

Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach

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Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved July 2, 2009 (received for review June 13, 2009)

Worldwide a number of fish stocks have collapsed because of overfishing and climate-induced ecosystem changes. Developing ecosystem-based fisheries management (EBFM) to prevent these catastrophic events in the future requires ecological models incorporating both internal food-web dynamics and external drivers such as fishing and climate. Using a stochastic food-web model for a large marine ecosystem (i.e., the Baltic Sea) hosting a commercially important cod stock, we were able to reconstruct the history of the stock. Moreover we demonstrate that in hindsight the collapse could only have been avoidable by adapting fishing pressure to environmental conditions and food-web interactions. The modeling approach presented here represents a significant advance for EBFM, the application of which is important for sustainable resource management in the future.

ecosystem-based fisheries management | sustainability

Atlantic cod (*Gadus morhua*) is among the commercially most important fish species of the European waters. Many of the stocks have declined dramatically and still remain at historically low levels (1, 2). These collapses have largely resulted from overfishing (3, 4) and climate-driven declines in productivity (5, 6). The climate effect generally works through changes in the physical environment (e.g., temperature and salinity), but also through altered food supply for early life-history stages, eventually affecting recruitment (5, 6). In accordance with this effect, recruitment failure of Eastern Baltic cod was caused mainly by high egg and larval mortalities as a result of climate-induced hydrographic change (7, 8). In several areas the collapses of cod stocks were part or major drivers of large-scale reorganizations of ecosystems (9). These so-called regime shifts are frequently caused by climatic changes (9, 10) and/or over-exploitation resulting in cascading trophic interactions (11, 12). Similarly to other areas, the Baltic Sea underwent both regime shifts and trophic cascades (8, 13). Such alterations in ecosystem structure typically affect species interactions, eventually influencing food-web dynamics through both positive and negative feedback loops (14).

The recognition of the ecosystem context in the collapse of fish stocks has led to the development of more holistic ecosystem-based fisheries management (EBFM) approaches (15, 16). To be of value in decision making and management, ecosystem-based models require a manageable degree of complexity, to incorporate ecological detail, represent environmental and fishing effects, and provide estimates of uncertainty (17, 18). Statistical models have proven useful in incorporating key ecological and environmental drivers and evaluating multiple sources of uncertainty (19–21), an advantage over existing multispecies models for the Baltic Sea (22, 23). Multivariate autoregressive models [MAR(1)] provide a statistical framework for modeling food-web interactions at multiple trophic levels (14). Within this modeling framework, stochastic events such as environmental variability can be included to account for external forcing on the system's dynamics. By integrating multiple drivers and uncertainties the MAR(1) framework thus provides an important tool

for EBFM. Surprisingly, it has rarely been extended beyond theory, and its application to real food webs (24, 25) has, to our knowledge, never been used in fisheries management.

We applied the MAR(1) approach to the food web of the Baltic Sea, host to one of the formerly most productive cod stocks (7). The Baltic Sea upper trophic food web is dominated by cod and two competing planktivorous fish species, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Additionally, the species are forced top-down by fishing and bottom-up through zooplankton and environmental effects (Fig. 1). We modeled this simple food web by fitting a MAR(1) state-space model to a time series of population biomasses, fishing mortalities (F), and a number of abiotic and biotic variables, selected based on prior knowledge of their effects on fish stocks (see Table S1 and SI Text). Finally, the most parsimonious model in terms of the number of parameters and the explained variance was selected (Table S2 and Fig. S1).

Model Results and Validation

Model parameters of the selected model (Tables S3–S6) accurately captured the known mechanisms of species interactions within the food web and the effects of fishing, zooplankton, and environmental variability on the three species (Fig. 1). Density dependence was detected for all species. The strong effect on cod probably is caused by cannibalism (26), whereas food competition (27) and egg cannibalism may explain the effect on herring and sprat (28). Herring is additionally affected by sprat competition (27), although the opposite is not seen. Cod predation influences both prey species negatively, whereas only herring shows a significant net positive foraging effect on cod. Sprat predation on cod eggs may underlie the lack of positive effect on cod (29).

Climate-induced hydrographic change has markedly altered the Baltic Sea ecosystem (8, 13). Changes in salinity and oxygen conditions act both directly on cod recruitment (i.e., through egg and larval survival) or indirectly on the availability of *Pseudocalanus acuspes*, the main food source for larval cod (7). In our model, a 3-year lagged positive effect of salinity indicates a stronger direct environmental effect (Fig. 2B). The time lag corresponds to the recruitment phase of Baltic cod reaching maturity at the age of 4. Sea surface temperature (SST) lagged by 1 year strongly affects sprat (Fig. 2D), demonstrating its positive effect on recruitment (30). Although increased prey availability may indirectly add to this effect (30), the interaction with *Acartia* spp. did not significantly explain the variance in sprat spawning stock biomass (SSB). On the contrary, our model

Author contributions: M.L. and C.M. designed research; M.L., C.M., and A.N. performed research; and M.L., C.M., A.N., and N.C.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0906620106/DCSupplemental.

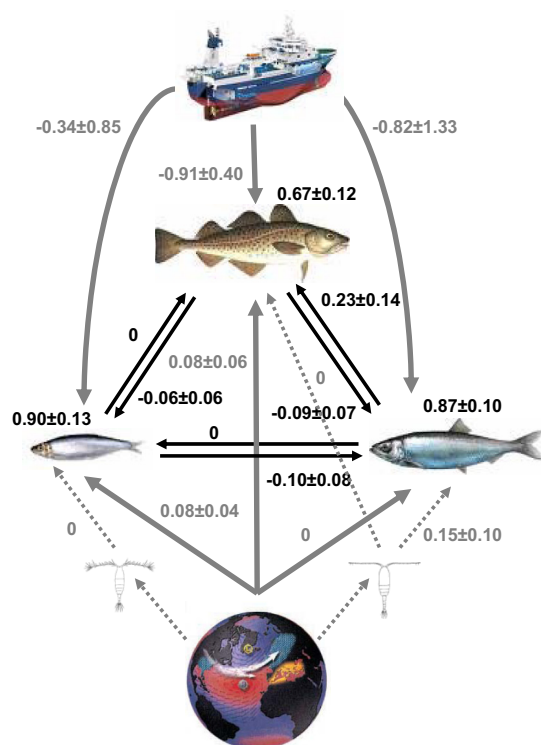


Fig. 1. A schematic view of the Baltic Sea upper-trophic food web. Black arrows and parameters represent species interactions between cod (Top), sprat (Left), and herring (Right). Gray arrows and parameters demonstrate the effects of fishing, climate, and zooplankton on the three species. Interactions with the key zooplankton species *Acartia* spp. (Left) and *P. acuspes* (Right) are illustrated by dotted arrows. Negative parameter values indicate negative effects on the biomass of the species and vice versa. Intraspecific parameters <1 indicate an increasing degree of density dependence in the population. Zero parameter values indicate interactions excluded during model selection. Note that even though it is statistically uncertain we decided to include the fishing effect on sprat and herring because they are heavily exploited by commercial fishing. Climate image is from www.ideo.columbia.edu/res/pi/NAO.

displays a significant effect of *P. acuspes* on herring (Fig. 2F). With *P. acuspes* being a key prey species for herring (27), this interaction indicates a stronger indirect environmental effect on herring, i.e., because *P. acuspes* critically depends on high salinities for reproduction (31). We found a negative effect of commercial fishing on all three species, with the largest effect on cod.

By combining internal food-web dynamics with external forcing through fishing, zooplankton and the physical environment our fitted model clearly reproduces the observed fish stock dynamics in the Baltic Sea. These are characterized by the decrease of cod from high levels during the early 1980s (Fig. 2A), the drastic increase of sprat since the late 1980s (Fig. 2C), and a constant decline of herring (Fig. 2E). We validated our model by sequentially refitting the model for varying time periods and hindcasting the observed dynamics based on only the starting biomass values (Fig. S2). Forced by the observed time series of fishing mortality and salinity (Fig. 2B) the simulations recreate accurately both the sharp increase in cod biomass of the late 1970s, the so-called “gadoid outburst,” and the dramatic decline and collapse of the stock in the early 1990s (Fig. S2b).

The gadoid outburst in the North Sea has been explained mainly by indirect climate forcing caused by “match–mismatch” in the timing and abundance of key copepod prey for larval cod (i.e., *Calanus finmarchicus* and *Calanus helgolandicus*; ref. 5). In our model, the gadoid outburst of Baltic cod is explained mainly

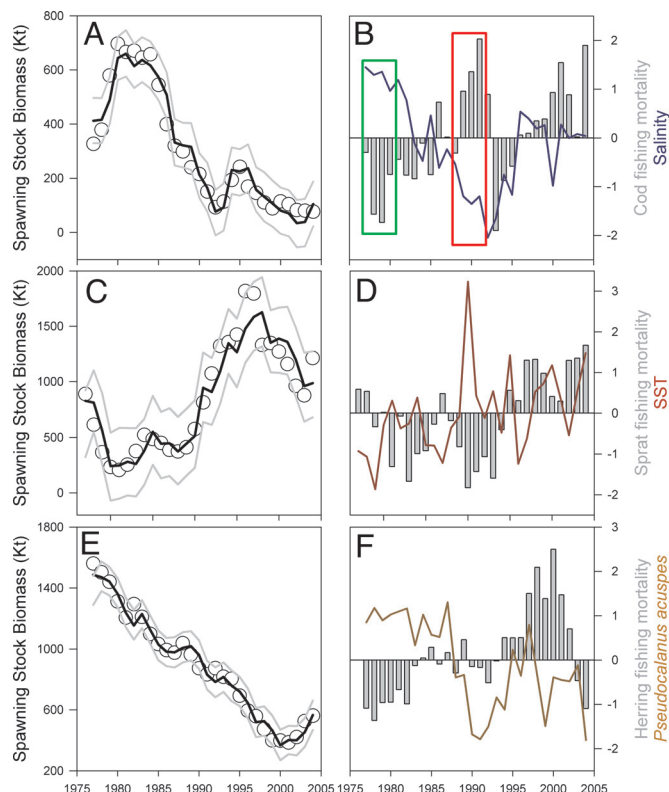


Fig. 2. Historical development of the Baltic Sea fish populations. (A, C, and E) The fitted biomass values (black lines) represent well the observed biomasses (circles) of cod ($r^2 = 0.95$) (A), sprat ($r^2 = 0.89$) (C), and herring ($r^2 = 0.98$) (E) from 1977 to 2004. Upper and lower 95% prediction intervals are displayed by gray lines. (B, D, and F) The main external drivers, i.e., fishing mortalities and environmental variables are shown as anomalies (i.e., standardized to zero mean and unit variance) for each species. In B a combination of low fishing mortalities and record high salinities explains the sharp increase in cod during the late 1970s, i.e., the gadoid outburst (green box). On the contrary, decreasing salinities combined with high fishing pressure explain the dramatic decline and collapse of the cod stock in the early 1990s (red box).

by a period of anomalously low fishing mortalities in combination with record high salinities (Fig. 2B), enabling successful spawning and strong recruitment caused by high egg and larvae survival in the entire Baltic Sea (7, 32). Although the ecological mechanisms differ between areas, the largely synchronous outburst of cod in the North and Baltic Seas suggests a common underlying driver. Because both variability in *C. finmarchicus* and *C. helgolandicus* and hydrographic conditions suitable for recruitment of Baltic cod (i.e., salinity and oxygen) have been strongly linked to oceanic inflow events from the North Atlantic (33, 34), climate-driven changes in large-scale circulation patterns (35, 36) seem to be the most likely driver.

Management Scenarios and Simulations

The validated model was then used to explore whether given the present knowledge on environmental forcing and species interactions, we in hindsight could have managed the cod stock in ways to avoid a collapse. To this end we applied an adaptive management approach (37), taking into account both environmental conditions and food-web interactions in deciding precautionary exploitation levels for Baltic cod. First, to derive precautionary exploitation levels (38), we performed multiple stochastic simulations over a range of fishing mortalities (F from 0 to 1.2) and salinity levels (i.e., corresponding to the observed salinity range from 1974 to 2004). The response of the cod stock was calculated as the percentage of simulations where SSB

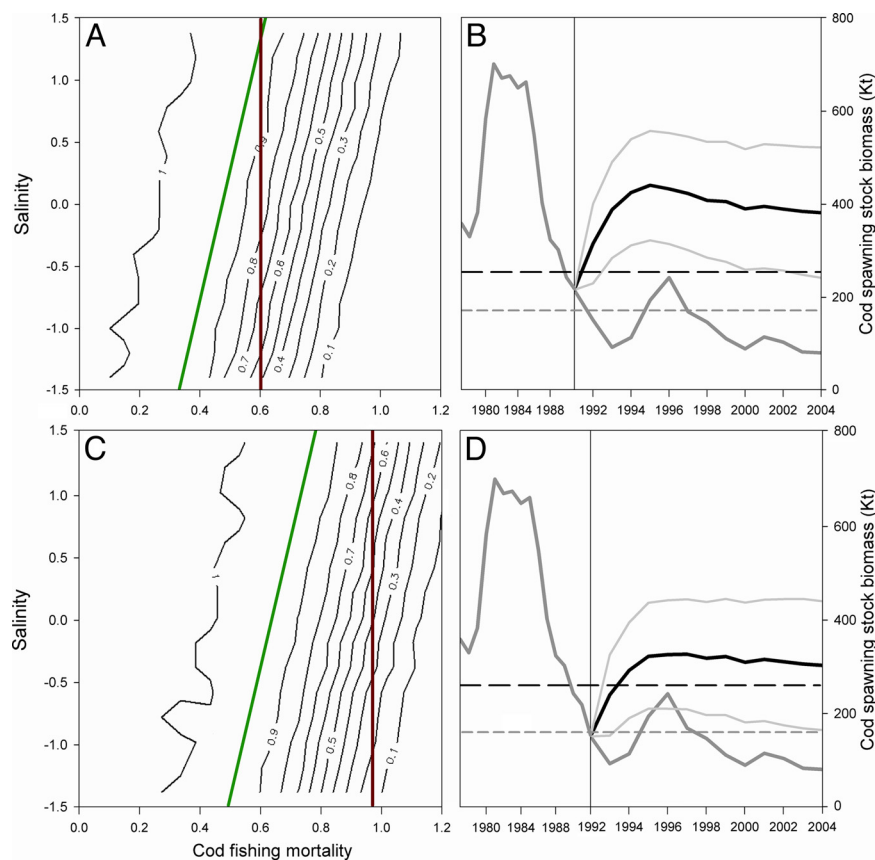


Fig. 3. An adaptive management strategy for Baltic cod. (A and C) The probability of cod stock recovery above B_{pa} (A) and B_{lim} (C) in 1992–2004 is shown over a range of fishing mortalities (F from 0 to 1.2) and salinity levels (i.e., corresponding to the observed standardized salinity range from 1974 to 2004). The red vertical lines show the recommended fixed reference levels, F_{pa} and F_{lim} , and the green diagonal lines show the adaptive management approach deciding F levels based on salinity conditions. (B and D) The dark gray line represents the observed biomass and the black line represents the simulated biomass following the adaptive management strategy outlined in A and C. The simulations are initialized in 1991 (B) and 1992 (D), the years after the collapse below B_{pa} and B_{lim} , respectively. Light-gray lines indicate the upper and lower 95% confidence interval of the simulations. Horizontal lines define the ecologically safe levels B_{pa} (long dash) and B_{lim} (short dash) above which the stock is considered recovered.

recovers above the precautionary stock level (B_{pa}) and the limiting stock level (B_{lim}) in 1992 and 2004, respectively, providing a measure of the probability of stock recovery above ecologically safe levels.

In both scenarios the probability of recovery increase rapidly with decreasing F and increasing salinity levels (Fig. 3 A and C). At F levels close to 0.3 and 0.5 the probability of recovery above B_{pa} and B_{lim} , respectively, approach 100% regardless of salinity level, whereas at exploitation >1.0 and 1.2 a collapse below ecologically safe levels is inevitable. It is noteworthy that the actual F before the collapse and in several recent years were well above this critical threshold (e.g., 1.41 in 1991 and 1.29 in 2004). During a period of highly unfavorable salinity conditions for spawning and recruitment (i.e., because of a lack of inflows from the North Sea) these extreme exploitation levels (Fig. 2B) no doubt caused the decline and collapse of Baltic cod (7). Furthermore, when fished according to the previously recommended reference levels, the precautionary fishing mortality (F_{pa}) may promote a stock recovery above B_{pa} only during highly favorable salinity conditions, whereas at the limiting fishing mortality (F_{lim}) not even maximum observed salinity levels can guarantee a recovery above B_{lim} . Hence, fixed reference levels not taking into consideration environmental forcing and indirect effects of food-web interactions seem far from precautionary and would not have promoted a recovery of the stock.

Based on the above analysis of recovery potential at different environmental conditions we formulated our adaptive

management strategy by assigning exploitation levels relative to the observed salinity conditions during 1992–2004. As such, our adaptive strategy allow F levels to increase during favorable salinity conditions, whereas during unfavorable conditions lower F levels may compensate for recruitment reductions. To ensure precautionary management (38) we applied F levels corresponding to a $<5\%$ risk of population decline below ecologically safe levels. By adopting this strategy, we initialized the simulations in 1991 and 1992, the years after the collapse below B_{pa} and B_{lim} , and managed the stock forward until 2004. By running 1,000 stochastic simulations, we show that our precautionary management strategy, by adapting fishing pressure to environmental conditions and food-web interactions, could significantly have prevented the cod stock from collapsing and promoted a stock recovery above ecologically safe levels (Fig. 3 B and D).

Additionally, to demonstrate that our adaptive management strategy is essential in preventing future stock collapses we simulated a set of long-term dynamics of Baltic cod under three different management scenarios: (i) fishing mortalities fluctuate at mean historical levels (1974–2004); (ii) fishing mortalities remain fixed at $F_{pa} = 0.6$; and (iii) fishing levels are adapted to salinity conditions (i.e., F varies according to 0.6 ± 0.3). Forced under the same environmental scenario (i.e., resembling the historical range of fluctuations in SST and salinity conditions) only the adaptive management approach may prevent future stock collapses and maintain the stock stably above ecologically

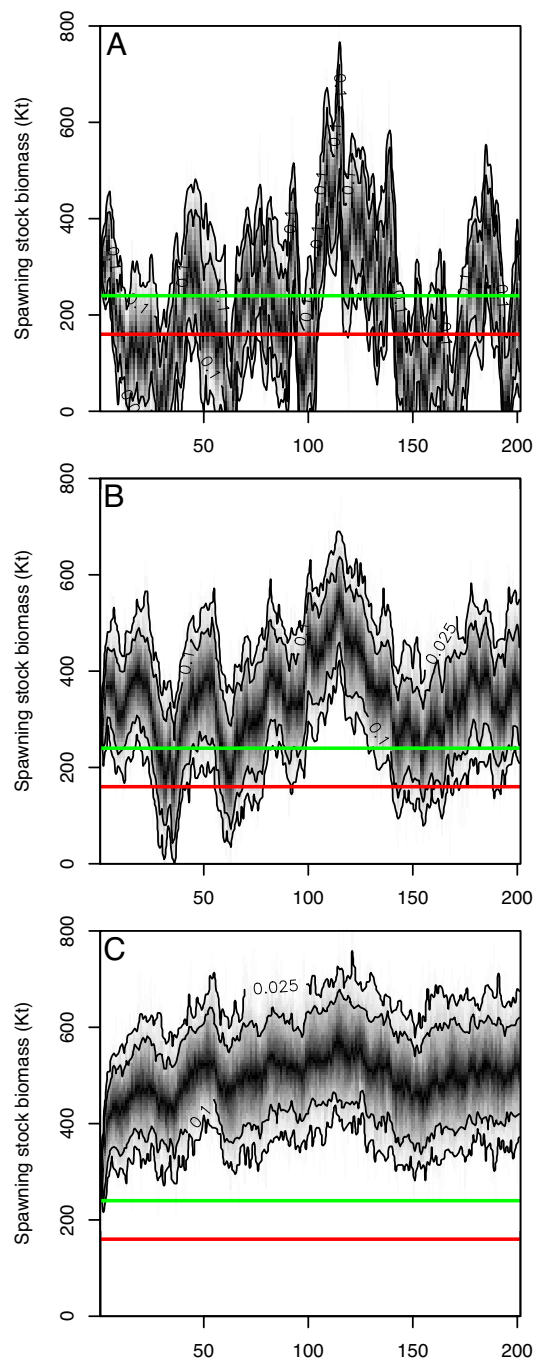


Fig. 4. Simulated long-term dynamics of Baltic cod under different management scenarios. (A) Fishing mortalities fluctuate at mean historical levels. (B) Fishing mortalities are fixed at F_{pa} (0.6). (C) Fishing levels are adapted to salinity conditions (i.e., $F = 0.6 \pm 0.3$). To resemble the historical range of fluctuations in SST and salinity, environmental conditions were simulated based on the mean, variance, and autocorrelation structure of the observed time series (1974–2004) using an approach for modeling “red-shifted,” i.e., positively autocorrelated marine environments (39, 40). Simulations were initialized at the mean historical SSB levels for each species and replicated 1,000 times including stochastic process noise. Solid horizontal lines mark the recommended ecologically safe levels of Baltic cod, the precautionary stock level, B_{pa} (green), and limiting stock level, B_{lim} (red). Black contour lines show the 90% and 95% prediction intervals within which the cod stock dynamics of each replicated run fluctuates.

sustainable levels, B_{pa} and B_{lim} (Fig. 4C). Although the fixed reference approach may reduce large-scale variability in SSB (Fig. 4B) compared with a more “random” harvesting scenario

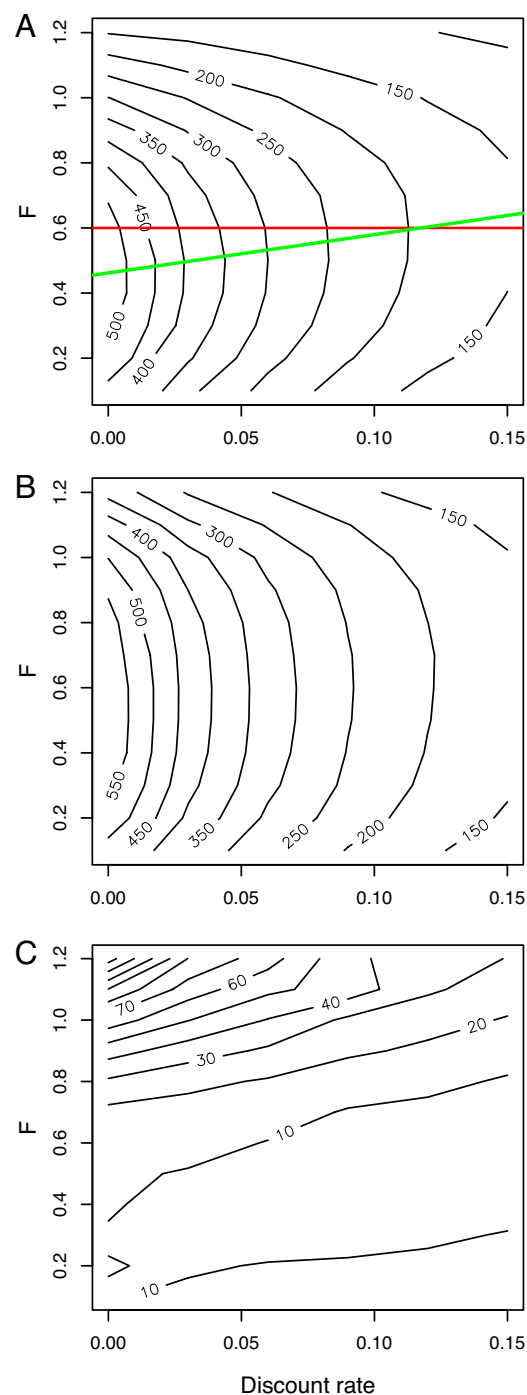


Fig. 5. Economic revenue (m€) of the Baltic cod fishery. (A and B) Revenue is shown under a fixed (A) and adaptive management (B) strategy. NPVs are shown over a range of fishermen discount rates (0–15%) and fishing mortalities (F from 0 to 1.2). Fishing mortalities for sprat and herring are maintained at mean historical levels. (C) The net revenues (i.e., the percentage difference between the adaptive and fixed management scenario) are shown. The economically optimal exploitation levels (F_{opt}) is shown in green, and the horizontal red line marks the precautionary fishing mortality, F_{pa} .

(Fig. 4A), it does not sufficiently buffer against climate-driven recruitment failure nor prevent recurrent stock collapses.

Bio-Economic Scenarios

In an effort to adopt a holistic management perspective we finally coupled the food-web model to a simple bio-economic

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