Economic repercussions of fisheries-induced evolution

Anne Maria Eikeset[a,b,c], Andries Richter[a,d], Erin S. Dunlop[c,e,f], Ulf Dieckmann[c], and Nils Chr. Stenseth[a,1]

[a]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Blindern, N-0316 Oslo, Norway; [b]Center for BioComplexity, Princeton Environmental Institute, and the Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; [c]Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria; [d]Biometris, Department of Mathematical and Statistical Methods, Wageningen University, 6700 AC Wageningen, The Netherlands; [e]Institute of Marine Research, Nordnes, N-5817 Bergen, Norway; and [f]Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Peterborough, ON, Canada K9J 7B8

Fish stocks experiencing high fishing mortality show a tendency to mature earlier and at a smaller size, which may have a genetic component and therefore long-lasting economic and biological effects. To date, the economic effects of such ecoevolutionary dynamics have not been empirically investigated. Using 70 y of data, we develop a bioeconomic model for Northeast Arctic cod to compare the economic yield in a model in which life-history traits can vary only through phenotypic plasticity with a model in which, in addition, genetic changes can occur. We find that evolutionary changes toward faster growth and earlier maturation occur consistently even if a stock is optimally managed. However, if a stock is managed optimally, the evolutionary changes actually increase economic yield because faster growth and earlier maturation raise the stock's productivity. The optimal fishing mortality is almost identical for the evolutionary and nonevolutionary model and substantially lower than what it has been historically. Therefore, the costs of ignoring evolution under optimal management regimes are negligible. However, if fishing mortality is as high as it has been historically, evolutionary changes may result in economic losses, but only if the fishery is selecting for medium-sized individuals. Because evolution facilitates growth, the fish are younger and still immature when they are susceptible to getting caught, which outweighs the increase in productivity due to fish spawning at an earlier age.

Atlantic cod | genetic adaptations | harvest control rule | marine governance | adaptive management

Life-history theory, experiments, and field-based studies strongly suggest that fishing is capable of inducing genetic adaptations, especially when it removes individuals with characteristics such as large body size (1–5). Even if fishing is not size-selective, high fishing mortality may be sufficient to induce genetic change (6, 7). It is difficult to predict how genetic changes at the individual level affect population-level properties. Genetic adaptations may, in principle, be beneficial for the state of a stock, by enabling individuals to invest more into reproduction and growth (1, 8). As a consequence, the stock may become more productive, allowing exploited populations to withstand higher fishing mortalities than they could in the absence of such adaptation, possibly permitting higher yields. However, although an individual's increased reproductive investment leads to larger gonads, this happens at the expense of slower postmaturation growth. Maturing earlier may also reduce fecundity, because individuals are smaller when they reproduce (9). Moreover, adapting to fishing may bear a cost of maladaptation, resulting in increased natural mortality (10, 11). Therefore, fisheries-induced evolution (FIE) may reduce yield (2, 4, 12, 13) and may even imply a "Darwinian debt" (14) to be paid back by future generations, at least if genetic changes are difficult to reverse (1, 15, 16). Clearly, FIE has the potential for causing positive and negative effects on key stock properties such as spawning stock biomass (SSB) and yield, making its economic effect ambiguous. It is also an open question whether the expected size of the economic effects are substantial, largely because any evolutionary changes are closely intertwined with ecological effects. For example, the release of density dependence when population biomass is fished down could be an important driver of phenotypic

change (1, 17, 18) and might override effects of FIE on yield. However, the economic consequences of FIE and its effects on optimal fishing mortalities in wild populations have yet to be determined. Here, we ask how evolutionarily informed management differs from classical fisheries management. First, we determine how an evolving fish population should be optimally managed. Second, we analyze how these management strategies differ compared with optimal management derived for a population whose development is purely determined by ecological processes. Third, we ask how substantial the losses are if a fishery's manager—unaware of any evolutionary changes—manages an evolving population as if it were not evolving. Fourth, we analyze how FIE affects the performance of the fishery that is not optimally managed, but heavily exploited.

Northeast Arctic (NEA) cod is currently the world's largest stock of Atlantic cod (*Gadus morhua*) and provides substantial ecosystem services. The stock's fishery is an important economic resource for Norway and Russia, with annual catches by Norway being worth more than 500 million US dollars in 2010, and Russia obtaining about the same revenue. Traditionally, harvesting focused on adult cod at the stock's spawning grounds along the Norwegian coast. From the 1930s, when industrial trawlers were introduced in the stock's feeding grounds in the Barents Sea, immature fish came under substantial fishing pressure, and total fishing mortality increased (19). Evolutionary changes have been predicted to be a factor in explaining the observed declines in age and length at maturation in NEA cod, although the predicted extent has varied among studies (17, 20, 21).

We develop a bioeconomic model to investigate if and how FIE affects economic yield (Fig. 1). Our model is a comprehensive compilation of a life-history model for a harvested species with economic components relying on individual vessel data, making this a unique empirically derived bioeconomic model for investigating genetic adaptations to harvesting. This model has been specifically built for NEA cod to investigate the ecological and evolutionary effects of exploitation on the changes in maturation that occurred after fishing mortality was intensified in the 1930s in the feeding grounds (17). To match the observed trends in the biological model as closely as possible, we recreated the historical selection pressure to determine the evolvability (i.e., the coefficient of genetic variation) in the life-history traits (17). Although we focus on the feeding ground fishery in the Barents Sea, we also included fishing in the spawning grounds at the historic levels between 1932 until 2005, and at a constant rate after 2006. Hence, we consider the spawning ground fishery to
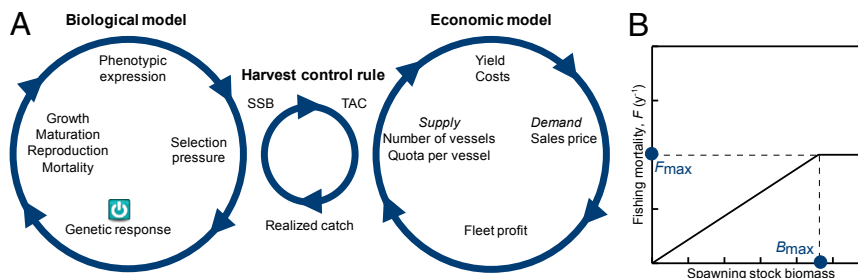
Fig. 1. An overview of the bioeconomic model. (*A*) The biological and economic model components are coupled by the harvest control rule (HCR). The individual-based biological model describes the evolution of key life-history traits if genetic changes are allowed to occur in the model. The economic model accounts for the supply and demand side of the fishery, as well as for fleet profit generated. (*B*) The shape of the HCR depends on two parameters: above the level B_{max} of spawning stock biomass, the maximum fishing mortality F_{max} is allowed. Between B_{max} and a biomass level of zero, fishing mortality linearly decreases from F_{max} to zero. The structure of this HCR is in agreement with that advised in 2004 by the International Council for the Exploration of the Sea for the Northeast Arctic cod fishery.

be beyond the control of the manager. The biological model component is built on the individual-based ecogenetic model framework developed by Dunlop et al. (1), describing four evolving life-history traits capturing key aspects of growth, maturation, and reproduction (Table S1). Changes in life-history traits may be driven both by ecological processes, such as phenotypic plasticity and density dependence, and genetic processes. To evaluate whether accounting for FIE requires a special harvest strategy, we also analyze a nonevolutionary version of the biological model in which the genetic traits cannot evolve. We therefore compare a nonevolutionary model, in which changes in populations are driven only by phenotypic plasticity, with an evolutionary model that allows, in addition, for genetic adaptations. The economic model component consists of production and cost functions estimated specifically for the Norwegian cod trawler fleet (Table S1). We incorporate a demand function, also estimated from empirical data, to account for how total catch affects the price of landings (22). Our model incorporates feedbacks between the stock development and the economic gains through an optimal harvest control rule (HCR), which is constrained by the two parameters B_{max} and F_{max} (Fig. 1). This shape makes it directly comparable to the HCR that is being implemented for NEA cod since 2004 (23, 24). We search for the parameter combination that gives the highest net present value (NPV) of fleet profits. We derive HCRs that are optimized in either the evolutionary or nonevolutionary versions of the model.

Results

We first compare the emerging properties of the evolutionary model with the nonevolutionary model, when both are managed according to what an HCR recommends that has been optimized for fleet profits (Table 1, Evolution vs. Ecology). We find that the optimal fishing mortality is almost identical for the evolutionary and nonevolutionary models and substantially lower than what it has been historically. Despite this, the emerging biomass

levels and the total allowable catch (TAC) are higher in the evolutionary model, indicating that evolution indeed makes the stock more productive, permitting higher yields for the same fishing mortality. Overall, the NPV of the fishery is higher when evolution occurs, even though the total effect is very small. Given that the recommended fishing mortalities are almost identical, the loss of disregarding any evolutionary effects is negligible, and the NPV is still higher if evolution occurs and is ignored by managers (Table 1, Evolution ignored). The key message here is that a low fishing mortality is optimal, regardless of whether genetic changes occur. This prediction holds for different discount rates (Table S2), when sales prices are assumed to be independent of the total catch, and when the price that can be obtained per kilogram of cod rises with the weight of the fish (Table S3).

Given that fishing mortality has not been low for the NEA cod fishery in the past, and considering that worldwide most fisheries are still far from being managed optimally, we also investigate how evolution affects the stock when it is overexploited. To do so, we use historic fishing mortalities between 1932 and 2006, and the average fishing mortality afterwards to simulate a scenario of high fishing pressure; this is then contrasted with a counterfactual scenario that analyzes how the fate of the fishery would have developed if an optimal HCR had been introduced already in 1932 (as given in Table 1, Evolution). We find that using an optimal HCR leads to higher biomass levels in the evolutionary model, compared with the case where only ecological effects are present. The opposite is true for the scenario of historically high fishing mortality, where biomass is slightly lower in the evolutionary model (Fig. 2*A*). As a result, the corresponding TAC and NPV are also slightly lower when evolution occurs and fishing mortality is high (Table S4).

It is not immediately obvious why evolution has a positive effect on the fishery if fishing mortality is set optimally, but a negative effect if fishing mortality is high. Inspecting key life-history traits reveals that age at maturation declines over time in all scenarios (Fig. 2*B*), and although this also occurs in the nonevolutionary model (solely as a result of phenotypic plasticity), the decline is even more severe when evolution takes place. A decline in length at maturation occurs in all scenarios as well, and is even more pronounced if fishing mortality is high (Fig. 2*C*). Despite reduced age and length at maturation, the reproductive output per unit of SSB, a measure of the stock's productivity, is increasing over time when evolution occurs (Fig. 2*D*). To better understand the population structure, we take a closer look at the age composition at the simulation endpoints (Fig. 3). We find that despite individual fish being smaller at maturation, the size at a given age is consistently larger for the evolutionary model compared with the nonevolutionary model, irrespective of the fishing mortality being optimal or high (Fig. 3*A*). Indeed, the underlying genetic trait changes show that the evolving population invests more in intrinsic somatic growth

Table 1. Optimal HCR for the evolutionary model (evolution) and nonevolutionary model (ecology)

Model	F	TAC	SSB	NPV
Evolution	0.34	469 (60)	767 (163)	25.4
Ecology	0.35	443 (48)	643 (118)	25.3
Evolution ignored	0.35	470 (60)	735 (155)	25.4

Values shown are averages for 1932–2100 of fishing mortality (*F*), total allowable catch (TAC), spawning stock biomass (SSB), with temporal SDs in parentheses, and net present value (NPV) is given for a discount rate of 2%. "Evolution ignored" uses the evolutionary model with the ecologically optimal harvest control rule (HCR). Units: *F* (y^{-1}), TAC and SSB (1,000 tonnes), NPV (in billions, US dollars).

Fig. 2. The first scenario (*Left*) is based on an optimal harvest control rule (HCR) maximizing fleet profit (green shading shows the period for which we have data), and the second scenario (*Right*) is based on the observed historic fishing mortalities for 1932–2005 (red shading), and from 2006 onward follows the average fishing mortality for 1946–2005. For each scenario, the emerging properties for an evolutionary model (black) are compared with those of the corresponding nonevolutionary model (gray). (*A*) Total biomass from age 3 y is lower in the evolutionary model when fishing mortality is high, but higher in the evolutionary model when the optimal HCR is used. (*B*) Predicted age at maturation and (*C*) length at maturation is lower in the evolutionary model than in the nonevolutionary model. The historic scenario predicts age and length at maturation to fall to between ages 6 and 7 y, and 60 and 70 cm in 2005, in agreement with the observed data. (*D*) Stock productivity, i.e., mean gonad mass divided by total spawning stock biomass, increases when evolution occurs, and more if fishing mortality is high.

capacity and reproduction, resulting in overall larger body sizes and higher reproductive output (Fig. 3*A*; Fig. S1). Looking closer at the age structure of the fish stock makes it immediately clear that

the evolutionary loss occurs because the number of individuals in each age class is much lower if fishing mortality is high and evolution occurs (Fig. 3*B*). The fish grow quicker and mature earlier in the evolutionary scenario when fishing pressure is high, but these genetic changes do not pay off in terms of population biomass, TAC or NPV, because fish are also younger (and still immature) when they are potentially caught by trawlers, which in the model spare all fish below the minimum size limit of 45 cm. It might seem surprising that these genetic changes toward faster growth occur, given that this makes the fish more vulnerable to fishing at an earlier age. However, faster growth also means maturing earlier, which enables individuals to have a higher probability to reproduce and pass on genes before being captured by the fishery.

If certain environmental conditions are responsible for the evolutionary loss, it may be sufficient to tweak the environment to avoid or reverse these losses. Indeed, we find that changing the minimum size limit is sufficient to avoid any evolutionary costs (Fig. 4). With a very low minimum size limit, evolution is unambiguously good for the fishery, because it leads to individual growth that is fast enough to negate any detrimental effects of early maturation on TACs (Fig. 4*A*). As expected, evolution has little effect on the TAC when the minimum size limit is high, because selection acting on maturation and growth is weaker, so and there is little difference between the evolutionary and non-evolutionary predictions (Fig. 4*C*; Fig. S2). Therefore, the loss in NPV due to evolution only occurs for intermediate minimum size limits, where the beneficial effects of growing faster are

Fig. 3. Ecoevolutionary dynamics and age truncation. The optimal HCR scenario is shown by green bars, and the scenario with historic (high) fishing mortality is indicated with red bars. The evolutionary model outcome is shown with full bars, and the nonevolutionary one is shown by gray inner bars. (*A*) The mean size is larger for all age classes if evolution occurs. (*B*) The number of individuals in each age class is much lower if evolution occurs, but only if fishing mortality is high.
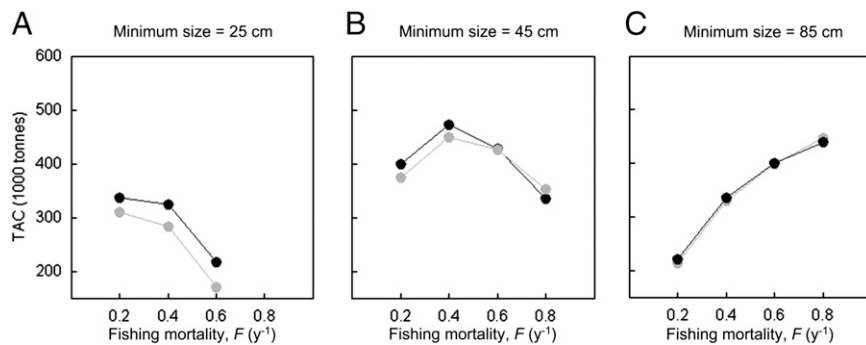
Fig. 4. (*A–C*) Total allowable catch (TAC) under different minimum size limits and for different constant fishing mortalities, *F*. The evolutionary model (black) predicts higher TAC than the nonevolutionary model (gray) when selection also acts on very young fish. For a minimum size limit of 85 cm, the two model predictions become essentially indistinguishable. At the intermediate minimum size limit of 45 cm, the TAC is highest for the evolutionary model when fishing mortality is low, but as fishing intensity increases, the TAC is smaller for the evolutionary model.

overriden by making those fish more vulnerable that are larger, but also younger and still immature (Table S5).

In this study, the coefficient of genetic variation was set at a level that resulted in the best fit to empirical observations in age and length at maturation (Table S1), but we nonetheless investigated the effect of this parameter (the evolvability of traits) on model predictions. As expected (1, 16, 25, 26), higher genetic variance resulted in fish maturing at even younger ages and smaller sizes, while also growing faster. Consequently, higher TACs can be obtained when the evolvability is high, suggesting that stronger evolutionary forces can have a positive effect on the fishery (Fig. S3).

Discussion

Our model predicts that evolutionary change occurs even if fishing mortality is low, which implies that a management strategy aimed at avoiding genetic change might not be feasible. At the same time, we find that fisheries-induced evolution is not necessarily bad for the fishery, and most of the time even beneficial—especially a fishery that is managed according to what is ecologically optimal can safely ignore any evolutionary effects, at least for the stock and under the conditions that we are considering. This finding is very surprising and in contrast to much of the existing literature, which tends to sketch a gloomy picture of the potential consequences of FIE. It is also comforting that fishing can cause evolution of faster growth, allowing the population to withstand higher harvest pressure and prevent stock collapse (Fig. S3). Nonetheless, the life-history changes we predict could have management implications because they affect important indicators that are commonly used to assess the state of the stock. Evolution tends to increase the ratio between SSB and total biomass (Fig. S4), which could mask a decreasing trend in total biomass and affect the stock-recruitment relationship (26); this may have important management implications when biomass levels approach SSB-based limit reference points (27, 28). Even more worrisome is our finding that evolutionary effects tend to be more important when a fish stock is overexploited and the fishery is intermediately size-selective. Admittedly, such an exploitation regime is a special case, but unfortunately the one that, worldwide, most fisheries are facing. Surprisingly, an economic cost of evolution under these conditions does not materialize because of a drop in reproductive output or, as many might expect, because of a reduction in growth or size-at-age (29). On the contrary, evolution here promoted faster growth, yet still could exact an economic cost. These results underscore the importance of management taking into account the detailed age and size structure of the stock (30–32).

Although we find that selectively removing individuals of intermediate size may result in economic losses due to evolutionary change, we do not find any evidence that targeting only large fish results in evolutionary loss (Fig. 4). These findings may shed light on the discussion whether harvesting should be balanced or selective (33). In this study, we assume a knife-edge selectivity in our model (34, 35), so different gear types with other selectivity patterns remain to be explored by further research. Although gear regulations can, in principle, be easily changed, our findings may also hint at broader problems. If predation is size-selective, evolutionary changes may affect natural mortality which may lead to similar consequences as fishing mortality (10, 11). Investigating how FIE acts in concert with natural mortality, climatic changes, or other driving forces remains to be explored, especially in the light of recovery potential (16).

Although our biological model is complex, the optimal HCR was constrained by two parameters, resembling the shape of the HCR currently adopted for NEA cod. It would be interesting to see to what extent our results carry over to a simpler biological model that could then be used for more flexible optimization routines treating the minimum size limit, for example, as a choice variable. Another interesting avenue is to separately optimize HCRs for the NEA cod's feeding and spawning grounds. Previous research has found predictions for FIE to differ depending on whether management actions target feeding or spawning grounds (36). Here, we focused on the fishery in the stock's feeding grounds and kept the fishing mortality at observed levels in the stock's spawning grounds to mimic the historic selection pressure on mature fish, while parsimoniously asking what can be changed for the trawler fleet in the Barents Sea.

Together, our results show that the economic consequences of FIE are rather small, and mostly beneficial, largely because of the positive effects of fishing on growth. This prediction is made possible because of the crucial ecoevolutionary feedbacks among biomass, growth, and maturation, and the inclusion of growth as an evolving trait. Models that do not include these crucial factors might incorrectly predict a larger economic cost of evolution. Regardless, low fishing mortality is the key for successful management. Today, many fish stocks are still far from being managed in an ecologically optimal way. In such a case, our model predicts that FIE enables the stock to withstand higher harvests, but only if fishing mortality is not intermediately size-selective; otherwise, FIE may reduce economic yield and make the stock less viable. Admittedly, these evolutionary costs are small, but they may just be enough to push a fish stock from the state of overexploitation into collapse.

Materials and Methods

Our bioeconomic model consists of two model components: the biological model, describing the life cycle of NEA cod, and the economic model, describing details such as cost and demand for the NEA cod trawl fishery. Each of

these components have been specifically estimated and calibrated for this stock by using data from 1932 to 2007 (Table S1). A more extensive model description can be found in *SI Materials and Methods: Model and Data Description*.

Biological Model. The biological model component is individual-based and has been developed in ref. 17, building on the ecogenetic modeling framework derived in ref. 1. The model describes each individual's growth, maturation, reproduction, and mortality in each year and follows the fate of ~50,000 superindividuals (37, 38). If a fish reproduces, genetic traits are inherited by offspring and expressed phenotypically. Mortality acts on these phenotypic traits, resulting in selection that may cause a genetic response in the life-history traits (Fig. 1A). We studied two versions of our model, an evolutionary and a nonevolutionary version, each modeling their respective population of individuals to compare a population that has the propensity to evolve with a population that does not evolve. We consider the evolution of four quantitative life-history traits: maturation tendency given by the (*i*) slope and (*ii*) intercept of a probabilistic maturation reaction norm (20), (*iii*) growth capacity, and (*iv*) reproductive investment. The genetic traits evolve independently, and we therefore do not account for pleiotropy or genetic linkage between traits. Our model has limitations, but thanks to the data availability for NEA cod, we are able to include estimates of the initial mean life-history trait values and annual exploitation rates, as well as parameters specifying the stock-recruitment relationship (describing fecundity and newborn mortality) and the density dependence of growth on stock biomass (17). Furthermore, a growth-survival tradeoff is included; the strength of this tradeoff was determined by matching the ecological properties for data on age and length at maturation, phenotypic growth, and biomass from 1932 to 1950 in the nonevolutionary version of the model after reaching demographic equilibrium (17). In the evolving population, the coefficient of genetic variation ($CV_{z,G}$) has been determined empirically for each trait (17) by matching trends in age and length at maturation over a 74-y period (from 1932 to 2005). In this calibration, the historic selection pressure was mimicked by using annual harvest probabilities in the feeding and spawning grounds from 1932 until 2005. The resultant $CV_{z,G}$ has been found to be lower than what was assumed in previous studies using the same modeling framework but not based on specific stocks (1, 16, 25, 26), as was the case here. For the non-evolving population, which is only driven by ecological processes, the $CV_{z,G}$ is equal to zero.

Economic Model and Harvest Control Rule. The economic model specifies (i) the harvest function, (ii) the profit function, (iii) the procedure for allocating fishing quotas, and (iv) the demand function. All of these functions have been estimated and derived in detail in ref. 39 and used in ref. 22. We assume

a knife-edge selectivity (34, 35) that targets all fish above the size of 45 cm (17, 40). The biological and economic model components are linked through an annual feedback loop: SSB is fed into the economic model component where ultimately the TAC is determined by a HCR, and the derived TAC feeds back into the biological model component where it affects the stock size (Fig. 1, realized catch). The shape of the HCR is based on the one that has been implemented for NEA cod since 2004 (23, 24): the maximum fishing mortality F_{max} is allowed above a certain SSB level, given by the parameter B_{max}. Below B_{max}, fishing mortality decreases linearly to the origin (Fig. 1B). We explore model simulations over a large grid of combinations of F_{max} and B_{max}, searching for those combinations that achieve the economic objective of maximizing the net present value of fleet profits. All results, such as those for SSB and TAC, are given for a population that has been scaled up by a factor of 100,000. Because the model is stochastic, we ran each scenario for 15 independent replicates, and then averaged across these, presenting the mean in the tables and figures.

Historic Fishing Pressure. The observed harvest pressure in the feeding ground increased steadily from the 1930s to the middle of the 1960s and remained high until mid-2000. In the historic fishing scenarios, we use observed fishing mortalities from 1932 to 2005 and then assume a constant fishing mortality in the feeding ground (0.68 y^{-1}) being maintained from 2006 into the future. This constant (0.68 y^{-1}) is an average of the historic fishing mortality between 1946 and 2005 and is higher than what is considered to be precautionary for NEA cod (0.4 y^{-1}) (40).

1. Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. *Ecol Appl* 19(7):1815–1834.
2. Hutchings JA (2009) Avoidance of fisheries-induced evolution: Management implications for catch selectivity and limit reference points. *Evolutionary Applications* 2(3):324–334.
3. Hutchings JA, Fraser DJ (2008) The nature of fisheries- and farming-induced evolution. *Mol Ecol* 17(1):294–313.
4. Jørgensen C, et al. (2007) Ecology: Managing evolving fish stocks. *Science* 318(5854): 1247–1248.
5. Carlson SM, et al. (2007) Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecol Lett* 10(6):512–521.
6. Sharpe DMT, Hendry AP (2009) Life history change in commercially exploited fish stocks: An analysis of trends across studies. *Evol Appl* 2(3):260–275.
7. Roff DA (1992) *The Evolution of Life Histories: Theory and Analysis* (Chapman & Hall, New York).
8. Andersen KH, Brander K (2009) Expected rate of fisheries-induced evolution is slow. *Proc Natl Acad Sci USA* 106(28):11657–11660.
9. Marshall CT, Needle CL, Yaragina NA, Ajiad AM, Gusev E (2004) Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. *Can J Fish Aquat Sci* 61(10):1900–1917.
10. Jørgensen C, Fiksen Ø (2010) Modelling fishing-induced adaptations and consequences for natural mortality. *Can J Fish Aquat Sci* 67(7):1086–1097.
11. Swain DP (2011) Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evol Appl* 4(1):18–29.
12. Hard JJ, et al. (2008) Evolutionary consequences of fishing and their implications for salmon. *Evol Appl* 1(2):388–408.
13. Sutherland WJ (1990) Evolution and fisheries. *Nature* 344(6269):814–815.
14. Dieckmann U, Heino M, Rijnsdorp AD (2009) The dawn of Darwinian fishery management. *ICES Insight* 46:34–43.
15. Conover DO, Munch SB, Arnott SA (2009) Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proc Biol Sci* 276(1664):2015–2020.
16. Enberg K, Jorgensen C, Dunlop ES, Heino M, Dieckmann U (2009) Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol Appl* 2(3):394–414.

17. Eikeset AM, Dunlop ES, Heino M, Stenseth NC, Dieckmann U (2010) Is evolution needed to explain historical maturation trends in Northeast Atlantic cod? PhD thesis (University of Oslo, Oslo).
18. Eikeset AM, Richter AP, Diekert FK, Dankel DJ, Stenseth NC (2011) Unintended consequences sneak in the back door: Making wise use of regulations in fisheries management. *Ecosystem Based Management for Marine Fisheries: An Evolving Perspective*, eds Belgrano A, Fowler CW (Cambridge Univ Press, Cambridge, UK), pp 183–217.
19. Godø OR (2003) Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. *Fish Fish* 4(2):121–137.
20. Heino M, Dieckmann U, Godø OR (2002) Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: A new technique illustrated by application to Northeast Arctic cod. *ICES J Mar Sci* 59(3):562–575.
21. Heino M, Dieckmann U, Godø OR (2002) Reaction norm analysis of fishery-induced adaptive change and the case of the Northeast Arctic cod. *ICES CM Series, Report Y:14*. Available at http://brage.bibsys.no/imr/handle/URN:NBN:no-bibsys_brage_3050.
22. Eikeset AM, et al. (2013) A bio-economic analysis of harvest control rules for the Northeast Arctic cod fishery. *Mar Pol* 39:172–181.
23. Bogstad B, et al. (2005) Harvest control rules for management of fisheries on Cod and Haddock and optimal long term optimal harvest in the Barents Sea ecosystem. *Report of the Basic Document Working Group (BDWG) to the Joint Norwegian–Russian Fisheries Commission*. Available at www.regjeringen.no/upload/kilde/fkd/prm/2005/0084/ddd/pdfv/262877-vedlegg_11_bdwg-2005_final.pdf.
24. International Council for the Exploration of the Sea (ICES) (2011) Report of the ICES Advisory Committee, 2011. *ICES Advice* (ICES, Copenhagen).
25. Dunlop ES, Baskett ML, Heino M, Dieckmann U (2009) Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evol Appl* 2(3): 371–393.
26. Enberg K, Jørgensen C, Mangel M (2010) Fishing-induced evolution an changing reproductive biology of fish: The evolution of steepness. *Can J Fish Aquat Sci* 67(10): 1708–1719.
27. Marshall CT, Needle CL, Thorsen A, Kjesbu OS, Yaragina NA (2006) Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock:

ENVIRONMENTAL SCIENCES

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Implications for stock-recruit theory and management. *Can J Fish Aquat Sci* 63(5): 980–994.

28. Heino M, et al. (2013) Can fisheries-induced evolution shift reference points for fisheries management? *ICES Journal of Marine Science* 70(4):707–721.

29. Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. *Science* 297(5578):94–96.

30. Diekert FK, Hjermann DO, Naevdal E, Stenseth NC (2010) Spare the young fish: Optimal harvesting policies for North-East Arctic Cod. *Environ Resour Econ* 47(4): 455–475.

31. Sinclair AF, Swain DP, Hanson JM (2002) Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Can J Fish Aquat Sci* 59(2):361–371.

32. Tahvonen O (2009) Economics of harvesting age-structured fish populations. *J Environ Econ Manage* 58(3):281–299.

33. Garcia SM, et al. (2012) Conservation. Reconsidering the consequences of selective fisheries. *Science* 335(6072):1045–1047.

34. Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. *Fish Investment Series 2* (U.K. Ministry of Agriculture, Fisheries and Food, London), Vol 19.

35. Food and Agricultural Organization of the United Nations (FAO) (1998) Introduction to tropical fish stock assessment. Part 1: Manual. *FAO Fisheries Technical Paper* (FAO, Rome).

36. Jørgensen C, Ernande B, Fiksen O (2009) Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evolutionary Applications* 2(3):356–370.

37. Huse G, Johansen GO, Bogstad L, Gjosaeter H (2004) Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES J Mar Sci* 61(7):1201–1213.

38. Scheffer M, Baveco JM, Deangelis DL, Rose KA, Vannes EH (1995) Super-individuals a simple solution for modeling large populations on an individual basis. *Ecol Modell* 80(2-3):161–170.

39. Richter AP, Eikeset AM, Van Soest DP, Stenseth NC (2011) Towards the optimal management of the Northeast Arctic cod fishery. *Fondazione Eni Enrico Mattei Working Paper 591*. Available at www.feem.it/userfiles/attach/20115201140194NDL2011-040.pdf.

40. International Council for the Exploration of the Sea (ICES) (2009) *Report of the Arctic Fisheries Working Group* (ICES, Copenhagen).

Supporting Information

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SI Text

SI Text consists of two main sections: *SI Materials and Methods* and *SI Results*. In the first section, we describe the biological and economic components of the bioeconomic model, including a description of the data used to parameterize the model (Table S1). At the end of *SI Materials and Methods*, we discuss model limitations. In *SI Results*, we show in greater depth the emerging properties of the historic fishing scenario that may give rise to an evolutionary cost. Also, we investigate the implications of alternative discount rates for deriving optimal harvest control rules (HCRs). Furthermore, we probe into the robustness of our results. Simulating different levels of constant fishing mortality rates (0.2–0.8 y^{-1}), we evaluate the impact of changing the minimum size limit, assuming a constant price, weight-dependent price, and, finally, changing the coefficient of genetic variation (i.e., evolvability) of the genetic life-history traits.

SI Materials and Methods: Model and Data Description

Biological Model. The biological model is an individual-based model that uses the framework developed in ref. (1). This model combines quantitative genetics with ecological processes taking place at the individual level to derive knowledge on how fishing pressure progressively affects the stock at the population level. The genetic component of this model allows individuals to adapt to the selection pressure brought about by harvesting. The individual-based model follows about 50,000 superindividuals (2, 3). All models results, such as spawning stock biomass (SSB) and catch, are given for a population that has been scaled up by a factor of 100,000 to recreate realistic stock levels. Parameter values for our model (Table S1) are based on published sources, data collected by the Norwegian Institute of Marine Research (IMR), Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), and the Norwegian Directorate of Fisheries, and survey data made available through the International Council for the Exploration of the Sea (ICES). This model has been developed and calibrated for the Northeast Arctic (NEA) cod stock in ref. 4. A similar model was used in ref. 5 for the same stock, without considering any evolutionary dynamics.

Evolutionary dynamics. This section describes first how we model the phenotypic expression of the genetic traits for individual maturation tendency, growth, and reproductive investment; second, how we introduce the distribution of the evolving genetic traits in the initial population; and finally, how the traits are inherited by offspring. Each genetic trait value z_G (denoted by subscript G) has a corresponding phenotypic trait value z_P (denoted by subscript P), with a genetic variance $\sigma^2_{z,G}$ and phenotypic variance $\sigma^2_{z,P}$. At the population level, we assume phenotypic variance to be the sum of the genetic and environmental variance ($\sigma^2_{z,P} = \sigma^2_{z,G} + \sigma^2_{z,E}$). Based on quantitative genetics (6), each trait has a heritability, $h^2_z = \sigma^2_{z,G}/\sigma^2_{z,P}$, which allows us to calculate the environmental variance $\sigma^2_{z,E} = \sigma^2_{z,G}(h^{-2}_z - 1)$ for each trait in the initial population (where $\sigma^2_{z,G}$ is empirically determined for each trait; see below). This environmental variance was then subsequently kept constant through time. The four considered quantitative genetic traits are the maturation tendency by a probabilistic maturation reaction norm (PMRN): (*i*) slope $z_G = s_G$ and (*ii*) intercept $z_G = i_G$; and (*iii*) growth capacity $z_G = g_G$ and (*iv*) reproductive investment, given by the gonadosomatic index $z_G = \text{GSI}_G$. In the initial population, the genetic traits are assumed to be normally distributed with mean initial trait values and genetic variances determined by the coefficient of genetic variation $\text{CV}_{z,G}$, both based on empirical data (Table S1). The genetic traits are expressed phenotypically by random draws from a normal distribution with means equal to the respective genetic trait (see Table S1 for initial values), with the corresponding environmental variances σ^2_E. We examined an evolutionary and a nonevolutionary version of the model, each modeling their respective population of individuals to compare a population that has the propensity to evolve with a population that does not evolve. First, the nonevolutionary model was calibrated to accomplish a match with data on NEA cod phenotypic growth, biomass, and age and length at maturation for the period 1932–1950 (4). For the nonevolving population, which is only driven by ecological processes, the $\text{CV}_{z,G}$ by definition equals zero. In the evolving population, $\text{CV}_{z,G}$ was determined by matching trends in age and length at maturation over a 74-y period (1932–2005); for all four evolving traits, these were then varied to determine the amount of evolution needed to match the maturation trends for 1932–2005. Based on previous models, the range of evaluated $\text{CV}_{z,G}$ was between 0% and 12% (1, 7–9). All possible combinations were systematically evaluated and ranked by log-likelihood. The combination that ranked best was consequently selected and used to define the $\text{CV}_{z,G}$ values for each trait.

Offspring inherited genetic trait values from their parents by drawing randomly from normal distributions with means equal to the midparental genetic trait values (i.e., the arithmetic mean trait value of the two parents) and variances equal to half the variance for a given genetic trait in the initial population (thus assuming a constant recombination–segregation–mutation kernel) (1, 10). After the initial year (e.g., the first year in the simulation), genetic means, heritabilities, and the trait distributions could change freely as determined by the processes of maturation, somatic growth, reproduction, natural mortality, and harvesting mortality. These processes were applied sequentially in each year to all individuals.

Maturation, growth, reproduction, and mortality. Each year, the probability p_m that an immature individual will mature is described by a PMRN (11, 12); this is a function of the individual's length l and age a and given by $p_m = [1+\exp(-(l-l_{p50,a})/v)]^{-1}$. The length $l_{p50,a}$ is where the maturation probability p_m is equal to 50% at age a, as given by $l_{p50,a} = i_P + s_P a$, with a phenotypic intercept i_P and slope s_P. The parameter v is determined by the lower bound probability p_l (25%) and the upper bound probability p_u (75%) of the maturation envelope (1, 4), together with the PMRN width w, as given by $v = w/\ln\frac{p_l^{-1}-1}{p_u^{-1}-1}$.

To reflect density dependence in growth brought about by changes in abundance, and consequently competition and resource availability, we used an estimated relationship of phenotypic growth $g_{P,D,t} = g_{P,t}\exp(-xB_t)$, depending on total stock biomass B_t in year t. The hypothetical length increment where biomass B_t is zero is referred to as the maximum growth increment, and x is the strength of density dependence reducing growth relative to this maximum. For this estimation (Table S1), derived in detail in ref. 4 and used in ref. 5, we used data on annual growth increments and biomass for the period 1978–2009, obtained from survey data and stock assessment (4, 13). The parameters were estimated by regressing log-transformed mean annual growth increments for ages 0–5 y in the winter survey against total biomass and other covariates ($R^2 = 73\%$) (4). For the immature individuals, denoted by a superscript I, the body length in a given year depends on the length in the previous year and the growth increment in that year, $l^I_t = l^I_{t-1} + g_{P,D,t-1}$. Mature individuals, denoted by a superscript M, also allocate re-

sources to reproduction, depending on the reproductive investment; this is given by the phenotypic gonadosomatic index GSI_P and a conversion factor γ, needed to account for the higher energy content of gonadic tissue relative to somatic tissue (14, 15). Consequently, the length of a mature individual is given by $l_t^M = 3(l_{t-1}^M + g_{P,D,t-1})/(3 + \gamma GSI_{P,t-1})$. An individual female's fecundity f is determined by its length l and gonadosomatic index phenotype GSI_P and given by $f = kl^j GSI_P D$, where D is the weight-specific packing density of oocytes (16), and k and j are allometric constants relating body length to body mass. The gonad weight at a given age can be calculated from fecundity by dividing it by the weight-specific packing density (shown in Fig. S1). An individual's probability to mate is proportional to its gonad mass, where large gonads due to larger body size and/or gonadosomatic index result in a higher production of gametes (eggs and sperm), and therefore in the production of more offspring. In our model, sex was assigned randomly at birth at a 1:1 primary sex ratio. Atlantic cod are batch spawners and so may mate with several different partners (17, 18). We therefore assumed mating to be random with replacement.

The individuals can die from natural or fishing mortality. In our model, natural mortality originated from three sources: newborn mortality, cost of growth, and a constant background natural mortality. The density-dependent newborn mortality was modeled by using an estimated Beverton–Holt stock-recruitment relationship (19) from virtual population analysis (VPA) data (20, 21). Recruitment depends on SSB_t in year t and sea surface temperature SST_t, reflecting the impact of climate. The sea surface temperature stretches from the Kola meridian transect (33°50' E, 70°50' N to 72°50' N) and has been shown to be a good indicator for recruitment for NEA cod (22–25). The expected number $R_{3,t}$ of recruits at age 3 y is then given by $R_{3,t+3} = c_0 SST_t + (c_1 SSB_t/(1 + c_2 SSB_t))$, where c_0, c_1, and c_2 are statistically estimated parameters ($R^2 = 58.9\%$). The two density-dependent parameters c_1 and c_2 were scaled to the modeled population (Table S1). Annual temperature data from 1932 to 2005 was fed into the modeled stock-recruitment relationship, and after 2006 we used the average from 1995 to 2005. In this stock-recruitment model, we ignore cannibalism, even though it has been shown to be important for natural mortality in young age classes (24, 26). We found the expected number $R_{0,t}$ of newborn recruits by back-calculating the predicted number of 3-y olds, assuming an annual total natural mortality probability equal to 0.2 y^{-1}, as conventionally done for this stock in assessment (21). The survival probability of the offspring of a given spawning pair was equal to $R_{0,t}$ divided by the total fecundity of the spawning population.

The second source of mortality, the growth–survival tradeoff, accounts for less energy available for maintenance (27, 28) and lower survival as growth increases, which may be a result of, for example, risky foraging behavior (29, 30). We therefore included a tradeoff between an individual's survival and genetic growth capacity g_G through the extra mortality probability $m_g = g_G/g_{max}$, where g_{max} is the maximal genetic growth increment at which the survival probability drops to zero, and determines the strength of this tradeoff. The parameter g_{max} is a priori unknown and has been determined in a nonevolutionary model to imitate the stock demographically from 1932 to 1950 (4), by varying g_{max} from 50 to 200 cm, in steps of 5 cm, resulting in 31 evaluated combinations. This grid covered the range of values being assumed in published versions of this model (1, 7). Comparing model predictions with time-series data on phenotypic growth, biomass, and mean age and length at maturation for the period 1932–1950, the growth–survival tradeoff g_{max} was determined by log-likelihood (Table S1). Together, the background natural mortality and the additional mortality resulting from the growth–survival tradeoff produced annual natural mortality probabilities m equal to 0.18, as assumed by ICES in its VPA analyses (Table S1).

As is the case for NEA cod, harvesting was implemented in the model separately in the feeding grounds and spawning grounds. In the feeding grounds, harvesting was size-selective with minimum size limits within the range recorded for NEA cod from the 1980s onward (31). In the spawning grounds, only mature individuals were harvested, and there was no minimum size limit. Due to annual spawning migration out of the feeding grounds for approximately one-quarter of the year, the harvest probability of mature fish on the feeding grounds was $1 - (1 - p_0)^{3/4}$, where p_0 is the harvest probability for the immature fish.

Economic Model. To calculate the welfare effects of harvesting, we first specify the harvest function; second, specify the profit function; third, derive a procedure for allocating fishing quotas; and fourth, derive the demand function. All of these functions have been estimated and derived in detail in ref. 32 and used in ref. 5. Furthermore, we specify the objective functions to derive an optimal HCR.

Harvest function. Following refs. 33 and 34, the harvest function of vessel i in year t is given by a Cobb–Douglas production function $h_{it} = qB_t^\alpha e_{i,t}^\beta$, where q is a catchability coefficient, B_t is the amount of total stock biomass, and $e_{i,t}$ is fishing effort. In our model, effort is defined as the number of days a boat is fishing cod north of 62° N, multiplied by the size (given in gross tonnage) of the boat. The stock–output elasticity α and effort–output elasticity β describe how harvest changes when the respective inputs, biomass, and effort change.

Profit function. The cost data for each vessel contains expenses made for labor wages and shares to crew; social expenses (i.e., payroll-related expenses, such as employer contributions to pension and the employer portion of social security tax); fuel and lubrication oil; bait, ice, salt, and packaging; food expenses to crew, as well as maintenance on vessel, maintenance and investment on gear, insurance on vessel, other insurances, depreciation on vessel, and other operating expenses (35). In total, there are 11 cost components, which are indexed $k = 1 \ldots 11$. Total costs incurred by vessel i in year t are given by the vector of nominal cost components $C_{ik,t}$, which are subsequently corrected for inflation using the Producer Price Index (PPI). We calculate the part of the total costs incurred for catching cod by the share of days vessel i spends on catching cod in the total number of days vessel i is fishing at sea. Using index j to enumerate all eight fish species caught (with cod being $j = 8$) and denoting the number of days in year t that vessel i catches species j by $D_{ij,t}$, the total number of days vessel i spends catching fish in year t is equal to $\sum_{j=1}^{8} D_{ij,t}$. Therefore, the costs attributed to catching cod by vessel i in year t are $C_{i,t} = (D_{i8,t} \sum_{k=1}^{11} c_{ik,t})/(PPI_t \sum_{j=1}^{8} D_{ij,t})$.

We empirically determine which fraction of the costs of fishing per boat $C_{i,t}$ comprise fixed and variable costs by estimating $C_{i,t} = c_f + c_v e_{i,t}$, where c_f can be interpreted as fixed costs, and c_v are variable costs. Multiplying the catch $h_{i,t}$ of vessel i with the price of cod P_t yields the revenue $P_t h_{i,t}$ of vessel i. The profit $\pi_{i,t}$ of vessel i is then given by offsetting this revenue with the costs of vessel i and given by $\pi_{i,t} = P_t h_{i,t} - c_f - c_v e_{i,t}$.

Issuing individual quotas. Harvest quotas could in principle be allocated through a market mechanism, such as an auction, or handed out by the government to the boat owners. It is not clear a priori what the most efficient allocation (or market outcome) is, because the size of the quota and number of quotas can vary. Each boat faces a fixed cost, but is harvesting less efficiently when the size of the quota per boat increases, determined by the estimated effort–output elasticity (parameter β in Table S1). For each year t, we identify an optimal number n_t^* of vessels harvesting an optimal number e^* of tonnage days for a given total allowable catch (TAC) and total stock biomass (for details, see ref. 32), where $n_t^* = H_t q^{-1} e^{*-\beta} B_t^{-\alpha}$.

Demand function. The NEA cod fishery contributes a large part of the world's cod landings and therefore affects the international

market price for cod. To describe this relationship, we use a linear demand function, $P_t = b_0 - b_1 H_t$, where P_t is the price for cod in year t, H_t is the total harvested biomass in year t (as determined by the TAC), and b_0 and b_1 are parameters. The inverse price elasticity is estimated to be 0.5, i.e., if the supply of cod increases by 1%, the world price drops by 0.5% (32). Using the average kilogram price in the period 1998–2007 [in 2000 Norwegian kroner (NOK)] of 12.59 NOK, and the average landing of 527,800 tonnes allows us to solve for b_0 and b_1 (Table S1).

Objective function and HCR. Each year, the NEA cod fishery generates economic profits for the fishing fleet, given by Π_t. Finding the maximum economic yield requires us to maximize the NPV of the fishery over T years, as given by NPV $= \sum_{t=0}^{T} \Pi_t (1/(1+\delta))^t$, where δ is the discount rate.

The HCR implemented for the NEA cod fishery in 2004 translates precautionary reference points into a management plan (21, 36). Below these reference points, the stock is at risk for being harvested unsustainably. The implemented HCR for the NEA cod in 2004 consists of two parameters (37, 38): a maximum fishing mortality F_{pa} is followed if the spawning stock biomass level is above the precautionary biomass level B_{pa}; below this biomass level, the fishing mortality decreases linearly to the origin, i.e., fishing mortality is zero at a biomass level of zero.

Here, we generalize a HCR with two parameters (Fig. 1B), which can be compared with the implemented management plan. If the SSB is between zero and B_{max}, the instantaneous fishing mortality for the given year is given by $F_{max}\text{SSB}/B_{max}$. If the SSB is larger than B_{max}, the fishing mortality is equal to F_{max}. The current HCR is therefore recovered as a special case when $B_{max} = B_{pa}$ and $F_{max} = F_{pa}$. In our model, we vary the parameters in the HCR over a wide range of values, not constraining them to existing precautionary reference points. We search for the combination of parameter values B_{max} and F_{max} that deliver the best results for the objective function (maximize the net present value of fleet profits) and identify those as optima. The grid for the parameters covered 4,141 different HCRs. The parameter B_{max} was varied from 0 to 800,000 tonnes in steps of 20 tonnes, and the instantaneous fishing mortality F_{max} was varied from 0.2 to 1.2 y^{-1} in steps of 0.01 y^{-1}. Our model is individual-based, and for some of these HCRs, fishing could make the abundance very low. To avoid stochastic effects at low abundances, we therefore set a threshold below which the population was classified as extinct (at 20 modeled mature superindividuals) (3, 4). The computations were completed on Abel, a computer cluster with 10,000+ cores at the Research Computing Services at the University of Oslo.

Model Limitations. As with all models, our bioeconomic model has limitations and involves simplifications. A few assumptions merit special attention here. First, we assume an initial 1:1 sex ratio, although it has been shown that the sex ratio has fluctuated over time in this cod stock (39). Second, we assume no sexual selection, although it is possible that sexual selection may influence the evolutionary changes in life-history traits (40–42). Third, we do not include genetic correlations between the life-history traits describing maturation tendency, growth capacity, and reproductive investment (4). Fourth, we assume a constant minimum size limit that determines the harvestable biomass (Table S1), implicitly assuming knife-edge selectivity (19, 43), which may not be fully realistic. Although our size limit is based on data, the size selectivity has varied over the considered time period and across vessels since 1932 (for a sensitivity analysis with respect to minimum size limit, see Table S5). Fifth, the shape of the HCR we are considering is constrained by two parameters, reflecting the current management plan. Investigating completely different shapes or considering HCR parameters that change over time is an interesting avenue for further research. Sixth, we focused on the fishery

in the stock's feeding grounds and kept the fishing mortality at observed levels in the stock's spawning grounds; we did this because we wanted to mimic the historic selection pressure on the mature fish, while parsimoniously asking what can be changed for the trawler fleet in the Barents Sea. This assumption could be changed, and the next step would be to derive an optimal HCR for each of these fisheries.

SI Results

Historic Fishing Pressure. Table S4 shows the harvesting properties for the scenario of historic fishing pressure (i.e., high fishing mortality) presented in Fig. 2. The evolutionary model delivers lower TAC, total biomass from age 3 y, and lower NPV, whereas the SSB is slightly higher compared with the nonevolutionary model.

In Fig. S1 we show the life-history changes in the scenario of historic fishing pressure, corresponding to Figs. 2 and 3. Genetic adaptations caused by fishing pressure lead to higher reproductive investment (Fig. S1A) and genetic growth (Fig. S1B). As a result, the evolving population has consistently larger gonad weight (Fig. S1C) and higher phenotypic growth (Fig. S1D). Due to evolutionary changes, the ratio between spawning stock biomass and total biomass changes over time because of a change in maturation schedule (Fig. S4), and this may have implications for stock assessment and the target reference points that are used for management.

Alternative Discount Rates. Table S2 presents optimal HCR derived for alternative discount rates. As expected, higher discount rates lead to slightly higher fishing mortality, even though only marginally. This finding may seem surprising, but happens because larger catches result in lower prices, and hence profits. At a certain point, the resulting profit loss from lower prices outweighs the profit gain resulting from catching more fish, irrespective of the discount rate (5).

Alternative Scenarios with Constant Fishing Mortalities. *Constant and weight-dependent prices.* We probe the robustness of our results by varying the fishing mortality under alternative assumptions and investigating how this influences the effects of evolutionary changes. First, as a theoretical exercise, we assume that sales prices are independent of the total catch and the price is constant; this is clearly not realistic for the NEA cod fishery, but certainly the case for many other fisheries. As a constant price, we use the inflation-corrected average kilogram price in the period 1998–2007 of 12.59 NOK. Second, in addition, we assume that sales prices are weight-dependent, i.e., the price that can be obtained per kilogram of cod rises with the weight of the fish; we found little evidence that this is actually the case for the fleet of trawlers we are considering here, but it may be relevant for other vessel types, notably smaller coastal vessels. As a theoretical benchmark, we can rely on the minimum prices from the Norwegian fishermen's sales organization (44). The prices for the different weight classes are as follows. Cod that is heavier than 6.5 kg yields 17 NOK per kilogram. Cod that weighs between 2.5 and 6.5 kg yields 14.25 NOK per kilogram; cod that weighs between 1.0 and 2.5 kg yields 12.25 NOK per kilogram; and all cod that weighs less than 1.0 kg yields 9.25 NOK per kilogram. Table S3 shows the emerging properties of different fishing mortalities and the NPV for a constant price (NPV_{CP}) and for weight-dependent prices (NPV_{WP}). For comparison, we also show the NPV derived from the model used in the main text. We find that our earlier results presented in Table 1 fully carry over to the case where the price is constant or weight-dependent. Still, evolution increases the NPV of a fishery if fishing mortality is low, and it decreases the NPV of a fishery if fishing mortality is high (Table S4).

Emerging properties for minimum size limits of 25, 45, and 85 cm. Table S5 shows the emerging properties of TAC, total biomass above the age of 3 y, and NPV that complement Fig. 4. For a fishing mortality of $F = 0.8 \ y^{-1}$ and a minimum size limit equal to 25 cm, both the evolving and the nonevolving model population go extinct. When harvest pressure is high and the size limit is low (25 cm), the economic losses due to evolution that we see at a size limit of 45 cm disappear. The NPV values are overall lower, however, for the 25-cm size limit than for the 45-cm size limit. At a very high minimum size of 85 cm, the nonevolutionary model performs insignificantly better than the evolutionary model, suggesting that economic losses from evolutionary change are not increasing as minimum sizes increase. Instead, those evolutionary costs are highest (albeit still small) for a minimum size of 45 cm— a size that is based on historic values for the Norwegian and Russian cod fisheries (4, 21) and very close to the size currently used as a legal minimum size (45). Fig. S2 shows the final genetic trait values (year 2100) for different fishing mortalities ($F = 0.4$, $0.8 \ y^{-1}$) and for different minimum size limits. We find here that the evolutionary change is larger as fishing mortality increases for all traits except for growth, and that higher minimum size limits result in lower selective pressure and less evolution (Fig. S2).

Varying the coefficients of genetic variation and fishing mortality. In the evolutionary version of our model, the coefficient of genetic variation (Table S1) has been determined empirically by matching trends in age and length at maturation over a 74-y period (1932–2005) (4). The genetic changes emerging from this study are found to be lower than what has been predicted in comparable studies (1, 7–9). These studies assumed a coefficient of genetic variation for all traits equal to 8% and 6%, respectively. As a robustness check, we therefore used these higher coefficients of genetic variation (6% and 8%) and performed simulations for different fishing mortalities. After fishing with a particular fishing mortality from 1932 to 2100, we compare the simulation end-points for age at maturation and TAC with our calibrated evolutionary model (Table S1) and nonevolutionary model (for which all coefficients of genetic variation are equal to zero). As expected, we find that an assumed $CV_{z,G}$ of 6% and 8% results in predicting larger evolutionary responses, causing a much lower age at maturation in the year 2100 (Fig. S3A). As genetic variance increases, the fish mature at a younger age and at a smaller size, and also grow faster. As fishing mortality increases, age at maturation also declines for the nonevolutionary model, which is entirely due to phenotypic plasticity and density dependence in response to a lower abundance of the stock. For the case where the coefficients of genetic variation are set to 6% and 8%, we find that for a given fishing mortality, higher TACs can be obtained compared with the models where evolutionary change is weaker or even absent. This finding indicates that stronger evolutionary forces tend to have as positive effect on the TAC, and corroborates our earlier finding that evolution toward faster growth tends to have positive effects on the fishery.

1. Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. *Ecol Appl* 19(7):1815–1834.
2. Huse G, Johansen GO, Bogstad L, Gjosaeter H (2004) Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES J Mar Sci* 61(7):1201–1213.
3. Scheffer M, Baveco JM, Deangelis DL, Rose KA, Vannes EH (1995) Super-individuals a simple solution for modeling large populations on an individual basis. *Ecol Modell* 80(2-3):161–170.
4. Eikeset AM, Dunlop ES, Heino M, Stenseth NC, Dieckmann U (2010) Is evolution needed to explain historical maturation trends in Northeast Atlantic cod? PhD thesis (University of Oslo, Oslo).
5. Eikeset AM, et al. (2013) A bio-economic analysis of harvest control rules for the Northeast Arctic cod fishery. *Mar Pol* 39:172–181.
6. Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness components. *Heredity (Edinb)* 59(Pt 2):181–197.
7. Dunlop ES, Baskett ML, Heino M, Dieckmann U (2009) Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evol Appl* 2(3): 371–393.
8. Enberg K, Jorgensen C, Dunlop ES, Heino M, Dieckmann U (2009) Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol Appl* 2(3):394–414.
9. Enberg K, Jørgensen C, Mangel M (2010) Fishing-induced evolution an changing reproductive biology of fish: The evolution of steepness. *Can J Fish Aquat Sci* 67(10): 1708–1719.
10. Roughgarden J (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (Macmillan, New York).
11. Dieckmann U, Heino M (2007) Probabilistic maturation reaction norms: Their history, strengths, and limitations. *Mar Ecol Prog Ser* 335:253–269.
12. Heino M, Dieckmann U, Godø OR (2002) Reaction norm analysis of fishery-induced adaptive change and the case of the Northeast Arctic cod. *ICES CM Series*, Report Y: 14. Available at http://brage.bibsys.no/imr/handle/URN:NBN:no-bibsys_brage_3050.
13. International Council for the Exploration of the Sea (ICES) (2008) *Report of the Arctic Fisheries Working Group*, ICES CM 2008/ACOM:01 (ICES, Copenhagen).
14. Gunderson DR, Dygert PH (1988) Reproductive effort as a predictor of natural mortality-rate. *J du Conseil* 44(2):200–209.
15. Lester NP, Shuter BJ, Abrams PA (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: The cost of reproduction. *Proc Biol Sci* 271(1548):1625–1631.
16. Thorsen A, Kjesbu OS (2001) A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. *J Sea Res* 46(3-4):295–308.
17. Kjesbu OS, Witthames PR, Solemdal P, Walker MG (1998) Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J Sea Res* 40(3-4):303–321.
18. McEvoy LA, McEvoy J (1992) Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. *J Fish Biol* 41(Suppl B):125–136.
19. Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. *Fish Investment Series 2* (UK Ministry of Agriculture, Fisheries and Food, London), Vol 19.
20. Hylen A (2002) Fluctuations in abundance of Northeast Arctic cod during the 20th century. *ICES Mar Sci Symp* 215:543–550.
21. International Council for the Exploration of the Sea (ICES) (2009) *Report of the Arctic Fisheries Working Group*, ICES CM 2009/ACOM:2 (ICES, Copenhagen).
22. Bochkov YA (1982) Water temperature in the 0–200m layer in the Kola-Meridian in the Barents Sea, 1900–1981. *Sb Nauchn Trud PINRO* 46:113–122, Russian.
23. Tereshchenko VV (1996) Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. Report CM 1996/C:11 (Intl Council for the Exploration of the Sea, Copenhagen).
24. Hjermann DO, et al. (2007) Food web dynamics affect Northeast Arctic cod recruitment. *Proc Biol Sci* 274(1610):661–669.
25. Ottersen G, Hjermann D, Stenseth NC (2006) Changes in spawning stock structure strengthens the link between climate and recruitment in a heavily fished cod stock. *Fish Oceanogr* 15(3):230–243.
26. Yaragina NA, Bogstad B, Kovalev YA (2009) Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006. *Mar Biol Res* 5(1):75–85.
27. Billerbeck JM, Lankford TE, Jr., Conover DO (2001) Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. *Evolution* 55(9):1863–1872.
28. Nicieza AG, Metcalfe NB (1999) Costs of rapid growth: The risk of aggression is higher for fast-growing salmon. *Funct Ecol* 13(6):793–800.
29. Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. *Can J Fish Aquat Sci* 50:2058–2070.
30. Biro PA, Post JR (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc Natl Acad Sci USA* 105(8): 2919–2922.
31. Bjordal Å, Gjøsæter H, Mehl S (2004) Management strategies for commercial marine species in northern ecosystems. *Proceedings of the 10th Norwegian–Russian Symposium*. Norwegian Institute of Marine Research (IMR)/Polar Research Institute of Marine Fisheries and Oceanography (PINRO) Joint Report Series 1. Available at www.imr.no/filarkiv/2004/12/Imr-Pinro-1-2004.pdf/nb-no.
32. Richter AP, Eikeset AM, Van Soest DP, Stenseth NC (2011) Towards the optimal management of the Northeast Arctic cod fishery. *Fondazione Eni Enrico Mattei Working Paper 591*. Available at www.feem.it/userfiles/attach/20115201140194NDL2011-040.pdf.
33. Clark CW (1990) *Mathematical Bioeconomics: The Optimal Management of Renewable Resources* (Wiley, New York), 2nd Ed.
34. Grafton RQ, Kompas T, Hilborn RW (2007) Economics of overexploitation revisited. *Science* 318(5856):1601.
35. Norwegian Directorate of Fisheries (2009) Profitability survey on the Norwegian fishing fleet (Norwegian Directorate of Fisheries, Bergen, Norway). Available at www.ssb.no/a/english/aarbok/tab/tab-370.html.
36. International Council for the Exploration of the Sea (ICES) (2008) Report of the ICES Advisory Committee. *ICES Advice 2008* (ICES, Copenhagen).
37. Bogstad B, et al. (2005) Harvest control rules for management of fisheries on Cod and Haddock and optimal long term optimal harvest in the Barents Sea ecosystem. *Report of the Basic Document Working Group (BDWG) to the Joint Norwegian–Russian Fisheries Commission*. Available at www.regjeringen.no/upload/kilde/fkd/prm/2005/0084/ddd/pdfv/262877-vedlegg_11_bdwg-2005_final.pdf.
38. Kovalev YA, Bogstad B (2005) Evaluation of maximum long-term yield for Northeast Arctic cod. *Ecosystem Dynamics and Optimal Long-Term Harvest in the Barents Sea*

Fisheries, ed Shibanov V (Norwegian Institute of Marine Research/Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia), pp 1–18.

39. Marshall CT, Needle CL, Thorsen A, Kjesbu OS, Yaragina NA (2006) Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: Implications for stock-recruit theory and management. *Can J Fish Aquat Sci* 63(5):980–994.

40. Urbach D, Cotton S (2008) Comment: On the consequences of sexual selection for fisheries-induced evolution. *Evol Appl* 1(4):645–649.

41. Hutchings JA, Rowe S (2008) Response: On the consequences of sexual selection for fisheries-induced evolution. *Evol Appl* 1(4):650–651.

42. Hutchings JA, Rowe S (2008) Consequences of sexual selection for fisheries-induced evolution: An exploratory analysis. *Evol Appl* 1(1):129–136.

43. Food and Agricultural Organization of the United Nations (FAO) (1998) *Introduction to Tropical Fish Stock Assessment. Part 1: Manual*. FAO Fisheries Technical Paper (FAO, Rome).

44. Norwegian Fishermen's Sales Organization (2010) Minimum price list. Circular no. 2010/16 (Norwegian Fishermen's Sales Organization, Tromsø, Norway). Norwegian.

45. International Council for the Exploration of the Sea (ICES) (2012) *Report of the Arctic Fisheries Working Group* (ICES, Copenhagen).

Fig. S1. Life-history changes from 1932 to 2100 in the scenario with historic fishing pressure for the evolutionary (black lines) and nonevolutionary model (gray lines), corresponding to Figs. 2 and 3. (*A*) Genetic gonadosomatic index (GSI), (*B*) genetic growth capacity, (*C*) average gonad weight, and (*D*) phenotypic growth capacity.

Fig. S2. Predicted evolved life-history traits at the simulation endpoints in the year 2100 for different minimum size limits and different fishing mortalities. Fishing mortalities were applied from 1932 to 2100. Results shown are for the evolutionary model. Coefficients of genetic variation are the same as those used in the main text. Initial trait values are shown by the horizontal bold line, and the arrow shows the direction of evolution. Dark-gray lines and circles are for $F = 0.4 \ y^{-1}$, and light-gray lines and circles are for $F = 0.8 \ y^{-1}$. (*A*) Probabilistic maturation reaction norm (PMRN) intercept, (*B*) PMRN slope, (*C*) genetic gonadosomatic index (GSI), and (*D*) genetic growth capacity.

Fig. S3. Predicted stock characteristics at the simulation endpoints in the year 2100 for different coefficients of genetic variation, $CV_{z,G}$, and different fishing mortalities, F. Fishing mortalities were applied from 1932 to 2100. Open circles are for $CV_{z,G} = 6\%$ for all traits, and open squares are for $CV_{z,G} = 8\%$ for all traits; gray circles are for the nonevolutionary model, and black circles are for the evolutionary model used in the main text (Table S1). (*A*) Age at maturation and (*B*) total allowable catch (TAC).

Fig. S4. Ratio between spawning stock biomass (SSB) and total biomass from age 3 y in the scenario with historic fishing pressure for the evolutionary (black line) and nonevolutionary model (gray line).

Table S1. Parameter values and data sources for the bioeconomic model

Parameters	Value	Source
Biological model component		
Initial mean PMRN slope, $\bar{s}_G$	0.15 cm y^{-1}	4, 12
Initial mean PMRN intercept, $\bar{i}_G$	77.4 cm	4, 12
Initial mean reproductive investment, $\overline{GSI}_G$	0.15	17
Initial mean growth capacity, $\bar{g}_G$	11.08 cm	4, 5, M. Heino*
PMRN width, w	12.88 cm	4, 12
Coefficient of genetic variation in PMRN slope, $CV_{s,G}$	10%	4
Coefficient of genetic variation in PMRN intercept, $CV_{i,G}$	2%	4
Coefficient of genetic variation in reproductive investment, $CV_{GSI,G}$	12%	4
Coefficient of genetic variation in genetic growth, $CV_{g,G}$	4%	4
Initial heritability, h_z^2	0.2	6
Strength of density dependence in growth, x	2.08×10^{-5} kg^{-1}	4, 5, M. Heino*
Reproductive investment conversion factor, γ	0.60241	14
Allometric constant, k	3.2×10^{-6} kg cm^{-j}	O. S. Kjesbu*
Allometric exponent, j	3.24	O. S. Kjesbu*
Weight-specific oocyte density, D	4.45×10^6 kg^{-1}	16
Maximal growth capacity, g_{max}	105 cm	4
Stock recruitment constant, c_1	0.7549 kg^{-1}	4, 20, 21
Density-dependent stock recruitment constant, c_2	-6.0633 kg^{-1}	4, 20, 21
Temperature coefficient in stock recruitment, c_0	0.4241 $°C^{-1}$	PINRO**, 22, 23
Natural mortality probability, m	0.18	21
Immature fishing probability in spawning grounds pre-1932	0.38	M. Heino*, O. R. Godø*
Immature fishing probability in feeding grounds pre-1932	0.09	M. Heino*, O. R. Godø*
Minimum size limit on feeding grounds	45 cm	21, O. R. Godø*
Economic model component		
Intercept of the demand function, b_0	18.88 NOK kg^{-1}	32
Slope of the demand function, b_1	1.19×10^{-8} NOK kg^{-2}	32
Stock–output elasticity, α	0.58	32
Effort–output elasticity, β	0.85	32
Catchability coefficient, q	6.17×10^{-4} $tonnes^{-1}d^{-1}$	32
Fixed costs per boat, c_f	1.55×10^6 NOK	32
Variable costs per boat, c_v	131.6 NOK $tonnes^{-1}d^{-1}$	32
Optimal number of tonnage days, $e*$	66,712 tonnes/d	32

Economic data for the Northeast Arctic cod fishery: costs and harvests from the Norwegian Directorate of Fisheries, Bergen, Norway, provided by P. Sandberg; biomass and total landings are from ICES (21); and demand function is from Statistics Norway, Oslo, Norway, and Norwegian Directorate of Fisheries. Economic values have been inflation corrected using the Producer Price Index from the Organisation for Economic Cooperation and Development, Paris, France, with year 2000 as a baseline. The applied exchange rate is 1 US dollar = 5.6 NOK. Biological data for the Northeast Arctic cod stock is described below.
*IMR, Institute of Marine Research, Bergen, Norway: Survey data on growth from 1932 to 2009 provided by M. Heino; allometric data from survey 1999–2007 provided by O. S. Kjesbu; data on fishing mortality and minimum size limit provided by M. Heino and O. R. Godø.
**PINRO, Knipovich Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia: Temperature data.

Table S2. Optimal HCR with parameters F_{max}, B_{max}, and corresponding NPV for different discount rates (δ), 0%, 2%, and 4%

Model	δ, %	F_{max}	B_{max}	F	TAC	SSB	NPV
Evolution	0	0.33	100	0.33	467 (60)	801 (163)	96.0
	2	0.34	20	0.34	469 (60)	767 (163)	25.4
	4	0.35	20	0.35	470 (60)	735 (155)	12.6
Ecology	0	0.33	40	0.33	439 (48)	670 (125)	94.7
	2	0.35	100	0.35	443 (48)	643 (118)	25.3
	4	0.36	100	0.36	445 (48)	618 (114)	12.6

Averages of fishing mortality (F), total allowable catch (TAC), and spawning stock biomass (SSB) with temporal SDs in parentheses. Units: F_{max} and F (y^{-1}); B_{max}, TAC, and SSB (1,000 tonnes); NPV (in billions, US dollars). HCR, harvest control rule; NPV, net present value.

Table S3. Averages for different constant fishing mortalities from 1932 to 2100, showing TAC, total biomass from age 3 y, and NPV for a discount rate of 2% assuming NPV_{CP} and NPV_{WP}

F	Model	TAC	Biomass	NPV_{CP}	NPV_{WP}	NPV
0.2	Evolution	400 (55)	2,686 (375)	25.7	30.5	23.1
0.2	Ecology	375 (42)	2,503 (277)	24.6	29.2	23.0
0.4	Evolution	473 (60)	1,779 (216)	27.3	31.5	25.2
0.4	Ecology	449 (51)	1,711 (178)	26.47	30.8	25.1
0.6	Evolution	429 (70)	1,208 (176)	21.41	23.8	21.6
0.6	Ecology	427 (66)	1,246 (164)	22.1	24.8	22.3
0.8	Evolution	335 (90)	800 (191)	13.0	13.9	14.7
0.8	Ecology	354 (85)	889 (176)	15.10	16.6	16.7

For comparison we also show the NPV derived from the model used in the main text. Temporal SDs for total allowable catch (TAC) and biomass are shown in parentheses. Units: F (y^{-1}); TAC and total biomass (1,000 tonnes); NPV (in billions US dollars). NPV_{CP}, net present value for constant price; NPV_{WP}, net present value for weight-dependent prices.

Table S4. Mean values corresponding to the historic fishing pressure in Fig. 2

Model	F	TAC	SSB	Biomass	NPV
Evolution	0.68	360 (95)	267 (365)	1,103 (562)	17.8
Ecology	0.68	370 (93)	260 (356)	1,167 (526)	18.6

Averages of fishing mortality (F), total allowable catch (TAC), total biomass from age 3 y, and spawning stock biomass (SSB) with temporal SDs in parentheses, and finally net present value (NPV). The NPV is given for a discount rate of 2%. Units: F (y^{-1}); TAC, biomass, and SSB (1,000 tonnes); NPV (in billions, US dollars).

Table S5. NPV, TAC, and total biomass from age 3 y for the minimum size limits 25, 45, and 85 cm across different constant fishing mortalities, F

	Minimum size (cm)					
	25		45		85	
	Evolution	Ecology	Evolution	Ecology	Evolution	Ecology
TAC						
$F = 0.2$	337 (48)	310 (34)	400 (154)	375 (42)	222 (50)	215 (54)
$F = 0.4$	325 (58)	283 (49)	473 (60)	449 (51)	336 (65)	331 (55)
$F = 0.6$	217 (79)	170 (79)	429 (69)	426 (66)	401 (70)	398 (60)
$F = 0.8$	—	—	335 (91)	354 (86)	441 (71)	446 (67)
NPV						
$F = 0.2$	20.7	20.2	23.1	23	13.4	12.9
$F = 0.4$	16.9	15.5	25.2	25.1	19.1	19.7
$F = 0.6$	6.4	4.51	21.6	22.3	22.0	22.8
$F = 0.8$	—	—	14.7	16.7	23.6	24.5
Biomass						
$F = 0.2$	2,026 (309)	1,852 (221)	2,689 (374)	2,505 (276)	3,914 (535)	3,833 (479)
$F = 0.4$	1,034 (191)	896 (159)	1,778 (216)	1,709 (178)	3,639 (446)	3,590 (446)
$F = 0.6$	487 (183)	385 (184)	1,208 (176)	1,245 (165)	3,464 (395)	3,438 (423)
$F = 0.8$	—	—	798 (193)	888 (178)	3,341 (365)	3,324 (382)

Values shown for total allowable catch (TAC) and total biomass (1,000 tonnes) are averages for 1932–2100 with temporal SDs in parentheses. The net present value (NPV) (in billions, US dollars) is given for a discount rate of 2%. Units: F (y^{-1}); TAC and total biomass (1,000 tonnes); NPV (in billions, US dollars).