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Reference state, structure, regime shifts, and regulatory drivers in a coastal sea over the last century: The Central Baltic Sea case

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Abstract

The occurrence of regime shifts in marine ecosystems has important implications for environmental legislation that requires setting reference levels and targets of quantitative restoration outcomes. The Baltic Sea ecosystem has undergone large changes in the 20th century related to anthropogenic pressures and climate variability, which have caused ecosystem reorganization. Here, we compiled historical information and identified relationships in our dataset using multivariate statistics and modeling across 31 biotic and abiotic variables from 1925 to 2005 in the Central Baltic Sea. We identified a series of ecosystem regime shifts in the 1930s, 1970s, and at the end of the 1980s/beginning of the 1990s. In the long term, the Central Baltic Sea showed a regime shift from a benthic to pelagic-dominated state. Historically, benthic components played a significant role in trophic transfer, while in the more recent productive system pelagic–benthic coupling was weak and pelagic components dominated. Our analysis shows that for the entire time period, productivity, climate, and hydrography mainly affected the functioning of the food web, whereas fishing became important more recently. Eutrophication had far-reaching direct and indirect impacts from a long-term perspective and changed not only the trophic state of the system but also affected higher trophic levels. Our study also suggests a switch in regulatory drivers from salinity to oxygen. The "reference ecosystem" identified in our analysis may guide the establishment of an ecosystem state baseline and threshold values for ecosystem state indicators of the Central Baltic Sea.

Marine ecosystems worldwide are becoming increasingly affected by climate change and anthropogenic pressures. Such cumulative pressures, including a combination of eutrophication, overfishing, and climate, can in some cases lead to significant changes in ecosystem structure and function—a so-called regime shift (Hempson et al. 2018; Rocha et al. 2018). Here, we followed a pragmatic definition of marine regime shifts, considering a regime as a representation of an ecosystem state and regime shifts as "low-frequency, high-amplitude changes in aquatic systems that may be especially pronounced in biological variables and propagate through several trophic levels" (Collie et al. 2004). Depending on the type of shift, ecosystem scale, and the time factor (decadal or more, Scheffer et al. 2001; Andersen et al. 2009), some ecosystems respond with hysteresis, that is, they return to their original state along a different trajectory (Collie et al. 2004) while others may change irreversibly over longer time scales. While the operational definitions of regime shifts are subject to ongoing debate (Biggs et al. 2015; Conversi et al. 2015), it is clear that knowledge regarding the history, magnitude, and drivers of past change is essential for evaluating the current state of marine ecosystems or projecting future states.

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Additional Supporting Information may be found in the online version of this article.

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Special Issue: Nonlinear dynamics, resilience, and regime shifts in aquatic communities and ecosystems

Regime shifts have been reported for many marine ecosystems and in different contexts (Yletyinen et al. 2016; Vasilakopoulos et al. 2017; Nayak and Armitage 2018). In the systems adjacent to our study area, the Central Baltic Sea (Fig. 1), regime shifts have been detected in the North Sea in the late 1980s (Alheit et al. 2005), in the Kattegat in the late 1980s and the mid-1990s (Lindegren et al. 2012), and in some Baltic coastal ecosystems (Tomczak et al. 2013*a*; Olsson et al. 2015).

The Baltic Sea (Fig. 1) is a semi-enclosed, eutrophic brackish sea with strong physical gradients in temperature and salinity (Leppäranta and Myrberg 2009), low biodiversity (Feistel et al. 2008), and expanding hypoxia (Reusch et al. 2018). Low salinity is physiologically stressful for most higher trophic level organisms (Schubert et al. 2017); therefore, variations in hydrographical conditions may have a substantial impact on the Baltic biota. Intermittent inflows of saline water through the narrow Danish straits (Fig. 1) determine water column salinity and stratification and together with nutrient inputs, they determine deep-water oxygen conditions (Carstensen et al. 2014). Abiotic and trophic conditions have profoundly changed during the last century (Savchuk et al. 2008; Gustafsson et al. 2012). At the beginning of the 20th century, deep waters were largely oxygenated (Gustafsson et al. 2012), with large volumes of water suitable for cod reproduction (Savchuk et al. 2008; Gustafsson et al. 2012). The drastic increase in nutrient use on land, mainly fertilizers in agriculture (Hong et al. 2012; McCrackin et al. 2018), led to an increased transport of nutrients, stimulating primary production and consequently increasing sedimentation and oxygen consumption in the deep waters, which is associated with hypoxia (Gustafsson et al. 2012). The Baltic food web has experienced severe changes in the 20th century, including a well-described regime shift, trophic cascade, and food-web reorganization due to climate and fisheries impacts (Casini et al. 2009; Möllmann et al. 2009). At the beginning of the century, the catches and biomass of cod, herring, and sprat were low, but rapidly increased prior to the 1950s and again around the 1970s. Cod catches collapsed after the 1980s due to overfishing and unfavorable environmental conditions, while pelagic clupeid fisheries flourished (Reusch et al. 2018). In contrast, flatfish biomass peaked in 1920–1930 and

Fig. 1. The Central Baltic Sea (blue on main map), consisting of the Bornholm and Gotland basins, takes up the main water volume of the Baltic Sea. The Baltic Sea is located in Northern Europe (*see* map insert) and is connected to the world oceans through the shallow Danish straits (*see* circle on main map).

collapsed shortly after (Hammer et al. 2008) (*see* Supplementary Information S1). In the early 20th century, the dominant top predators in the Baltic were the marine mammals gray, ringed, and common seals (*Halichoerus grypus*, *Phoca hispida*, and *Phoca vitulina*) (Harding and Härkönen 1999; Österblom et al. 2007).

Marine ecology, conservation, and management have mostly focused on the last 20–50 yr of scientific monitoring data and rarely provide historical reference points that go back to the beginning of exploitation and other human impacts (Lotze et al. 2011; Duarte et al. 2020). Long-term reconstructions can help define reference conditions, or baselines against which to gauge change, as guidelines for setting management targets within various environmental policies, such as the EU Marine Strategy Framework Directive and the US Clean Water Act. Such reconstructions can be gleaned from a variety of sources, including paleoecological records, archeological findings, historical documents, long-term ecological data, and modeling (Samhouri et al. 2011).

This is especially important in marine systems where resource exploitation and human impacts have had noticeable effects over long time periods (e.g., since the Middle Ages). One example of such a system is the Baltic Sea (MacKenzie et al. 2007; Elmgren et al. 2015). Möllmann et al. (2009) identified regime shifts in the Central Baltic Sea ecosystem based on a dataset that described hydrographic conditions, nutrient and phytoplankton concentrations, and fish stocks, but their study was limited to three recent decades (1974–2005). Studies covering longer time periods (> 50 yr) are available only for separate ecosystem components, such as seals (Harding and Härkönen 1999), fish and fisheries (Eero et al. 2007*b*), nutrient and oxygen conditions (Gustafsson et al. 2012), and hydrography (Feistel et al. 2008). Food-web modeling frameworks exist for the Baltic Sea, covering different spatial extents from the very local and coastal (Tomczak et al. 2009) to the whole Baltic Sea (Bossier et al. 2021). Most food-web models span the mid-1970s to the present and some include future scenarios (Niiranen et al. 2013). To date, only Österblom et al. (2007) has addressed the dynamics of the modeled food web throughout the 20th century and suggested a shift at higher trophic levels from seal to cod and cod to sprat dominated periods; however, they did not take into account flatfish and benthic components. In that context, it is clear that there is a knowledge gap regarding the Baltic ecosystem at the holistic level and in the long-term perspective, since previous studies have not addressed (1) the entire food web and all trophic levels but instead focused mainly on the pelagic domain and (2) time periods reaching further back than the 1960s/1970s. The lack of monitoring data is often the reason for this gap; however, an increasing number of time series reconstructions and modeling results can now be used to address this.

To fill some of the knowledge gaps, we used a unique, almost century-long time series dataset covering practically all trophic levels, changes in pelagic–benthic coupling, and the main pressures (salinity and temperature fluctuations, eutrophication, and fishing) in the Baltic Sea ecosystem. To avoid gaps in observations, we used simulated time series for all ecosystem components, either from a well-validated biogeochemical model or from dedicated models of benthic and zooplankton components and reconstructed fish and seal populations. Similar to Möllmann et al. (2009) we applied principal component analysis (PCA) to identify regime shifts in ecosystem structure, followed by general additive modeling (GAM) to identify drivers of change in biological ecosystem components. Even though simulated time series are deterministically related to the forcing functions of the underlying models and are thus also partially correlated with each other, we show that by treating PCA and GAMs as metamodel tools for extracting the most influential processes and dominant patterns in ecosystem changes, important food-web processes and drivers can still be identified.

The present study demonstrates that despite data limitations, our analysis is useful for understanding and explaining the long-term dynamics of a large marine ecosystem, providing hypotheses regarding food-web changes and restructuring regime shifts, and setting a "reference ecosystem state" in the context of ecosystem-based management. In particular, we aimed to (1) identify abrupt changes in ecosystem structure over 80 yr, (2) identify major natural and anthropogenic drivers, and (3) describe the regulatory mechanisms leading to these changes.

Materials and methods

Long-term data

Here, we focused on the Central Baltic Sea (Fig. 1), as it includes the central deep areas with high vertical gradients, covering most of the Baltic Sea water volume. We collected time series data for important Central Baltic Sea ecosystem components covering the period 1925–2005, the maximum period for which homogeneous fish stock reconstructions are available. All time series were simulated using well-validated component models from previous studies or designed for this study. Temperature, salinity, oxygen, nutrient, phytoplankton, and two zooplankton variables were derived from the BALTSEM biogeochemical model (Gustafsson et al. 2012); the key zooplankton species *Pseudocalanus acuspes* and two macrobenthos species were simulated by population models forced with BALTSEM input (Timmermann et al. 2012; Otto et al. 2014, 2020). For fish stock dynamics, reconstructions based on catches were used.

We aimed to keep the structure of our dataset similar to the Central Baltic Sea regime shift study by Möllmann et al. (2009). Their study covered the time period between 1974 and 2005 and applied PCA to summarize ecosystem structure and identify regime shifts in the two dominant components. The authors selected time series that were representative of hydrographic conditions, nutrients, phyto- and zooplankton, and commercial

fish stocks. The number of time series was balanced to represent abiotic conditions as well as all trophic levels, while avoiding over-representing single ecosystem components (e.g., a trophic group or an abiotic driver). Similarly, we described the biotic part of the central Baltic ecosystem by key food-web components within fish, zoo-, and phytoplankton communities, and additionally included benthos and flatfish data. Thus, our final dataset contained 10 biological variables distributed over three fish stocks, three groups of zooplankton, two macrozoobenthos groups, and phytoplankton biomass during spring and summer or annually (Fig. 2; for details, *see* Supplementary Information S1).

We treated the abiotic time series as potential drivers of change in biotic variables. Abiotic time series were selected to describe climatic drivers and human pressures based on general knowledge of controlling factors in the Baltic Sea, similar as in Möllmann et al. (2009). The selected driver time series (Fig. 3 and Table S1 in Supplementary Information S1) consisted of eight nutrient and seven hydro-climatic variables together with three fisheries-related and one top-down predator (seals) pressures. Detailed information on previously unpublished modeled time series is presented in Supplementary Information S2–S4.

Environmental and anthropogenic drivers

We used modeled concentrations of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) derived from the BALTSEM biogeochemical model (Savchuk et al. 2008; Gustafsson et al. 2012) in surface and deeper water layers to describe the nutrient reservoir available on annual and longer time scales. Spring and summer temperatures were chosen from the surface and intermediate layers that are most influenced by atmospheric conditions; salinity from the surface layer affected by runoff and precipitation; and —as an indicator of major Baltic inflow events (Matthäus and Franck 1992)—from the bottom layer of the Gotland Basin. Additional modeled oxygen and salinity variables characterize deep-water conditions that are important for the recruitment of cod (Margonski et al. 2010) and flounder (Ustups et al. 2013) as well as for the living conditions of benthic species (Timmermann et al. 2012) and *P. acuspes* (Möllmann et al. 2003). Fishing pressures were originally represented by historical landings for sprat and flounder (Hammer et al. 2008) and cod fishing mortality (Eero et al. 2008). Thus, to better represent the fishing effect on fish stocks, the yield per reconstructed biomass was calculated from landings (*see* Fig. 2). Reconstructed gray seal biomass (Harding and Härkönen 1999) was treated as a pressure variable to investigate the effect of changes in predation on fishes.

Time series of low trophic levels

Phytoplankton were represented using the results of the biogeochemical model simulations from BALTSEM. The spring and summer phytoplankton biomass was divided into diatoms, which dominate the spring bloom, and the remaining phytoplankton, representing mainly dinoflagellates, flagellates, and cyanobacteria, to describe the summer communities.

Zooplankton were represented by the key species *P. acuspes* and the total zooplankton biomass. Long-term spring and summer biomass of *Pseudocalanus* sp. were reconstructed for the Gotland Basin using the model approach by Otto et al. (2014, 2020) and validated with historical data (Driver 1907; Kraefft 1908), whereas total zooplankton biomass was derived from BALTSEM for spring and summer. The BALTSEM model treats zooplankton as a lumped variable that incorporates all size classes of heterotrophic grazers on detritus and phytoplankton (Gustafsson et al. 2012). We used the simulated biomass in the upper part of the water column (0–60 m) to represent small copepod species, such as *Acartia* spp. and *Temora* spp.

Long-term benthos observations are very sparse, and only a few data points exist far back in time. Therefore, we used the modeling approach proposed by Timmermann et al. (2012) to reconstruct the dynamics of benthic organisms. Their physiological benthic fauna model simulates the growth of benthic groups in response to food availability, combined with an oxygen-dependent mortality term. The model was calibrated with data from benthic sampling sites collected between 1920 and 2005 (*see* Supplementary Information S3) using food and oxygen concentrations derived from BALTSEM as model forcing. As a proxy for benthic communities, we used *Macoma* (*Macoma baltica*) and suspension feeders (*Astarte borealis*, *Arctica islandica*, and *Mytilus* sp.) from the long-term simulation output (1925–2005) for the Bornholm Basin above the halocline. Bivalves, like *Macoma* sp., are the main diet component of Baltic flounder but do not significantly contribute to the diet of cod (Haase et al. 2020).

Time series of high trophic levels

High trophic levels represented by fish biomass are reconstructed based on the best available knowledge on population dynamics, biological processes, comprehensive compilations of fisheries data, statistics verified with independent survey data and historical observations (Eero et al. 2008; Hammer et al. 2008), and in the case of flounder, published modeling approaches (Horbowy and Tomczak 2017). Fish stocks are represented by the commercially most important species: cod (*Gadus morhua*) (Eero et al. 2008), sprat (*Sprattus sprattus*) (Eero 2012), and flounder (*Platichthys flesus*) (*see* Table S1 in Supplementary Information S1 and S4). The reconstructed biomasses were used to describe stock dynamics, while fishing ratio (yield per biomass) and reconstructed landings (Hammer et al. 2008) were chosen to represent fishing pressure (*see* Supplementary Information S1). A long-term herring (*Clupea harengus*) time series (Thurow 1997) was not used because the stepwise character of the reconstructed biomass caused artificial regime shifts in the analysis.

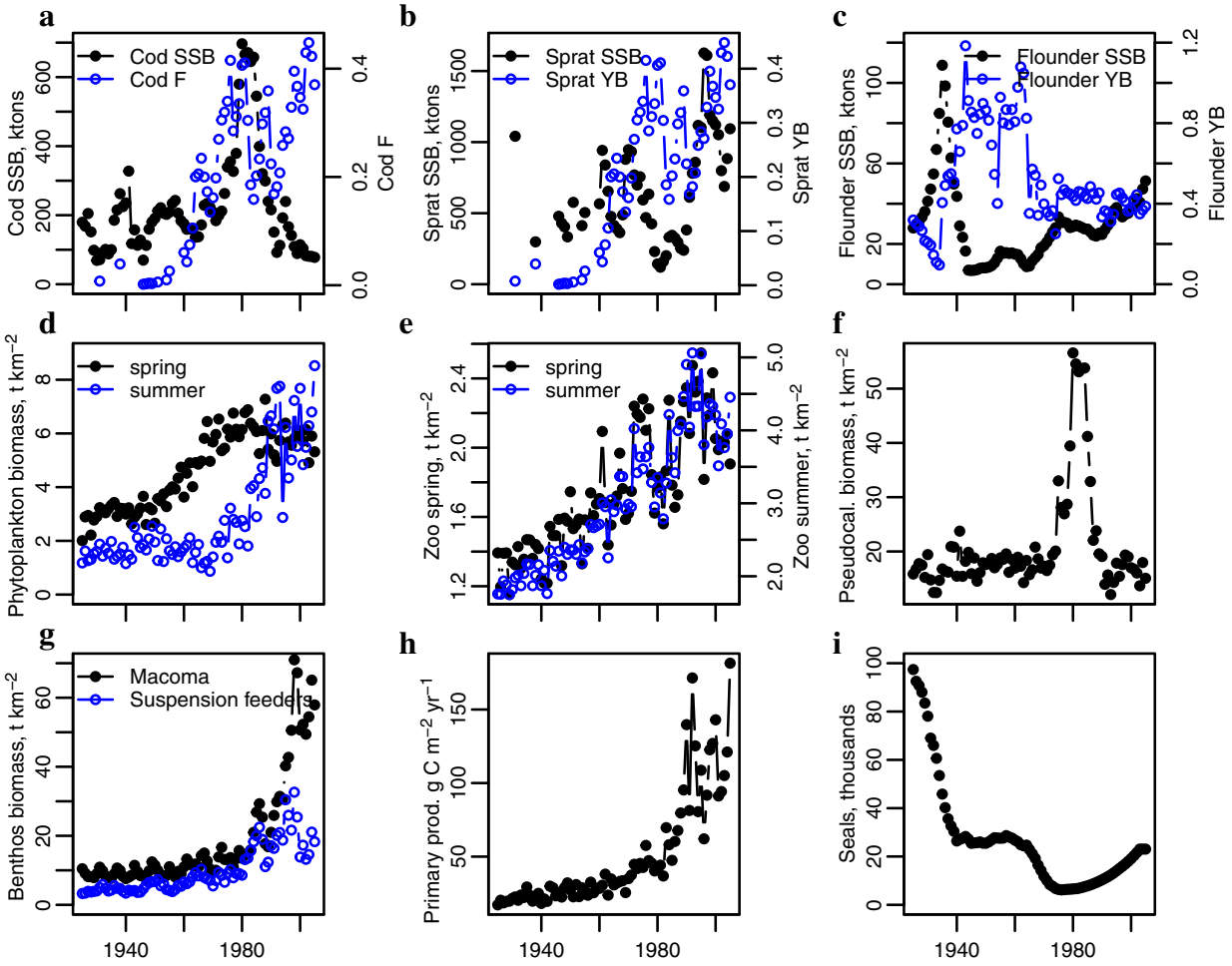

Fig. 2. Time series (1925–2005) of biological state variables and direct pressures. (**a**–**c**) Spawning stock biomass (SSB) of major fish stocks and their fishing pressure (F, fishing mortality; YB, yield per biomass). (**d**–**g**) Primary and secondary producers: phytoplankton (**d**), zooplankton (**e**), *Pseudocalanus* (**f**), and macrozoobenthos (**g**). (**h**) Long-term increase in primary production. (**i**) The number of seals. For a detailed description, *see* Supplementary Information S1.

The compiled time series differed in their spatial dimensions. In particular, fish stocks are generally assessed in terms of the areas encompassing their geographical distribution or the area covered by assessment models. Hence, cod in our dataset was representative of the Eastern Baltic cod stock (Eero et al. 2008), whereas sprat and flounder stock biomass referred to the entire Baltic Sea (Eero 2012) (*see* Supplementary Information S1). Despite this, all stocks employed in this analysis represent the major fish stocks in the Central Baltic Sea.

Our analysis focused on the Central Baltic Sea (Fig. 1), an area comprising the Bornholm and Gotland basins, excluding the big gulfs (Gulf of Bothnia, Gulf of Finland, and Gulf of Riga). It is important to note that data coverage is not perfect for long-term historical periods; often information is not available as data per se, i.e., collected during surveys, but rather as reconstructions based on the best available knowledge and modeling (i.e., biomasses or environmental time series) or, in the best case, compilations of historical time series from different sources (i.e., catches).

Admittedly, our assessment relies on long-term data series that have issues in terms of gaps in the data, coverage, and data quality, especially for time series data before the 1970s. Therefore, where necessary, we used modeled time series data that are well validated by historical information (Savchuk et al. 2008). Most importantly, the modeled time series for biogeochemical variables (primary production, nutrient, and bottom oxygen concentration) as well as major zooplankton and benthos species covered the observed changes in those variables, i.e., they reasonably reflected the spatiotemporal changes in hydrography and nutrient and oxygen concentrations. The modeled hydrographical variables (temperature and salinity) can be regarded as well justified because model performance is best for these variables (Gustafsson et al. 2012). The BALTSEM model has been extensively validated against field data and other models (Eilola et al. 2011) and has been used to hindcast the biogeochemical state of the Baltic Sea from 1850 to the present (Gustafsson et al. 2012). The modeled long-term dynamics in primary production and phytoplankton biomass, together with

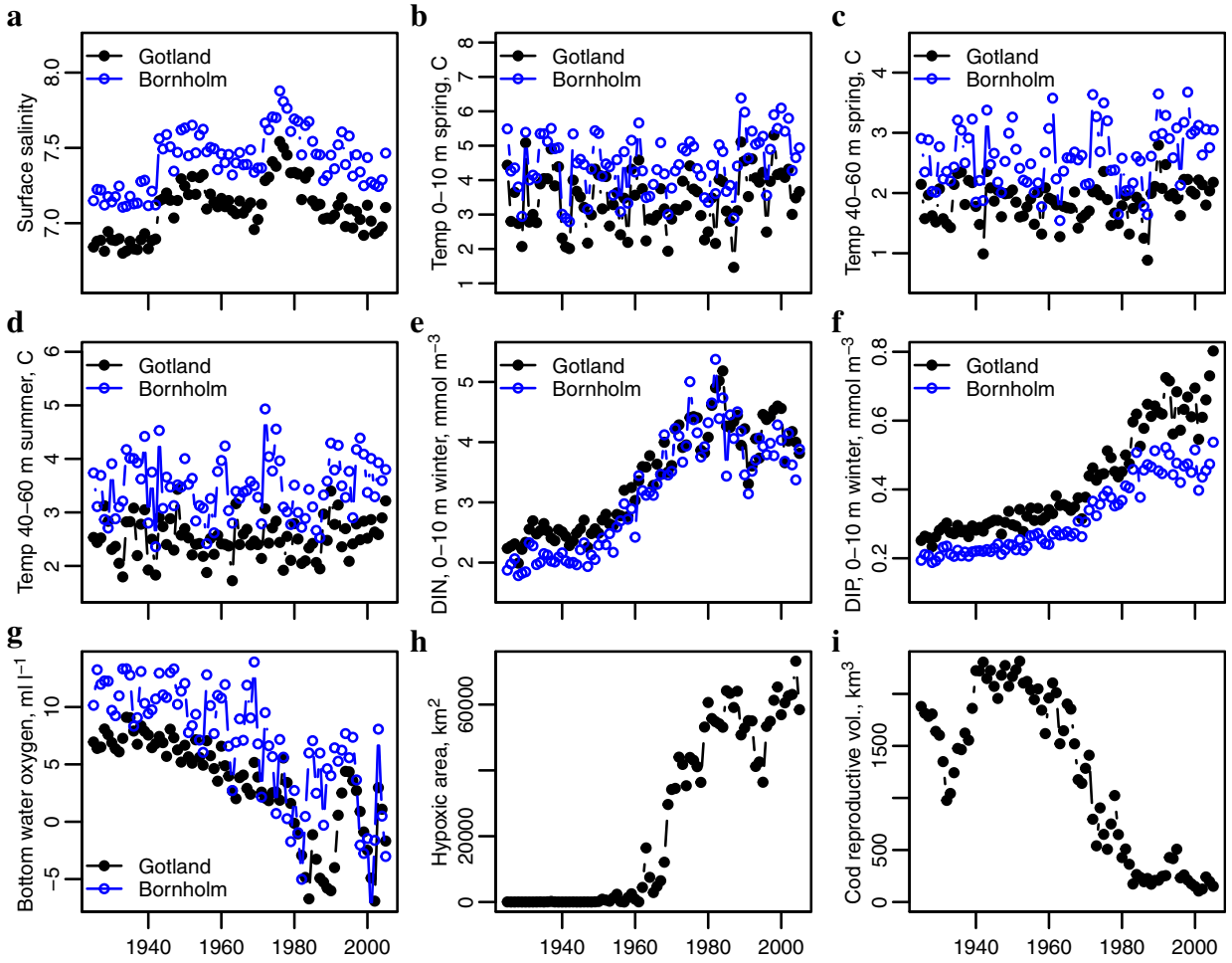

Fig. 3. Time series (1925–2005) of key environmental drivers. (**a**–**d**) Salinity and temperature in the Gotland and Bornholm basins: surface salinity (**a**); temperatures at the surface (**b**); and temperatures between the thermocline and halocline in spring (**c**) and summer (**d**). (**e**, **f**) Nutrient concentrations of DIN (**e**) and DIP (**f**). (**g**–**i**) Oxygen-related parameters: bottom oxygen concentration in the Gotland and Bornholm basins (**g**); hypoxic bottom area (**h**) and water volume suitable for cod reproduction (cod reproductive volume) (**i**). For a detailed description, *see* Supplementary Information S1.

oxygen loss below the halocline, have also been confirmed by other Baltic Sea biogeochemical models (Meier et al. 2012). Our estimates of benthos and zooplankton biomass as food for higher trophic levels are reasonably described at the level of available historical information. Model approaches used to hindcast long-term changes in individual food-web components include up-to-date understanding of ecological processes and relationships (Savchuk et al. 2012; Timmermann et al. 2012; Otto et al. 2014). *Pseudocalanus* sp. and benthic fauna time series were derived from published models applied to long time scales (Timmermann et al. 2012; Otto et al. 2014), with forcing from the BALTSEM biogeochemical model.

Statistical analysis of long-term ecosystem dynamics

Principal component analysis

To describe the most important modes of variability in the time series, we applied PCA as a multivariate technique to allow for direct comparisons with previous analyses (Möllmann et al. 2009). PCA is a common tool used in exploratory data analysis for better visualization of the variation present in a multivariate dataset by transforming linearly correlated variables into uncorrelated variables. Any correlation present in the dataset indicates redundancy of information, which can be reduced in the visualization. The method is purely correlative and does not allow any inference on causality. Any correlation between the input time series is caused by similar temporal patterns, such as trends, cycles, or autocorrelation. Whether these are caused by intrinsic sources, direct linkages, or a common driver cannot be inferred. In addition, if the input variables are modeled time series, as in our case, correlations between time series are likely to reflect similar configurations of the underlying models. In this study, we used PCA as a tool for dimensionality reduction and visualization. Similar PCA-based analyses have been widely employed for marine ecosystems and have

been applied as integrated trend assessments for the Baltic Sea (ICES 2008; Möllmann et al. 2009) and other areas (Lindegren et al. 2012; Heymans and Tomczak 2016). While applying this methodology, we were aware of the concerns such as the linearity of PCA and autocorrelation in reconstructed data, as described by Planque and Arneberg (2018), and we followed the method guidelines described in a recent ICES Workshop on integrated trend analyses in support to integrated ecosystem assessment (WKINTRA) (ICES 2018).

We first applied PCA on the full dataset of 10 biological variables for the entire time period (Table S1 in Supplementary Information S1), which was then repeated for each identified ecological regime period using two different change point detection methods. Because most of our data are model-based (*see* Table S1 in Supplementary Information S1), there were no missing values, except for sprat biomass (Eero 2012) whose missing values were replaced by 2 yr averages and in the case of longer gaps, by constant average values from the closest 3-yr period. Only 26 missing observations were replaced out of a total of 8000 data points. To improve the linearity between variables and reduce the relationship between the mean and variance, all biological variables were $\ln(x + 1)$ transformed. All PCAs were conducted based on the correlation matrix, after which the first factorial plane was visualized.

Regime shift identification

We employed two change point detection methods, a sequential *t*-test (STARS) (Rodionov 2004, 2006) and Bayesian analysis of the change point (bcp) (Erdman and Emerson 2007), to identify inflation points in the scores of the first two principal components (PCs). STARS was applied to detect sudden changes in the system by identifying abrupt changes in the PC scores (Diekmann et al. 2012). Because of the PCA limitations described above, we additionally applied STARS to the individual time series to identify synchronicity in the shifts across ecosystem components. To avoid false shifts caused by gradual linear increases, scores were detrended using linear functions, and STARS was performed on the residuals. No pre-whitening procedure was used to remove the red noise component from the time series (Rodionov and Overland 2005). The significance level (α) was set to 0.05 and the cutoff length (l) was set to 5 yr. The cutoff length defines the minimum regime length to be identified, but high magnitude shifts can still be detected for shorter periods. Huber's weight parameter, which controls the identification and weights assigned to outliers, was set to 3.

We also applied the bcp algorithm as an alternative method for detecting sudden changes in the PCs. Bcp estimates the probability of a change point at each location in a sequence. The probability level for detecting changes was set to 0.8. We assumed that change points detected by both STARS and bcp in the same or consecutive years should be treated as potential regime shifts in the ecosystem.

Identifying drivers of ecosystem change

We used generalized additive models (GAMs) (Hastie and Tibshirani 1990) to test for relationships between biotic variables and a set of pressure variables representing atmospheric and hydrographic conditions, nutrient availability, and fishing pressure. GAM is a nonparametric regression method that allows for greater flexibility in modeling non-normally distributed data and nonlinear relationships between the response and predictor variables (Hastie and Tibshirani 1990). GAMs are thus ideally suited for considering nonlinearities in ecological modeling.

Our dataset consisted of modeled biotic variables and a time series reconstructed from observations. The modeled biotic variables (phytoplankton, benthos, and zooplankton) were deterministically related to the set of pressure variables through the equations of the mechanistic model applied. Therefore, for the modeled variables, we treated GAMs as a tool to summarize the dynamics of the underlying biogeochemical, zooplankton, or benthos models. If a GAM with a low number of pressure variables reflected the mechanistic model dynamics, we assumed that these pressure variables were the most important drivers in the mechanistic simulation model.

On the other hand, fish time series were reconstructed independently of the pressure variables. For these time series, GAMs were used to identify the relationships between the set of driver variables and independent observations. In addition to atmospheric and hydrographic conditions, nutrient availability, and fishing pressure, we also treated seal abundance as a pressure variable to reflect their ecological role as top predators.

The following additive model formulation between biotic variables (BIO) and drivers (V) was used:

$$\mathrm{BIO}_i = a + s(V_1) + \ldots + s(V_n) + a + s(\mathrm{BIO}_1) + \ldots + s(\mathrm{BIO}_k) + e$$

where a is the intercept, s is spline smooth functions (Wood 2003), $V_{1\ldots n}$ and $\mathrm{BIO}_{1\ldots k}$ are the abiotic and biotic predictors, respectively (for the employed variables, *see* Table 2 and Supplementary Information S1), and e is the error term.

The generalized cross-validation criterion (Wood et al. 2016) was used as the main parameter for model selection. We constructed GAM models for all combinations of two predictors with no significant cross-correlation ($p < 0.05$) and selected models where (1) all model predictors were significant (partial *F*-test, $p < 0.05$), (2) model residuals followed a normal distribution (Shapiro–Wilk test, $p < 0.05$), and (3) had no significant autocorrelation at lags > 1 ($p < 0.05$). Furthermore, the spline smooth functions (s) were constrained to three equally spaced spline nodes ($k = 3$) to restrict the spline curvature during model fitting. Driver combinations were ranked according to AIC and checked for biological meaningfulness. All statistical analyses were conducted using R software (www.r-project.org).

Table 1. Change points detected in principal component scores for the entire time period (1925–2005; PC) as well as the historical (1925–1972; PChist) and present (1973–2005; PCnow) periods.

	1925–2005		1925–1972		1973–2005	
	PC1	PC2	PC1hist	PC2hist	PC1now	PC2now
Variance explained	51%	25%	51%	26%	58%	14%
1930s		**1936**		**1931**		
				1936		
				1938		
1940s				*1942*		
1960s				1961		
1970s	**1972**	**1975**			*1978*	
	1978	**1979**			1979	
1980s		1985			1984	**1988**
		1986				
		1989				
1990s	**1990**	**1991**			1991	**1996**
		1998				
2000s	2000				2001	

Change points simultaneously detected by both STARS and bcp analysis are marked in bold; normal and italic fonts mark change points detected by STARS or bcp, respectively.

Results

Detected shifts

Using the complete time series (1925–2005), shifts in the first principal component (PC1) at the beginning and end of the 1970s and in the 1990s were detected by both change point detection methods (Table 1). The first regime shift detected by both methods (in 1972), was used to divide the dataset into the historical (1925–1972) and present (1973–2005) periods, which we further analyzed in detail. Both detection methods identified abrupt changes in the mid-1930s, beginning and end of the 1970s, the end of the 1980s, and the beginning of the 1990s (Table 1).

Ecosystem structure in the detected regimes

For the entire time period (1925–2005), the first two PCs explained 75% of the data variance (Fig. 4a,b), whereas 51% of the variance was explained by PC1 alone. PC1 showed an

Table 2. Selected GAMs linking ecosystem components with environmental drivers.

Dependent variable	Driver 1	Driver 2	R2adj	GCV
Historical period				
Primary production GS	DIP GS winter (+)	Temperature GS 40–60 m summer (+)	0.866	0.00703
Macoma biomass	DIP BN winter (+)	Temperature BN 40–60 m spring (+)	0.450	0.01927
Flounder SSB	Surface salinity GS spring (−)	Surface temperature GS spring (+)	0.748	0.16965
Flounder SSB	Oxygen GS 220 m (+)	Founder yield per biomass (−)	0.535	0.31151
Present period				
Primary production GS	DIP GS winter (+)	Temperature GS 40–60 m spring (+)	0.895	0.02575
Macoma biomass	Sprat SSB (+)	Hypoxic area (+)	0.852	0.05795
Suspension feeder biomass	Oxygen GS 220 m (+)	Salinity GS 220 m (−)	0.658	0.06596
Cod SSB	Hypoxic area (−)	*Pseudocalanus* sp. (+)	0.879	0.07315
Cod SSB	Cod RV (+)	*Pseudocalanus* sp. (+)	0.853	0.08866
Sprat SSB	Hypoxic area (−)	Cod SSB (−)	0.729	0.14961
Flounder SSB	Oxygen GS 220 m (−)	Seals (+)	0.864	0.00574
Flounder SSB	Macoma (+)	NA	0.616	0.01551

BN, Bornholm Basin; GCV, general cross-validation criterion; GS, Gotland Sea; R2adj, explained variance; RV, reproductive volume; SSB, spawning stock biomass.
(+) and (−) indicate positive and negative correlations, respectively.

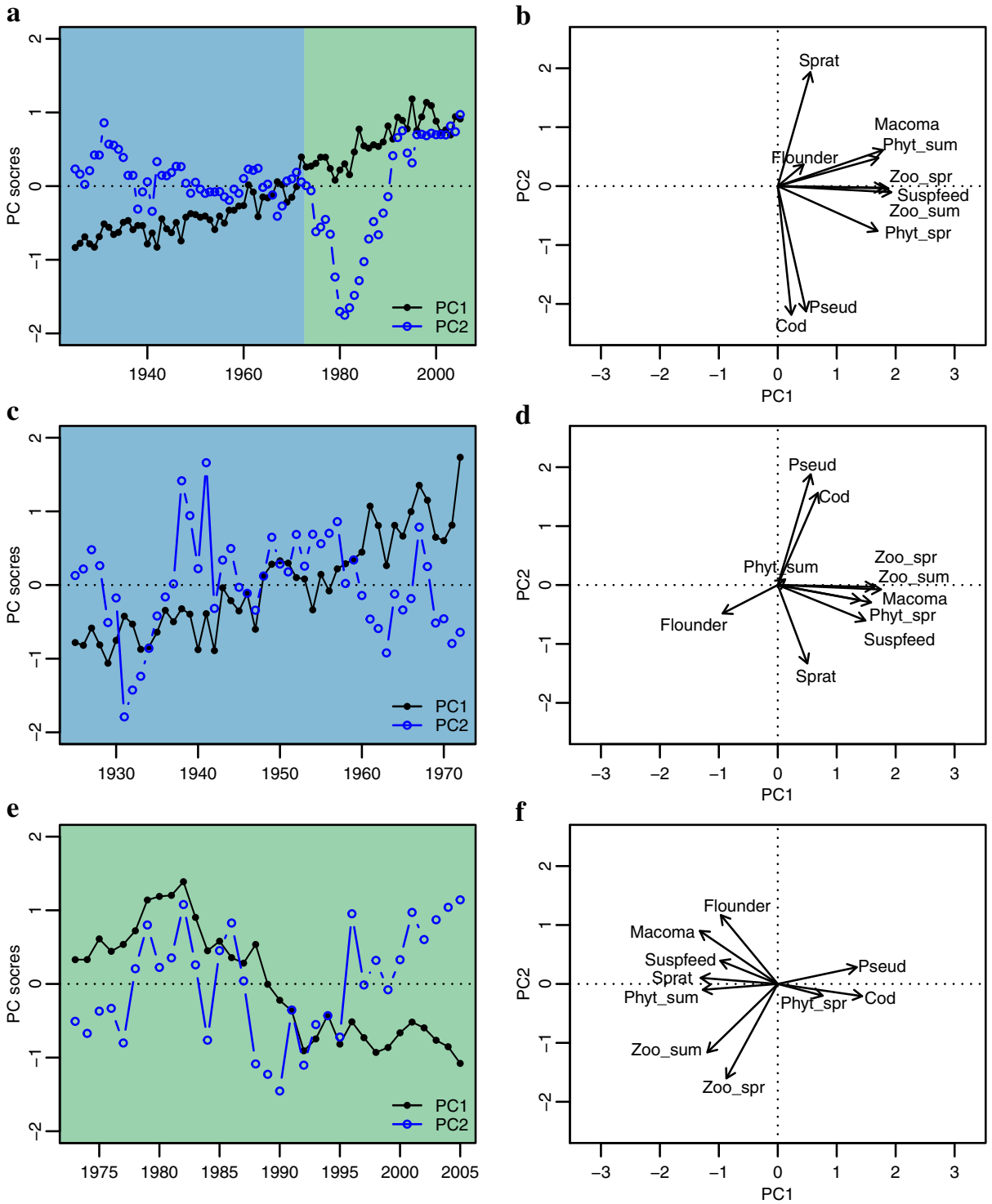

Fig. 4. Principal component scores (left panel) and variable loadings in the first two factorial planes (right panel). (**a**, **b**) The entire time period covered (1925–2005). (**c**, **d**) The historical (1925–1972) and (**e**, **f**) present (1973–2005) regimes. Variables are biomass of cod, sprat and flounder, *Macoma* sp., suspension feeders (Suspfeed), *Pseudocalanus* sp. (Pseud), zooplankton in spring (Zoo_spr) and summer (Zoo_sum), and phytoplankton in spring (Phyt_spr) and summer (Phyt_sum). Blue and green boxes represent low and high productive systems, respectively.

increasing trend throughout the entire time period (Fig. 4a), and all variables were positively correlated with PC1 (Fig. 4b). Productivity-related variables such as zooplankton biomass, benthos variables, and phytoplankton showed higher

correlations with PC1 than did fish components. The second PC (PC2; Fig. 4a) showed an initial sharp increase and then a decrease in scores during the late 1930s, followed by a slight change until the mid-1970s, after which scores drastically dropped to a minimum in the early 1980s, followed by a rapid rise to maximum values in the 1990s. Sprat, *Macoma* sp., summer phytoplankton, and flounder biomass were positively correlated with PC2, whereas cod, *Pseudocalanus* sp., and spring phytoplankton biomass were negatively correlated (Fig. 4b).

For the historical period (1925–1972), the first two PCs (PC1hist) explained 77% of the data variance (Fig. 4c,d). PC1hist scores were low at the beginning of the subset and increased almost linearly until the 1970s (Fig. 4c). All variables except flounder biomass (Fig. 4d) were positively correlated with PC1hist, with the highest loadings for productivity-related variables, that is, phytoplankton and benthos time series. In contrast to the long-term dataset, flounder biomass did not follow the increase in primary producers and benthic consumers. PC2hist scores oscillated during the first two decades, followed by moderate fluctuations and a sharp decrease that switched to a rapid increase between the late 1960s and early 1970s (Fig. 4c). Cod and *Pseudocalanus* sp. showed strong positive correlations, whereas sprat, suspension feeders, and flounder were strongly negatively correlated with PC2hist (Fig. 4d).

For the present period (1973–2005), both PCs (PCnow) explained 71% of the variance in the first factorial plane. PC1now scores first increased with the highest values at the beginning of the 1980s, followed by a gradual decrease throughout the remaining period (Fig. 4e). Cod, *Pseudocalanus* sp., and spring phytoplankton (Fig. 4f) were positively correlated with PC1now, whereas *Macoma*, suspension feeders, sprat, flounder, and summer phyto- and zooplankton were negatively correlated. In contrast to the historical period, the alternating cod and sprat biomass were described by the first instead of the second PC. Thus, after 1972, the interaction between cod and sprat became the dominant pattern in the food web of the Central Baltic. PC2now scores increased sharply in the beginning, followed by high fluctuations until the late 1980s (Fig. 4e). In 1990, PC2now dropped to a minimum, followed by an increase until the end of the time series. Flounder, *Macoma* sp., and suspension feeders showed positive correlations with PC2now, whereas zooplankton groups, and to some extent cod, were negatively correlated (Fig. 3f). The decrease in PC2now summarizes a strong temporary decline in benthic components at the beginning of the 1990s, paralleled by a strong increase in zooplankton.

Change points within the detected regimes

The earliest significant shift in PC1 (for the entire period) was detected in 1972 as a regime shift in ecosystem productivity, as indicated by the strong increase in phytoplankton, zooplankton, and benthic organism biomass (Fig. 2; Supplementary Information S1). The simulated primary production roughly tripled from a nearly constant 26.6 ± 6.0 g C m^{-2} yr^{-1} until 1972 to 83.9 ± 40.0 g C m^{-2} yr^{-1}. However, no significant shifts in PC1hist were detected by the two change point methods (Table 1), indicating a gradual change in the major ecosystem components before 1972. Sudden changes within the historical period were detected for the ecosystem structure described by PC2hist. PC2hist was related to changes in *Pseudocalanus* sp., cod, sprat, benthic suspension feeder, and flounder dynamics. STARS and bcp ($p > 0.8$) detected sudden changes at the beginning and end of the 1930s, suggesting that changes between 1925 and 1972 were associated with predator–prey interactions between cod, sprat, *Pseudocalanus* sp., and benthic ecosystem components.

For the present period (1973–2005), both detection methods found a shift in PC1now at the end of the 1970s. Based on variable correlations with PC1now, this shift was associated with cod interacting with its prey during the cod biomass maximum in the ecosystem. Other shifts in PC1now were detected by STARS only in the mid-1980s, the beginning of the 1990s, and in 2001. For PC2now, STARS and bcp detected identical breakpoints associated with ecosystem changes between the end of the 1980s and the mid-1990s (Table 1), when flounder and benthos biomass decreased and zooplankton biomass increased.

Key drivers

Only a few biological time series could be represented by simple GAM models (Table 2; Supplementary Information S5) with significant predictors ($p < 0.05$). During the historical period (1925–1972), GAM indicated that nutrient concentrations and water temperature were the most important drivers of primary production in the BALTSEM model. For the simulated benthic groups, *Macoma* sp. was correlated with increasing nutrient concentrations, suggesting that food supply was the most important driver of the simulated dynamics. Oxygen conditions did not significantly affect simulated benthic biomass during the historical period. For fish stock time series, which were reconstructed based on catches only, no significant GAM model was found for cod and sprat dynamics; in contrast, flounder was linked to warm and low salinity conditions, high bottom-water oxygen concentrations, and low fishing pressure (Table 2).

In contrast to the historical period, significant relationships were found between cod and sprat for the present period. Cod biomass was high when deep waters were well oxygenated and the cod reproductive volume was high. Sprat was negatively correlated with its predator cod, particularly when bottom-water salinity was high and oxygen concentrations were low. Flounder covaried with increases in their prey *Macoma* sp. and with high seal biomass and low cod biomass. In addition to food supply, represented by primary production, bottom-water oxygen affected the reconstructed *Macoma* sp. biomass. Oxygen effects were also observed for benthic suspension feeders. Similar to the historical period, high

winter DIP concentrations together with increasing temperatures corresponded with increased primary production (*see* Table 2).

Discussion

Identified ecosystem regimes and their drivers

Our comprehensive study, combining reconstructed long-term time series of multiple trophic levels and drivers, provides a unique perspective and new insights into the overall changes in ecosystem dynamics and regulatory mechanisms that have occurred in the Baltic Sea over the past century—a period in human history with several wars, industrialization, and the dynamic development of populations and societies (Davies 1998). Moreover, our study provides a potential ecosystem reference period that can be used to place more recent changes in context (Lotze and Worm 2009).

We identified three major ecosystem shifts in the Central Baltic Sea that occurred in (1) the mid-1930s, (2) the mid-1970s, and (3) between the late 1980s and early 1990s, which affected biological productivity, food-web structure, and environmental quality over 80 yr (Fig. 5). We divided the resulting four regimes into low (1925–1972) and high (1973–2005) productive phases. Based on food-web modeling, Österblom et al. (2007) also proposed a sequence of regime shifts from seals to cod (after the 1930s), from oligotrophic to eutrophic states (between 1951 and ca. 1970s), and from cod to clupeid dominated periods (ca. 1989), which largely agrees with our findings with respect to eutrophication and detected phases.

Below, we describe each identified regime within each production phase and discuss the potential underlying drivers and mechanisms of change, focusing on the cumulative effects of (1) climate, (2) eutrophication, and (3) commercial fishing.

Low production phase (1925–1972)

During the low production phase (Fig. 5), deep waters are largely oxygenated (Fonselius and Valderrama 2003) with large volumes of water suitable for cod reproduction (Savchuk et al. 2008). During this period, the productivity signal was

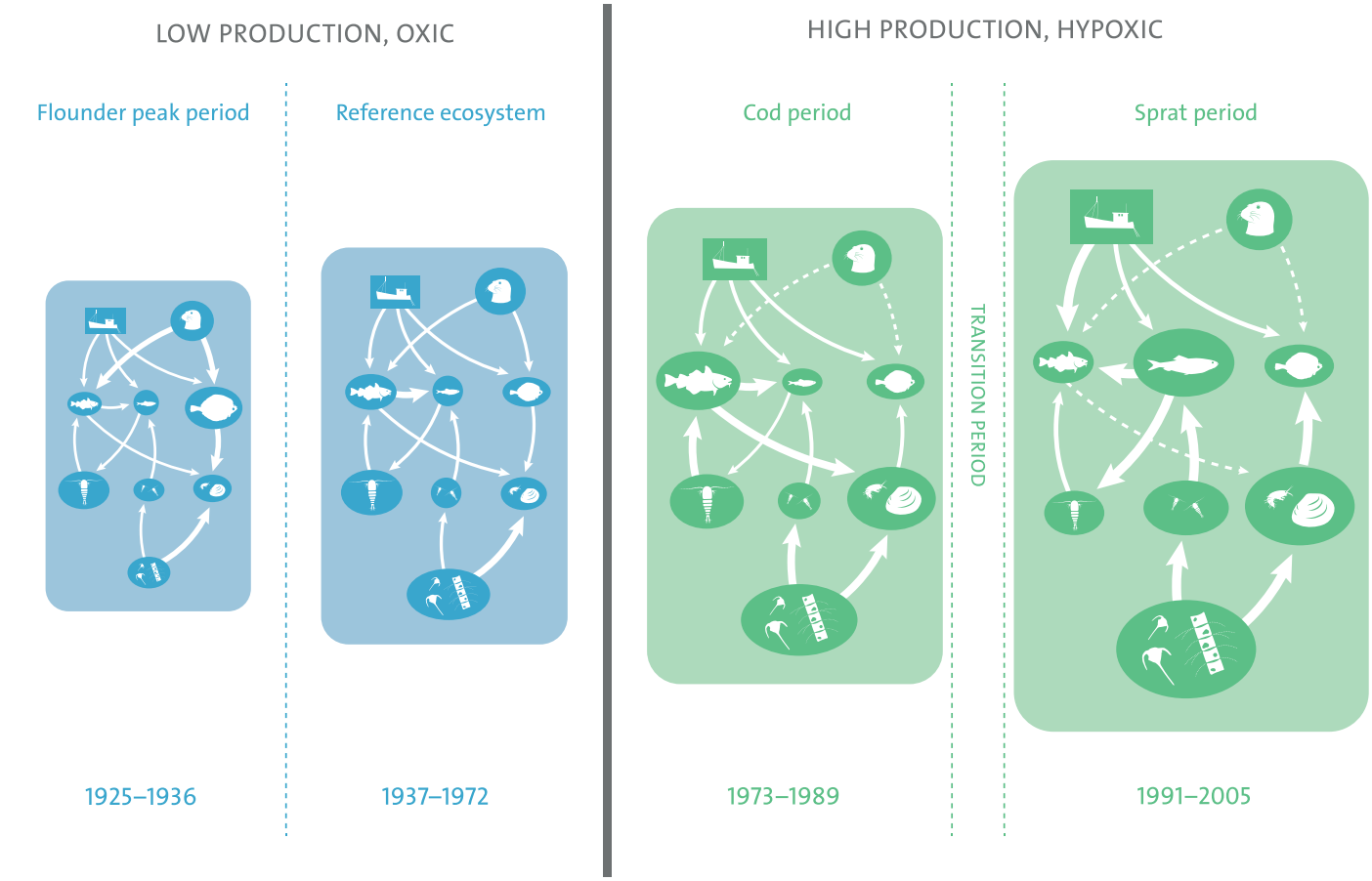

Fig. 5. Conceptual diagram displaying the changes in the Baltic Sea ecosystem between 1925 and 2005 with potential regime shifts. Blue and green boxes represent low and high productive systems, respectively. Arrows represent direction and strength of controls. Arrow width indicates strength of relationship. Dashed lines represent the weakening or loss of the trophic control. Circles and ellipsoids represent the natural elements of the food web; squares represent fisheries.

well described by PC1hist, but the negative relationship between productivity-related variables and benthos to flounder biomass (Fig. 4d) suggests top-down control of flatfish on benthic resources, particularly bivalves, and especially during 1925–1938, when flounder biomass was high (Fig. 3; Supplementary Information S5); this was also suggested by Persson (1981). Oxygen, a forcing in the biomass reconstructions of *Macoma* sp., benthic suspension feeders, and *Pseudocalanus* sp., was not identified as an important driver by the GAM models (Table 2).

Flounder peak period (1920–1936)

At the beginning of the 20th century, the biomass of cod, herring, sprat, and benthic fauna was low. In contrast, flounder biomass peaked in 1920–1930 and collapsed shortly after (Fig. 5; see also Supplementary Information S4) (Hammer et al. 2008). Several studies on the historical development of the Baltic flatfish community have linked this increase and collapse to fishing development, environmental conditions such as inflows and stagnation periods, nutrient dynamics, and compensatory growth triggered by high fishing pressure (Hammer et al. 2008). Because the mechanisms driving the flatfish assemblages extend beyond the time span and scope of this paper, we focused on flounder only and the time period after 1925. Elmgren (1989) described a large increase in benthic biomass in 1920–1923, likely overlapping with the peak of plaice biomass and catches. The highest historical biomass of flounder in the mid-1930s overlapped with a hydrographical "stagnation period" characterized by the absence of inflows from the North Sea leading to low salinity in deeper water layers (Fig. 4). Our hypothesis is that the low salinity caused unfavorable recruitment conditions for cod but was sufficient for the more euryhaline flounder, particularly in conjunction with high benthic food availability caused by low competition after the collapse of plaice and dab stocks in the 1930s (Hammer et al. 2008). The change point in PC2 and PC2hist detected at the beginning of the 1930s (Table 1) may thus reflect the increase in flounder and decrease in cod at the beginning of the stagnation period. Afterward, fishing pressure on flounder increased due to the motorization of fishing vessels, increased fishing effort, and development of trawls (Eero et al. 2008), in addition to the discovery of new, easily available resources for fisheries (Hammer et al. 2008). Flounder biomass increased initially because of compensatory growth (Smith 1994), after which extraordinarily high catches reduced flounder biomass to very low levels.

Reference ecosystem (1937–1972)

We refer to the period from the end of the 1930s to the early 1970s as the "reference ecosystem" (Fig. 5), since it was the longest period identified in our analysis without extraordinary bursts or collapses of individual groups in the food web (Fig. 3)—assuming that our data indicate the most relevant ecosystem changes. The reference ecosystem is part of the low production phase and is characterized by high salinity and good oxygen conditions (Fig. 4; Supplementary Information S1), relatively frequent inflows (Mohrholz 2018), and increasing productivity (Fig. 4) (Gustafsson et al. 2012). However, at the end of the period, hypoxic episodes became more frequent (Fig. 4) (Gustafsson et al. 2012).

After the collapse of the flounder stock in the beginning of the 1940s, cod biomass increased due to an increase in salinity and then decreased due to possible competition for benthic resources (Fig. 3). The flounder stock did not recover after its collapse in the 1940s, probably because of the high food competition and increased predation from cod, which showed faster growth and higher reproduction potential supported by improved spawning conditions during that period (Eero et al. 2007*a*). At the end of the 1950s, hypoxia eliminated the bottom fauna below the halocline, reducing feeding opportunities for cod and flounder (Österblom et al. 2007). This reduction in benthic fauna was not fully captured in our time series, as the data came from locations above the halocline.

Cod and flounder diets overlap (Haase et al. 2020), which is one of the potentially important mechanisms for Baltic food-web dynamics during this period. Generally, cod food items do not include a large share of mussels (Haase et al. 2020), but other benthic groups may make up to 70% of the cod diet, depending on the season and cod size (Neuenfeldt et al. 2020). The flounder diet is spread over mussels, crustaceans, and polychaetes. Unfortunately, our data and analysis covered only the mussel component of the benthic community, and we were thus unable to fully illustrate the effect of diet overlap and competition presented in other studies (Haase et al. 2020). Despite this, we believe that the poor condition of cod prior to the 1940s (Eero et al. 2011) suggests low benthic food availability due to flatfish competition, since the food base (the available biomass at lower trophic levels) was much smaller during the low productive historical period compared with today (1/4th of present levels) (Elmgren 1989), both in the benthic and pelagic domains.

We also hypothesized that the drastic changes in flatfish stocks caused a regime shift in the ecosystem during the 1930s, as indicated by PC2hist (Table 1), and via a trophic cascade, shifted the food web to a new state characterized by low flatfish biomass together with larger cod and sprat stocks. The collapse of flounder biomass in the early 1940s released part of the benthic resources from top-down control, leaving more food resources to cod. When deep-water salinity conditions improved again in the 1940s (Fig. 3), the biomass of cod and *Pseudocalanus* sp. increased, which also affected sprat biomass and initiated the cod–sprat oscillations described by the PC2hist dynamics after the regime shift at the end of the 1930s and the beginning of the 1940s (Table 1). The mechanism described above may be one possible explanation for the increase in cod biomass after the 1940s, a question raised by Eero et al. (2007*a*, 2011). As proposed by Österblom et al. (2007), the shift from seals to cod after the 1930s was a rapid transition from a top predator to a cod dominated state, and the cod biomass increase after 1930 was an effect of the

lack of top-down control by seals (Österblom et al. 2007). However, our GAM models do not confirm the dominant role of seals as a driver. The food-web model used by Österblom et al. (2007) does not include the flatfish component, and thus misses, in our opinion, key mechanisms of cod–flatfish competition and top-down control of flatfish on the benthic community.

High production phase (1973–2005)

During the high production phase (1973–2005; Fig. 5), the ecosystem reached a much higher overall biomass than during any previous decade (Savchuk et al. 2008). Based on PC1 loadings, this productive phase was best characterized by an increase in primary production and lower trophic level biomass, i.e., by the well-known primary effects of eutrophication (Elmgren 1989). Eutrophication, the main driver of PC1, changed the ecosystem regulatory drivers and had much larger effects on ecosystem structure than previously implied by short-term studies. Apart from eutrophication, represented by nutrients, increasing temperature also contributed to long-term dynamics, confirming previous findings (Savchuk et al. 2008; Gustafsson et al. 2012). Moreover, Österblom et al. (2007) had already suggested a true regime shift between oligotrophic and eutrophic states between the 1950s and 1970s, when oxygen deficiency became a chronic feature of the Baltic Sea.

Cod period (1973–1989)

The regime shift in the early 1970s marks an acceleration in the increasing biomass trends at almost all trophic levels (Fig. 3). As shown by PC2, the alternating dominance of key fish and zooplankton species, that is, cod and *Pseudocalanus* sp. vs. sprat, is an important ecosystem change. Besides the regime shift detected by Möllmann et al. (2003) at the end of the 1980s, we also found change points in PC2 at the end of the 1930s and in the mid-1970s. The mid-1970s shift occurred almost simultaneously with a productivity shift at PC1. During this time, cod reproduction was still possible in large parts of the Baltic Proper (Eero et al. 2011). We suggest that the accelerated increase in productivity combined with sufficient cod reproductive volume pushed the ecosystem into a cod dominated state.

During this "cod period," the food-web structure started to differ from that of the reference ecosystem (Fig. 5). The positive correlation between flounder and benthos, represented by bivalves, suggested bottom-up control on flounder while cod exerted top-down control on benthos and sprat (Casini et al. 2009). We suggest that after 1970, cod benefited from eutrophication by feeding on benthic and pelagic prey in similar proportions (Uzars 1994). Moreover, its fast growth and high reproduction (Heessen et al. 2015) helped cod benefit from the suitable reproduction conditions (Fig. 3). Another study suggested that mainly forage fish such as sprat benefit from eutrophication (Eero et al. 2016), whereas Cederwall and Elmgren (1980) showed positive effects of eutrophication on benthic resources above the halocline, which increased the food bases for cod and flounder. Eero et al. (2011, 2016) suggested that the increase in ecosystem productivity between the 1940s and 1980s had a minor effect on the cod stock and that climate/hydrographic conditions supporting recruitment and fishing were the main driving forces. Relationships between cod stock and cod reproductive volume in our driver analysis confirmed the importance of recruitment conditions, but we also identified strong coupling between cod and sprat as the dominant feature of the productive phase, linked to its first PC. We suggest that the cod period was an extraordinary ecosystem state within the highly productive phase, where the productive trophic state supported high cod biomass by combined pelagic and benthic feeding, using trophic pathways in parallel.

Sprat period (1991–2005)

Our analyses detected several change points between the late 1980s and mid-1990s that coincided with a sharp decrease in cod and increase in sprat biomass, marking a shift to a sprat dominated period (Fig. 5). During this period, cod switched to pelagic feeding (Neuenfeldt et al. 2020) because sprat was easily available with high biomass, and supported by good recruitment and feeding conditions (Möllmann et al. 2009). Similarly to Möllmann et al. (2009), we hypothesized that recruitment and fishing controlled cod during the sprat dominated period. Because the high biomass of sprat (> 1,000,000 tons) formed the food base, cod likely no longer controlled the benthic groups. At the same time, benthic food resources for cod, mainly amphipods or crustaceans such as *Saduria entomon*, may have become less available due to hypoxia. Our GAM models identified negative oxygen effects in benthic biomass reconstructions only for the more sensitive suspension feeders, whereas the simulated *Macoma* sp. biomass increased despite spreading hypoxia (Table 2). Thus, despite increasing benthos biomass above the halocline and increasing mussel biomass due to eutrophication (Elmgren 1989; Timmermann et al. 2012), benthic crustaceans, the main food items for cod in the previous periods, were replaced by clupeids after the late 1980s (Uzars 1994).

Benthic food resources did not support cod to the same extent as in the cod dominated period (Casini et al. 2016; Neuenfeldt et al. 2020); meanwhile mussels, the main food item for flounder, supported a steady increase in flounder stock since the 1990s (Fig. 3) (ICES 2019). Unfortunately, we were unable to test this hypothesis fully because our dataset does not cover important benthic components in the cod diet, such as *S. entomon* or *Bylgides sarsi*.

Our results are mostly in agreement with Möllmann et al. (2009) with regard to pelagic relationships and the timing of the shift at the end of the 1980s; however, our PCnow results also suggest changes in the benthic trophic pathway. A food-web modeling study conducted for that eutrophic phase (Tomczak et al. 2013*b*) also suggests a similar

mechanism for the abrupt shift from a cod to clupeid state of the system with a redirection of the trophic flows to the pelagic domain. However, modeled flows through flatfish functional groups are still lacking.

Cumulative drivers

Ecosystem changes, among them regime shifts, are caused by the interplay of multiple drivers and forces that can be both natural and anthropogenic (Lees et al. 2006). Since the beginning of the century, ecosystem productivity, expressed by the biomass of key ecosystem components, increased alongside nutrient enrichment as a primary effect (Gustafsson et al. 2012). In general, biogeochemical models for the historical and present periods indicated that nutrient (DIN and DIP) concentrations together with temperature and fisheries can explain a large part of the ecosystem dynamics. A shift from a benthic to pelagic-dominated state as a consequence of eutrophication and the opposite as an effect of nutrient reduction in coastal systems is not a newly identified phenomenon and has been described in a number of cases (Lindegren et al. 2012; Griffiths et al. 2017).

As described by Möllmann et al. (2009), shifts in the food web, in particular the cod–sprat relationship, are driven by salinity, deep-water oxygen concentration, temperature, and fishing intensity on sprat and cod. Our analysis includes two periods with limited inflows from the North Sea, the 1930s and the 1980s/1990s, as indicated by the low bottom-water salinity in the Bornholm and Gotland basins (Fig. 1). Due to the different productivity phases, these inflows had different consequences for the food-web structure and dynamics. In the 1930s (low production phase), the lack of inflows reduced deep-water salinity, but the oxygen concentration remained relatively high (Fig. 3). In the 1980/1990s (high production phase), the salinity decrease was followed by a high oxygen loss at the bottom (Fig. 3). Thus, during the latter period, bottom-water oxygen conditions started to shape the Baltic food web, and the oxygen supplied via inflows from the North Sea created an intermittent signal in cod recruitment that was channeled via sprat abundance into the food web.

Fisheries

Fisheries played different roles in the two periods. In accordance with our GAM results (Table 2), during the historical period only flounder fishing was important and affected only its target species. Sprat and cod fishing pressures became noticeable only after 1970, as fishing patterns changed from targeting flounder and clupeids to cod and sprat. As reported by Hammer et al. (2008), clupeid catches during the historical, low production period were comparable to flounder catches (clupeids $\sim$ 50,000 t yr^{-1} in 1920–1940, flounder $\sim$ 60,000 t yr^{-1} at peak), whereas cod catches were much lower ($\sim$ 10,000 t yr^{-1}), creating high fishing pressure on flounder and relatively low pressure on cod. After 1970, flounder catches did not exceed 20,000 t yr^{-1} and were minor compared with cod catches during the cod peak. Thus, as pointed out by other studies (Casini et al. 2008; Möllmann et al. 2009), cod fishery is one of the main anthropogenic pressures shaping the cod stock, impacting the entire Baltic Sea food web.

The role of seals

Österblom et al. (2007) suggested that seals were the main predator in the early 20th century (seals dominated period). The seal population declined by 95% during the last century as a result of hunting (1900–1940) and toxic pollutants (1965–1975) (Harding and Härkönen 1999); therefore cascading effects after the collapse of the seal population shifted the ecosystem into a cod dominated period as the predation pressure and top-down control on cod decreased (Österblom et al. 2007). In our driver analysis, seals appeared to noticeably affect only flounder during the historical period and all fish stocks during the present period, despite a much lower seal biomass (*see* Supplementary Information S5). Therefore, we argue that relationships with seal biomass are spurious correlations caused by significant (negative) correlations with the productivity signal. In addition, MacKenzie et al. (2011) concluded that even at the beginning of the 20th century, when the seal population was 10 times larger than in the 2000s, seal predation pressure alone was too small to control the cod stock. Elimination of the seal population brought a significant change to the ecosystem by removing an entire trophic level; however, it did not appear to trigger a regime shift.

Uncertainty and methods

Because surveys and monitoring data rarely cover more than a few decades, historical ecology uses different and often unconventional sources of information, such as modeling techniques, historical statistics, archived press news, notes, and anecdotes, to fill data gaps and extend existing time series (Thurstan et al. 2015). Here, we relied on a combination of reconstructed, modeled, published, verified, and validated time series (*see* Supplementary Information S1). Other biogeochemical models provided similar results for the essential drivers of food-web changes that we identified, in particular for the long-term increase in primary production and phytoplankton biomass as well as the oxygen loss below the halocline (Meier et al. 2012). In reconstructing fish dynamics, models depend on the quality of the catch data, and the Baltic Sea has relatively good data availability and quality (Hammer et al. 2008; Eero et al. 2011). It is evident that single-species fish modeling does not consider the entire species life history and ecological processes, which may differ under historical circumstances (Hoshino et al. 2014).

In addition, the spatial heterogeneity of the data used affects our analysis. For example, physical processes are modeled on a sub-basin scale, where fish stocks are modeled on the entire Central Baltic Sea scale. Some important ecosystem components, such as herring, birds, and some benthos groups could not be included due to a lack of suitable data or because they inhabit the coastal zone of the Baltic, where

different species and processes play a key role (Olsson et al. 2015). Therefore, our suggested mechanisms did not include these organisms. For the time being, the combined dataset presented here is the best available for characterizing the largest subsystem of the Baltic, the Central Baltic Sea.

Since we aimed to describe the long-term dynamics of the Central Baltic food web, we had to include simulated time series for lower trophic level variables, as no data are available prior to the 1970/1980s. We are also aware that the time series derived from the biogeochemical, *Pseudocalanus* sp., and benthos models are fully determined by deterministic relationships with their drivers. Therefore, we treated the results of the GAM models for these variables as model simplifications that highlight the importance of different drivers in shaping the simulated time series. For example, the temperature dependency of the zooplankton group (Savchuk et al. 2012), the oxygen and hypoxic area sensitivity of the benthic suspension feeders (Timmermann et al. 2012), and the sprat control on *Pseudocalanus* sp. are described in the respective submodels. Even though all simulation models used were well-calibrated and built based on known biota responses to abiotic conditions, our driver analysis may overestimate the importance of abiotic drivers for lower trophic level food-web components. Meanwhile, fish stock dynamics were reconstructed independent of hydro-physical conditions or lower trophic level biomasses, making our analysis more robust. For example, our analysis successfully detected the well-known dependency of the Eastern Baltic cod stock on deep-water salinity and oxygen conditions (Köster et al. 2016).

Furthermore, given that the regime shift detection method STARS often does not detect the exact year of a shift (Stirnimann et al. 2019), we interpreted the set of breakpoints identified by STARS and bcp at different probability levels with caution as the approximate time of major ecosystem changes.

Management context

Despite the many uncertainties caused by filling historical data gaps, our analysis helps us understand the mechanisms of ecosystem change from a long-term perspective and thus fosters solutions for contemporary marine conservation and ecosystem-based management (Thurstan et al. 2015). The nature of regime shifts makes it difficult to manage pressures and predict ecosystem response (Lees et al. 2006), but knowing previous ecosystem configurations and their controlling mechanisms would make it easier to define targets and baselines at the ecosystem level. This knowledge can help answer management questions, for example, whether it is possible to simultaneously reach the low eutrophication status and high cod stock of the 1980s.

Baselines are the purview of restoration ecology and represent the pristine state of an ecosystem, which may be subjectively interpreted as a preferred state or a situation in which the pristine state is not aligned with a realistic management goal (Samhouri et al. 2011). As posited by Samhouri et al. (2011), recognition of these types of reference levels is crucial for avoiding the shifting baselines syndrome—failing to identify the state of nature where human impacts are absent, making it impossible to determine the extent of modification. For example, the EU Marine Strategy Framework Directive requires threshold values as a "value or range of values that allows for an assessment of the quality level achieved for a particular criterion. Where available, these values should be determined based on long time-series data. Threshold values should reflect natural ecosystem dynamics, including predator–prey relationships, and describe a state that reflects prevailing conditions to which the ecosystem may recover after deterioration" (EU 2008). However, what are the "natural ecosystem dynamics" and "prevailing conditions" in the Baltic context? Most marine ecosystems have been assessed after many species had declined and historical amnesia contributed to a "shifting baseline syndrome," where the perception of "what is natural" shifted toward more degraded ecosystems (Pauly 1995; Lotze et al. 2011). Every baseline for an ecosystem state changes alongside human generations (Pinnegar and Engelhard 2008), sometimes slowly over centuries or decades (Lotze et al. 2011) and sometimes in quick, emergent reorganizations seen as regime shifts (Lotze and Worm 2009; Thurstan et al. 2015). As the Baltic Sea has been exploited over the ages (Hoffmann 2005), targeting pristine conditions at the ecosystem level would be impossible and unrealistic from a management perspective because of changes in climatic conditions and human impacts. A shift in baseline definition also occurred in the Baltic Sea, where the cod dominated period referred to by the media as the "good old times of Baltic Sea" is usually used as the reference point for public debate. However, we suggest that the period between the mid-1930s and the beginning of the 1970s as a potential reference period for the Baltic ecosystem, representing a long period with a relatively stable food-web configuration as shown in Fig. 5. Although this period does not represent "pristine" conditions, it may provide a reference for management and inform potential ecosystem recovery pathways after deterioration based on management actions, as proposed in the Baltic Sea Action Plan (HELCOM 2007). Because there are clear dependencies and trade-offs between environmental conditions, productivity of the system, and the configuration of higher trophic levels, cross-cutting multisectoral, integrated ecosystem management plans instead of sectoral or single-species plans are necessary to avoid contradictory objectives, goals, and measures leading to unsustainable, unbalanced, and economically unjustified management actions. Furthermore, climate change and other anthropogenic drivers may lead to conditions where reference conditions are not realistic for the future.

Conclusions

Our study demonstrates that at the scale of almost a century, several regime shifts occurred in the Baltic Sea, which reorganized its food web. During this sequence of shifts, the

trophic state of the ecosystem changed from low productivity, where benthic components played a significant role in trophic transfer, to a productive system where pelagic–benthic coupling was weak and pelagic components dominated. Based on our data analysis, productivity and environmental conditions, such as climatic and hydrographic factors, affected the food web. Fishing was an important driver in the present period, and the human-induced productivity increase caused by eutrophication has far-reaching direct and indirect impacts in the long term. Eutrophication changed not only the trophic state of the Baltic Sea system but may have also led to a switch in the main regulatory drivers from salinity and temperature to oxygen. The reference period proposed in our analysis may guide the establishment of ecosystem state baselines and threshold values for ecosystem state indicators, which may change over time. Overall, knowledge and identification of past ecosystem regimes is essential for informing the ecosystem-based management of sustainable seas.

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Conflict of Interest

None declared.

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