

# A metacommunity perspective on source–sink dynamics and management: the Baltic Sea as a case study

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**Abstract.** The degree to which metapopulation processes influence fish stock dynamics is a largely unresolved issue in marine science and management, especially for highly mobile species such as Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*). The Baltic Sea comprises a heterogeneous oceanographic environment that structures the spatial and temporal distribution of the dominant species cod, herring, and sprat (*Sprattus sprattus*). Despite local differences, the stocks are traditionally managed as homogeneous units. Here, we present a metacommunity-perspective on source–sink dynamics of Baltic Sea fish stocks by using a spatially disaggregated statistical food web model. The model is fitted to area-specific time series of multiple abiotic and biotic variables using state-space methods. Our analysis reveals pronounced net fluxes between areas, indicative of source–sink dynamics, as well as area-specific differences in species interactions (i.e., density dependence, competition, and predator–prey) and the degree of fishing and climate impact on survival and recruitment. Furthermore, model simulations show that decreasing exploitation pressure in the source area for cod (without reallocating fishing effort) produces an increase in neighboring sink habitats, but a decline of prey species in response to increased predation. Our approach provides valuable insight concerning metacommunity-structuring of marine fish and may serve as an important tool for implementing sustainable management strategies under the ecosystem approach to marine and fisheries management.

**Key words:** *Baltic Sea; cod, Gadus morhua; fisheries management; food web; herring, Clupea harengus; metacommunity; metapopulation; population dynamics; sprat, Sprattus sprattus; source–sink.*

## INTRODUCTION

The degree to which local population processes influence regional dynamics of fish stocks is a largely unresolved issue in marine science and management (Kritzer and Sale 2004). Source–sink dynamics is a theoretical framework (Holt 1985, Pulliam 1988) describing how excess production from sources (i.e., habitats where reproduction exceeds mortality) support sinks (i.e., habitats where reproduction is insufficient to balance local mortality) in a network of interlinked local populations, termed a metapopulation (Levins 1969, Hanski 1999). When expanded further to include species interactions, a metacommunity is defined as a set of local communities linked by dispersal of multiple interacting species (Wilson 1992, Leibold et al. 2004). By embedding local communities within a larger metacommunity context, spatial dynamics may directly

or indirectly alter local community processes that feedback to affect the regional biota (Leibold et al. 2004). Therefore, estimating rates of interpopulation exchange has large implications for marine spatial management and is hence considered a priority for future research (Kritzer and Sale 2004).

Empirical investigations of metapopulation dynamics are scarce due to difficulties in measuring dispersal rates in natural habitats (Dunning et al. 1992). Additionally, sources and sinks may be misclassified due to environmental variability and/or natural disasters. Empirical examples of metapopulation and source–sink dynamics stem mostly from terrestrial ecosystems (Keddy 1981, Dias 1996, Tittler et al. 2006), while marine examples concern mainly sedentary species with limited dispersal abilities (e.g., reef fish; James et al. 2002, Bode et al. 2006) or crustaceans (Botsford et al. 1998), although examples of highly motile fish species also exist (Casini et al. 2012). In open marine ecosystems, the metapopulation concept is questioned (Grimm et al. 2003). Yet, tagging studies (McQuinn 1997, Wright et al. 2006) and genetic analysis (Nielsen et al. 2005) suggests the existence of metapopulation dynamics also in highly

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mobile species such as Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*). Additionally, drift studies show how local recruitment may depend on advection of early life-stages from neighboring areas, at least during periods of locally unfavorable conditions for spawning (Svedäng 2003, Stein and Borovkov 2004). While these examples identify possible sources and sinks for single species separately, what constitutes a sink for one species may act as a source for other species (Leibold et al. 2004). Hence, studies adopting a metacommunity context of multiple interacting species are essentially needed in spatial management of marine resources, but, to our knowledge, presently lacking.

The Baltic Sea comprises a heterogeneous oceanographic environment largely influencing the spatial and temporal distribution of cod, herring, and sprat (*Sprattus sprattus*), the three dominant fish species in the area. Despite local differences in stock abundance, structure, and life history traits (Casini et al. 2011), the stocks are traditionally managed as geographically homogeneous units. In an effort to resolve local dynamics of Baltic fish stocks, area specific multispecies stock assessment has been conducted (Köster et al. 2001). However, without quantifying species interactions and migration between basins, as supported by tagging studies and modeling (Aro 1989, Hinrichsen et al. 2003), the approach is not designed for resolving local impact of source-sink dynamics within the Baltic Sea fish community. Although nonspatially resolved models may be sufficient to assess the overall stock status and response to various (nonspatial) management actions (e.g., Lindegren et al. 2009, Tomczak et al. 2012), we present a metacommunity perspective on source-sink dynamics and examples of spatial management alternatives for Baltic Sea fish stocks using a spatially disaggregated statistical food web model. Fitted to area-specific time series of multiple abiotic and biotic variables, our model shows clear regional patterns of exchange between areas dependent on local species interactions (density dependence, competition, and predation), commercial fishing, and climate effects (e.g., temperature, salinity, and oxygen) on recruitment and survival.

## MATERIAL AND METHODS

### *Ecosystem and site description*

The Baltic Sea is a large, semi-enclosed sea that, due to its brackish nature, is characterized by low species diversity, yet high productivity. The central part of the Baltic Sea encompasses three deep basins (Fig. 1), the Bornholm Basin (BB), the Gdansk Deep (GD), and the Gotland Basin (GB). Characteristic of the hydrography of these basins is a permanent halocline separating low salinity surface waters from high-saline deep waters. Deep water conditions can only be enhanced by inflows of saline and oxygenated water from the North Sea (Matthäus and Franck 1992). A lack or low-frequency of these events, as observed during the recent three

decades, leads to low salinity and oxygen levels, and, hence, detrimental reproductive conditions for fish (e.g., cod; Köster et al. 2005). Hydrological conditions since the late 1980s have significantly changed the living conditions for animal populations inhabiting the area. The main trends are lowered surface salinity and deepwater oxygen levels due to low frequency of inflows and increased temperatures (Fig. 2D–F; Möllmann et al. 2009).

The heterogeneous oceanographic environment of the Central Baltic Sea largely influences reproduction, growth, and survival of cod, herring, and sprat, the ecologically and commercially most important species in the area. For example, population indices of cod, estimated by bottom trawl surveys and ichthyoplankton sampling, revealed distinct trends in each basin (Sparholt and Tomkiewicz 2000, Köster et al. 2001), as well as substantial spatial differences in maturity and growth (Tomkiewicz et al. 1997). Furthermore, the herring-stock in the Central Baltic Sea is likely composed of a number of subpopulations exhibiting variations in spawning period and growth rates, as well as other meristic, morphometric, and otolith characteristics (e.g., Ojaveer 1981, Parmanne et al. 1994). Although sprat may form local stock components (Ojaveer 1989), as indicated by otolith characteristics (Aps et al. 1981) or number of vertebrae (Ojaveer and Kalejs 2010), the existence of distinct subpopulations is controversial, due to pronounced movement and mixing within the Baltic Sea (Parmanne et al. 1994).

### *Model setup and fitting*

We studied the spatial dynamics and exchange of cod, herring, and sprat between the basins of the central Baltic Sea using a spatially disaggregated statistical food web model, derived from the basic principles of a previous nonspatially resolved model (Lindegren et al. 2009). We used the division of the Baltic Sea from the International Council for the Exploration of the Sea (ICES) into subdivisions 25, 26, and 28, corresponding to the natural division of the Baltic Sea. These three distinct divisions are the Bornholm Basin (BB), the Gdansk Deep (GD), and the Gotland Basin (GB), respectively. This statistical approach is based on the multivariate autoregressive (MAR) model framework (Ives et al. 2003) and essentially functions as a set of lagged multiple linear regression equations (one for each species of the food web in each area) solved simultaneously to arrive at the most parsimonious model overall (Hampton et al. 2006). Written in state-space form, the model is given by

$$X_{i,t} = \mathbf{B}_i X_{i,t-1} + \mathbf{C}_i \mathbf{U}_{i,t-\Delta t} + \sum_j \mathbf{D}_{i,j} (X_{j,t-1}/X_{i,t-1}) + \mathbf{E}_{i,t} \quad (1)$$

$$Y_{i,t} = \mathbf{Z} X_{i,t} + V_{i,t} \quad (2)$$

where  $X_{i,t}$  are log-transformed abundance indices of juvenile cod, adult cod, sprat, and herring in basin  $i$  at

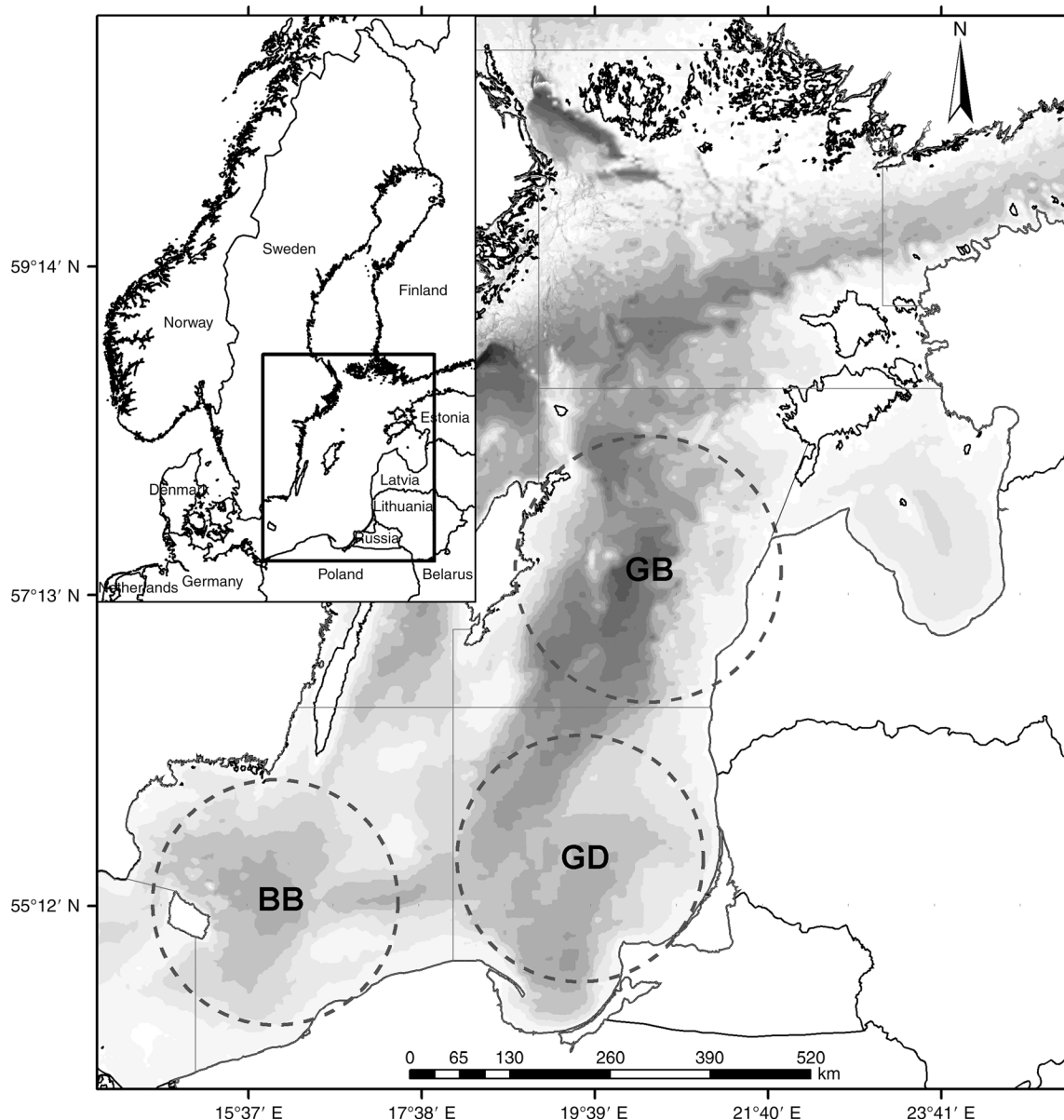


FIG. 1. Map of the Baltic Sea and its location within Northern Europe. The central part of the Baltic Sea encompasses three deep ( $<70$  m) spawning basins for marine fish populations, the Bornholm Basin (BB), the Gdansk Deep (GD), and the Gotland Basin (GB); largely corresponding to the International Council for Exploration of the Seas (ICES) subdivisions 25, 26, and 28, respectively (thin lines).

time  $t$ .  $\mathbf{B}$  is a matrix of basin-specific species interaction parameters, analogous to the community matrix used by May (1972) and Pimm (1982). In order to account for important spatial differences in cod recruitment (Bagge et al. 1994, Köster et al. 2001, 2005), cod is represented by a simple stage-structure including a juvenile stage (i.e., log-transformed recruitment [ $R$ ] indices at age two) and adult cod.  $R$  is modeled as the sum of a linear and quadratic effect of the adult stock size ( $S$ ) in each basin lagged by two years (i.e.,  $R_{i,t} = aS_{i,t-2} + bS_{i,t-2}^2$ ). The additional parameters are estimated as part of the matrix  $\mathbf{B}$ . The

vector  $\mathbf{U}$  contains basin-specific covariate time series that influence the abundance of each species differentially through the parameter matrix  $\mathbf{C}$ . The covariate vector  $\mathbf{U}$  includes basin-specific exploitation rates (Fig. 2A–C); climate through selected abiotic variables known to affect recruitment of cod, herring, and sprat (Appendix: Table A1); and potential seal predation (in the GB only). Note that, since climate influences cod primarily during the early life-stages (Köster et al. 2005), the climate effect is included only for the recruitment stage (two years of age); and, therefore lagged with two years. In order to reflect

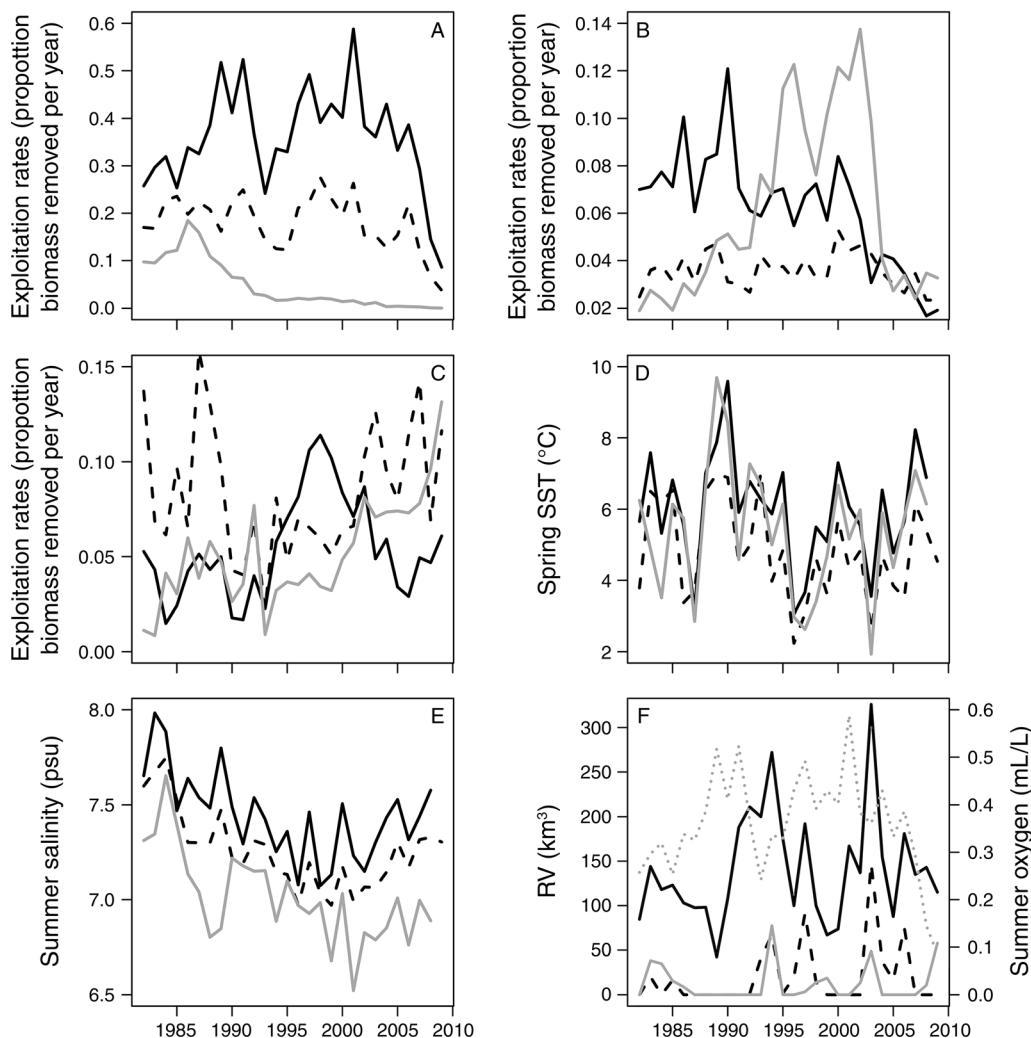


FIG. 2. Time series of a number of covariates used during model fitting. Exploitation rates of (A) cod (*Gadus morhua*), (B) herring (*Clupea harengus*), and (C) sprat (*Sprattus sprattus*), estimated as the proportion of total spawning stock biomass removed each year by landings. In addition, the climate conditions shown are (D) spring sea surface temperature (SST); (E) summer surface salinity; and (F) cod reproductive volume (RV; the volume of water with salinity >11 psu and oxygen content >2 mL/L that is necessary for the survival of cod eggs) and summer deep water oxygen for GB (dotted line). Data for the Bornholm Basin is in black, the Gdansk Deep is dashed, and the Gotland Basin appears gray.

the timing of herring and sprat recruitment, climate variables were lagged by one year (ICES 2010).

Potential pairwise exchange between basins is assumed to be proportional to the ratio between the logarithmic abundances in each basin (i.e.,  $X_j/X_i$ ). Hence, our assumption aims to reflect a directed flux (i.e., diffusion) to neighboring habitats in accordance with the so-called basin model, where density and habitat size is assumed to vary with abundance (MacCall 1990). The actual species- and basin-specific fluxes are contained and estimated as part of the diffusion matrix **D**. Finally, the vector **E** contains multivariate, normally distributed, and temporally uncorrelated process errors. In the state-space formulation, the process model Eq. 1 is complemented by a measurement model Eq. 2. Here, the data  $Y_{i,t}$  reflects

observations of the hidden state  $X_{i,t}$ . The observations and the hidden state are connected by the covariance matrix  $\mathbf{Z}_{i,t}$  and subject to the observation error described by  $V_{i,t}$ . The parameters were estimated by maximum-likelihood estimation using a Kalman filter (Harvey 1989). The Kalman filter is a recursive estimator that sequentially calculates the unobserved values  $X_{i,t}$  from the previous time step ( $t - 1$ ) using the model formula specified in Eq. 1. Predictions of the hidden state given in  $X_t$  are then updated using the observed values,  $Y_t$  of the true state (Eq. 2). As a complement to the Kalman filter, regression parameters (i.e., Table 1, matrices **B**, **C**, and **D**) were also fitted using ordinary linear regression. Model-fitting was performed on available time series covering the period 1984–2009.



TABLE 1. Final parameters with standard errors of species interactions (the community matrix, **B**), the effects of fishing, climate, and seal predation (the environmental covariate matrix, **C**), and the effect of migration (the diffusion matrix, **D**) for each species and basin (BB, GD, and GB).

	BB			
	Cod recruitment	Cod	Herring	Sprat
Community matrix, <b>B</b>				
BB				
Cod recruitment		†		
Cod	0.37 ± 0.22		0.51 ± 0.31	0
Herring		−0.13 ± 0.11	0.29 ± 0.03	0
Sprat		0	0	0.78 ± 0.30
GD				
Cod recruitment				
Cod				
Herring				
Sprat				
GB				
Cod recruitment		0.36 ± 0.27		
Cod				
Herring				
Sprat				
Environmental covariate matrix, <b>C</b>				
Fishing		−3.30 ± 2.07	−3.32 ± 3.31	0
Climate	0.01 ± 0.01		1.5 × 10 <sup>−3</sup> ± 0.5 × 10 <sup>−3</sup>	0.14 ± 0.14
Seal (GB)				
Diffusion matrix, <b>D</b>				
BB				
GD		0	0	2.59 ± 1.39
GB		0	0	0
R <sup>2</sup>	0.51	0.52	0.89	0.42

Notes: Predictor variables are along the columns for the **B** matrix but along the rows for the **C** and **D** matrices. The climate effects correspond to reproductive value (RV) for cod, sea surface temperature (SST) for herring and sprat, and oxygen (summer) for sprat in GB. Blank cells represent parameters not included in the model setup and zero values interactions reduced during model selection (see the Appendix: Table A2). Note that cod is divided into a juvenile stage (i.e., log-transformed recruitment indices at age two) and adult cod. Recruitment ( $R$ ) is modeled as the sum of a linear and quadratic effect of the adult stock size ( $S$ ) in each basin lagged by two years (i.e.,  $R_{i,t} = aS_{i,t-2} + bS_{i,t-2}^2$  in basin  $i$  at time  $t$ , where  $a$  and  $b$  are regression parameters). Conditional explained variance ( $R^2$ ) is also presented.

† Linear effect of spawning numbers on cod recruitment in BB is  $1.58 \pm 0.56$  and quadratic effect is  $-0.15 \pm 0.10$ .

‡ Linear effect of spawning numbers on cod recruitment in GD is  $1.27 \pm 0.51$  and quadratic effect is  $-0.10 \pm 0.09$ .

### Data description

The data required for the fitting comprise abundance indices of each population  $Y_{i,t}$  and potential environmental covariates or exploitation rates  $U_{i,t}$ . Note that we do not use fishing mortalities or biomasses as these are not directly observed but are model-estimates from stock assessments. In order to reflect the adult component of the populations, the abundance indices were summed over all ages having reached maturity, given by the corresponding maturity ogives (ICES 2010). In order to characterize the area-specific abiotic and biotic conditions  $U_{i,t}$ , a number of variables were collected from each basin (Appendix: Table A1). Abundance indices of juvenile (age two) and adult cod originate from spring trawl surveys, whereas abundances of sprat and herring originate from autumn hydroacoustic surveys. In order to account for potential seal predation, particularly in the GB, we used a time series of gray seal (*Halichoerus grypus*) abundance (MacKenzie et al.

2011). Furthermore, basin-specific exploitation rates (i.e., the annual proportion of the total spawning stock biomass [ICES 2010] removed by fishing in each of the three basins) were included as proxies for the extent and allocation of exploitation. In order to reflect climate effects on recruitment in each basin, time series on temperature, salinity, and oxygen-concentrations at the surface and in deep water during spring and summer were collected from the stations BY5 (BB), BMPK01 (GD), and BY15 (GB), available through the Swedish Meteorological and Hydrological Institute and ICES (data available online).<sup>6,7</sup> In addition, reproductive volume (RV) or the volume of water with salinity >11 psu and oxygen content >2 mL/L that is necessary for the survival of cod eggs, as well as maximum ice cover, the winter North Atlantic Oscillation (NAO), and Baltic

<sup>6</sup> [http://www.smhi.se/oceanografi/oce\\_info\\_data/SODC/download\\_sv.htm](http://www.smhi.se/oceanografi/oce_info_data/SODC/download_sv.htm)

<sup>7</sup> <http://ecosystemdata.ices.dk>

TABLE 1. Extended.

GD				GB			
Cod recruitment	Cod	Herring	Sprat	Cod recruitment	Cod	Herring	Sprat
$0.69 \pm 0.28$	$0^{\ddagger}$	$0.19 \pm 0.19$	0	$0.76 \pm 0.26$	$0.27 \pm 0.27$	$0.53 \pm 0.41$	$-0.34 \pm 0.26$
	$-0.34 \pm 0.29$	$0.77 \pm 0.19$	$-0.31 \pm 0.25$		$-0.14 \pm 0.07$	$0.88 \pm 0.14$	$-0.22 \pm 0.07$
	$-0.27 \pm 0.30$	0	$0.44 \pm 0.19$		$-0.12 \pm 0.21$	0	$0.83 \pm 0.16$
$4 \times 10^{-3} \pm 0.5 \times 10^{-3}$	0	0	$-7.72 \pm 6.05$	$0.01 \pm 0.01$	0	0	0
	$0.08 \pm 0.10$	0	0		$0.05 \pm 0.06$	$0.07 \pm 0.13$	0
	0	0	0		0	0	0
0.28	$1.87 \pm 1.60$	$2.09 \pm 1.47$	0	0.45	0	$2.22 \pm 0.96$	$1.91 \pm 2.11$
	0	$2.26 \pm 1.03$	$0.45 \pm 0.13$		$0.76 \pm 0.74$	$4.60 \pm 3.38$	$3.60 \pm 2.20$
	0.21	0.6	0.58		0.67	0.64	0.27

Sea Index (BSI) were used as covariates of recruitment success (MacKenzie et al. 2000, Lehmann et al. 2002).

#### *Model selection and validation*

In order to avoid overparameterization, we limited the number of climate covariates in  $\mathbf{U}_{i,t}$  to only one variable per species and basin in the full model. Prior to model reduction, the full model was fitted with each climate covariate separately (Appendix: Table A2). The covariates were then chosen based on minimizing the Akaike's information criterion (AIC; Anderson et al. 1998). Then stepwise-model reduction of the full model was used to further penalize for complexity (Appendix: Table A3). We minimized the negative log-likelihood function and applied the likelihood ratio test to compare full and reduced models. In order to validate the predictive ability of the model, we assessed the degree to which the model is capable of recreating the historical population trajectories by hindcasting the food web dynamics, based on only the first year values as initial conditions. This procedure is fundamentally different from a simple fit to the data, as the observed values from the second year onwards are not used during the hindcast simulations (Hjermann et al. 2004). In order to account for unexplained sources of variability, including potential cross-boundary fluxes outside the area investigated (e.g., Casini et al. 2012), simulations were run 1000 times

with random noise, resampled from the residuals of the model, and added at each time step. Mean values and 95% confidence intervals of the predictions were computed. Residuals were checked for normality and temporal autocorrelation. All statistical analyses were conducted using the R software v. 2.12.1 (R Development Core Team 2010).

#### *Model simulations and management scenarios*

As a simulated case study, the validated model was used to explore the response of the food web to a fishing closure of the main spawning area in the BB and a drastic improvement in hydrographic conditions necessary for cod recruitment in the three different basins. In the first scenario, exploitation rates for cod in the BB were set to zero, while exploitation rates of cod in GD and GB and exploitation rates for herring and sprat in all the basins were maintained at mean historical levels throughout a simulated period of 50 years. Climate conditions were set fluctuating at mean historical levels based on the mean, variance, and degree of autocorrelation of the observed climate time series (Lindegren et al. 2010a). In the second scenario, exploitation rates for all species were set at mean historical levels in all three basins, while an increase in the RV by 100% compared to observed (mean) levels from 1984–2009 was simulated. The response of the food web to the fishing and climate scenarios was evaluated as

the relative change in stock abundance compared to a baseline scenario with both exploitation rates and climate conditions maintained at mean historical levels throughout the simulated period. For each scenario, 1000 simulations were run with random process noise, resampled from the residuals of the model, and added at each time step. Mean values and a 95% confidence interval of the simulations were computed.

### RESULTS

The final model illustrates clear, basin-specific effects of species interactions, fishing, and hydrographic conditions on local population dynamics of Baltic cod, herring, and sprat, as well as pronounced fluxes within the metacommunity (Fig. 3, Table 1, Appendix: Table A4). Significant negative effects (parameters) of cod on herring are found in all the three basins but primarily in the GD, while negative interactions of cod on sprat are significant in the GD and GB. In addition, positive interactions on (adult) cod are found only for herring, while negative effects of sprat on cod occur in the GB. Significant negative interactions from sprat on herring are seen in GD and GB, while negative effects from herring on sprat are not supported in any of the basins. Density-dependence was found for all species and basins, illustrated by intraspecific parameters of the community matrix lower than one (Table 1B), as well as a significant (negative) quadratic effect of cod spawning stock abundance on cod recruitment in BB and GD. Commercial fishing was found to negatively affect all species with spatial differences in the main areas of impact. While cod and herring seem to be impacted mainly in the BB, sprat is influenced primarily in the GD. In contrast to the targeted impact of fishing, hydrographic conditions have a significant effect in all basins. Recruitment variability of cod is best explained by the RV, while for herring and sprat, sea surface temperature (SST) in spring (BB and GD) and summer (BB and GB) are the dominant climate predictors with the exception of summer oxygen conditions being the most significant variable for sprat in the GB (Appendix: Table A2). Seals in GB did not have an effect on any of the species (Table 1).

In addition to basin-specific effects of species interactions, fishing, and climate, fluxes from neighboring basins were significant for most species and basins (Table 1). Adult cod demonstrate a clear preference for the BB. If the log(abundance) ratio between adjacent basins increases (e.g., through local declines due to fishing or unfavorable hydrographic conditions for reproduction), the fluxes are primarily towards the south. The opposite pattern is seen for cod recruitment in the GB, where local abundance of adults alone was insufficient to explain local recruitment variability without including the effect of adults in the main spawning area of the BB. In contrast to the mainly unidirectional flux of adult cod, herring, and sprat show significant linkages between all basins, especially between the GD and the GB (Table 2).

By combining basin-specific species interactions with external forces through fishing, climate, and migration, our fitted model clearly reproduces the observed long-term dynamics of the Baltic Sea food web. These are characterized by a long-term decrease of cod in the GD and GB (Fig. 4E and F), but a recent increase in recruitment and adult abundance in the BB (Fig. 4A and D). Herring demonstrate similar dynamics in all basins with high abundances during the late 1980s, followed by a pronounced decline and a recent increase during the past decade (Fig. 4G–I). In contrast, sprat show basin-specific trends with a recent decline in the BB and GD but a marked increase in the GB (Fig. 4J–L). While the model accurately recreates long-term trends, the pronounced interannual variability is less well reproduced for some species and basins, as illustrated by lower conditional  $R^2$  values (i.e., reporting the proportion explained variance from time  $t$  to  $t + 1$ ; Table 1). We validated our model by hindcasting the observed food web dynamics, based on only the starting abundance indices for each species and basin. Forced by the observed time series of exploitation rates and hydrographic conditions in each basin, the simulations reproduce the long-term abundance trends, although underrepresenting the magnitude of interannual fluctuations (Appendix: Fig. A1). Model residuals were normally distributed and temporally uncorrelated (Appendix: Figs. A2 and A3).

In our scenario simulation, a fishing closure of the main cod spawning area in the BB yields a mean long-term increase in adult cod abundance in all areas, with the BB showing a doubling of the adult stock relative to the baseline scenario (Fig. 5A). While no significant effect on recruitment is shown in the GD and BB, an increase is seen in the GB. As a response to increasing cod abundance, sprat show a moderate decrease, especially evident in GB, while herring seem less affected across basins. In the second scenario, a doubling of the RV results in a strong increase in cod recruitment and adult biomass across all basins, with a comparatively less pronounced effect on the adult population in the BB (Fig. 5B). In contrast to the first scenario, both herring and sprat demonstrate a long-term decrease, with the exception of herring in the BB.

### DISCUSSION

The influence of metacommunity structuring and source-sink dynamics is a largely unresolved issue in marine science and management (Kritzer and Sale 2004). Local recruitment success of marine fish populations may depend on advection of early life-stages from neighboring source areas, at least during periods of locally unfavorable conditions for spawning (Svedäng 2003, Stein and Borovkov 2004). In the Northern Baltic Sea, cod recruitment is believed to be dependent on advection and dispersal of eggs and larvae from southern areas, especially during stagnation periods with adverse hydrographic conditions for successful

reproduction (Bagge et al. 1994, Hinrichsen et al. 2003). On the other hand, following large inflows from the North Sea, high salinity and oxygen concentrations markedly increase the available spawning habitat (i.e., RV; MacKenzie et al. 2000) allowing for egg and larvae survival and successful reproduction and growth throughout large parts of the Central Baltic Sea (Bagge et al. 1994). Such major inflow events (Matthäus and Franck 1992) may, therefore, explain abundant year-classes and peak biomasses (e.g., as experienced during the high stock levels of the late 1970s [Bagge et al. 1994, Köster et al. 2005, Lindegren et al. 2009]).

Our results confirm the influence of hydrographic conditions on cod population dynamics by demonstrating a positive effect of reproductive volume on local recruitment in all basins. In addition, our findings are consistent with tagging studies (Aro 1989) and modeling (Hinrichsen et al. 2003), indicating a potential net flux of adults toward the south, as well as a significant contribution of recruits from the main spawning area of the BB to the GB. It is important to note that the estimated fluxes are based on statistical relationships aiming to represent potential cross-basin interactions. Although our model does not allow for a detailed understanding of the underlying processes, we suggest that the mechanisms are mediated through larvae transport and/or juvenile active dispersal. To that end, the BB may be considered as a source habitat providing individuals to sinks in the northern Central Baltic Sea, where local reproduction is limited due to hydrographical constraints on early-life survival (Casini et al. 2012).

Recruitment dynamics of Baltic herring and sprat are primarily restricted by temperature-dependent processes, involving both physiological responses as well as availability of key zooplankton prey (MacKenzie and Köster 2004, Dickmann et al. 2007, Cardinale et al. 2009, Margonski et al. 2010, Lindegren et al. 2011). In addition, deep oxygen concentrations have been found important for sprat egg survival, especially in the northern GB (Nissling et al. 2003). The significant temperature effects on herring and sprat, as well as the influence of deep oxygen concentrations for sprat in the GB found in our study, may therefore reflect the conditions necessary for successful recruitment in the

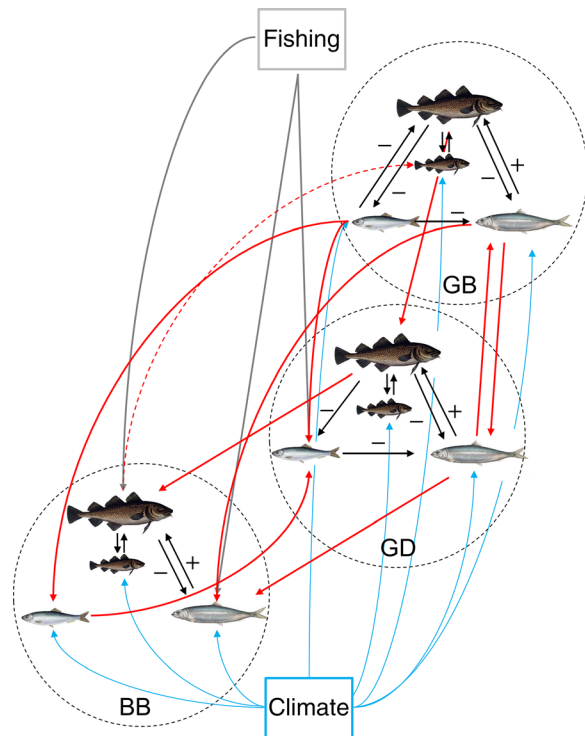


FIG. 3. A schematic view of the Central Baltic Sea metacommunity model. Black arrows represent estimated species interactions (positive [+]) and negative [-]) between cod (top of each interaction triangle), sprat (left), and herring (right). (Intraspecific interactions are not shown.) Gray and blue arrows indicate basin-specific fishing and climate effects on the dynamics of the three species, respectively. Red solid arrows represent fluxes between local fish populations in each basin of the metacommunity, while the dotted red line represents dispersal of cod larvae and/or juveniles.

different spawning basins of the Baltic Sea. In contrast to the simple dispersal pattern of Baltic cod, herring, and sprat demonstrate widespread fluxes between basins and neighboring areas, confirming previous studies (Aro 1989, Parmanne et al. 1994). The net mean fluxes estimated by our model, illustrate higher mobility of pelagic species not primarily bound by particular benthic habitats. Furthermore, they indicate a preference of herring for the southern BB, while sprat seems to

TABLE 2. Pairwise exchanges (diffusion) between basins estimated as the relative contribution of the diffusion terms for each species and basin.

Basin	Cod contribution (%)			Herring contribution (%)			Sprat contribution (%)		
	BB	GD	GB	BB	GD	GB	BB	GD	GB
BB		34 ± 5	0		40 ± 2	46 ± 2		0	13 ± 3
GD	0		12 ± 4	0		86 ± 7	45 ± 7		38 ± 4
GB	52 ± 8	0		0	37 ± 3		0	27 ± 7	

Notes: Exchanges are estimated by setting the diffusion parameters (in matrix **D**, Table 1) to zero and assessing the degree of change in log(abundance) while maintaining the remaining parameters unchanged and the covariates at their observed values during the period used for fitting. Values are mean ± SE. Pairwise (antidiagonal) differences indicate net fluxes. Zero values indicate statistically insignificant fluxes (parameters) reduced during model selection. Influx due to larvae or juvenile dispersal from BB are included for cod recruitment dynamics in GB.



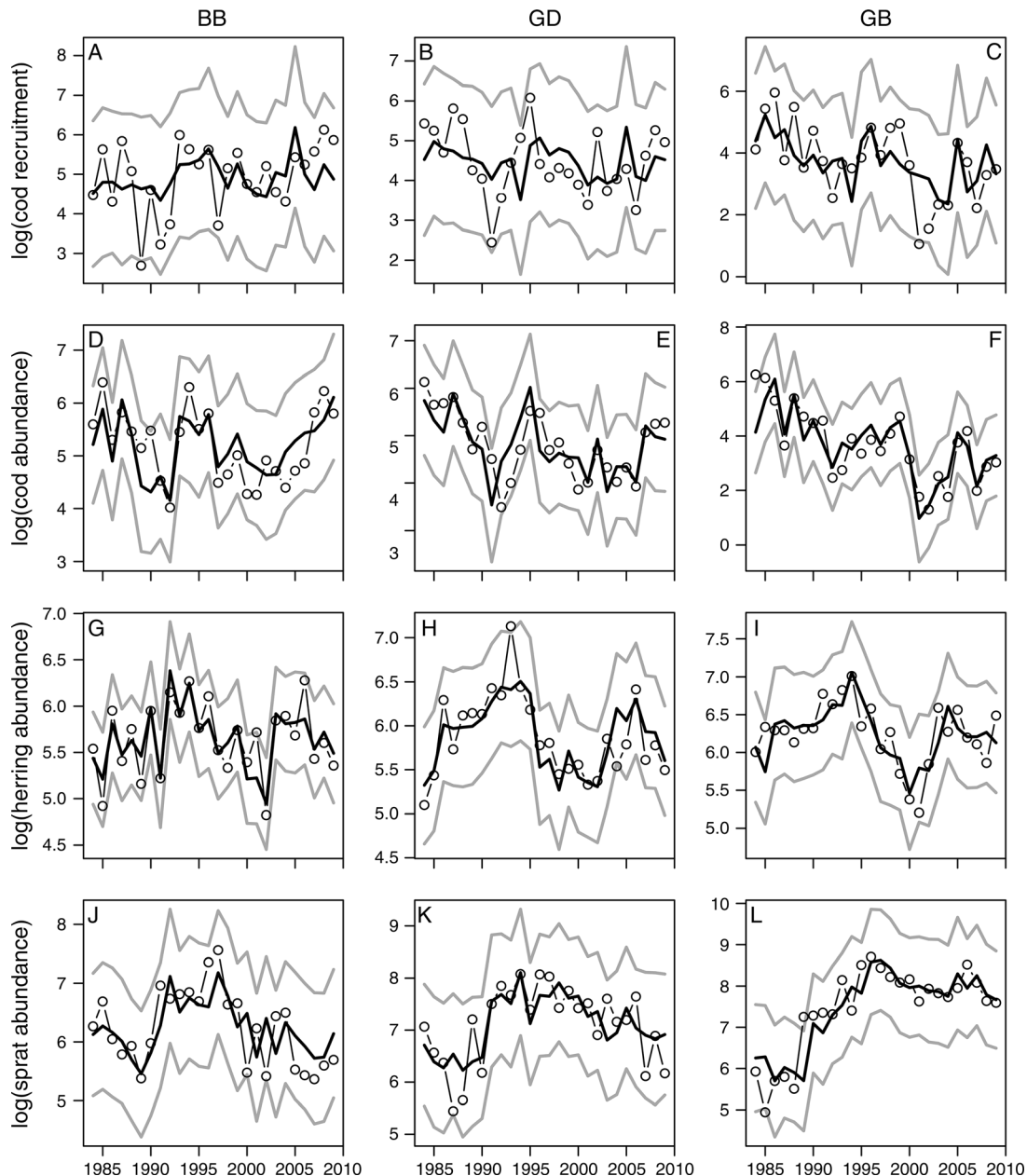


FIG. 4. Historical dynamics of (A–C) cod recruitment, and (D–F) adult cod, (G–I) herring, and (J–L) sprat, based on survey indices, i.e.,  $\log(\text{abundance})$ , from (A, D, G, J) the Bornholm Basin, (B, E, H, K) the Gdansk Deep, and (C, F, I, L) the Gotland Basin. The fitted values ( $X$  in Eq. 1 and depicted in black) represent the observed dynamics ( $Y$  in Eq. 2 and shown as circles) of the species from 1984–2009. Upper and lower 95% prediction intervals are displayed by gray lines.

increase and concentrate in the northern GB (Casini et al. 2011). Although these areas of aggregation may act as local source habitats, potential fluxes between basins and the likely existence of multiple subpopulations call for further investigations on source–sink dynamics and metapopulation structuring of Baltic herring and sprat populations.

As a result of the different patterns of aggregation, basin-specific species interactions (i.e., competition and predator–prey relations) are determined by spatiotem-

poral overlap between cod, herring, and sprat (Neuenfeldt 2002, Neuenfeldt and Beyer 2003). Therefore, competition between sprat and herring occur primarily in the GD and GB (Casini et al. 2011), likely caused by competition for *Pseudocalanus acuspes*, the key zooplankton prey also for cod larvae (Sparholt 1994, Voss et al. 2003). While significant cod predation on herring is noted in all basins, the positive foraging effect from herring to cod is the strongest in the BB, likely due to increased vertical overlap during favorable hydrograph-

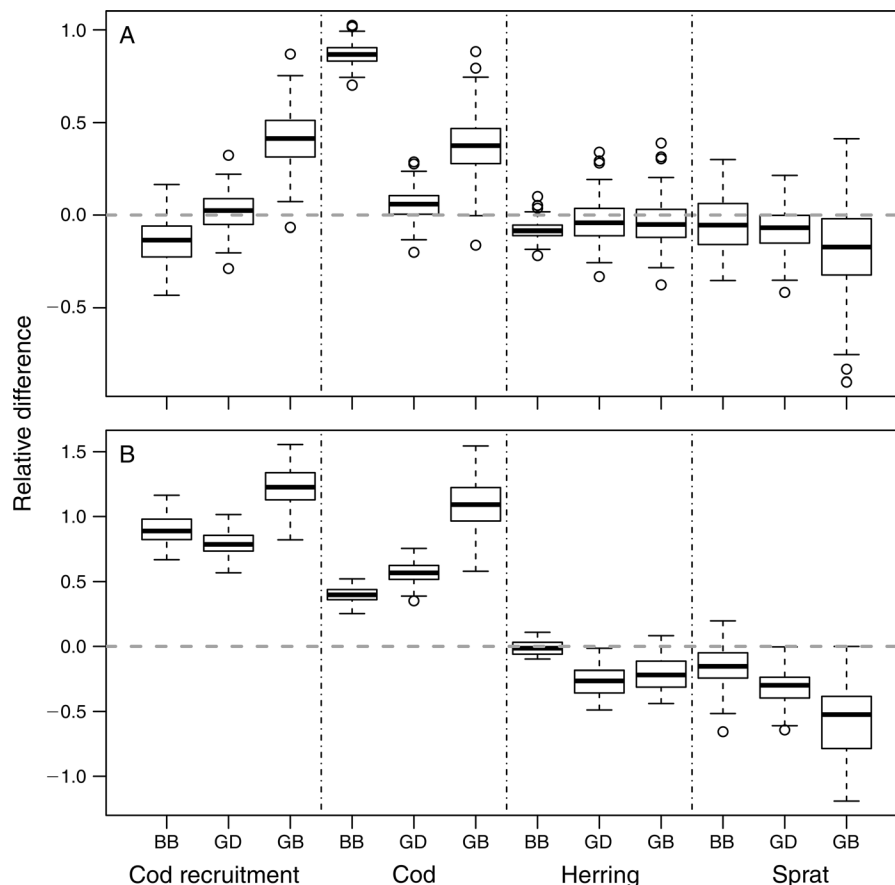


FIG. 5. Relative difference in simulated abundances of cod, herring, and sprat from the Bornholm Basin (BB), the Gdansk Deep (GD), and the Gotland Basin (GB) given a (A) fishing closure scenario for cod in the BB and (B) a scenario of favorable climate conditions for cod spawning and recruitment in all basins (defined as a 100% increase in the cod reproductive volume). Changes are calculated as the difference in  $\log(\text{abundance})$  relative to a baseline scenario (i.e., a value of 1 indicates a 100% increase) with fishing and climate variables maintained at historical levels (1982–2009) throughout a simulated 50-year period. The lines, boxes, whiskers, and circles mark the median, first and third quartiles, the corresponding 95% confidence intervals, and extreme values (outliers), respectively.

ic conditions (Neuenfeldt 2002). In addition, significant negative effects of sprat on cod are restricted to the GD and GB where the sprat population has increased the most (Casini et al. 2011). In the GB, sprat predation on cod eggs and/or competition for *Pseudocalanus acuspes* may explain the negative interaction and lack of positive foraging effect on cod (Köster and Möllmann 2000, Möllmann et al. 2003, Lindegren et al. 2010b). Intraspecific competition was detected for both sprat and herring in all the basins, whereas negative effects of sprat on herring were detected in GD and GB (Casini et al. 2011). Density dependence between adult and juvenile cod was evidenced for BB, illustrated by a negative quadratic effect of cod-spawning stock abundance on cod recruitment (Table 1), a process likely mediated by cannibalism in the area of highest cod abundance (Neuenfeldt and Köster 2000).

In order to maximize economic profit, commercial fisheries generally target high-density areas to optimize catch-per-unit effort. To that end, the largest landings of

cod and the highest proportion of stock biomass are taken from the BB. Consequently, the significant negative effect of fishing found in the BB may reflect the vulnerability to harvesting in an important source habitat (i.e., the main spawning ground), causing immediate negative consequences for recruitment in neighboring sinks, and the long-term persistence of the metapopulation as a whole, especially during unfavorable environmental conditions expected in the future (Meier et al. 2012). Likewise, the largest proportion of herring removed and the significant negative effect of fishing is found in the BB, the main area of aggregation (i.e., highest net mean flux) for the stock. On the contrary, the dominant area of the sprat fishery, as well as the significant effect of fishing, is found in the GD; hence, outside the main area of aggregation in the GB. The relatively low fishing pressure on sprat in the GB, in combination with improved hydrographic conditions for spawning and reduced spatial overlap with the declining population of cod, may explain the pronounced increase

of sprat in the GB (Casini et al. 2011). However, the steep increase in fishing pressure in GB during the latest years could have an impact on sprat population in the near future.

It is important to stress that all parameters, including species interaction coefficients and the estimated cross-basin fluxes, contain a degree of uncertainty, due to data limitations (e.g., different sampling times for cod and clupeids) and unexplained sources of variability not accounted for by the model setup, notably intra-annual shifts in distribution and predator–prey overlap (due to seasonal migration), as well as potential migration outside our study area (Aro 1989, Parmanne et al. 1994, Casini et al. 2012). Nevertheless, our model is capable of recreating the long-term dynamics of the metacommunity, representing key external and internal forcing (i.e., through climate, fishing, and species interactions) affecting the population dynamics of each species, as well as highlighting potential source–sink dynamics consistent with previous tagging and drift studies (Aro 1989, Hinrichsen et al. 2003).

Spatial management tools, involving permanent or seasonal closures of certain areas to different fishing gears, as well as more general protection measures through National Parks and other forms of Marine Protected Areas (MPAs), is a commonly advised practice within marine and fisheries management (e.g., Halpern 2003, Bellwood et al. 2004, Botsford et al. 2009). However, empirical evidence for positive outcomes of MPAs is largely limited to coral reefs (e.g., Little et al. 2009). In open marine ecosystems MPAs often show little or no effect at all (Pastoors et al. 2000), due to effort spatial reallocation and motility of the target species. As illustrated by our management simulation, efforts to decrease exploitation in the source area for cod (BB), without reallocating effort to neighboring areas, produce immediate positive effects on adult survival, as well as recruitment in the sink habitats where lower stock size and density-dependence (e.g., cannibalism) does not limit juvenile survival. We also show how, under favorable hydrographic conditions, recruitment success and population size increase throughout the metacommunity, while prey species decline in response to increased predation.

The main challenges for appropriate design of spatial management measures and MPAs rely on the understanding of ecological connectivity through migration and dispersal of adults and larvae (Botsford et al. 2009, Gruess et al. 2011). In addition, the consideration of local species interactions, fisheries effects, and stochastic environmental conditions on recruitment and survival is crucial in the design and implementation of successful management actions (West et al. 2009). Our findings provide valuable insight concerning metacommunity structuring and source–sink dynamics of marine fish populations and may serve as an important tool for developing sustainable management strategies under the

ecosystem approach to marine and fisheries management (McLeod and Leslie 2009).

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#### LITERATURE CITED

- Anderson, D. R., K. P. Burnham, and G. C. White. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture–recapture studies. *Journal of Applied Statistics* 25:263–282.
- Aps, R., U. Falk, and R. Oeberst. 1981. Morphological variability of otolith growth zones in the Baltic sprat. *Fischerie-Forschung* 19:27–30.
- Aro, E. 1989. A review of fish migration patterns in the Baltic. *Baltic Sea Fishery Resources* 190:72–96.
- Bagge, O., F. Thurow, E. Steffensen, and J. Bay. 1994. The Baltic cod. *Dana* 10:1–24.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bode, M., L. Bode, and P. R. Armsworth. 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series* 308:17–25.
- Botsford, L. W., D. R. Brumbaugh, C. Grimes, J. B. Kellner, J. Largier, M. R. O'Farrell, S. Ralston, E. Soulanille, and V. Wespestad. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries* 19:69–95.
- Botsford, L. W., C. L. Moloney, J. L. Largier, and A. Hastings. 1998. Metapopulation dynamics of meroplanktonic invertebrates: the dungeness crab (*Cancer magister*) as an example. *Canadian Special Publication of Fisheries and Aquatic Sciences* 125:295–306.
- Cardinale, M., et al. 2009. Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. *Marine Ecology Progress Series* 388:221–234.
- Casini, M., T. Blenckner, C. Moellmann, A. Gardmark, M. Lindegren, M. Llope, G. Kornilovs, M. Plikshs, and N. C. Stenseth. 2012. Predator transitory spillover induces trophic cascades in ecological sinks. *Proceedings of the National Academy of Sciences USA* 109:8185–8189.
- Casini, M., G. Kornilovs, M. Cardinale, C. Möllmann, W. Grygiel, P. Jonsson, T. Raid, J. Flinkman, and V. Feldman. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. *Population Ecology* 53:511–523.
- Dias, P. C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11:326–330.
- Dickmann, M., C. Möllmann, and R. Voss. 2007. Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. *Marine Ecology Progress Series* 342:277–289.

- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Grimm, V., K. Reise, and M. Strasser. 2003. Marine metapopulations: a useful concept? *Helgoland Marine Research* 56:222–228.
- Gruess, A., D. M. Kaplan, S. Guenette, C. M. Roberts, and L. W. Botsford. 2011. Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* 144:692–702.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13(Supplement):S117–S137.
- Hampton, S. E., M. D. Scheuerell, and D. E. Schindler. 2006. Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. *Limnology and Oceanography* 51:2042–2051.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Harvey, A. C. 1989. *Forecasting, structural time series models, and the Kalman filter*. Cambridge University Press, Cambridge, UK.
- Hinrichsen, H. H., U. Bottcher, F. W. Köster, A. Lehmann, and M. A. St John. 2003. Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. *Journal of Sea Research* 49:187–201.
- Hjermann, D. O., N. C. Stenseth, and G. Ottersen. 2004. The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1747–1755.
- Holt, R. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181–208.
- International Council for the Exploration of the Sea (ICES). 2010. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 15–22 April 2010. ICES, Copenhagen, Denmark.
- Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. Estimating community stability and ecological interactions from time series data. *Ecological Monographs* 73:301–330.
- James, M. K., P. R. Armsworth, L. B. Mason, and L. Bode. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proceedings of the Royal Society B* 269:2079–2086.
- Keddy, P. 1981. Experimental demography of the sand dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology* 69:615–630.
- Köster, F. W., and C. Möllmann. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science* 57:310–323.
- Köster, F. W., et al. 2005. Baltic cod recruitment: the impact of climate variability on key processes. *ICES Journal of Marine Science* 62:1408–1425.
- Köster, F. W., C. Möllmann, S. Neuenfeldt, M. A. St John, M. Plikshs, and R. Voss. 2001. Developing Baltic cod recruitment models: resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1516–1533.
- Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131–140.
- Lehmann, A., W. Krauss, and H. H. Hinrichsen. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus Series A Dynamic Meteorology and Oceanography* 54:299–316.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Lindegren, M., C. Möllmann, and L. Hansson. 2010b. Biomanipulation: a tool in marine ecosystem management and restoration? *Ecological Applications* 20:2237–2248.
- Lindegren, M., C. Möllmann, A. Nielsen, K. Brander, B. R. MacKenzie, and N. C. Stenseth. 2010a. Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society B* 277:2121–2130.
- Lindegren, M., C. Möllmann, A. Nielsen, and N. C. Stenseth. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences USA* 106:14722–14727.
- Lindegren, M., O. Östman, and A. Gårdmark. 2011. Interacting trophic forcing and the population dynamics of herring. *Ecology* 92:1407–1413.
- Little, L. R., A. E. Punt, B. D. Mapstone, G. A. Begg, B. Goldman, and N. Ellis. 2009. Different responses to area closures and effort controls for sedentary and migratory harvested species in a multispecies coral reef line fishery. *ICES Journal of Marine Science* 66:1931–1941.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. University of Washington Press, Seattle, Washington, USA.
- MacKenzie, B. R., M. Eero, and H. Ojaveer. 2011. Could seals prevent cod recovery in the Baltic Sea? *PLoS ONE* 6:e18998.
- MacKenzie, B. R., H. H. Hinrichsen, M. Plikshs, K. Wieland, and A. S. Zezera. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. *Marine Ecology Progress Series* 193:143–156.
- MacKenzie, B. R., and F. W. Köster. 2004. Fish production and climate: sprat in the Baltic Sea. *Ecology* 85:784–794.
- Margonski, P., S. Hansson, M. Tomczak, and R. Grzebielec. 2010. Climate influence on Baltic cod, sprat, and herring stock: recruitment relationships. *Progress in Oceanography* 57:277–288.
- Matthäus, W., and H. Franck. 1992. Characteristics of major Baltic inflows: a statistical analysis. *Continental Shelf Research* 12:1375–1400.
- May, R. M. 1972. Will a large, complex system be stable? *Nature* 238:413–414.
- McLeod, K., and H. Leslie. 2009. *Ecosystem-based management for the oceans*. Island Press, Washington, D.C., USA.
- McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* 7:297–329.
- Meier, H. E. M., R. Hordoir, H. C. Andersson, C. Dieterich, K. Eilola, B. G. Gustafsson, A. Hoglund, and S. Schimanke. 2012. Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. *Climate Dynamics* 39:2421–2441.
- Möllmann, C., R. Diekmann, B. Müller-Karulis, G. Kornilovs, M. Plikshs, and P. Axe. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biology* 15:1377–1393.
- Möllmann, C., G. Kornilovs, M. Fetter, F. W. Köster, and H. H. Hinrichsen. 2003. The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fisheries Oceanography* 12:360–368.



- Neuenfeldt, S. 2002. The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. *Fisheries Oceanography* 11:11–17.
- Neuenfeldt, S., and J. E. Beyer. 2003. Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. *Journal of fish biology* 62:168–183.
- Neuenfeldt, S., and F. W. Köster. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES Journal of Marine Science* 57:300–309.
- Nielsen, E. E., P. Grønkaer, D. Meldrup, and H. Paulsen. 2005. Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:2219–2225.
- Nissling, A., A. Muller, and H. H. Hinrichsen. 2003. Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. *Journal of Fish Biology* 63:280–299.
- Ojaveer, E. 1981. Fish fauna of the Baltic. Pages 275–292 in A. Voipio, editor. *The Baltic Sea*. Elsevier Oceanography Series 30. Elsevier Scientific Publishing, New York, New York, USA.
- Ojaveer, E. 1989. Population structure of pelagic fishes in the Baltic. *Baltic Sea Fishery Resources* 190:17–21.
- Ojaveer, E., and M. Kalejs. 2010. Ecology and long-term forecasting of sprat (*Sprattus sprattus balticus*) stock in the Baltic Sea: a review. *Reviews in Fish Biology and Fisheries* 20:203–217.
- Parmanne, R., O. Rechlin, and B. Sjöstrand. 1994. Status and future of herring and sprat stocks in the Baltic Sea. *Dana* 10:29–59.
- Pastors, M. A., A. D. Rijnsdorp, and F. A. Van Beek. 2000. Effects of a partially closed area in the North Sea on stock development of plaice. *ICES Journal of Marine Science* 57:1014–1022.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, London, UK.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- R Development Core Team. 2010. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- Sparholt, H. 1994. Fish species interactions in the Baltic Sea. *Dana* 10:131–162.
- Sparholt, H., and J. Tomkiewicz. 2000. A robust method for compiling trawl survey data used in the assessment of central Baltic cod (*Gadus morhua* L.). *Archive of Fishery and Marine Research* 48:125–151.
- Stein, M., and V. A. Borovkov. 2004. Greenland cod (*Gadus morhua*): modeling recruitment variation during the second half of the 20th century. *Fisheries Oceanography* 13:111–120.
- Svedäng, H. 2003. The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources. *ICES Journal of Marine Science* 60:23–31.
- Tittler, R., L. Fahrig, and M. A. Villard. 2006. Evidence of large-scale source–sink dynamics and long-distance dispersal among wood thrush populations. *Ecology* 87:3029–3036.
- Tomczak, M. T., S. Niiranen, O. Hjerne, and T. Blenckner. 2012. Ecosystem flow dynamics in the Baltic proper: using a multi-trophic dataset as a basis for food web modelling. *Ecological Modelling* 230:123–147.
- Tomkiewicz, J., M. Eriksson, T. Baranova, V. Feldman, and H. Müller. 1997. Maturity ogives and sex ratios for Baltic cod: establishment of a database and time series. *ICES CM 1997/CC*. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Voss, R., F. Köster, and M. Dickmann. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea RID A-6113-2011. *Fisheries Research* 63:97–111.
- West, C. D., C. Dytham, D. Righton, and J. W. Pitchford. 2009. Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. *ICES Journal of Marine Science* 66:1919–1930.
- Wilson, D. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73:1984–2000.
- Wright, P. J., F. C. Neat, F. M. Gibb, I. M. Gibb, and H. Thordarson. 2006. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology* 69:181–199.

## SUPPLEMENTAL MATERIAL

### Appendix

Tables and figures showing the model selection routine, validation exercises, residual diagnostics, and details regarding the input data used during model fitting (*Ecological Archives* A024-208-A1).