Supporting Information

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SI Text

Model Fitting and Selection. In fitting the MAR(1) food-web model, we used data on SSB of cod, sprat, and herring from 1974 to 2004 derived from multispecies stock assessment (MSVPA) in the Baltic Sea (1). Model fitting was performed separately on both log-transformed and normalized SSB values. To include the top-down effect of commercial fishing on the dynamics of the three species, time series on mean annual fishing mortality (F) of cod, sprat, and herring were used as covariates. Further, to encompass environmental and zooplankton effects, abiotic and biotic variables known to affect recruitment of cod, sprat, and herring were included (Table S1). To take into account any geographical differences in hydrographic forcing (2), environmental variables were taken separately from the two main subbasins of the Central Baltic Sea, the southern Bornholm Basin and the northern Gotland Basin. Egg and larval survival of Central Baltic cod is affected mainly by salinity and oxygen conditions in the deep Baltic basins (3). The effect works directly on the eggs (4), but also indirectly on the availability of the copepod *P. acuspes* (5), the main food source for larval cod. Furthermore, *P. acuspes* is the dominant prey for herring (6). To address both these effects, we included salinity and oxygen concentration in the deepwater and $\ln(x + 1)$-transformed biomass of *P. acuspes* as potential covariates. We further used the reproductive volume (i.e., the water volume with a salinity >11 psu and an oxygen content >2 mL·l^{-1}) representing the minimal conditions for successful cod egg development in the deep Baltic basins (7). Temperature is the main environmental variable influencing sprat recruitment (8) by directly affecting egg and larval survival (4). Indirectly temperature affects the production and hence the availability of the copepods *Acartia* spp (6), which are important for the survival of larval sprat (9). Thus, we included both temperature and $\ln(x + 1)$-transformed biomass of *Acartia* spp. as potential covariates in the analysis. Hansson et al. (10) argue that eutrophication has a strong impact on the Baltic ecosystem, because enhanced primary production increases total fish production but at the same time it may induce hypoxia in bottom waters. To account for this effect, we used $\ln(x + 1)$-transformed values of spring and summer chlorophyll (*a* Chl. *a*) in the analysis. Finally, the Baltic Sea Index (BSI) was included because it reflects the impact of climate variability on oceanographic processes in the area (11).

To avoid colinearity between environmental and zooplankton covariates, we included only one abiotic and biotic variable per species in the full model. Before model reduction the full model was therefore fitted with each covariate separately and at different time lags (1–3 years). The time lags aim to represent the period until recruitment of the species to the fisheries. The covariates included in the full model were then chosen based on the significance level of the parameters (Table S1). Then by stepwise model reduction, the full model was penalized for complexity. We minimized the negative log-likelihood function and applied the likelihood ratio test to compare full and reduced models (Table S2).

Model Diagnostics. A number of diagnostics were applied to assess whether the final MAR(1) model gave a reasonable description of the food-web dynamics. The assumption of normality of the error terms is supported by an analysis of the residuals (Fig. S1). A partial autocorrelation analysis of the residuals further indicates that the model errors were independent for all species and lags, the only exception being a slight autocorrelation in the fifth- and sixth-year lag for sprat and cod, respectively (Fig. S1). Both R^2 values and conditional R^2 values, reporting the proportion of

change from t to $t + 1$ show a high degree of explained variance for all species (Table S3). Finally, a stability analysis of the final parameters of the community matrix reveals a dominant eigenvalue below one ($\lambda 1 = 0.93$) (Table S5), indicating a stable, stationary food web (12, 13). Our model thus has captured the essential dynamics of a natural, stable system. The log-transformed version of the model showed a considerably lower degree of conditional explained variance and marked autocorrelation in the residuals compared with the normalized version. The subsequent simulations were therefore based only on the normalized version.

Model Validation. A way of validating the predictive capabilities of a model is to fit on a subset of the available data and then check the model by forecasting the remainder of the data (14). Therefore, we adopted a sequential refitting procedure where the model was initially fitted to only the first 10 years of the dataset and then refitted on a yearly basis, producing a prediction for each consecutive year. The predicted values and associated 95% prediction intervals were compared with the observed values to assess the predictive accuracy of the model. The sequential refitting procedure serves a purpose not only to validate the model but as a realistic stock assessment tool, where we in retrospect forecast the future stock size to give sound management advice for the coming year. Additionally, the food-web dynamics was simulated by using only the first-year values as initial conditions. This procedure is fundamentally different from a simple fit to the data, because the observed values from the second year onward are not used (15). Simulations were run 1,000 times with random process noise added at each time step. Mean values and a 95% confidence interval of the predictions were computed. To assess the relative contribution of environmental and species interactions in affecting the food-web dynamics, we performed an additional hindcast simulation by using a simpler single-species MAR(1) model fitted only to fishing mortalities and biomasses of each individual species separately. Both the sequential refitting and the simulated dynamics demonstrated a distinct ability to "recreate the past" dynamics of cod, herring, and sprat (Fig. S2). The hindcast simulations without accounting for environmental forcing and species interactions, however, did not at all explain nor recreate the past dynamics of the three species, especially in the case of cod and sprat (Fig. S2). All statistical analysis were conducted with R software (www.r-project.org).

Model Simulations. To compare alternative management strategies we estimated the mean annual yield of the Baltic cod fishery and the probability of stock decline below B_{lim} given a fixed- and adaptive management scenario. In the fixed scenario, reference levels (F) remain fixed in the range from 0.3 to 1.0, whereas in the adaptive scenario we allow F levels to additionally vary with ± 0.3 dependent on climate conditions (i.e., hence F 0–0.6 and 0.6–1.2 corresponds to the lowest and highest adaptive exploitation pressure, respectively). Furthermore, to study yield curves and probabilities during variable climate we performed multiple stochastic simulations over a range of salinity levels corresponding to the observed fluctuations in salinity from 1974 to 2004.

In both the fixed and adaptive scenarios mean annual yield (Kt) increase with salinity levels, reflecting the increased input of recruits to the fishable stock caused by enhanced egg and larvae survival (3) (Fig. S3 *a* and *b*). On average, the adaptive

scenario gives higher yields as it guarantees stock biomass to remain at higher mean levels compared with the fixed approach (Fig. 4). Given an adaptive approach we can show how under highly unfavorable salinity conditions the adaptive approach allows for a yield $\approx$3–4 times the fixed yield (i.e., $\approx$35 and $<$10 Kt). During favorable salinity conditions for spawning and recruitment, however, the difference in mean yield decreases, illustrated by an adaptive and fixed yield of $\approx$120 and $\approx$90 Kt, respectively. Finally, concerning the probability of collapse below B_{lim} the adaptive approach (Fig. 3d) by buffering against climate variability considerably reduces the risk of future stock collapse compared with a fixed strategy (Fig. 3c), despite equal mean F levels.

1. The International Council for the Exploration of the Sea (1996) *Report of the Working Group on Multispecies Assessments of Baltic Fish* (International Council for the Exploration of the Sea, Copenhagen)
2. MacKenzie BR, Gislason H, Möllmann C, Köster FW (2007) Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biol* 13:1348–1367.
3. Köster FW, et al. (2005) Baltic cod recruitment: The impact of climate variability on key processes. *ICES J Mar Sci* 62:1408–1425.
4. Nissling A (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea: Implications for stock development. *Hydrobiologia* 514:115–123.
5. Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can J Fish Aquat Sci* 59:1858–1873.
6. Voss R, Köster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin. *Baltic Sea Fish Res* 63:97–111.
7. MacKenzie BR, Hinrichsen HH, Plikshs M, Wieland K, Zezera AS (2000) Quantifying environmental heterogeneity: Habitat size necessary for successful development of cod (*Gadus morhua*) eggs in the Baltic Sea. *Mar Ecol Prog Ser* 193:143–156.
8. Köster FW, et al. (2003) Recruitment of Baltic cod and sprat stocks: Identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. *Sci Mar* 67:129–154.
9. Dickmann M, Möllmann C, Voss R (2007) Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: Implications for survival. *Mar Ecol Prog Ser* 342:277–289.
10. Hansson S, et al. (2007) Managing Baltic Sea fisheries under contrasting production and predation regimes: Ecosystem model analyses. *Ambio* 36:265–271.
11. Lehmann A, Krauss W, Hinrichsen HH (2002) Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus A* 54:299–316.
12. Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. *Ecol Monogr* 73:301–330.
13. May RM (1972) Will a large complex system be stable? *Nature* 238:413–414.
14. Chatfield C (1989) *The Analysis of Time Series, An Introduction* (Chapman & Hall, London).
15. Hjermann DO, Stenseth NC, Ottersen G (2004) The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: An analysis based on survey data. *Can J Fish Aquat Sci* 61:1747–1755.
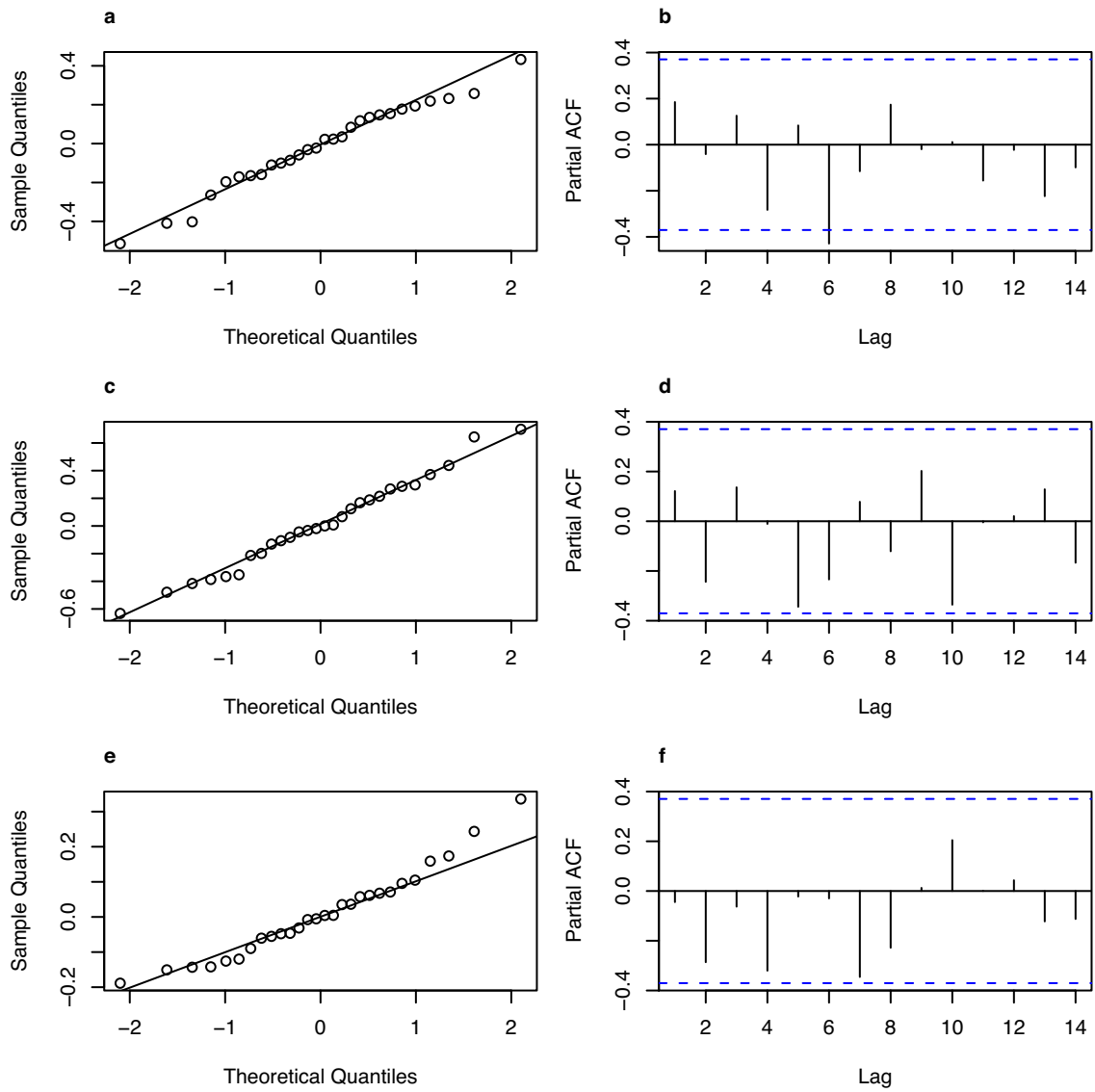
Fig. S1. Model diagnostics. Normal probability plots (*a*, *c*, and *e*) and partial autocorrelation coefficients (*b*, *d*, and *f*) of residuals for cod (*a* and *b*), sprat (*c* and, *d*), and herring (*e* and *f*) from the final MAR(1) model.
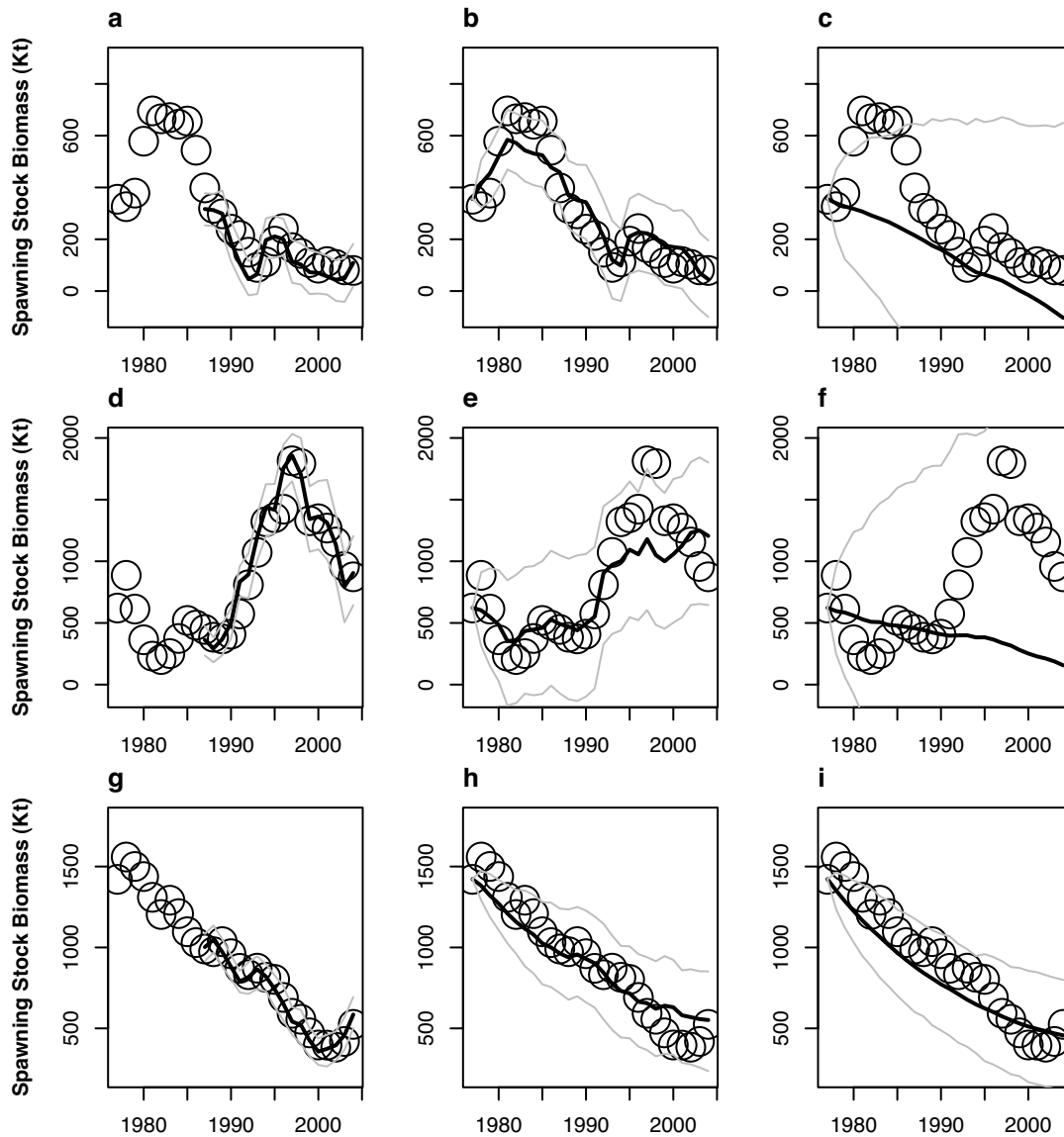
Fig. S2. Model validation through hindcasting. Observed (open circles) and simulated biomass (solid lines) of Baltic cod (*a*–*c*), sprat (*b*–*f*), and herring (*g*–*i*) from 1977 to 2004, showing the MAR(1) model's ability to recreate the food-web dynamics. (*a*, *d*, and *g*) Yearly predictions from the sequential refitting approach, where the model was initially fit to only the first 10 years and for each following year it was refitted. (*b*, *e*, and *h*) The results from simulations using only the first-year values in 1977 as initial conditions are shown. Simulations were replicated 1,000 times (each time with random process noise added). (*c*, *f*, and *i*) Simulations from a model fitted only to fishing mortalities and biomasses for each species separately are shown. Gray lines indicate the upper and lower 95% confidence intervals of the simulations.
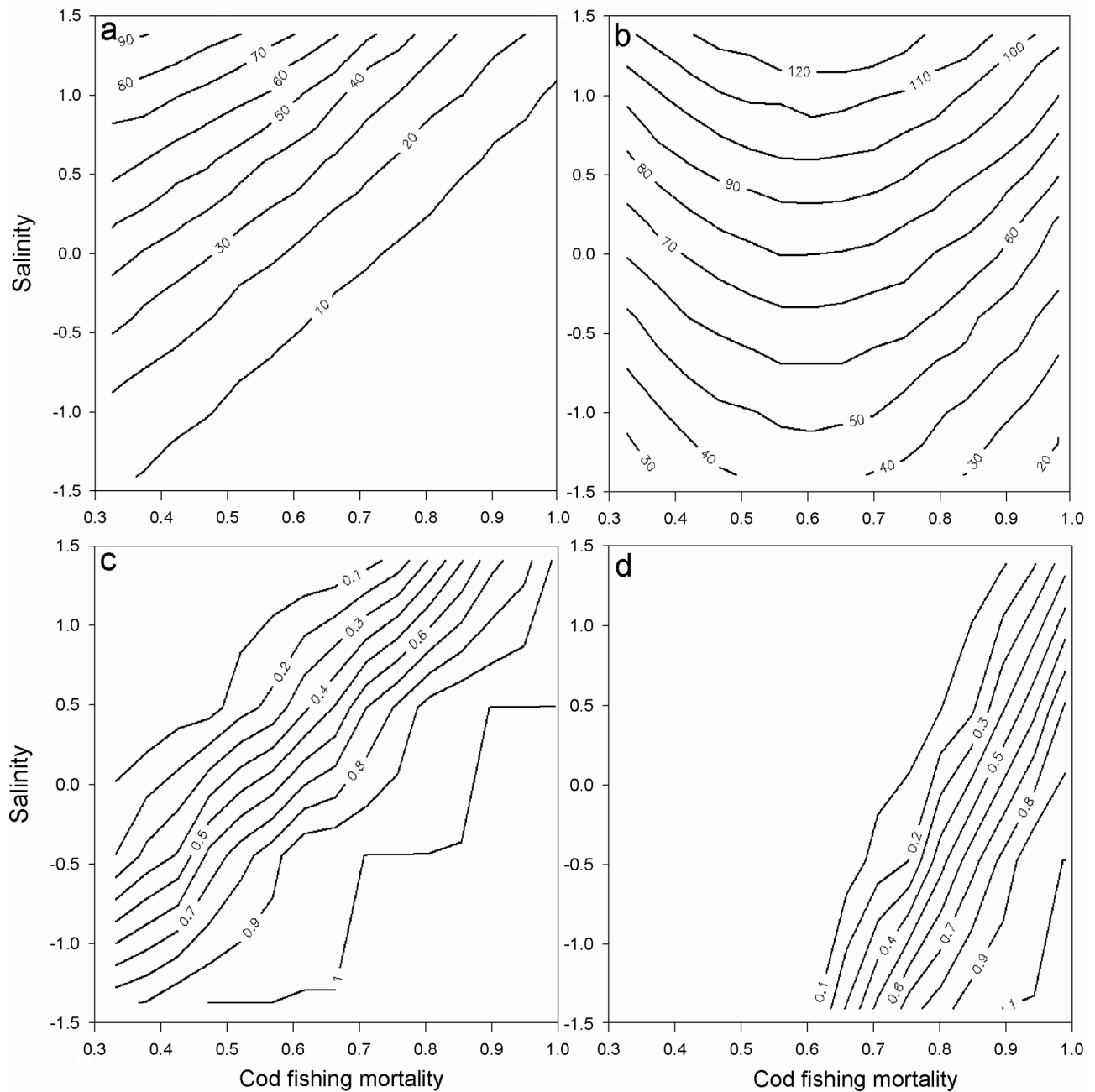
Fig. S3. Simulated mean annual yield (Kt) and the probability of stock collapse below B_{lim} (i.e., the percentage of simulations where SSB < B_{lim}) given a fixed- and adaptive management scenario. While in the fixed management scenario (*a* and *c*) fishing mortalities remain constant at the specified *F* levels over the entire modeled time period (i.e., ranging from 0.3 to 1.0), the adaptive scenario (*b* and *d*) allows for additional temporal variability in *F* levels by ± 0.3 depending on salinity conditions. Climate conditions were simulated as to resemble the historical range of fluctuations in SST and salinity conditions in the Baltic Sea. Salinity conditions are presented as anomalies where ± 1.5 psu indicates the minimum and maximum observed levels from 1974 to 2004. Simulations were initialized at the mean historical SSB levels for each species and replicated 1,000 times, including stochastic process noise.

Table S1. Covariates and parameter *P* values from the full model fitting

Covariate	Cod	Herring	Sprat
Spring temperature (0–10 m) GB	0.69	0.91	0.007**
Spring temperature (40–60 m) GB	0.86	0.21	0.008**
Summer temperature (0–10 m) GB	0.54	0.18	0.15
Summer temperature (40–60 m) GB	0.62	0.84	0.04*
Spring temperature (0–10 m) BB	0.48	0.13	0.30
Spring temperature (40–60 m) BB	0.53	0.30	0.08
Summer temperature (0–10 m) BB	0.33	0.30	0.01*
Spring salinity (0–10 m) GB	0.16	0.06	0.04*
Spring salinity (80–100 m) GB	0.05*	0.15	0.21
Summer salinity (0–10 m) GB	0.12	0.05*	0.04*
Summer salinity (80–100 m) GB	**0.05***	**0.04***	0.32
Spring salinity (0–10 m) BB	0.30	0.11	0.04*
Spring salinity (70–90 m) BB	0.18	0.21	0.01*
Winter bottom oxygen BB	0.56	0.16	0.49
Winter bottom oxygen GB	0.68	0.39	0.90
Reproductive volume	0.06	——	——
Baltic Sea Index (BSI)	0.11	0.62	0.08
Spring *Acartia* spp. GB	——	——	**0.007***
Summer *Acartia* spp. GB	——	——	0.07
Spring *Pseudocalanus* spp. GB	0.66	0.68	——
Summer *Pseudocalanus* spp. GB	**0.17**	**0.01***	——
Spring [Chl. *a*] BB	0.31	0.41	0.49
Summer [Chl. *a*] BB	0.30	0.87	0.22
Spring [Chl. *a*] GB	0.52	0.48	0.78
Summer [Chl. *a*] GB	0.70	0.18	0.88

Climate variables are taken from the Gotland Basin (GB) and the Bornholm Basin (BB) separately. The bold values show the most significant climate and zooplankton variables chosen to be included in the full model. The variable for cod is lagged by 3 years, whereas the variables for sprat and herring are lagged by 1 year.

Table S2. Model reduction

Eq.1	−log(L)	P value	R^2	Conditional R^2
Full model	−15.66		[0.96, 0.90, 0.98]	[0.57, 0.39, 0.55]
Cod:zooplankton	−15.66	0.99	——	——
Sprat:zooplankton	−14.90	0.47	——	——
Cod:sprat	−14.53	0.52	——	——
Sprat:herring	−14.52	0.69	——	——
Herring:salinity	−12.05	0.21	[0.95, 0.89, 0.98]	[0.56, 0.36, 0.53]

Final model evaluation using negative log likelihood estimation and the likelihood ratio test for model reduction. The total and conditional explained variance for cod, sprat, and herring are shown for the full and the final models only. $P > 0.05$ indicate that the complex model does not fit the data significantly better than the reduced model. The parameter can thus be excluded.

Table S3. Fit of the model for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004

Variate	Total R^2	Conditional R^2
Cod	0.95	0.56
Sprat	0.89	0.36
Herring	0.98	0.53

Table S4. Parameter estimates for species interactions, the community matrix for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004

	Cod	Sprat	Herring
Cod	0.67 [0.55, 0.80]	0	0.23 [0.08, 0.37]
Sprat	−0.06 [−0.12, 0.00]	0.90 [0.73, 1.06]	0
Herring	−0.09 [−0.16, −0.02]	−0.10 [−0.19, −0.02]	0.87 [0.77, 0.97]

Table S5. Eigenvalue analysis of the community matrix for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004

Variate	Eigenvalue
Cod	$0.93 + 0.00i$
Sprat	$0.76 + 0.13i$
Herring	$0.76 - 0.13i$

Table S6. Parameter estimates with 95% confidence intervals for covariates, fishing, climate, and zooplankton for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004

Variate	Fishing	Climate	Zooplankton
Cod	−0.91 [−1.31, −0.52]	0.08 [0.02, 0.14]	0
Sprat	−0.34 [−1.20, 0.51]	0.08 [0.04, 0.13]	0
Herring	−0.82 [−2.14, 0.51]	0	0.15 [0.05, 0.26]