

An empirical model of the Baltic Sea reveals the importance of social dynamics for ecological regime shifts

Steven J. Lade^{a,b,1}, Susa Niiranen^a, Jonas Hentati-Sundberg^a, Thorsten Blenckner^a, Wiebren J. Boonstra^a, Kirill Orach^a, Martin F. Quaas^c, Henrik Österblom^a, and Maja Schlüter^a

^aStockholm Resilience Centre, Stockholm University, 106 91 Stockholm, Sweden; ^bNordic Institute for Theoretical Physics, KTH Royal Institute of Technology and Stockholm University, 106 91 Stockholm, Sweden; and ^cDepartment of Economics, University of Kiel, 24118 Kiel, Germany

Edited by Bonnie J. McCay, Rutgers, The State University of New Jersey, New Brunswick, NJ, and approved June 23, 2015 (received for review March 12, 2015)

Regime shifts triggered by human activities and environmental changes have led to significant ecological and socioeconomic consequences in marine and terrestrial ecosystems worldwide. Ecological processes and feedbacks associated with regime shifts have received considerable attention, but human individual and collective behavior is rarely treated as an integrated component of such shifts. Here, we used generalized modeling to develop a coupled social–ecological model that integrated rich social and ecological data to investigate the role of social dynamics in the 1980s Baltic Sea cod boom and collapse. We showed that psychological, economic, and regulatory aspects of fisher decision making, in addition to ecological interactions, contributed both to the temporary persistence of the cod boom and to its subsequent collapse. These features of the social–ecological system also would have limited the effectiveness of stronger fishery regulations. Our results provide quantitative, empirical evidence that incorporating social dynamics into models of natural resources is critical for understanding how resources can be managed sustainably. We also show that generalized modeling, which is well-suited to collaborative model development and does not require detailed specification of causal relationships between system variables, can help tackle the complexities involved in creating and analyzing social–ecological models.

social–ecological systems | fisheries | generalized modeling | human decision making | feedback analysis

In recent decades, the world's biological and physical systems have experienced dramatic change (1, 2). Many marine ecosystems, for example, have undergone abrupt changes known as regime shifts (3, 4). In one prominent case, the Baltic cod fishery suddenly changed in the 1980s from historically high cod biomass and catches (henceforth the “cod boom”) to a sprat-dominant ecosystem with low cod abundance (5–8). This collapse, generally understood to have been precipitated by deteriorating environmental conditions and overfishing (7), had substantial negative socioeconomic impact on Baltic Sea fisheries, including among others the small-scale coastal fishery (9).

Ecological analyses of regime shifts, such as of the Baltic cod fishery (10), can capture the complex interplay of ecological and physical processes and drivers that trigger the shift. Numerous studies, however, have shown that understanding individual and collective human behavior is also critical for managing natural resources (11, 12) such as marine ecosystems (13, 14). Social–ecological system research responds to the need to incorporate humans as part of ecosystems by treating natural resource use as arising from linked systems of humans and nature, so-called social–ecological systems. Social–ecological system dynamics result from feedback loops involving biophysical processes, human behavior, and institutional processes within given social and biophysical contexts (15). Formal, quantitative analyses of the contributions of the social and biophysical subsystems to a social–ecological system's dynamics are rare, however, because

knowledge of social–ecological systems is often partial and spread over multiple disciplines (16).

Here, we tested the influence of social dynamics on a regime shift in a marine ecosystem using a formal modeling framework. Specifically, we investigated the significance of fisher decision making, as influenced by psychological, economic, and regulatory factors, on the 1980s boom and collapse of the Eastern Baltic cod stock. In a significant advance for natural resource modeling, and for social–ecological modeling more generally, use of the generalized modeling approach (17, 18) enabled us to empirically parameterize, dynamically model, and analyze the qualitative social and ecological dynamics of the Baltic cod fishery at comparable levels of detail and without detailed specification of causal relationships. The Baltic cod fishery was selected because the ecological dynamics during the cod boom and collapse have been well-studied (10, 19, 20), and information about fisher behavior and institutional settings, such as regulation and subsidy policy, is available. Additionally, the cod boom and collapse are qualitatively distinct features of the social–ecological system's dynamics that are amenable to the concepts and methods of dynamical systems theory (21), such as stability.

Model

We constructed a social–ecological model to investigate the role of social dynamics in the boom and collapse of the Baltic cod fishery during the 1980s. Due to available data, we based our

Significance

“Natural resource management is people management” is a cliché, but the effects of human behavior on the condition of natural resources, and vice versa, are often still not sufficiently acknowledged when modeling and managing natural resources. We constructed an empirically parameterized model of the boom and collapse of Baltic cod fisheries in the 1980s that explicitly took these two-way interactions between human action and ecological dynamics into account. We used novel methods of analysis based on generalized modeling to demonstrate how the interplay of social and ecological processes can be critically important for understanding and managing the dynamics of cod stocks and fisher welfare in the Baltic, as well as ecosystems and human well-being in general.

Author contributions: S.J.L. and M.S. designed research; S.J.L., S.N., J.H.-S., T.B., W.J.B., K.O., M.F.Q., H.Ö., and M.S. performed research; S.J.L. analyzed data; S.J.L., S.N., J.H.-S., T.B., W.J.B., K.O., M.F.Q., H.Ö., and M.S. wrote the paper; and S.N., J.H.-S., W.J.B., and M.F.Q. contributed data.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹To whom correspondence should be addressed. Email: steven.lade@su.se.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1504954112/-DCSupplemental.

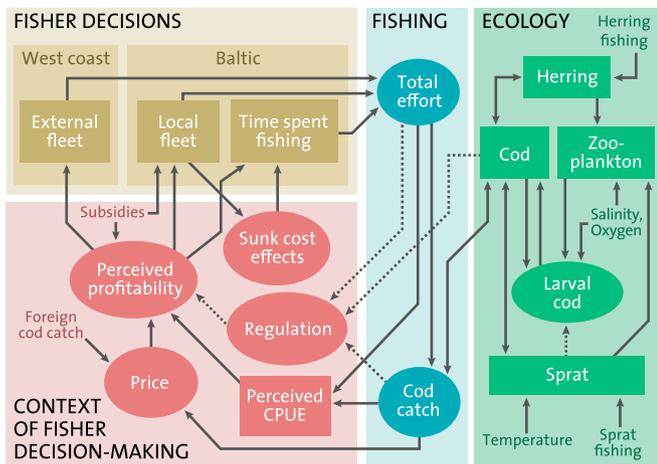


Fig. 1. Illustration of the model. Simplified version of the collaboratively developed causal loop diagram (Fig. S1), illustrating the main processes and feedbacks in the model. Arrows indicate the direction of influence of one quantity on another. Boxes indicate stocks; ovals denote intermediate variables; smaller text indicates some of the external drivers. Dotted lines indicate interactions included in hypothetical model “experiments.”

model on the Swedish cod fishery. Under these temporal and spatial system boundaries, a team of Baltic Sea experts from the natural and social sciences collaboratively developed a conceptual model of the key ecological and social quantities and processes that contributed to cod stock dynamics (Fig. 1 and Fig. S1).

This conceptual model was further formalized into a generalized model (SI Appendix), a dynamical systems model in which processes are represented only with abstract “placeholder functions” (17, 18, 22). Instead of parameterizing the model functions directly, generalized modeling requires values for the three classes of the so-called generalized parameters: α parameters, which determine the time scale at which different state variables operate; β parameters, which specify the relative contributions of two processes to a state variable; and elasticities, which can be interpreted as the local nonlinearities of links. The generalized parameters, combined with the generalized model, allow system stability to be calculated. In the dynamical systems sense used here, a social–ecological system is stable if it can recover from small social or ecological shocks to its previous state. Stability is important because a regime shift, such as the cod collapse, can often be associated with a loss of stability (18, 23, 24). We do not use “stability” in any normative sense but rather as a predicted or observed property of a system’s dynamics. Generalized parameters were obtained from a combination of empirical data, such as stock assessment and fleet composition data, analysis of pre-existing empirically calibrated models, and theoretical assumptions.

Social Processes. The Swedish Baltic cod fishing fleet in the early 1980s consisted of relatively small vessels fishing mainly with passive gear, such as gillnets. An external fleet, mostly from the Swedish west coast, started to fish Baltic cod around the same time (25). Three factors influencing fishing pressure exerted by these fisher groups on the cod stock were identified and modeled (Fig. 1): the size of the fleet of local fishers; the average amount of time that a vessel was used for fishing during a season; and the size of the external fleet. Heterogeneities in the fishing fleet beyond the distinction between local and external (26) were not modeled. Investment in fishing vessels, changes in time spent fishing, and the movement of the external fleet in turn resulted from complex decisions taken by the fishers involved. We now describe the factors influencing fisher decision making that were included in our model (Fig. 1).

Because fishers relied on cod for a substantial proportion of their income (27), we assumed that the profitability of the cod fishery was an important influence on their decisions. We modeled fishers’ expectations of future returns on fishing effort based on their current perception of catch per unit effort (CPUE) for cod and the price of cod on the Swedish domestic market. Price was modeled as an imperfectly elastic market response to domestic supply and was affected by the availability of non-Swedish cod as a substitute for domestic supply. Fishery regulations were largely either nonexistent (for example, no catch quotas for cod existed at that time) or not significant due to lack of consistent monitoring (8) and were not modeled. The unemployment benefits, fleet purchase subsidies, and price supplements for catches that had been present for several decades (8, 28) were assumed to affect local fisher decision making.

A number of noneconomic factors that could have affected fisher decision making were also included in the model. Social identity (29), risk aversion (30), and other factors may have contributed to delaying fishers’ responses to changing stock levels (31, 32). Time spent fishing was therefore treated as a “stock” in the system dynamics sense (33): that is, a quantity that only gradually responds to changes in input. In the model, fishers tend to maintain their time spent fishing at the same level, with changing ecological or socioeconomic conditions leading only to a gradual response to that change. These noneconomic factors may additionally have influenced updating of perceptions about the state of the resource; perceived CPUE was therefore also treated as a stock. Lastly, sunk cost effects, the tendency to continue an endeavor once an investment in money, effort, or time has been made (34, 35), are believed to have contributed to the persistence of a high level of cod fishing despite the collapse of the cod stock (36). Sunk cost effects were represented by giving the local fleet variable, which is also a system dynamics stock, a long characteristic time scale and including a directed influence from local fleet size onto time spent fishing.

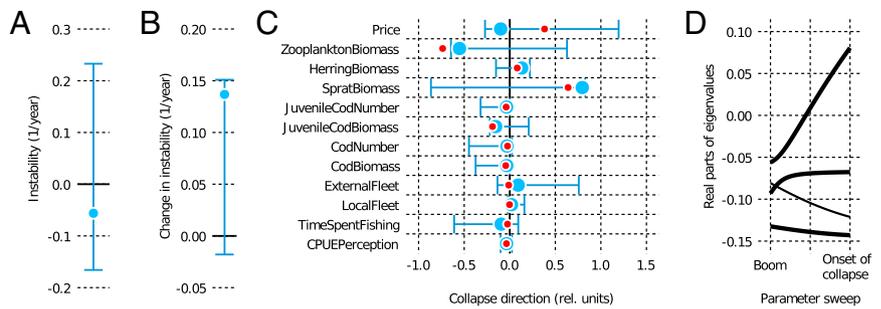
Ecological Processes. Important ecosystem dynamics were included by modeling biomasses of sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and the zooplankton species *Pseudocalanus acuspes* (hereafter “zooplankton”), in addition to cod (*Gadus morhua*). Sprat and herring were important prey species for cod, as was zooplankton for sprat, herring, and cod larvae (20, 37). Biomasses of sprat and zooplankton displayed rapid changes at a similar time to the cod collapse (38) and are believed to have been involved in a prey-to-predator loop that encouraged a low-cod, high-sprat state after the collapse (7). The relatively short maturation times of these three prey species meant that their populations could each be approximated as a single biomass pool with instantaneous recruitment. The long maturation time of cod (typically 42 mo) demanded that both biomasses and numbers of cod be modeled in two separate stages: juveniles and adults (SI Appendix).

Biophysical drivers, such as salinity and temperature, are known to have contributed to triggering the cod collapse (7). Although we did not model these drivers directly, their impacts are indirectly present through their effects on the empirical catch and diet data that we used to parameterize the ecological components of the system.

Results

Is the Model a Valid Representation of the Baltic Cod Fishery Social–Ecological System? The generalized modeling procedure is designed to assess stability; it cannot produce time series output and therefore cannot be calibrated against historical time series like a simulation model. There were known features of the Swedish Baltic cod fishery’s dynamics, however, against which the model could be validated (7, 19, 38). First, a high biomass of cod persisted over several years during the boom; the coupled social–ecological system should therefore be stable during this period.

Fig. 2. Model validation. (A) Stability of the social-ecological system during the boom (positive/negative numbers indicate an unstable/a stable system). (B) Change in stability at the onset of the collapse (positive/negative numbers indicate an increased/decreased instability). (C) The predicted directions of changes in the social-ecological system at the time of collapse, calculated from the eigenvector of the dominant eigenvalue (18) relative to the known collapse in cod biomass, using the Jacobian during the boom (blue) and the start of the collapse (red) (positive/negative numbers indicate a predicted increase/decrease in the quantity during the collapse). (D) Eigenvalue spectrum, as generalized parameters were simultaneously and linearly swept from their values during the boom to the onset of the collapse. The real parts of the five most dominant eigenvalues are shown, consisting of three purely real eigenvalues (thick lines) and one complex conjugate eigenvalue pair (thin line). In A–C, dots indicate mean values, and bars indicate 95% confidence interval. For the uncertainty in B, only the contributions of those parameters with data available on their change (or lack thereof) were included.



Second, by 1985, the cod stock was beginning to collapse, which, as discussed above, can generally be associated with a decrease in stability. Third, a catastrophic loss of stability, such as the fold bifurcation (39), is consistent with the Baltic cod's large and sudden collapse. Fourth, the biomasses of cod and zooplankton decreased steeply as a consequence of the collapse (herring stock also decreased, but more gradually) whereas sprat biomass increased, cod price increased, and the local fishing fleet size started to decline (40). Although the empirical uncertainties were large, the mean estimated results passed all validation tests (Fig. 2 A–D), with the exception of partial success for the directions in which system variables changed during the collapse (Fig. 2C). The generalized model best predicted changes in the social-ecological system associated with the cod collapse when data closest to the actual collapse were used (Fig. 2C). We conclude that the social-ecological model is qualitatively consistent with the boom and collapse of the Swedish Baltic cod fishery.

Two key model assumptions about fisher decision making and the ecology were also tested. The first assumption was that fishers behaved such as to maximize short-term profit (32). Modeling fishers instead as satisficers (41) who sought to maintain a particular level of income over time and therefore were likely to increase time spent fishing with decreasing perceived profitability had only a small effect on stability (Fig. 3). Second, including the proposed feedback whereby sprat consume cod eggs (42) had little effect on stability (Fig. 3) at the estimated level of egg consumption. We concluded that the model results were largely independent of these assumptions. Because higher rates of cod egg consumption by sprat, however, led to a strong destabilizing influence in the model, the strength of this link should receive further empirical investigation.

How Did Social and Ecological Processes Contribute to Social-Ecological System Dynamics? We tested the relative importance of social and ecological processes for the stability of the social-ecological system by comparing its stability with those of its decoupled subsystems. The ecological system under assumption of constant fishing effort, thus decoupled from social processes, may in fact have been unstable during the cod boom (Fig. 4A). Specific ecological feedbacks contributing to this instability are described in detail in *Which Feedbacks Drove the Cod Collapse?*. In the coupled social-ecological system, however, social feedbacks involving adaptive fisher decision making may have stabilized an otherwise unstable ecosystem during the boom (Fig. 4A), ensuring that the cod boom persisted at least temporarily. However, the social feedbacks could not mitigate the later increases in ecosystem instability (Fig. 4B).

At the time of the collapse, the instability of the social-ecological system may actually have increased more than in the ecosystem alone (Fig. 4B) (again, a process-based explanation is provided in *Which Feedbacks Drove the Cod Collapse?*). An ecosystem-only

analysis, therefore, might have underestimated the increase in instability of the actual social-ecological system. Emergence of large-scale dynamics (here, destabilization) not present in the component subsystems is indeed a classic complex systems phenomenon (43).

Which Feedbacks Drove the Cod Collapse? A prey-to-predator loop, in which sprat when present in large numbers can outcompete larval cod for its zooplankton prey (44, 45), is likely to have been the dominant destabilizing feedback in the coupled social-ecological system, both during the boom and at the onset of the collapse (Fig. 4D). This feedback loop strengthened significantly between the boom and the onset of the collapse (Fig. 4D). Increased mortality of zooplankton due to consumption by sprat contributed most to this change in strength although other components of the loop were also important (Fig. S2).

Applying the same feedback loop analysis to the decoupled ecological system (Fig. 4C) provided a possible explanation for the different changes in stability in the ecological and social-ecological systems described above (Fig. 4B). During the boom, the dominant destabilizing feedback loop in the decoupled ecological system may actually have been the risk of depensatory collapse (46, 47) in the cod stock, in which a population becomes unable to sustain itself. Therefore, in the stability analysis of the decoupled ecological system, the strengthening of the prey-to-predator loop was partially masked by the cod depensation feedback loop. In the coupled social-ecological system, this masking was not present due to adaptive fisher behavior reducing the risk of depensatory cod collapse.

The overlapping nature of the social feedback loops complicated feedback loop analysis of the decoupled social system (in

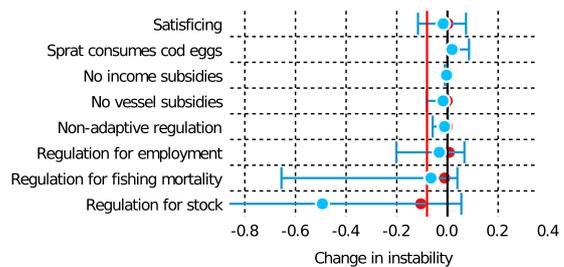


Fig. 3. Model experiments. Effect on instability during the cod boom (blue) and at the onset of the cod collapse (red) of hypothetical modifications to the system to (from top to bottom): test sensitivity to model assumptions (two experiments); remove subsidies (two experiments); apply fixed regulations (one experiment); and apply adaptive regulations (three experiments). The minimum change in instability that would have been required to stabilize the social-ecological system at the onset of the collapse is indicated (red line). Dots indicate mean values, and bars indicate 95% confidence interval.

Discussion

Our analysis of the Baltic cod fishery social–ecological system highlighted the importance of human individual and institutional behavior for ecosystem regime shifts. Using a generalized modeling approach, we showed that adaptive fishing effort arising from fisher decision making contributed to temporarily maintaining an otherwise unstable high cod stock in the Baltic Sea. Limitations to fisher adaptability, however, meant that ecosystem nonlinearities, strengthened by environmental changes, eventually led to a regime shift. Ecological feedbacks also affected social processes: the ability of strengthened fishery regulations in the Baltic to avert the regime shift would have been highly dependent on ecological nonlinearities, in addition to characteristics of fisher decision making and regulatory settings. Adaptive management based on ecosystem feedback (such as the status of the cod stock) was more likely to have been successful than fixed regulation. Although the cod boom was too short (only 6 y) and uncertainties therefore too large to allow for a definitive conclusion, these quantitative, empirically based results indicate that social processes and feedbacks can be critical for how and when ecological regime shifts unfold.

Ecological models are capable of reproducing the dynamics of ecological regime shifts by using time-varying inputs, such as catch data, to represent human impacts. They can investigate, however, neither the processes driving changing catch and effort nor the social–ecological feedbacks in which these processes participate and which drive the social–ecological system into a new state. Our social–ecological model, which incorporated feedbacks between complex ecosystem change and complex human responses, showed that, without a social–ecological perspective, the increase in instability in the Baltic cod fishery may have been greatly underestimated. In particular, the lack of adaptive fisher behavior in the decoupled ecological model led to inaccurate estimation of initial system instability based on that model. Our results underline that social processes, noneconomic as well as economic, are important for understanding and governing the dynamics of natural resources.

The model presented here represents a significant advance for natural resource management and social–ecological system research. Building on a rich history of empirical reflections on sustainable and unsustainable natural resource use (15, 58, 59) and theoretical investigations of generic processes (60–64), we sought a middle ground by studying the Baltic Sea cod fishery social–ecological system using a formal and empirically grounded social–ecological model. The generalized modeling framework allowed us to empirically parameterize models of social and ecological processes even though their precise causal relationships were often not known. The resulting model permitted a range of thorough and mathematically rigorous analyses that are not commonly available to other social–ecological models, such as agent-based models (65, 66). Especially when combined with causal loop diagrams as a collaborative or participatory modeling tool, generalized modeling can be used to understand the qualitative dynamics of many natural resource management problems, as well as social–ecological systems more generally (18).

Our study provides managers and policy makers with an in-depth, empirically grounded analysis of the role of social processes for the dynamics of natural resources. Expanding the boundaries of an ecosystem model to include these social processes allowed a nuanced understanding to be developed of the interactions between the nonlinear dynamics of a natural resource, decision making regarding exploitation of the resource, the resource governance system, markets, and different fisher groups. For example, we showed that the success of regulations to avoid regime shifts may depend on the proximity of the regulatory responses to the processes responsible for system

collapse. Results from the study highlight the importance of human adaptive responses but also point to limitations to adaptation resulting from psychological and institutional constraints and biophysically driven ecological dynamics. These insights and the new modeling techniques developed here contribute toward future policy development for sustainable ecosystems for the well-being of current and future generations.

Materials and Methods

Generalized Model. As described in *Model*, a conceptual model was developed (Fig. S1) that outlined the key state variables and their interactions. This conceptual model was translated into a mathematical form known as a generalized model (17, 18), which contains symbolic placeholder functions instead of fully specified functional forms (SI Appendix).

Derivation of Jacobian. The fishery system was assumed to be in a ‘dynamic regime’ in the vicinity of a fixed point (18, 39). State variables were rescaled and the Jacobian matrix of the system symbolically calculated at that fixed point (SI Appendix), to quantify the stability of that dynamic regime.

Parameterization of Jacobian (Dataset S1). Based on time series of cod biomass (67), the years 1980–1984 were identified as the cod boom and the principal time period for which parameters were estimated. We used the year 1985 to investigate changes in the social–ecological system associated with the onset of the cod collapse, avoiding later time periods during the collapse due to generalized modeling’s requirement for the system to be near a fixed point.

Ecological β parameters were extracted from annual catch data (67) and estimates of diet following Tomczak et al. (10). Ecological data were aggregated across the open Baltic Proper [International Council for the Exploration of the Sea (ICES) areas 25–28, excluding the Gulf of Riga], the main region of cod abundance and where commercial fishing was concentrated. The ecological α parameters were either basic life history characteristics, such as maturation time, or commonly made assumptions, such as natural mortality. Ecological elasticities, which cannot be obtained directly from catch data, were extracted from the functional forms in the Ecosim simulation model of the Central Baltic Sea (10), which itself had been calibrated against fishery and lower trophic level data.

For the social system, data were available on fleet composition (68), income subsidies (27), external cod supply (69), and catch elasticities (48). The remaining β parameters were based on qualitative information from subsidy policy (28) and fisher interviews (26). For α parameters, the key assumption was an ordering (from slowest to fastest) of LocalFleet < ExternalFleet < CPUEPerception < TimeSpentFishing. Many social elasticities listed in Dataset S1 are 1 (that is, linear) by definition; for the remaining elasticities, a value of 1 with a range 0.5–2 was used. Except for the market data, none of the social data had sufficiently fine temporal resolution to estimate parameters for both 1980–1984 (boom) and 1985 (beginning of collapse); in the parameterization, we therefore assumed no change.

Analysis of Generalized Model. After removal of localized modes (SI Appendix), various properties of the Jacobian matrix were calculated (18). In this article, the “instability” of the system refers to the real part of the dominant eigenvalue of the Jacobian matrix. Unless otherwise indicated, dots on all graphs indicate the mean values for the respective time period, and the error bars represent a 95% confidence interval. For parameters calculated from annual ICES data, we calculated the means of the parameters during the boom (1980–1984) and assigned uniform probability distributions covering their ranges as their uncertainty distributions. For other parameters without annual data during the boom, uncertainty ranges were conservatively estimated. For the onset of the cod collapse, confidence intervals were not estimated because only 1 y of data (1985) was used.

ACKNOWLEDGMENTS. We thank Beth Fulton and Carl Folke for helpful comments on the manuscript. The research leading to these results received funding from the European Research Council under the European Union’s Seventh Framework Programme (FP/2007–2013)/ERC Grant Agreement 283950 SES-LINK (to S.J.L., K.O., and M.S.); a core grant to the Stockholm Resilience Centre by Mistra; Project Grants 2009–252 and 2013–1293 from the Swedish Research Council Formas; the Baltic Ecosystem Adaptive Management programme (to H.Ö. and T.B.); and the Nordic Centre for Research on Marine Ecosystems and Resources under Climate Change.

1. Steffen W, Broadgate W, Deutsch L, Gaffney O, Ludwig C (2015) The trajectory of the Anthropocene: The Great Acceleration. *Anthropocene Rev* 2(1):81–98.
2. Steffen W, et al. (2015) Planetary boundaries: Guiding human development on a changing planet. *Science* 347(6223):1259855.
3. Möllmann C, Folke C, Edwards M, Conversi A (2014) Marine regime shifts around the globe: Theory, drivers and impacts. *Philos Trans R Soc Lond B Biol Sci* 370(1659): 20130260.
4. Rocha J, Yletyinen J, Biggs R, Blenckner T, Peterson G (2014) Marine regime shifts: Drivers and impacts on ecosystems services. *Philos Trans R Soc Lond B Biol Sci* 370(1659): 20130273.
5. Österblom H, et al. (2007) Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10(6):877–889.
6. Eero M, Köster FW, MacKenzie BR (2008) Reconstructing historical stock development of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea before the beginning of intensive exploitation. *Can J Fish Aquat Sci* 65(12):2728–2741.
7. Möllmann C, et al. (2009) Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: A discontinuous regime shift in the Central Baltic Sea. *Glob Change Biol* 15(6):1377–1393.
8. Statens Offentliga Utredningar (1993) *Svenskt Fiske: Slutbetänkande av Utredningen om Fiskerinäringens Utvecklingsmöjligheter* (Allmänna Förlaget, Stockholm).
9. Hentati-Sundberg J, Hjelm J, Boonstra WJ, Österblom H (2015) Management forcing increased specialization in a fishery system. *Ecosystems* (N Y) 18(1):45–61.
10. Tomczak MT, Niiranen S, Hjerne O, Blenckner T (2012) Ecosystem flow dynamics in the Baltic Proper: Using a multi-trophic dataset as a basis for food–web modelling. *Ecol Modell* 230:123–147.
11. Fulton EA, Smith ADM, Smith DC, Van Putten IE (2011) Human behaviour: The key source of uncertainty in fisheries management. *Fish Fish* 12(1):2–17.
12. Palmer PI, Smith MJ (2014) Earth systems: Model human adaptation to climate change. *Nature* 512(7515):365–366.
13. Österblom H, et al. (2013) Modeling social-ecological scenarios in marine systems. *Bioscience* 63(9):735–744.
14. Hilborn R (2007) Managing fisheries is managing people: What has been learned? *Fish Fish* 8(4):285–296.
15. Berkes F, Folke C, eds (1998) *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience* (Cambridge University Press, Cambridge, UK).
16. Schlüter M, et al. (2012) New horizons for managing the environment: A review of coupled social-ecological systems modeling. *Nat Resour Model* 25(1):219–272.
17. Gross T, Feudel U (2006) Generalized models as a universal approach to the analysis of nonlinear dynamical systems. *Phys Rev E Stat Nonlin Soft Matter Phys* 73(1 Pt 2): 016205.
18. Lade SJ, Niiranen S, Schlüter M (2015) Generalized modeling of empirical social-ecological systems. arxiv.org/abs/1503.02846.
19. Casini M, et al. (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proc Biol Sci* 275(1644):1793–1801.
20. Köster F, et al. (2005) Baltic cod recruitment: The impact of climate and species interaction. *ICES J Mar Sci* 62(7):1408–1425.
21. Kuznetsov Y (2010) *Elements of Applied Bifurcation Theory* (Springer, New York).
22. Kuehn C, Siegmund S, Gross T (2013) Dynamical analysis of evolution equations in generalized models. *IMA J Appl Math* 78(5):1051–1077.
23. Biggs R, et al. (2012) *Encyclopedia of Theoretical Ecology*, eds Hastings A, Gross LJ (Univ of California Press, Oakland, CA), pp 609–617.
24. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413(6856):591–596.
25. Berggren M (2013) Is growing larger the same as becoming resilient? A case study of the Gothenburg pelagic offshore fishery. Masters dissertation (Stockholm University, Stockholm).
26. Boonstra WJ, Hentati-Sundberg J (2014) Classifying fishers' behaviour: An invitation to fishing styles. *Fish Fish*, 10.1111/faf.12092.
27. Statistics Sweden (1982) *Fiskeristatistik Årsbok 1982* (Allmänna Förlaget, Stockholm).
28. Swedish Code of Statutes (1978) *Förordningen om statligt stöd till fiskets rationalisering, m. m.*, Svensk författningssamling (SFS) 1978:516.
29. Sonvisen SA (2014) Contemporary fisher images: Ideologies, policies and diversity. *J Rural Stud* 34:193–203.
30. Dowling NA, Wilcox C, Mangel M (2015) Risk sensitivity and the behaviour of fishing vessels. *Fish Fish* 16(3):399–425.
31. Boonstra WJ, Österblom H (2014) A chain of fools: Or, why it is so hard to stop overfishing. *Marit Stud* 13:15.
32. Van Putten IE, et al. (2012) Theories and behavioural drivers underlying fleet dynamics models. *Fish Fish* 13(2):216–235.
33. Sterman JD (2000) *Business Dynamics: Systems Thinking and Modeling for a Complex World* (Irwin/McGraw-Hill, Boston).
34. Arkes HR, Blumer C (1985) The psychology of sunk cost. *Organ Behav Hum Decis Process* 35(1):124–140.
35. Janssen MA, Scheffer M (2004) Overexploitation of renewable resources by ancient societies and the role of sunk-cost effects. *Ecol Soc* 9(1):6.
36. Hildén M (1997) Boundary conditions for the sustainable use of major fish stocks in the Baltic Sea. *Ecol Econ* 20(3):209–220.
37. Uzars D (1994) Feeding of cod (*Gadus morhua callarias* L.) in the Central Baltic in relation to environmental changes. *ICES Marine Sci Symp* 198:612–623.
38. Casini M, et al. (2009) Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc Natl Acad Sci USA* 106(1):197–202.
39. Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol Evol* 18(12):648–656.
40. Statistics Sweden (1971–1993) *Statistiska meddelanden Serie J* (Statistics Sweden, Stockholm).
41. Holland DS (2008) Are Fishermen Rational? A Fishing Expedition. *Mar Resour Econ* 23(3):325–344.
42. Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J Mar Sci* 57(2):310–323.
43. Levin SA (2005) Self-organization and the emergence of complexity in ecological systems. *Bioscience* 55(12):1075–1079.
44. Möllmann C, Müller-Karulis B, Kornilovs G, St John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: Regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES J Mar Sci* 65(3):302–310.
45. Walters C, Kitchell JF (2001) Cultivation/depensation effects on juvenile survival and recruitment: Implications for the theory of fishing. *Can J Fish Aquat Sci* 58(1):39–50.
46. De Roos AM, Persson L (2002) Size-dependent life-history traits promote catastrophic collapses of top predators. *Proc Natl Acad Sci USA* 99(20):12907–12912.
47. Liermann M, Hilborn R (2001) Depensation: Evidence, models and implications. *Fish Fish* 2(1):33–58.
48. Kronbak LG (2005) The dynamics of an open-access fishery: Baltic Sea cod. *Mar Resour Econ* 19:459–479.
49. IBSFC (1974) *Fishery Rules* (International Baltic Sea Fishery Commission, Warsaw).
50. Lindegren M, Möllmann C, Nielsen A, Stenseth NC (2009) Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proc Natl Acad Sci USA* 106(34):14722–14727.
51. Anderies JM, Rodriguez AA, Janssen MA, Cifaloz O (2007) Panaceas, uncertainty, and the robust control framework in sustainability science. *Proc Natl Acad Sci USA* 104(39):15194–15199.
52. Sethi G, Costello C, Fisher A, Hanemann M, Karp L (2005) Fishery management under multiple uncertainty. *J Environ Econ Manage* 50(2):300–318.
53. Council of the European Union (2007) *Council Regulation (EC) No. 1098/2007 of 18 September 2007 Establishing a Multiannual Plan for the Cod Stocks in the Baltic Sea and the Fisheries Exploiting Those Stocks, Amending Regulation (EEC) No. 2847/93 and Repealing Regulation (EC) No. 779/97* (European Commission, Brussels).
54. Saltelli A, et al. (2008) *Global Sensitivity Analysis: The Primer* (Wiley, Chichester, England).
55. Erisman BE, et al. (2011) The illusion of plenty: Hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Can J Fish Aquat Sci* 68(10):1705–1716.
56. Harley SJ, Myers RA, Dunn A (2001) Is catch-per-unit-effort proportional to abundance? *Can J Fish Aquat Sci* 58(9):1760–1772.
57. Hilborn R, Walters CJ (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty* (Kluwer, Boston).
58. Folke C (2006) Resilience: The emergence of a perspective for social–ecological systems analyses. *Glob Environ Change* 16(3):253–267.
59. Liu J, et al. (2007) Complexity of coupled human and natural systems. *Science* 317(5844):1513–1516.
60. Biggs R, Carpenter SR, Brock WA (2009) Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proc Natl Acad Sci USA* 106(3):826–831.
61. Carpenter S, Brock W, Hanson P (1999) Ecological and social dynamics in simple models of ecosystem management. *Conserv Ecol* 3(2):4.
62. Carpenter SR, Brock WA (2004) Spatial complexity, resilience, and policy diversity: Fishing on lake-rich landscapes. *Ecol Soc* 9(1):8.
63. Lade SJ, Tavoni A, Levin SA, Schlüter M (2013) Regime shifts in a social-ecological system. *Theor Ecol* 6(3):359–372.
64. Quaas MF, van Soest D, Baumgärtner S (2013) Complementarity, impatience, and the resilience of natural-resource-dependent economies. *J Environ Econ Manage* 66(1):15–32.
65. Fulton EA, et al. (2011) Lessons in modelling and management of marine ecosystems: The Atlantis experience. *Fish Fish* 12(2):171–188.
66. Lansing JS, Kremer JN (1993) Emergent properties of Balinese water temple networks: Coadaptation on a rugged fitness landscape. *Am Anthropol* 95(1):97–114.
67. ICES (2013) *Report of the Baltic Fisheries Assessment Working Group (WGBFAS)* (ICES Headquarters, Copenhagen).
68. Statens Offentliga Utredningar (1989) *Fiskprisregleringen och Fiskeriadministrations: Betänkande av 1989 års fiskerikutredning* (Allmänna Förlaget, Stockholm).
69. ICES (2013) *Report of the Arctic Fisheries Working Group (AFWG)* (ICES Headquarters, Copenhagen).
70. Kampmann CE (2012) Feedback loop gains and system behavior (1996). *Syst Dyn Rev* 28(4):370–395.
71. Kampmann CE, Oliva R (2009) *Encyclopedia of Complexity and Systems Science*, ed Meyers RA (Springer, New York), pp 8948–8967.
72. Oliva R (2004) Model structure analysis through graph theory: Partition heuristics and feedback structure decomposition. *Syst Dyn Rev* 20(4):313–336.
73. Quaas MF, Requate T (2013) Sushi or fish fingers? Seafood diversity, collapsing fish stocks, and multispecies fishery management. *Scand J Econ* 115(2):381–422.
74. Nielsen M (2006) Trade liberalisation, resource sustainability and welfare: The case of east Baltic cod. *Ecol Econ* 58(3):650–664.
75. Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev Fish Biol Fish* 7(2): 139–172.
76. Walters C, Pauly D, Christensen V, Kitchell JF (2000) Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* (N Y) 3(1):70–83.
77. Walters C, Christensen V, Walters W, Rose K (2010) Representation of multistanza life histories in ecosystem models for spatial organization of ecosystem trophic interaction patterns. *Bull Mar Sci* 86(2):439–459.
78. Aufderheide H, Rudolf L, Gross T (2012) Mesoscale symmetries explain dynamical equivalence of food webs. *New J Phys* 14(10):105014.