Human-induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea

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ABSTRACT

The ecosystems of coastal and enclosed seas are under increasing anthropogenic pressure worldwide, with Chesapeake Bay, the Gulf of Mexico and the Black and Baltic Seas as well known examples. We use an ecosystem model (Ecopath with Ecosim, EwE) to show that reduced top-down control (seal predation) and increased bottom-up forcing (eutrophication) can largely explain the historical dynamics of the main fish stocks (cod, herring and sprat) in the Baltic Sea between 1900 and 1980. Based on these results and the historical fish stock development we identify two major ecological transitions. A shift from seal to cod domination was caused by a virtual elimination of marine mammals followed by a shift from an oligotrophic to a eutrophic state. A third shift from cod to clupeid domination in the late 1980s has previously been explained by overfishing of cod and climatic changes. We propose that the shift from an oligotrophic to a eutrophic state represents a true regime shift with a stabilizing mechanism for a hysteresis phenomenon. There are also mechanisms that could stabilize the shift from a cod to clupeid dominated ecosystem, but there are no indications that the ecosystem has been pushed that far yet. We argue that the shifts in the Baltic Sea are a consequence of human impacts, although variations in climate may have influenced their timing, magnitude and persistence.

Key words: eutrophication; fishing; marine mammal; predation; regime shift; trophic cascade.

INTRODUCTION

Our knowledge of marine ecosystem dynamics has increased substantially during recent years, in part due to an increased understanding of the importance of historical human impacts (Jackson and others 2001), and in part due to an increased appreciation of the complexity of ecosystems (Hughes and others 2005). A number of studies have shown that complex ecosystems can exhibit multiple ''stable'' states, with abrupt transitions, known as regime shifts, between these states (Scheffer and others 2001). The ''stable'' states are maintained by internal feedback processes, but these internal processes can also interact with large-scale external forces (such as climate) to trigger regime shifts (Scheffer and others 2001; Carpenter 2003). Gradual changes in conditions, caused by for example, human-induced eutrophication or continuous fishing pressure, may alter internal feedbacks processes of an ecosystem
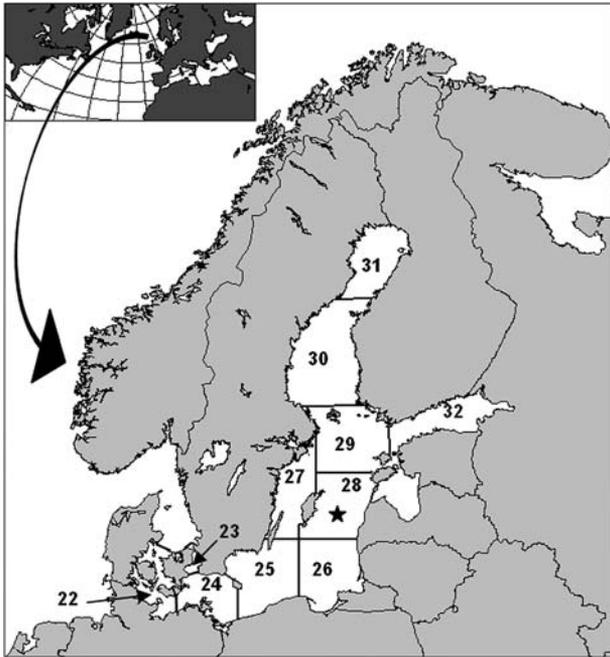
Figure 1. The Baltic Sea and the N. Atlantic (*insert*). *Numbers* refer to ICES (International Council for the Exploration of the Sea) Sub-Divisions (SD). The Baltic Sea is defined as SD 22–32, the modeling area is SD 25–29 + 32. The Danish straits are located in SD 22–23. *Star* indicates Eastern Gotland Basin sampling station for oxygen (Figure 6).

and push it closer to a threshold, increasing the likelihood that a shift to an alternate state will occur (Scheffer and others 2001). Crossing a threshold may cause a sudden and dramatic change in the responding state variables, for example, when lake systems shift from clear to turbid water (Carpenter 2003). In other cases, although the dynamics of the system have shifted from one direction to another, the transition of the state variables is more gradual as described by Walker and Meyers (2004).

Regime shifts and trophic cascades in marine ecosystems have been documented in both coastal and offshore food webs (Scheffer and others 2001; Jackson and others 2001; de Young and others 2004; Frank and others 2005), as results of natural (for example, climate) as well as anthropogenic forcing (for example, fishing and eutrophication), but the underlying mechanisms are often difficult to clarify (Scheffer and others 2001; Jackson and others 2001). In this article we investigate likely regime shifts in the Baltic Sea throughout the twentieth century and address the underlying mechanisms that could help stabilize ecosystem states.

THE BALTIC SEA

The Baltic Sea (Figure 1) is a species-poor, semi-enclosed brackish sea, with a mixture of marine and freshwater organisms. Cod (*Gadus morhua* L.), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are the dominating fish species and constitute around 80% of the total fish biomass (Elmgren 1984; Thurow 1984). The low salinity is physiologically stressful to most of the organisms, and variations in hydrographical conditions may have substantial impacts. Climate influences ice conditions, freshwater inputs, winds, and also the influxes of saline water through the narrow Danish straits (Figure 1) that determine the salinity and temperature stratification of the water column and the oxygen content of the deep water (Hänninen and others 2000; Fonselius and Valderrama 2003; MacKenzie and Köster 2004). However, the system is also influenced by anthropogenic factors like toxic substances, eutrophication, hunting and fishing.

The Baltic has undergone drastic changes in the twentieth century, including a well-documented shift from cod to clupeids (sprat and herring) as dominants in the fish community (for example, Rudstam and others 1994). This change has been referred to as a regime shift (Alheit and others 2005). Data from the previous century indicate that this shift was preceded by other major changes in the ecosystem. In the beginning of the century the production of cod, herring and sprat was low, but increased rapidly prior to the 1950s and again around the 1970s (Thurow 1997). The available biomass estimates, commercial catches and a number of observations (Segerstråle 1965; Thurow 1999a, b; MacKenzie and others 2002) all indicate that the first shift started with a rapid increase in cod biomass already in the 1930s followed by an increase in herring biomass during late the 1940s when cod biomass had stabilized. The second shift started with a rapid increase in clupeid biomass in the late 1960s followed by an increased cod biomass in the late 1970s. Since the publication of these suggested dynamics, new modeling tools have become available (Harvey and others 2003), which provide alternative ways of estimating historical fish production and ecosystem interactions.

In the early twentieth century, the dominant top predators in the Baltic were marine mammals (gray *Halichoerus grypus*, ringed *Phoca hispida* and common seals *Phoca vitulina*, and the porpoise, *Phocoena phocoena*; Elmgren 1989; Harding and Härkönen 1999; MacKenzie and others 2002). These species feed largely on cod and clupeids (Söderberg 1972;

MacKenzie and others 2002). The seal populations declined by some 95% during the last century (Harding and Härkönen 1999) as a result first of hunting (1900–1940) and later of toxic pollutants (1965–1975). The harbor porpoise was also radically reduced by, for example, hunting and incidental catches in gill nets (MacKenzie and others 2002), but there are also indications of severe winters causing substantial mortalities (Svärdsson 1955). Seals consumed much of the total fish production in the early twentieth century (Elmgren 1989) and may have controlled the cod stock. Both increases in fish biomass occurred after drastic reductions in seal stocks, indicating that reduced top-down control contributed to these changes in the fish community.

A century ago, the Baltic proper was an oligotrophic, clear-water sea (Sandén and Håkansson 1996). The deep waters were oxygenated (Fonselius and Valderrama 2003), with generally large volumes of water with favorable conditions for cod reproduction (see Methods). Extensive draining of wetlands and lakes in the late nineteenth and early twentieth century and growing use of agriculture fertilizers meant increased transport of nutrients to the sea (Hoffmann and others 2000). This stimulated primary production and most likely also fish production (Thurow 1997). The higher primary production led to increased consumption of oxygen in the deep waters and reduced spawning habitat for cod (Hansson and Rudstam 1990). The first signs of eutrophication were observed early in the last century, in coastal areas close to major cities (Johansson and Wallström 2001; Laurila and Laakkonen 2004), whereas the effects of eutrophication in the offshore areas became clearly evident in the 1950s (see below).

In this article we use an ecosystem model (Ecopath with Ecosim, EwE) to explore if top-down (seal predation) or bottom-up (eutrophication) mechanisms could explain the low biomass estimated for the early century as well as the first shift from very low fish biomass in the early century to intermediate levels in the mid century, and the second shift to the current high levels of fish. In addition to investigating the food-web dynamics, we also try to explain the mechanisms leading to the likely regime shifts in the nutrient enriched Baltic Sea and discuss whether these shifts are true regime shift, that is, including hysteresis phenomenon. This defined as: systems with more than one stable state, separated by an unstable equilibrium and with catastrophic transitions between states occurring at different critical conditions (Scheffer and others 2001). The degree of hysteresis may vary strongly even in the same kind of ecosystem. For example, shallow lakes can have a pronounced hysteresis in response to nutrient loading whereas deeper lakes may react smoothly. We thus investigate possible mechanisms that could stabilize the new ecosystem states. We also discuss the implications for management of the potential difficulty of reversing the observed shifts.

METHODS

The fish biomass time series used in this study are hindcasts from Thurow (1997, 1999a, b) for cod (1903–1969), herring (1903–1977) and sprat (1903–1972) and official stock assessments from ICES (2004a) for cod (1970–2003), herring (1980–2003) and sprat (1974–2003). Data on observed fish and seal populations are for the entire Baltic Sea, except for herring 1980–2003, when data from ICES SD 22–24 are excluded (for the period 1991–2003 this was on average ∼15% of biomass, ICES 2004a, b). These hindcasts were compared to simulation results from an ecosystem model (Harvey and others 2003, see below) developed for a somewhat smaller area, the Baltic proper and the adjacent Gulfs (that is, ICES subdivisions 25–29 + 32, Figure 1). The bulk of the cod and clupeid biomass is found in the area covered by the model, and modeled biomasses follow recorded biomasses in the entire Baltic Sea (Figure 2), making comparisons between estimated and modeled fish biomasses relevant.

The ecosystem model was developed using the Ecopath with Ecosim (EwE) software (http://www.ecopath.org, Christensen and others 2005) and is described in detail by Harvey and others (2003). In short, the model was parameterized by expanding the carbon flow model of Sandberg and others (2000), by adding a more detailed description of fish stocks (that is, juvenile and adult sprat, herrring and cod as separate groups, Figure 3). In total the model contains 15 functional groups, from primary producers to seals and fishery.

A mass-balanced budget was calculated for 1974 based on diets, production, consumption, fishing and biomass changes for all functional groups (Harvey and others 2003). The model dynamics during the calibration period (1974–2000) were driven by observed fishing patterns, environmental forcing on cod recruitment (multiplied by the reproductive volume, RV, see below) and the emergent stock recruitment relationships. EwE enables the user to specify the predator–prey relationships in terms of for example, degree of top-down versus bottom-up controll and feeding time
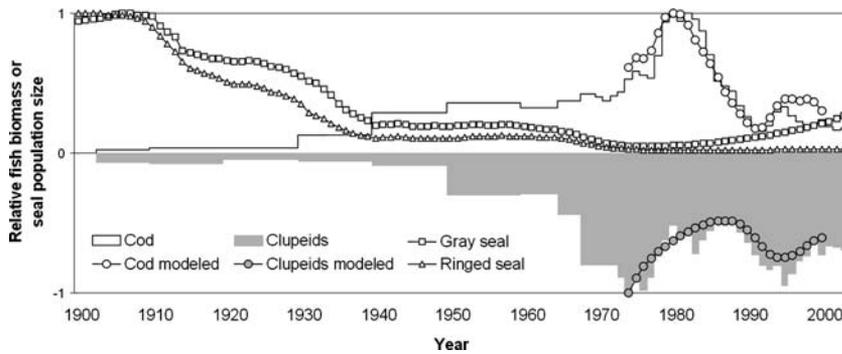
Figure 2. Relative abundance of key species at high trophic levels (excluding humans) and Ecosim modeled fish biomasses for the period used to calibrate that model. One unit represents 1.1 and 5.6 million tons (Mt) of cod, and clupeids, respectively, and 0.9 and 4.3 Mt of modeled cod and clupeids. For seals, one unit represents 75,000 and 200,000 individuals of gray- and ringed seal, respectively.

adjustment rates in response to prey availability. These predator–prey relationships were specified to maximize the fit of modeled dynamics in fish biomasses (sprat, herring and cod) to stock assessments presented by the International Council for Exploration of the Sea (ICES 2001). To make the model behavior more realistic with the new data input, some modifications were made to the model of Harvey and others (2003). The changes are detailed in the appendix at http://www.springerlink.com (see also Hansson and others 2007).

The calibrated EwE model was first used to simulate three main scenarios (1900, 1950 and 1970) where we used the primary production, cod reproductive volume and seal predation pressure in the (scenario 1900) early, (scenario 1950) mid, and (scenario 1970) late twentieth century to derive model predictions of fish densities during corresponding periods. To explore the relative importance of the top-down (changes in seal abundances) and bottom-up (primary production) mechanisms, the three main scenarios were complemented with four scenarios where the seal population size (S) and the primary production and cod RV (P) from historically adjacent main scenarios where combined. We refer to these four as scenario $P_{1900}S_{1950}$, $P_{1950}S_{1900}$, $P_{1950}S_{1970}$, and $P_{1970}S_{1950}$ (see below).

Each model scenario was run with three different fishing intensities, corresponding to the average fishing mortality in 1996–2000 (Status quo, SQ), the maximum levels suggested to be in agreement with the precautionary approach (PA, ICES 2001) and half the suggested precautionary approach levels (PA/2, Table 1). The simulations started with a rerun of the calibration period (1974–2000), followed by a 30-year period during which the changes in the driving input parameters mentioned above were introduced gradually to avoid instability and prevent the model from crashing. The simulations continued for another 70 years and the results presented here are the averages from the
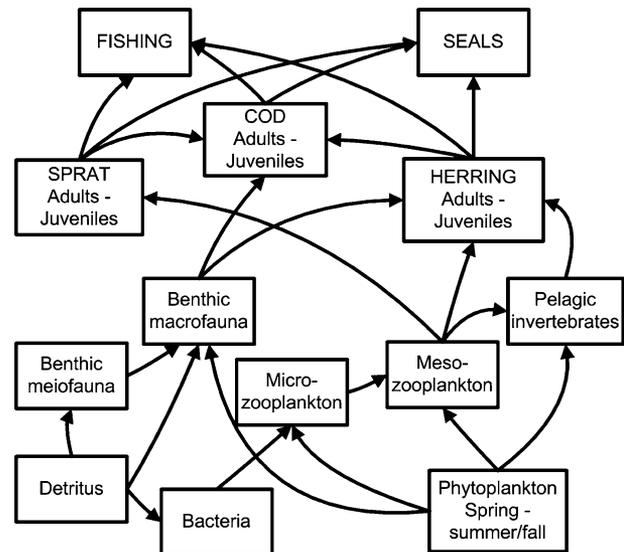

Figure 3. A simplified Baltic Sea food web. The 15 functional groups in the Ecopath with Ecosim model are: (1) spring phytoplankton (spring bloom algae, important food source for benthos), (2) other phytoplankton (summer and autumn algae, main food source for mesozooplankton), (3) bacteria (except for cyanobacteria), (4) microzoop. (small pelagic invertebrates that pass a 90 μ mesh net), (5) mesozoop. (medium-sized pelagic invertebrates that are retained by a 90 μ mesh net), (6) mysids (that is, large pelagic invertebrates), (7) meiobenthos (small benthic invertebrates that pass a 1 mm mesh sieve), (8) macrobenthos (large benthic invertebrates, retained by a 1 mm mesh sieve), (9) juv. sprat (younger than 2 years), (10) juv. herring (younger than 3 years), (11) juv. cod (younger than 4 years), (12) sprat (2 years and older), (13) herring (3 years and older), (14) cod (4 years and older) and (15) seals (all seal species combined).

last 20 years when the biomasses had become reasonably stable; they changed and sometimes fluctuated substantially in the intermediate prediction period. Finally we compare the modeled biomass of cod (juveniles and adults combined) and clupeids (juvenile and adults of herring and sprat

Table 1. Three Different Fishing Intensities are used to Drive the Model

	Scenario	Species		
		Sprat	Herring	Cod
Fishing mortality	SQ	0.299	0.329	0.833
	PA	0.379	0.130	0.555
	PA/2	0.190	0.065	0.278
Fishing intensity in relation to PA	SQ	79%	253%	150%
	PA	100%	100%	100%
	PA/2	50%	50%	50%

The SQ (status quo) scenario corresponds to the average fishing mortality in 1996–2000, the PA scenario to the highest fishing mortality in agreement with the precautionary approach and the PA/2 scenario to half the PA fishing mortality. The fishing mortalities are not identical to the ones given by ICES (2001), because the definition of the adult group is somewhat different.

combined) for the Baltic proper with the biomasses from the corresponding periods in the entire Baltic Sea. Because model output during the calibration period (1974–2000) fitted observed data (Harvey and others 2003), we tried to make comparisons easier by scaling biomasses of both actual and model data to 1.

Different seal predation pressures were modeled based on estimated (Harding and Härkönen 1999; Härkönen unpublished) abundances around 1900, 1950 and 1970. The gray and ringed seal populations in the early 1900s have been estimated at almost 100,000 and 200,000 individuals, respectively (Figure 2), and decreased to approximately 15% until 1950 and to less than 5% in the 1970s. In the model the two species are pooled into one group assuming that the smaller ringed seal eats about half as much as a gray seal (Elmgren 1989). Assuming that 50% of the seals inhabited the Baltic proper we used 100,000, 15,000 and 1,400 seals (in gray seal units) in the early-(1900), mid-(1950) and late (1970) twentieth century scenarios, respectively. The daily consumption per biomass was 3.5% (Elmgren 1989), but because approximately 50% of the seal diet consists of fish other than cod, herring and sprat, only half the seal population was included in the model. The diet composition was proportional to fish biomasses (Thurow 1997, 1999a, b).

Historical primary production has been estimated at approximately 35% of the current level in the early 1900s (Schneider and Kuss 2004; Wulff and others 2005) and at 50% in the 1950s (Stigebrandt 1991). In the oligotrophic scenarios we therefore multiplied the phytoplankton production per biomass with forcing functions that decreased the primary production to approximately 35 and 50%
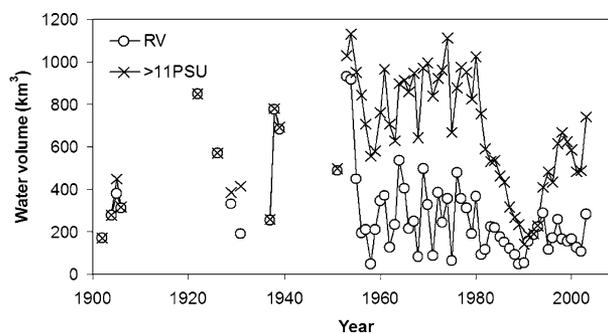

Figure 4. The cod reproductive volume (*RV*, >11 PSU and >2 ml O_2/l) and the entire volume of water with a salinity above 11 PSU (including water <2 ml O_2/l) in the Baltic Sea from year 1900 onwards. Before 1950, the entire volume of water with a salinity high enough for cod reproduction (>11 PSU) was mostly well oxygenated and available for cod reproduction. After 1950, the volume of water above 11 PSU is on average larger than before 1950, but the RV is lower, indicating that the decrease in RV was caused by eutrophication induced oxygen deficiency and not by decreased inflows of saline water.

of the level applied for the calibration period (1974–2000). The applied forcing functions were the same in all scenarios corresponding to the 1900 and 1950 primary production, respectively, but because of trophic cascade effects (compare Carpenter and others 2001), the reduction in the phytoplankton production varied slightly with fishing mortality and seal population size.

We have used data (http://data.ecology.su.se/models/bed.htm) provided by ICES and a range of marine institutes (see Acknowledgement), to show the historical oxygen content in the Eastern Gotland basin (see Figure 1) and to calculate corresponding cod reproductive volumes (see Figure 4). Interpolations and calculations of volumes of water were made with the DAS numerical tools described by Sokolov and others (1997).

Cod recruitment depends on the volume of water in the deep basins with a salinity (>11 PSU) and an oxygen content (>2 ml O_2/l) high enough for cod egg survival (Vallin and others 1999). This reproductive volume (RV) is influenced negatively by eutrophication, due to increased oxygen consumption in the bottom water (Karlsson and others 2002), but positively by occasional inflows of water with high salt and oxygen content from the North Sea (Matthäus and Franck 1992). The relative importance of these two processes is hard to estimate. The average RV in the early 1900s (estimated for 11 years between 1900 and 1950 from data in the Baltic Environmental Database using the DAS
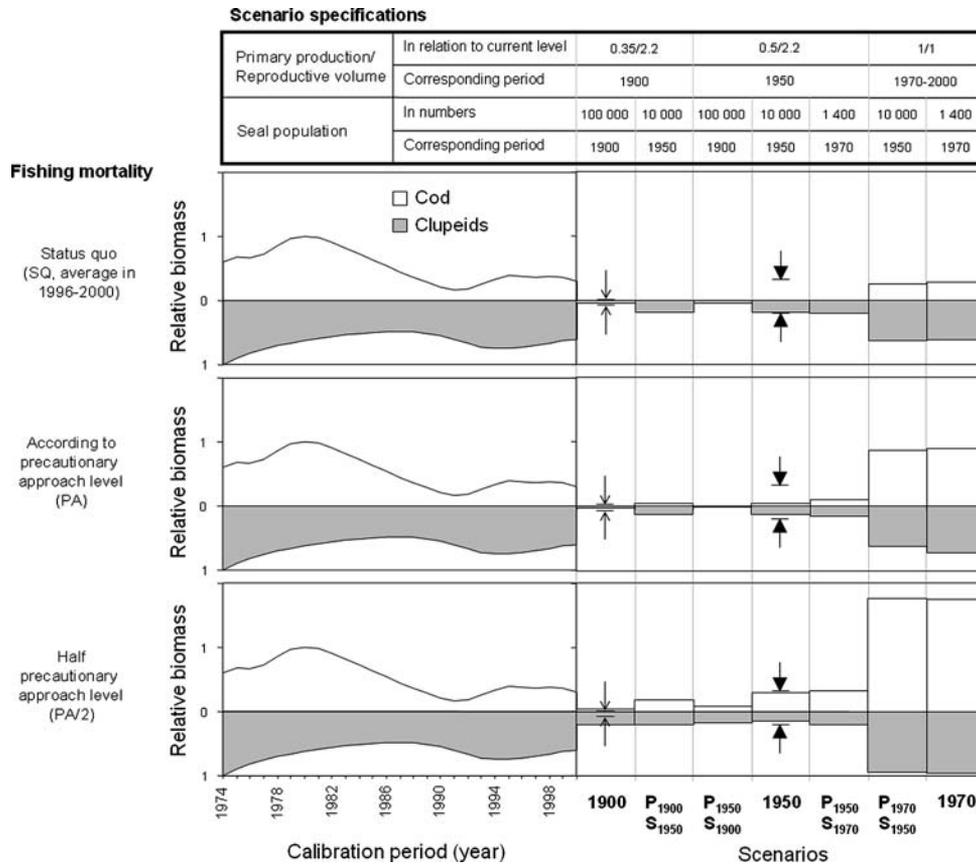
Figure 5. Ecosim-modeled relative cod and clupeid biomasses (1 is the maximum biomass during the calibration period), showing effects of different levels of seal predation and primary production at three levels of fishing mortality (*SQ, PA* and *PA/2*). The three panels at *left* are identical and show the modeled biomass of cod and clupeids during the model calibration period (1974–2000). The other panels show average fish biomass after the models have stabilized (last 20 years of a 100-year simulation). The generally low biomasses estimated when primary production and seal predation is set to the 1900 level (scenario 1900) agree reasonably with the hindcasts by Thurow (1997, indicated by *open arrows*). Primary production and seal predation pressure at the 1950 level also generate biomasses in line with the hindcasts (*closed arrows*) for clupeids and for cod if fishing intensity is low (PA/2). The model explains the increased fish biomass between 1900 and 1950 by decreased seal predation (scenario $P_{1900}S_{1950}$) rather than eutrophication (scenario $P_{1950}S_{1900}$). The modeled fish biomass under current primary production levels and seal predation pressure at the 1970 level (scenario 1970) is comparable to the calibration period (and hindcasts), but for cod depends largely on fishing intensity. The model explains increased fish biomass after 1950 by eutrophication (scenario $P_{1970}S_{1950}$) rather than by decreased seal predation (scenario $P_{1950}S_{1970}$).

software, Sokolov and others 1997 and http://data.ecology.su.se/Models/das) was on average 2.2 times higher than during the calibration period. Because the average total volume of water with a salinity over 11 PSU was slightly smaller in 1900–1950 than during the calibration period, we interpret the difference in RV as caused by lower oxygen concentration, that is, eutrophication, and not by differences in inflow volumes (Figure 4), although increased water temperatures might also contribute (Fonselius and Valderrama 2003). In the 1970 scenario we use the average RV from the calibration period (1974–2000) and in the 1900 and 1950 scenarios the RV is set 2.2 times larger.

RESULTS

The model results presented in Figure 5 predict generally low fish biomasses when seal and primary production are set to the levels of the early 1900s (scenario 1900), in agreement with the low fish biomass estimate by Thurow (1997). In this scenario, both status quo (SQ) and precautionary (PA) fishing mortalities are high enough to practically eradicate fish, whereas fishing intensities corresponding to the half precautionary approach (PA/2) result in cod and clupeid biomasses somewhat higher than Thurow's estimates. A modeled decrease in seal predation pressure and an increase

in primary production to the 1950s level (scenario 1950) results in clupeid biomasses similar to the averages estimated for 1940–1960 by Thurow (1999b). When applying the SQ or PA fishing intensity, a very low cod biomass is predicted, but with the PA/2 fishing intensity the estimated cod biomass is similar to Thurow's values (1999a). To explore the possible reason for the increase in fish between 1900 and 1950 (Figure 2), we compare a scenario with the 1900 level of primary production (P) and the seal predation (S) of 1950 (scenario $P_{1900}S_{1950}$), with a scenario with the 1950 level of primary production and the seal predation of the 1900s (scenario $P_{1950}S_{1900}$). These runs indicate that it was a reduced seal predation (a top-down control) and not an increased productivity that was the major reason for the increase in fish stocks in the first half of the previous century.

As expected, given how the EwE model was parameterized, decreasing the seal predation and increasing primary production to the 1970 levels (scenario 1970), results in cod and clupeid biomasses of the same order of magnitude as during the calibration period. Predicted cod biomass, however, depends largely on the fishing pressure. SQ fishing intensity results in a cod biomass similar to that at the end of the calibration period, but at lower fishing intensities (that is, PA/2) the cod stock increases to almost twice its maximum during the calibration period. Maintaining primary production at the 1950s level and decreasing seal predation to the 1970 level (scenario $P_{1950}S_{1970}$) hardly changed fish biomass at all. In contrast, maintaining seal predation at the level of 1950 and increasing primary production to the 1970 level resulted in almost the same fish biomass increases (scenario $P_{1970}S_{1950}$) as the 1970 seal predation level (scenario 1970). These results indicate that the second increase in fish biomass was caused by bottom-up forcing (eutrophication), not by top-down release from sea predation.

The mechanisms driving the eutrophication-related food web changes can be illustrated by the long-term change in oxygen content in the Gotland Deep in the central Baltic proper (Figure 6), which exemplifies the deteriorating oxygen situation during the last century. The marked oxygen deficiency after about 1950 caused a release of accumulated phosphorus from the sediments (Fonselius 1981), and the oxygen content can be regarded as a proxy for phosphorus release from the sediments. Recent studies have shown that redox conditions in the deep basins to a large extent control nutrient levels. During a stagnation period, up to three times more phosphorus is released from the sediments
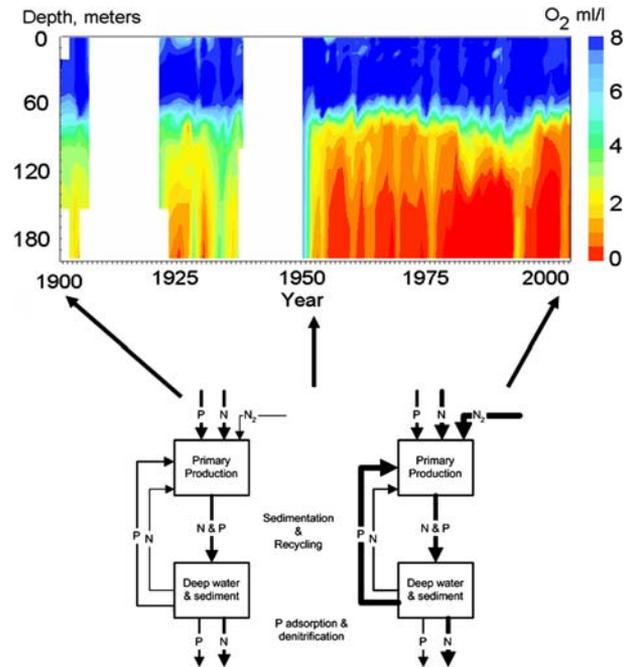

Figure 6. Oxygen content in the Eastern Gotland basin between 1902 and 2002. Data are missing from the two world war periods. The *lower panel* illustrates schematically the two nutrient regimes: before and after 1951. In the more oligotrophic Baltic (>1951) where most of the deep basins were oxidized, internal recycling of both nitrogen (N) and (P) was limited due to sediment P adsorption and nitrogen (N) losses though denitrification and/or anammox transfer to nitrogen gas (N_2). After 1951, when hypoxic conditions prevail, P recycling is enhanced due to poor sediment adsorption of reduced sediments, but denitrification is enhanced and proportionally less N is recycled. Increased P-stimulated nitrogen fixation (N_2) maintains high primary production, sedimentation and deep water oxygen consumption.

than is added as input from land (Conley and others 2002). High rates of denitrification (Rönner 1985) and poor P adsorption (Blomqvist and others 2004) maintain the low Baltic N:P ratio, which favors N_2-fixing cyanobacterial blooms (Niemi 1979; Larsson and others 2001; Nausch and others 2003, Vahtera and others 2007). A 'vicious circle' (Figure 6) characterizes the Baltic Sea since the 1950s, similar to that in many lakes, where internal source and sink terms maintain the system in a eutrophic state, long after external loads are reduced.

DISCUSSION

The ecosystem model outputs presented above are consistent with previously published hind-casts of fish stock dynamics (Figure 5), which allows us to use the model to explore possible mechanisms be-

hind these dynamics. We found that human impacts were important driving forces throughout the last century, as already suggested by Elmgren (1989): first hunting reduced seals and allowed cod to become the dominant top predator, then increased nutrient loading took the system from an oligotrophic to a eutrophic state and most recently fishing reduced the cod stock and allowed ecosystem domination for clupeid fish (the major prey of cod). Of these shifts, only the change to a eutrophic state is likely to be a true regime shift, with a documented mechanism for a hysteresis effect. Although the results indicate that all changes were probably ultimately the result of human impacts, the timing of some shifts was probably influenced by hydrographic events. The virtual elimination of top-level predators (seals and cod) has resulted in an ecosystem with strongly reduced populations of long-lived species, and we speculate that this increases the likelihood of drastic population fluctuations of lower trophic levels in today's Baltic Sea.

The Shift from Seals to Cod

Thurow (1999a) hypothesized that the first increase in cod biomass was due to good spawning conditions in 1922–1939 (that is, high oxygen and salinity levels in the deep basins). However, conditions were favorable also earlier in the century (MacKenzie and others 2002; Fonselius and Valderrama 2003) and the second increase (late 1970s) occurred under worse spawning conditions (compare this study) and higher fishing intensity (MacKenzie and others 2002) than earlier in the century. This indicates that other factors influenced the cod stock more the than spawning conditions. Based on our modeling results we propose that reduced predation from seals made this first increase of cod possible.

Estimated herring and sprat biomasses early in the century (Thurow 1999b; this study) indicate that these clupeids did not initially respond as positively as cod to the decreased predation by seals, probably because predation by cod increased. Around 1950, when the cod stock had stabilized, estimated herring and subsequently also sprat stocks increased (Thurow 1999b; this study). A possible explanation for this increase is the shift to more eutrophic conditions that started in this decade (see below). The modeling results also indicate that decreased seal predation was more important in the early twentieth century, whereas increased productivity was a primary driver during the latter half of the century. After the mid-1970s, when cod increased again, clupeid stocks decreased as a probable result of increased cod predation and an intensive fishery. Cod predation on clupeids probably intensified as cod were forced to prey more on pelagic fish as benthic conditions deteriorated (see below). To conclude, we suggest that there was a major ecosystem change after the 1930s, from a state with marine mammals as top predators to a cod-dominated state. We are unaware of any changes caused by cod that could stabilize the reduced mammal population and a pattern of hysteresis is unlikely between these ecosystem ''states''.

The Shift to a Eutrophic Sea

According to the modeling results presented, eutrophication has resulted in a substantial increase in fish production. We regard the changes from an oligotrophic to a eutrophic sea as a regime shift, in part due to the substantial effects these changes appear to have had on the food web. The synthesized data on oxygen content indicate that the regime shift from an oligotrophic to a more eutrophic sea were triggered in 1951, when the largest inflow of saline water of the century was followed by a long stagnation period (Fonselius and Valderrama 2003). Since then, oxygen depleted deep water has been a chronic feature of the Baltic, only occasionally interrupted by inflows of saltier sea water rich in oxygen (Schinke and Matthaus 1998), which is soon depleted. Increasing anthropogenic nutrient loads after the Second World War (Larsson and others 1985) boosted primary production (Stigebrandt 1991) causing increased sedimentation of organic matter and oxygen consumption. Surface layer concentrations of phosphate were still relatively low when regular measurements started in the early 1960s, but increased rapidly from the mid-1960s (during ~10 years). About half a decade later, a similar rapid increase in nitrate concentration was recorded (Nehring and Matthäus 1991), perhaps partly due to increased nitrogen fixation by cyanobacteria, stimulated by increased phosphorus availability (Poutanen and Nikkilä 2001). This state is presumably maintained by a combination of continued high anthropogenic nutrient loads and inefficient phosphorus precipitation (Blomqvist and others 2004). A mechanism for a hysteresis effect for transitions between these states thus exists.

Hypoxic conditions have occurred previously in the deep basins during long stagnations periods (Hallberg 1974), without the help of anthropogenic nutrient enrichment, but the areal extent was

probably much smaller than today. Actual observations are available from early 1900 and show a maximum area of less than 10,000 km^2, compared to more than 40,000 km^2 in the most recent decades.

Hypoxia had eliminated bottom fauna over vast areas below the halocline by 1958–1959 (Shurin 1960), causing a major disruption of the benthic food web (Elmgren 1989; Karlson and others 2002), and reducing feeding opportunities for cod (Shurin 1960). Benthic crustaceans were the main food of cod in the early twentieth century (Hessle 1923), but were replaced by clupeids in the second half of the century (Rudstam and others 1994), despite an increased biomass of benthic macrofauna above the halocline between 1920–1923 and 1976–1977 (Elmgren 1989).

The Shift from Cod to Clupeids

After the mid-1970s, fishing for cod increased and a few years of very strong recruitment resulted in catches of nearly 450,000 tons in 1984 (ICES 2004a), or 22% of the global cod catch (FAO 2007). Then cod recruitment declined due to worsening oxygen and salinity conditions during a long deep-water stagnation period, although fishing effort remained high (MacKenzie and others 2002; Fonselius and Valderrama 2003; ICES 2004a; Figure 6). Intensive fishing and eutrophication had synergetic effects—degraded environmental conditions made the cod stock more sensitive to fishing, and high fishing mortality made it more sensitive to adverse environmental conditions. When the cod stock plummeted in the late 1980s, sprat stocks increased dramatically (Figure 2). This increase has been ascribed to a combination of reduced cod predation (Rudstam and others 1994; MacKenzie and others 2002; Möllmann and others 2004) and favorable conditions for sprat reproduction (MacKenzie and Köster 2004). There was a significant negative correlation between cod and sprat biomass between 1974 and 2003 ($P < 0.0001$), possibly indicating top-down control (Worm and Myers 2003), but climate driven changes in zooplankton composition probably contributed to the shift. The main prey of cod larvae (*Pseudocalanus* sp.) decreased due to lower salinities (Köster and others 2005), whereas the main pray of sprat larvae (*Acartia spp.* and *Temora longicornis*) increased due to higher temperatures (Alheit and others 2005). By 1995, when the sprat stock had reached a historic record level, feeding conditions (zooplankton biomass) had deteriorated for adults of

both herring and sprat (Möllmann and others 2000; Casini and others 2006), indicating increased food competition (Möllmann and others 2004), as manifested in decreased stomach fullness and low mean weight at age in both herring and sprat (ICES 2004a; Möllmann and others 2004). This appears to have had cascading effects even on the piscivorous seabird common guillemot *Uria aalge* (Österblom and others 2006). As an alternative explanation to lower zooplankton biomass, Vuorinen and others (1998) and Hänninen and others (2000) proposed that lower salinity led to dominance by smaller zooplankton. The salinity reduction was caused by the same reduction of inflows of saline water from Kattegat that hampered cod reproduction and contributed to the cod stock decline and hence the increase in sprat. This makes it difficult to determine the ultimate cause of the changes in zooplankton.

Clupeids have been proposed to stabilize this clupeid-dominated regime by feeding on cod eggs and larvae (Köster and Möllmann 2000) and possibly also by competing with young cod for their main zooplankton prey (Hinrichsen and others 2002; Möllmann and others 2004). Similar shifts between predatory and prey fish species are well documented elsewhere (De Roos and Persson 2002; Carpenter 2003; Worm and Myers 2003), but so far there is nothing to suggest that a strong reduction in the cod fishery would not lead to a rapid recovery of the stock. On the contrary, the annual stock production (defined as landings plus the change in age 2+ stock biomass) per biomass is still high, and has actually increased slightly, from 0.46 in the 1970s to 0.49 in 2001–2004 (data for the cod population east of Bornholm, ICES 2006), despite less favorable oxygen and salinity conditions for cod reproduction. Predation by clupeids on cod roe and larvae, and competition over zooplankton prey, provide possible mechanisms for a dominance shift from cod to clupeids. However, there is no indication of an irreversible regime shift and it is still realistic to hope that the cod stock will rebound if managed properly.

Vulnerabiliy, Stability and Regime Shifts

Predation, hunting and fishing affect the most critical life-history trait in seal, cod and zooplanktivorous fish populations, as iteroparous organisms are most vulnerable to variations in adult survival (Jonsson and Ebenman 2001). We have depleted the Baltic Sea of omnivorous top predators (seals and cod), thereby substantially altering the abundance of key species. As a consequence, large

Table 2. Summary of Proposed Trophic Cascades, Regime Shifts and Stabilizing Mechanisms

Ecosystem change	Timing	Geographical extent	Character	Maintained by
The shift from seals to cod	After the 1930s	Entire Baltic (ICES SD 22–32)	Rapid transition in upper trophic levels: cod main predator	Hunting before1960. By the 1970s seal populations were kept low by reproduction impairment caused by toxic pollutants
The shift to a eutrophicated sea	1951 to ~1970	Basin scale change (ICES SD 23–29)	Shift to widespread hypoxia in deep waters and frequent algal blooms	External N and P inputs, boosted by internal P recycling, which stimulates nitrogen fixation (stabilizing new state)
The shift from cod to clupeids	~1989	Entire Baltic (ICES SD 22–32)	Rapid transition in upper trophic levels: reduced top-down control	Overfishing and bad conditions for reproduction of cod, clupeids also eat cod eggs and larvae, and compete with young cod for zooplankton (possibly stabilizing new state)

population fluctuations at lower trophic levels become more likely (Jackson and others 2001), as described here for zooplanktivorous fish stocks and zooplankton. Examples from lakes (Carpenter 2003) as well as large marine ecosystems (Frank and others 2005) show that such dynamics can change the grazing pressure on phytoplankton and amplify the effect of nutrient enrichment on algal blooms.

Rapid changes in species composition will occur when the dynamic balance of consumer and resource control is distorted (Worm and others 2002). In this study, there was a striking change in species composition in the mid-1970s, when primary production increased simultaneously with a further reduction of the seal stock, although our model results suggest that the effects of the reduced top-down control by seals during this period had small effects.

We have discussed three rather abrupt ecological transitions in the Baltic Sea, which we describe as regime shifts. We have also identified potential positive feedbacks that may have stabilizing effects on two of these shifts (Table 2). We argue that the shift from an oligotrophic to a eutrophic state represents a true regime shift, stabilized by a hysteresis effect, caused by a well-documented mechanism. There are also mechanisms that could stabilize the shift from a cod to a clupeid dominated ecosystem, but there is no evidence the system has been pushed that far yet. Similar observations of reduced top-down control (mammal and cod predation) and eutrophication-related hypoxia have been made elsewhere (Jackson and others 2001; Frank and others 2005). To our knowledge, this is the first study that demonstrates a sequence of three successive shifts involving such mechanisms.

The described shifts were caused mainly by human impacts, but were also influenced by abiotic conditions and food web interactions. The oligotrophic regime appeared initially relatively resilient to increased nutrient loading, as long as internal nutrient sinks, P adsorption and denitrification, buffered the increase. Given that more nutrients are now in circulation, a shift back to an oligotrophic state may require both drastically reduced nutrient inputs and large and repeated deep water inflows that give longer periods of deep water oxygenation. There is a risk that today's anthropogenically nutrient-enriched Baltic is more resilient than the original, oligotrophic state. In addition, the current clupeid dominated state, which may exacerbate eutrophication, may be more resilient than a cod-dominated state.

Future of the Baltic Sea Ecosystem

Measures implemented so far have not sufficiently reduced nutrient loads. Anoxic conditions in 2005 affected over 40,000 km^2, which is unparalleled in recorded history. We must expect this ecosystem to show large food web changes, even regime shifts, also in the future. Such likely but unpredictable ecological restructurings, in combination with (and possibly driven by) changes in climate (MacKenzie and others 2002; Döscher and Meier 2004; MacKenzie and Köster 2004), will be a difficult challenge for international management of the Baltic environment and fishery.

The cod stock is now so overfished that its recruitment is seriously diminished. It is realistic to fear that a continued reduction of the stock may result in a situation where clupeids become able to control cod, through predation on eggs and larvae and competition for zooplankton. The ecosystem will then have undergone another true regime shift, which may make it very difficult to restore an exploitable cod stock. To prevent this, time is precious. The seal populations are now increasing rapidly and their predation may again become a bottleneck for cod, reducing our chances of rebuilding the cod stock through wise fisheries management. Rebuilding measures (that is, reduced fishing effort) is likely to have a substantial effect on the cod stock and could be especially efficient after a large inflow of saline water.

Similar management measures, coupling strong management efforts to favorable conditions, have been proposed for restoring degraded arid ecosystems by grazer control during El Niño Southern Oscillation (ENSO) events (Holmgren and Scheffer 2001).

Conclusions

We can identify four different ecosystem states in terms of fish production in the Baltic Sea during the twentieth century, separated by three rather distinct shifts. Modeling analyses suggest that the first shift, from a seal-dominated system with very low fish biomass and production, to a system with intermediate levels of fish biomass, can be explained mainly by release from seal predation. We have no reason to believe that this shift was a true regime shift (that is, no reasonable mechanism for a hysteresis phenomenon). The second shift, from intermediate to high fish production and even smaller seal populations, can be explained mainly by anthropogenic eutrophication. This shift may be a true regime shift, as increased phosphorus release from anoxic bottoms and enhanced nitrogen fixation can provide stabilizing mechanisms. The last shift from a cod- to a clupeid-dominated system appears not to be a true regime shift, although a potential stabilizing feed-back mechanism exists (clupeid predation on zooplankton and cod eggs and larvae). Continued overfishing of cod, or increased populations of clupeids, may force the ecosystem to a true regime shift.

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