1948					
1949					
1950					
1951					
1952					
1953					
1954					
1955					
1956					
1957					428.72
1958					35.71
1959					38.32
1960					54.70
1961					166.11
1962					474.68
1963	4676.00				40.74
1964	21767.00	145.17			42.74
1965	13266.00	133.91			91.21
1966	26980.00	125.47			34.33
1967	25021.00	124.53			29.18
1968	29092.00	139.47			29.37
1969	22834.00	178.90		4.2	28.71
1970	10117.00	167.68		12.9	30.52
1971	11722.00	155.98		0.9	27.99
1972	27189.00	178.99		80.6	29.26
1973	20552.00	323.00		230.13	22.80
1974	18031.00	802.15		252.37	54.14
1975	13185.00	81.69	75.54	18.86	58.13
1976	13989.00	2080.67	38.02	46.34	111.36
1977	27778.00	1611.96	40.54	803.19	110.10
1978	65508.00	1014.29	28.32	703.18	121.56
1979	25313.00	947.82	19.02	268.96	57.08
1980	28684.00	453.44	12.78	73.08	66.11
1981	15292.00	886.61	4.82	165.85	164.67
1982	52698.00	1508.73	6.00	39.51	74.63
1983	12712.00	383.24	3.88	159.34	80.38
1984	34636.00	1210.83	6.70	144.41	419.43
1985	13281.00	418.04	14.24	42.19	107.31
1986	7751.00	392.18	4.36	91.68	119.15
1987	4881.00	313.65	5.98	386.02	95.04
1988	10519.00	906.90	5.50	270.93	246.08
1989	49350.00	1139.52	14.16	134.68	117.68
1990	28380.00	658.09	5.98	147.22	60.42
1991	21881.00	926.88	2.28	155.22	44.69
1992	52985.00	1000.98	2.08	109.97	56.04
1993	13663.00	373.06	1.80	189.56	89.54
1994	9905.00	565.07	2.82	41.93	137.70
1995	22291.00	985.92	6.84	28.79	135.14
1996	31988.00	1106.13	3.22	267.42	113.35
1997	15237.00	600.91	4.00	372.95	
1998	17042.00	830.78	4.50	166.21	
1999	26833.00	1023.88	15.16	53.01	
2000	44575.00	528.67	21.42	60.06	

Table A1 (*continued*)

Recruitment age	1	0	1	4	3
Year class	Walleye pollock	Pacific cod	Greenland turbot	Pacific herring	Rockfish[b]
2001	19678.00	462.63	32.66	83.44	
2002	11092.00	429.28	7.78	163.08	
2003	5861.00	394.65	4.22		
2004	9411.00	303.43	5.48		
2005	22415.00	675.08	7.98		
2006					
2007					

Togiak herring: 1969–1972, Williams and Quinn (2000).
Togiak herring: 1973–2002, from Charles Brazil, Alaska Department of Fish and Game, March 20, 2007.
Walleye pollock: Ianelli et al. (2006a).
Pacific cod: Thompson et al. (2006a).
Greenland turbot: Ianelli et al. (2006b).
Rockfish: Northern rockfish, Spencer and Ianelli (2006b); Pacific ocean perch, Spencer and Ianelli (2006a).

[a] Data sources.

[b] Total Rockfish computed by summing (assessment year) northern rockfish and Pacific ocean perch.

Table A2
Gulf of Alaska ecosystem recruitment time series (millions of recruits).[a]

Recruitment age	2	0	6	3	2–3
Year class	Walleye pollock	Pacific cod	Pacific halibut	Pacific herring	Rockfish[b]
1940					
1941					
1942					
1943					
1944					
1945					
1946					
1947					
1948					
1949					
1950					
1951					
1952					
1953					
1954					
1955					
1956					
1957					
1958					
1959	384.70				42.27
1960	425.53				42.24
1961	455.74				254.75
1962	102.82				39.61
1963	264.66				215.42
1964	141.15	55.74			100.86
1965	350.89	52.19			212.26
1966	415.38	48.53			25.03
1967	723.49	45.57			28.25
1968	343.02	44.43	1.61		68.77
1969	740.78	46.72	1.51		21.61
1970	1392.85	54.41	2.99		14.38
1971	1061.40	70.45	1.73		12.44
1972	3465.71	122.51	2.31		10.75
1973	702.47	184.44	3.89		11.57
1974	441.68	85.13	2.33		11.95
1975	2012.74	71.92	3.22		39.72
1976	2737.99	107.17	2.66		152.49
1977	2494.66	470.64	6.45	260.97	73.66
1978	3498.40	137.50	2.17	123.08	36.89
1979	1776.31	246.88	6.91	142.49	30.22
1980	431.49	324.30	8.27	433.52	46.27

(*continued on next page*)

Table A2 (*continued*)

Recruitment age Year class	2 Walleye pollock	0 Pacific cod	6 Pacific halibut	3 Pacific herring	2–3 Rockfish[b]
1981	491.11	172.39	4.39	416.72	46.65
1982	206.93	191.67	5.57	146.58	59.01
1983	480.01	200.01	14.31	114.60	43.77
1984	1624.79	390.20	9.47	1009.25	146.86
1985	555.76	288.73	6.43	92.97	67.39
1986	161.08	184.59	7.67	70.95	281.38
1987	377.42	395.21	17.22	80.52	90.36
1988	1614.38	226.66	12.40	894.03	76.22
1989	1007.97	411.55	6.46	106.71	47.22
1990	403.01	285.68	6.82	90.83	53.75
1991	240.41	285.13	5.21	51.93	40.35
1992	145.64	241.66	4.78	154.38	60.30
1993	220.98	256.29	4.17	155.07	44.63
1994	857.92	281.41	8.23	161.81	134.45
1995	409.35	342.68	8.04	63.08	144.33
1996	176.21	211.20	5.54	14.18	59.23
1997	161.10	212.39	4.89	21.49	83.40
1998	234.09	254.12	6.83	16.69	107.91
1999	945.97	376.53	6.80	245.98	83.21
2000	783.83	284.48		61.09	79.94
2001	141.12	136.38		29.85	60.27
2002	156.89	154.79		41.66	55.10
2003	146.05	173.05		31.07	56.73
2004	1331.37	160.53			15.74
2005					
2006					
2007					

Prince William Sound Pacific herring: 1977–2003, data from Steve Moffitt (personal communication, Alaska Department of Fish and Game); Hulson et al. (2008).
Walleye pollock: Dorn et al. (2006).
Pacific cod: Thompson et al. (2006b).
Pacific halibut: Area 3A data from Steven Hare (personal communication, International Pacific Halibut Commission).
Rockfish: Northern rockfish, Courtney et al. (2006); dusky rockfish, Lunsford et al. (2003); rougheye rockfish, Shotwell et al. (2003); Pacific ocean perch 1961–1976, Hanselman et al. (2003); Pacific ocean perch 1977–2005, Spencer and Ianelli (2005).

[a] Data sources.

[b] Total rockfish computed by summing northern rockfish, dusky rockfish, rougheye rockfish, and Pacific ocean perch.

Table A3

Gulf of Maine/Georges Bank ecosystem recruitment time series (millions of recruits).[a]

Recruitment age Year class	2 Atlantic herring	1 Atlantic mackerel	1 NW Atlantic Cod	1 Haddock	1 Yellowtail Flounder	1 Rockfish
1940						27.29
1941						27.39
1942						27.05
1943						26.53
1944						29.99
1945						23.66
1946						53.44
1947						77.76
1948						56.02
1949						55.19
1950						57.26
1951						47.88
1952						71.63
1953						76.87
1954						69.93
1955						61.92
1956						66.34
1957						70.56
1958						50.57

Table A3 (*continued*)

Recruitment age	2	1	1	1	1	1
Year class	Atlantic herring	Atlantic mackerel	NW Atlantic Cod	Haddock	Yellowtail Flounder	Rockfish
1959						71.54
1960						43.13
1961						85.53
1962		178.18				47.94
1963		205.99		462.19		97.41
1964		360.44		32.37		76.78
1965		991.39		4.09		33.56
1966		1810.59		14.69		7.64
1967	2632.73	5853.03		0.48		4.17
1968	2526.74	1459.17		1.05		2.52
1969	1846.02	2271.61		4.70		2.70
1970	8086.56	840.05		0.32		4.10
1971	504.40	1171.37		8.61		246.00
1972	393.00	1149.12		19.73		6.41
1973	1325.79	1847.44		10.62	52.19	2.47
1974	1095.61	2161.91		7.86	70.63	1.85
1975	1077.23	521.63		105.60	24.73	1.64
1976	1912.32	164.73		14.03	17.28	1.48
1977	1715.75	108.96		6.18	54.44	2.07
1978	409.24	492.62	23.51	83.91	25.51	51.96
1979	748.51	144.04	20.10	10.59	24.03	2.47
1980	681.45	422.50	41.39	7.40	63.00	2.89
1981	868.92	1238.94	17.47	2.51	22.85	10.21
1982	709.90	3414.16	17.15	3.21	6.58	20.73
1983	1677.99	265.43	37.86	17.57	10.84	8.47
1984	1045.76	215.59	15.67	1.84	16.75	19.75
1985	1299.24	291.24	52.91	15.27	8.47	13.28
1986	1660.32	285.23	28.91	2.00	9.20	5.33
1987	2715.39	827.53	48.65	17.05	22.88	4.32
1988	3518.78	1283.55	19.97	1.11	9.73	21.90
1989	3963.37	524.99	13.22	2.84	11.54	56.74
1990	3568.62	771.18	24.91	2.55	22.79	9.31
1991	1288.60	760.39	13.30	10.40	18.34	42.85
1992	1592.01	231.29	17.81	15.42	13.96	280.72
1993	1916.12	690.64	8.77	16.09	10.66	62.11
1994	7223.45	766.26	6.94	12.44	11.12	46.11
1995	3068.76	651.84	9.44	12.22	13.18	27.01
1996	2978.81	938.17	16.02	25.11	18.43	38.68
1997	1768.03	647.57	9.68	13.72	23.89	94.09
1998	5519.54	806.92	20.64	46.91	25.52	152.87
1999	1158.36	5035.60	12.33	18.90	20.98	81.71
2000	1520.82	1088.03	4.49	90.86	23.70	30.58
2001	2410.82	804.30	10.41	5.36	15.91	25.39
2002	4768.13	1758.13	5.35	1.34	17.13	26.28
2003	1483.90	2794.35	43.30	788.89	11.88	30.18
2004			16.71	9.88	9.19	
2005						
2006						
2007						

NW Atlantic herring: Overholtz (2006a).
Atlantic mackerel: Overholtz (2006b).
NW Atlantic cod: Mayo and O'Brien (2006a).
Haddock: Brodziak and Traver (2006).
Yellowtail flounder: Legault and Cadrin (2006).
Rockfish: Mayo et al. (2006b).

[a] Data source.

Table A4
Barents and Norwegian Sea ecosystem recruitment time series (millions of recruits).[a]

Recruitment age Year class	0 NSS herring	0 NE Atlantic mackerel	3 Cod[b]	3 Haddock	1 Blue whiting	5 Greenland halibut	3 Rockfish
1940							
1941							
1942							
1943			728.14				
1944			425.31				
1945			442.59				
1946			468.35				
1947			704.91	76.59			
1948			1083.75	633.31			
1949			1193.11	69.42			
1950	750680.00		1590.38	1184.84			
1951	146355.00		641.58	140.27			
1952	96644.00		272.78	59.17			
1953	86102.00		439.60	193.61			
1954	42086.00		804.78	59.97			
1955	24971.00		496.82	78.47			
1956	29858.00		683.69	372.27			
1957	25397.00		789.65	274.31			
1958	23094.00		916.84	124.00			
1959	412478.00		728.34	273.23		42.84	
1960	197514.00		472.06	314.41		51.69	
1961	76103.00		338.68	365.69		57.83	
1962	19003.00		776.94	116.59		70.44	
1963	168931.00		1582.56	273.23		64.28	
1964	93903.00		1295.42	339.59		55.93	
1965	8491.00		164.96	20.49		41.11	
1966	51409.00		112.04	20.12		31.55	
1967	3947.00		197.11	188.25		33.56	
1968	5187.00		404.77	109.17		31.06	
1969	9785.00		1015.32	1156.18		26.64	
1970	661.00		1818.95	306.17		22.54	
1971	236.00		523.92	60.15		22.10	
1972	957.00	2190.48	621.62	55.33		23.69	
1973	12884.00	4880.25	613.94	62.53		20.59	
1974	8631.00	4113.00	348.05	126.98		19.70	
1975	2971.00	5014.75	638.49	198.11		18.61	
1976	10068.00	5035.56	198.49	162.27		17.88	
1977	5095.00	1014.28	137.74	28.02		18.94	
1978	6201.00	3288.70	150.87	12.55		19.01	
1979	12498.00	5363.80	151.83	15.83		17.82	
1980	1474.00	5664.02	166.83	8.96	3307.00	19.93	
1981	1100.00	7365.37	397.83	12.08	4165.17	19.88	
1982	2343.00	2080.80	611.61	289.50	15350.51	19.44	
1983	343398.00	1613.65	1111.87	526.28	18855.08	23.00	
1984	11528.00	7398.80	321.90	115.57	10787.49	20.76	
1985	36608.00	3385.43	241.50	55.07	8649.18	14.54	
1986	6042.00	3482.60	212.88	26.50	9019.77	12.69	
1987	9090.00	5090.89	286.90	36.26	6776.13	10.57	44.91
1988	30204.00	3588.52	454.06	104.28	9481.37	13.00	37.43
1989	74349.00	4294.50	781.94	210.71	24343.81	18.39	30.29
1990	121734.00	3258.29	945.26	686.78	8364.12	17.92	32.01
1991	341838.00	3688.43	841.37	306.90	5461.83	18.48	15.14
1992	406020.00	4480.66	685.21	98.94	5185.76	20.47	11.98
1993	121213.00	5218.57	471.71	105.86	5653.69	18.57	8.92
1994	42863.00	4437.98	755.96	116.06	8233.82	15.03	10.23
1995	15667.00	4028.98	876.94	62.18	23351.82	15.76	6.62
1996	70204.00	3945.16	578.44	235.66	44850.29	15.08	11.77
1997	47279.00	3204.55	636.94	93.18	29478.47	17.75	5.52
1998	305200.00	3026.30	554.71	395.97	24142.51	16.38	6.11
1999	241941.00	3400.80	461.44	369.66	40003.05	19.83	3.55
2000	68362.00	1426.20	654.17	235.75	65081.69	27.21	6.57

Table A4 (*continued*)

Recruitment age Year class	0 NSS herring	0 NE Atlantic mackerel	3 Cod[b]	3 Haddock	1 Blue whiting	5 Greenland halibut	3 Rockfish
2001	47910.00	5087.07	333.37	224.26	46670.18	39.27	24.50
2002	358142.00	9335.00	565.86	338.88	41036.19		13.74
2003	76000.00	2882.66	416.53	134.56	26288.52		17.46
2004	314000.00	1827.93	9.784		29955.35		
2005	76000.00	780.23					
2006							
2007							

Norwegian Spring Spawning (NSS) herring: ICES (2006a).
NE Atlantic mackerel: ICES (2006b).
Cod: Northeast Atlantic cod, ICES (2007); Coastal cod, ICES (2007).
Haddock: ICES (2007).
Blue whiting: ICES (2006a).
Greenland halibut: ICES (2007).
Rockfish: ICES (2007).

[a] Data source.

[b] Total cod computed by summing northeast Atlantic cod and coastal cod.

Table A5

Bering Sea ecosystem spawning biomass time series (1000 metric tons).[a]

Year	Walleye pollock	Pacific cod	Greenland turbot	Pacific herring	Rockfish[b]
1940					
1941					
1942					
1943					
1944					
1945					
1946					
1947					
1948					
1949					
1950					
1951					
1952					
1953					
1954					
1955					
1956					
1957					
1958					
1959					
1960			153.76		261.26
1961			146.47		253.76
1962			133.71		235.97
1963			117.92		224.48
1964	526.00	185.22	106.88		201.25
1965	641.00	189.38	95.11		156.26
1966	734.00	192.68	92.90		117.89
1967	902.00	193.74	97.99		88.29
1968	1098.00	186.94	128.79		68.27
1969	1345.00	165.88	204.81		58.84
1970	1614.00	144.46	306.31		52.57
1971	1781.00	113.95	397.66		43.84
1972	1731.00	96.76	453.51		43.56
1973	1413.00	83.36	470.49		42.19
1974	997.00	70.61	472.15		42.13
1975	834.00	58.68	454.86		36.03
1976	867.00	54.08	431.91		30.63
1977	921.00	56.59	405.13	24.53	64.01
1978	940.00	78.33	389.57	48.63	63.73
1979	921.00	114.79	369.10	61.75	64.49

(*continued on next page*)

Table A5 (*continued*)

Year	Walleye pollock	Pacific cod	Greenland turbot	Pacific herring	Rockfish[b]
1980	1046.00	181.76	350.48	72.40	66.53
1981	1749.00	290.79	328.12	117.97	69.36
1982	2675.00	424.05	303.93	185.26	73.06
1983	3274.00	544.85	282.29	233.34	78.59
1984	3457.00	613.83	257.35	249.48	84.97
1985	3703.00	630.51	244.71	293.14	92.63
1986	3926.00	622.98	235.74	295.28	100.90
1987	4045.00	619.32	227.98	304.26	109.97
1988	4020.00	607.29	218.53	256.55	120.52
1989	3603.00	564.84	208.68	219.90	130.57
1990	2889.00	516.55	196.76	191.88	138.94
1991	2145.00	454.82	182.27	187.23	147.92
1992	2259.00	378.06	170.46	184.93	157.16
1993	3166.00	344.16	160.42	161.66	162.04
1994	3536.00	351.99	147.30	175.30	170.33
1995	3824.00	360.54	135.20	159.83	182.01
1996	3840.00	350.86	124.94	154.28	192.66
1997	3656.00	343.04	115.99	136.17	200.49
1998	3340.00	314.64	106.70	132.00	209.24
1999	3325.00	308.69	96.22	110.41	216.37
2000	3343.00	319.54	88.36	105.87	220.25
2001	3369.00	342.44	80.01	114.49	223.40
2002	3193.00	366.97	73.52	126.32	225.05
2003	3517.00	376.43	68.41	148.81	225.39
2004	3709.00	376.59	63.85	147.07	224.62
2005	3348.00	360.26	60.97	154.17	225.30
2006	2837.00	326.40	59.42	141.87	227.91
2007	2170.00		60.33		227.42

Togiak herring: 1969–1972, Williams and Quinn (2000).
Togiak herring: 1973–2002, from Charles Brazil, Alaska Department of Fish and Game, March 20, 2007.
Walleye pollock: Ianelli et al. (2006a).
Pacific cod: Thompson et al. (2006a).
Greenland turbot: Ianelli et al. (2006b).
Rockfish: Northern rockfish, Spencer and Ianelli (2006b); Pacific ocean perch, Spencer and Ianelli (2006a).

[a] Data source.

[b] Total rockfish computed by summing, by assessment year, northern rockfish, and Pacific ocean perch.

Table A6
Gulf of Alaska ecosystem spawning biomass time series (1000 metric tons).[a]

Year	Walleye pollock	Pacific cod	Pacific halibut	Pacific herring	Rockfish[b]
1940					
1941					
1942					
1943					
1944					
1945					
1946					
1947					
1948					
1949					
1950					
1951					
1952					
1953					
1954					
1955					
1956					
1957					
1958					

Table A6 (*continued*)

Year	Walleye pollock	Pacific cod	Pacific halibut	Pacific herring	Rockfish[b]
1959					
1960	82.13				
1961	93.51				163.59
1962	108.67				170.46
1963	128.49				183.72
1964	150.64	79.43			174.60
1965	162.60	79.57			165.29
1966	162.13	79.51			114.45
1967	153.92	78.95			100.01
1968	148.00	77.15			95.38
1969	145.96	74.50			86.80
1970	162.83	70.69			84.17
1971	181.58	66.21			85.29
1972	201.26	62.32			77.73
1973	238.44	57.51			65.89
1974	295.28	52.80	27.84		58.81
1975	412.65	50.73	27.93		50.71
1976	515.76	52.22	26.92		39.48
1977	556.57	59.44	25.77		78.65
1978	565.52	70.19	26.83		72.67
1979	621.60	73.59	28.03		71.83
1980	503.00	75.69	30.77	53.56	70.78
1981	572.26	80.78	34.91	65.85	68.21
1982	692.67	94.81	38.93	57.59	65.71
1983	719.27	108.19	44.36	63.54	65.23
1984	647.35	118.68	49.31	75.85	67.24
1985	524.26	132.79	53.84	95.81	70.67
1986	440.42	144.86	57.10	84.42	76.28
1987	399.62	149.10	57.28	82.34	82.09
1988	388.70	154.82	58.88	104.75	87.41
1989	349.95	165.83	57.49	106.48	90.01
1990	331.99	170.81	58.17	91.63	90.29
1991	295.08	162.77	62.83	78.61	90.50
1992	331.35	155.56	67.83	86.09	92.14
1993	379.05	150.69	71.36	28.93	97.30
1994	345.52	159.23	76.99	14.52	104.97
1995	312.01	168.73	84.37	16.67	114.51
1996	269.10	164.03	94.10	22.59	124.67
1997	205.06	156.51	102.37	31.62	135.21
1998	187.73	145.90	108.54	25.25	144.05
1999	176.18	141.12	112.12	19.00	150.05
2000	172.19	133.17	111.64	15.09	152.58
2001	146.46	127.93	110.18	10.46	154.38
2002	140.53	127.80	100.87	13.79	155.93
2003	157.04	131.20	99.18	18.81	156.62
2004	200.61	139.25	95.13	22.96	157.68
2005	212.25	139.16	88.85	15.79	159.94
2006		132.84		12.20	
2007					

Prince William Sound Pacific herring: 1977–2003, data from Steve Moffitt (personal communication, Alaska Department of Fish and Game); Hulson et al. (2008).
Walleye pollock: Dorn et al. (2006).
Pacific cod: Thompson et al. (2006b).
Pacific halibut: Area 3A data from Steven Hare (personal communication, International Pacific Halibut Commission).
Rockfish: northern rockfish, Courtney et al. (2006); dusky rockfish, Lunsford et al. (2003); rougheye rockfish, Shotwell et al. (2003); Pacific ocean perch 1961–1976, Hanselman et al. (2003); Pacific ocean perch 1977–2005, Spencer and Ianelli (2005).

[a] Data sources.

[b] Total rockfish computed by summing northern rockfish, dusky rockfish, rougheye rockfish, and Pacific ocean perch.

Table A7
Gulf of Maine/Georges Bank ecosystem spawning biomass time series (1000 metric tons).[a]

Year	Atlantic herring	Atlantic mackerel	NW Atlantic cod	Haddock	Yellowfin sole	Rockfish
1940						580.88
1941						577.52
1942						553.81
1943						514.28
1944						454.39
1945						420.01
1946						387.81
1947						340.37
1948						292.91
1949						263.25
1950						229.54
1951						196.90
1952						175.03
1953						161.46
1954						149.74
1955						142.53
1956						141.00
1957						132.72
1958						124.72
1959						119.32
1960						116.48
1961						114.95
1962		298.22				112.22
1963		302.20		160.71		111.05
1964		316.14		124.91		112.83
1965		335.92		143.93		115.87
1966		370.18		178.27		118.80
1967	1450.95	444.87		111.11		121.61
1968	1244.41	830.78		74.44		124.91
1969	979.69	1363.65		50.76		130.03
1970	794.64	1595.94		36.11		129.27
1971	686.29	1649.84		27.16		123.87
1972	530.88	1702.46		18.49	21.90	113.28
1973	687.45	1232.66		14.75	14.77	100.59
1974	530.30	937.70		17.25	8.97	90.30
1975	359.46	722.83		22.18	9.95	84.32
1976	217.53	662.75		24.76	8.35	82.00
1977	134.35	677.08		43.27	6.16	80.91
1978	161.00	781.90	80.64	72.19	8.42	75.34
1979	173.41	803.03	89.51	71.86	10.90	67.22
1980	180.16	797.68	92.77	67.37	10.41	53.79
1981	139.61	774.04	86.62	59.89	13.41	43.77
1982	108.21	779.49	113.84	49.94	11.35	35.16
1983	105.47	858.71	97.34	40.21	4.27	29.67
1984	138.01	1091.05	81.87	30.27	3.51	27.15
1985	163.85	1359.02	71.51	26.75	4.61	24.55
1986	218.47	1298.59	74.54	26.58	3.49	23.58
1987	215.24	1148.50	83.63	26.42	3.04	22.96
1988	225.63	1069.98	90.12	24.28	6.65	23.34
1989	288.67	961.61	94.64	23.86	5.72	24.70
1990	352.94	1029.83	92.51	25.75	4.52	27.10
1991	460.32	1247.15	73.63	22.98	4.60	28.66
1992	632.95	1268.87	52.41	18.29	4.24	29.89
1993	806.92	1161.18	40.09	14.63	2.91	31.79
1994	735.92	1083.99	31.25	18.96	2.65	35.04
1995	739.41	1057.13	32.34	29.11	4.34	39.45
1996	795.29	1143.53	31.63	37.73	5.67	46.51
1997	984.78	1171.52	29.66	45.05	6.98	60.58
1998	1031.83	1194.20	30.57	52.64	9.54	77.80
1999	1048.57	1262.61	35.18	61.87	10.44	94.83
2000	1168.85	1327.62	39.79	73.65	9.44	112.70
2001	1265.53	1847.91	53.82	95.97	10.48	124.45

Table A7 (*continued*)

Year	Atlantic herring	Atlantic mackerel	NW Atlantic cod	Haddock	Yellowfin sole	Rockfish
2002	1054.08	2265.87	50.85	113.50	10.39	138.39
2003	1033.18	2353.68	43.96	131.92	6.38	155.41
2004		2323.05	41.36	116.79		
2005						
2006						
2007						

Atlantic herring: Overholtz (2006a).
Atlantic mackerel: Overholtz (2006b).
NW Atlantic cod: Mayo and O'Brien (2006a).
Haddock: Brodziak and Traver (2006).
Yellowtail flounder: Legault and Cadrin (2006).
Rockfish: Mayo et al. (2006b).

[a] Data source.

Table A8

Barents and Norwegian Sea ecosystem spawning biomass time series (1000 metric tons).[a]

Year	NSS herring	NE Atlantic mackerel	Cod[b]	Haddock	Blue whiting	Greenland halibut	Rockfish
1940							
1941							
1942							
1943							
1944							
1945							
1946			1112.78				
1947			1165.06				
1948			1019.11				
1949			729.88				
1950	14178.00		615.34	130.67			
1951	12519.00		568.71	97.79			
1952	10921.00		520.60	55.48			
1953	9345.00		396.42	83.41			
1954	8656.00		429.69	115.38			
1955	9274.00		346.92	177.31			
1956	10924.00		299.82	239.72			
1957	9646.00		207.84	179.13			
1958	8695.00		195.38	148.42			
1959	7187.00		432.49	120.85			
1960	5855.00		383.48	103.52			
1961	4389.00		404.23	119.75			
1962	3446.00		311.68	109.62			
1963	2667.00		208.21	73.51			
1964	2527.00		186.57	57.54		72.64	
1965	3062.00		102.32	89.75		69.25	
1966	2804.00		120.72	120.90		68.56	
1967	1471.00		129.78	144.46		76.71	
1968	344.00		227.22	157.94		90.72	
1969	145.00		151.87	170.29		116.54	
1970	71.00		224.48	142.45		139.62	
1971	32.00		311.66	153.17		111.28	
1972	16.00	4038.60	346.51	115.27		94.88	
1973	85.00	4128.48	332.91	105.93		95.80	
1974	91.00	3976.21	164.49	188.47		91.52	
1975	79.00	3724.32	142.03	226.04		79.76	
1976	138.00	3400.48	171.24	177.30		62.69	
1977	286.00	3230.69	341.39	106.43		45.32	
1978	358.00	3192.12	241.54	83.50		35.94	
1979	388.00	2740.19	174.70	74.08		35.66	
1980	471.00	2300.86	108.25	72.99		34.66	
1981	504.00	2349.33	166.93	87.40	2934.62	39.59	
1982	503.00	2256.42	326.13	88.14	2387.67	38.44	

(*continued on next page*)

Table A8 (*continued*)

Year	NSS herring	NE Atlantic mackerel	Cod[b]	Haddock	Blue whiting	Greenland halibut	Rockfish
1983	575.00	2529.25	327.18	55.10	1941.54	42.81	
1984	602.00	2528.34	403.24	49.80	1708.21	39.28	
1985	515.00	2493.29	322.11	49.75	1992.08	41.21	
1986	437.00	2483.43	304.77	50.16	2317.48	40.66	
1987	926.00	2455.43	246.50	63.65	2032.28	30.42	
1988	2907.00	2461.64	328.27	72.66	1847.17	26.90	
1989	3537.00	2521.00	335.52	85.38	1767.05	24.18	
1990	3692.00	2368.84	426.46	93.13	1575.25	21.12	66.71
1991	3845.00	2632.08	837.24	110.01	1990.04	25.07	69.25
1992	3718.00	2638.90	1052.69	125.67	2612.48	16.23	72.20
1993	3615.00	2467.29	954.33	129.26	2517.50	18.33	74.55
1994	4130.00	2268.60	803.21	151.79	2404.83	15.90	75.12
1995	5086.00	2402.41	702.37	170.28	2228.11	14.52	75.32
1996	6788.00	2364.84	758.99	217.37	2086.01	14.53	74.45
1997	8237.00	2424.82	725.60	200.54	2219.57	15.82	71.75
1998	7618.00	2333.71	492.45	155.21	3258.05	17.61	67.27
1999	7174.00	2383.01	378.53	123.81	4041.30	18.17	60.66
2000	6147.00	2175.40	316.91	114.82	4281.53	21.45	54.82
2001	5168.00	2145.92	426.21	144.71	4710.38	28.78	48.74
2002	5319.00	1731.02	589.72	160.35	5803.77	37.24	46.06
2003	6807.00	1713.00	609.35	204.73	7037.43	41.87	43.10
2004	7725.00	1884.20	723.25	217.47	6466.52	44.92	39.75
2005	8299.00	2352.72	665.84	248.18	5508.42	40.35	36.49
2006	10300.00		642.95	226.66	4751.28	35.75	32.57
2007							

Norwegian Spring Spawning (NSS) herring: ICES (2006a).
NE Atlantic mackerel: ICES (2006b).
Cod: Northeast Atlantic cod, ICES (2007); coastal cod, ICES (2007).
Haddock: ICES (2007).
Blue whiting: ICES (2006a).
Greenland halibut: ICES (2007).
Rockfish: ICES (2007).

[a] Data source.

[b] Total cod computed by summing Northeast Atlantic cod and coastal cod.

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