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Economic repercussions of fisheries-induced evolution

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The economic repercussions of fisheries-induced evolution

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Abstract

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 eco-evolutionary dynamics have not been empirically investigated. Using 70 years of data, we develop a bio-economic 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 towards 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 non-evolutionary 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. As evolution facilitates growth, the fish are younger and still immature when they are susceptible to getting caught. This outweighs the increase in productivity due to fish spawning at an earlier age.

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Introduction

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, while an individual's increased reproductive investment leads to larger gonads, this happens at the expense of slower post-maturation 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 the 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. To our knowledge, no study has yet to empirically investigate the economic consequences of FIE in wild populations, and how these alter optimal fishing mortalities. 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 to 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, while 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).

We develop a bio-economic 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, and the economic components rely on individual vessel data, making this, as far as we are aware, the first empirically bio-economic model for investigating genetic adaptations to harvesting. It 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). While we focus on the feeding grounds 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 be beyond the control of the manager. The biological model component is built upon the individual-based eco-genetic model framework developed by ref. (1), describing four evolving life-history traits capturing key aspects of growth, maturation, and reproduction. Changes in life-history traits may be driven by both ecological processes, like phenotypic plasticity and density-dependence, and through genetic processes. To evaluate whether accounting for FIE requires a special harvest strategy, we also analyze a non-evolutionary version of the biological model in which the genetic traits cannot evolve. We therefore compare a non-evolutionary 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. We incorporate a demand function, also estimated from empirical data, to account for how total catch affects the price of landings (21). 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). Such shape makes it directly comparable to the HCR that was implemented for NEA cod in 2004 (22, 23). We search for the parameter combination that gives the highest net present value (NPV) for the objective fleet profits. We derive HCRs that are either optimized in the evolutionary or non-evolutionary version of the model.

Results

We first compare the emerging properties of the evolutionary model with the non-evolutionary model, when both are managed according to what an HCR recommends that has been optimized for fleet profits (see Table 1, "Evolution" vs. "Ecology"). We find that the optimal fishing mortality is almost identical for the evolutionary and non-evolutionary model and substantially lower than what it has been historically. In spite of 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 ignored by managers (Table 1, "Evolution ignored"). The key message here is that a low fishing mortality is optimal, no matter whether genetic changes occur or not. This prediction holds for different discount rates (Table S3), when sales prices are assumed independent of the total catch, and when the price that can be obtained per kg of cod rises with the weight of the fish (Table S4).

Given that fishing mortality has not been low for the NEA cod fishery in the past, and 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 already introduced 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 to the case where only ecological effects are present. The opposite is true for the scenario of historically high fishing mortality, where biomass is actually slightly lower in the evolutionary model (Fig. 2A). As a result, the corresponding TAC and NPV are also slightly lower when evolution occurs and fishing mortality is high (Table S2).

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 reveal that age at maturation declines over time in all scenarios (Fig. 2B). While this occurs in the non-evolutionary 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. 2C). In spite of 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. 2D). In order to better understand the population structure, we take a closer look at the age composition at the simulation endpoints (Fig. 3). We find that in spite of individual fish being smaller at maturation, the size at a given age is consistently larger for the evolutionary model compared to the non-evolutionary model, irrespective of the fishing mortality being optimal or high (Fig. 3A). Indeed, the underlying genetic trait changes show that the evolving population invests more in intrinsic somatic growth capacity and reproductive investment, with the end result being overall larger body sizes and higher reproductive output (Fig. 3A, S1). Looking closer at the age structure of the fish 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. 3B). 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 spare all fish below the minimum size limit of 45 cm. It might seem surprising that these genetic changes towards 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 interactions with the environment 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. 4A). 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 and there is little difference between the evolutionary and non-evolutionary predictions (Fig. 4C and S4). Therefore, the loss in NPV due to evolution only occurs for intermediate minimum size limits, where the beneficial effects of growing faster are swamped out by making those fish more vulnerable who 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, 24, 25), 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, predicting 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. S2), which could mask a decreasing trend in total biomass and affect the stock-recruitment relationship with associated accuracy of predictions (25). This may furthermore have important management implications when biomass levels approach SSB-based limit reference points (26). 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 institutional setting 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 (27). To 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 (28-30).

While we find that removing selectively 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 new light on the discussion whether harvesting should be balanced or selective (31). While we assume a knife-edge selectivity in our model (32, 33), different gear types with selectivity patterns remain to be explored for further research. While gear regulation 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).

While our biological model is very 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 harvest control rules for the NEA cod's feeding and spawning grounds. Previous research has found predictions for fisheries-induced evolution to differ depending on whether management actions target feeding or spawning grounds (34). 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.

Altogether, our results show that the economic consequences of FIE are rather small, and mostly beneficial. This is largely because of the positive effects of fishing on growth. This prediction is made possible because of the crucial eco-evolutionary feedbacks between biomass, growth and maturation and because of the inclusion of growth as an evolving trait. Models that don't 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 away 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 selective. Otherwise, FIE may reduce economic yield and make the stock actually less viable. Admittedly, these evolutionary costs are very small, but they may just be enough to push a fish stock from the state of overexploitation into collapse.

Materials and methods

Our bio-economic model consists of two sub-models: “the biological model” which is a description of 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 the sub-models have been specifically estimated and calibrated for this stock by using data from the time period 1932-2007 (Table S1). A more extensive model description can be found in SI Materials and Methods.

The biological model

The biological model is individual-based and has been developed in ref. (17) building upon the “eco-genetic” 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 about 50,000 super-individuals (34, 35). 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 made two versions of our model, an evolutionary and a non-evolutionary version, each modeling their respective population of individuals in order 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 (i.e., newborn mortality) and the density dependence of growth on stock biomass (17). Furthermore, a growth-survival tradeoff is included and the strength of this trade-off was determined by matching the ecological properties for data on age and length at maturation, phenotypic growth and biomass from 1932-1950 in the non-evolutionary version of the model to reach demographic equilibrium (17). In the evolving population, the coefficient of genetic variation (CV) has been determined empirically for each trait (17) by matching trends in age and length at maturation over a 74 year period (i.e. from 1932-2005). In this calibration, the historic selection pressure was mimicked by using annual harvest probabilities in the feeding and spawning ground from 1932 until 2005. The resultant CV 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, 24, 25), as was the case here. For the non-evolving population, which is only driven by ecological processes, the CV is equal to zero.

The economic model and harvest control rule

The economic model (i) specifies the harvest function, (ii) specifies the profit function, (iii) derives a procedure for allocating fishing quotas, and (iv) derives the demand function. All of these functions have been estimated and derived in detail in ref. (36) and used in ref. (21). We assume a knife-edge selectivity (32, 33) that targets all fish above the size of 45 cm (17, 37). The biological and economic models are linked together through an annual feedback loop: spawning stock biomass (SSB) is fed into the economic model where ultimately the total allowable catch (TAC) is determined by a harvest control rule (HCR). The derived TAC feeds back into the biological model and affects the stock size (Fig. 1, “realized catch”). The shape of the HCR is based on the one that was implemented for NEA cod in 2004 (22, 23): 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 maximize the economic objective, fleet profit. 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. As 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 the mid- 2000. In the “historic fishing” scenarios, we use observed fishing mortalities from 1932-2005 and then assume a constant fishing mortality in the feeding ground (0.68 year^{-1}) being maintained from 2006 and into the future. This constant (0.68 year^{-1}) is an average of the historic fishing mortality between 1946-2005 and is higher than what is considered to be precautionary for the NEA cod (0.4 year^{-1}) (37).

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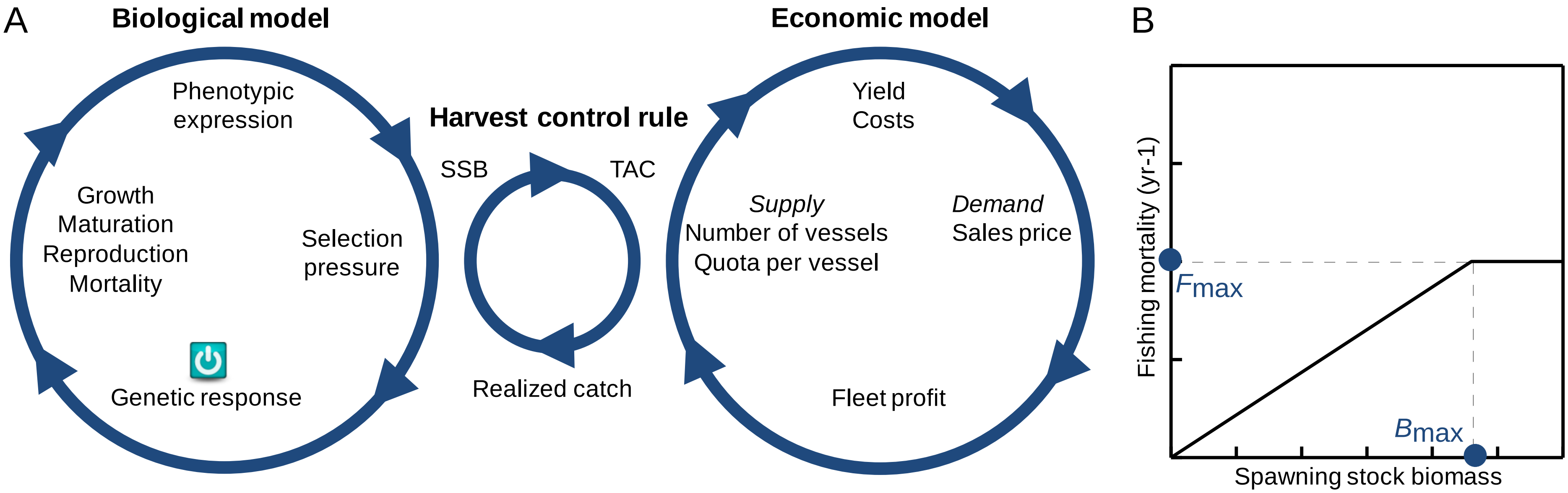
Figure legends

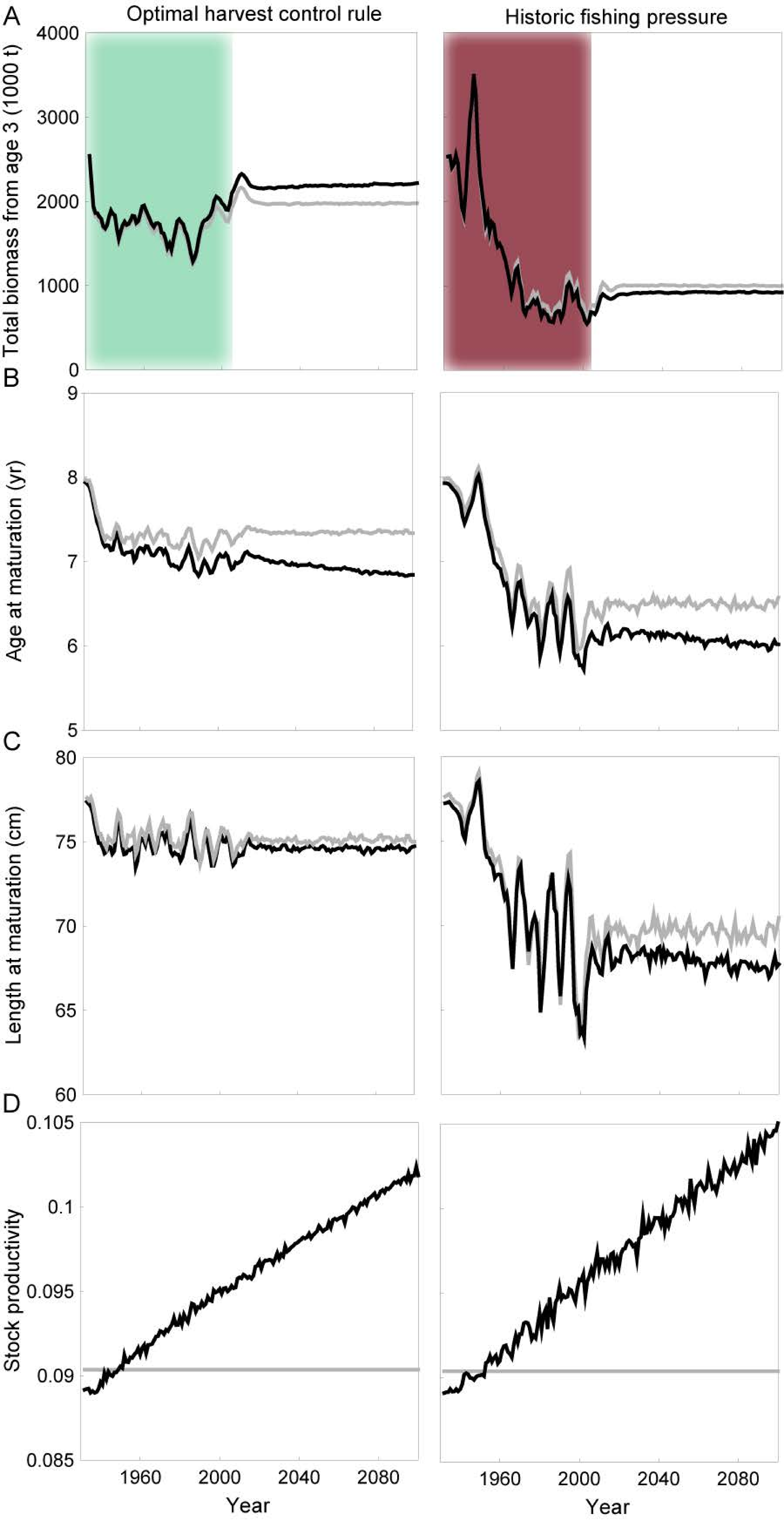
Fig. 1. An overview of the bio-economic model. **(A)** The biological and economic models are coupled by the harvest control rule (HCR). The individual-based biological model describes the evolution of key life-history traits if genetic changes are allowed to occur in the model. The economic model accounts for the supply and demand side of the fishery, as well as 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 ICES (The International Council for the Exploration of the Sea) for the NEA cod fishery.

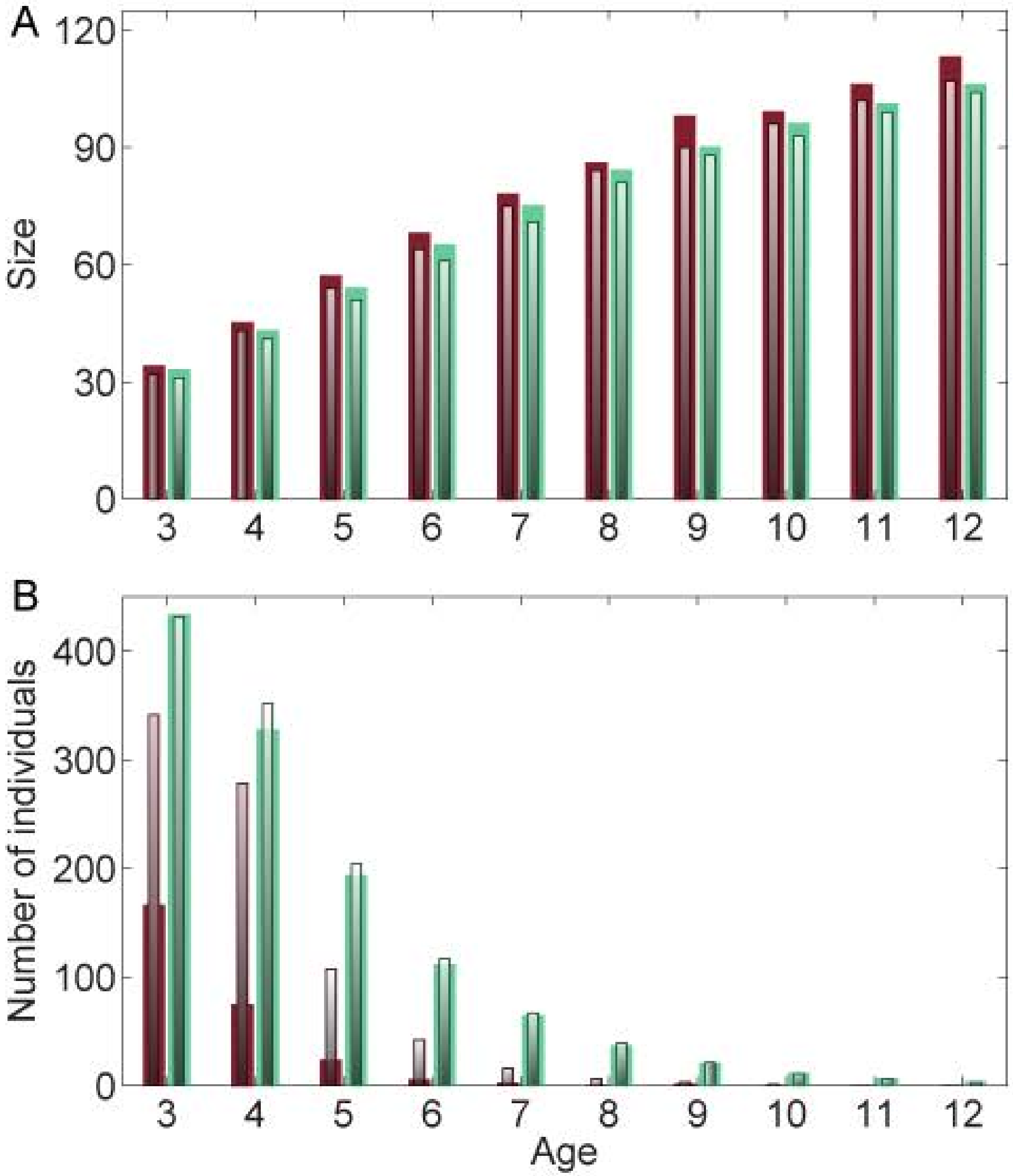
Fig. 2. The first scenario is based on an optimal harvest control rule (HCR) maximizing fleet profit (green shading shows the period for which we have data), and the second scenario of historic fishing mortality is based on the observed fishing mortalities for 1932-2005 (red shading), and from 2006 onwards follows the average fishing mortality for 1946-2005. For each scenario, the emerging properties from an evolutionary model (black) are compared with those of the corresponding non-evolutionary model (grey). **(A)** Total biomass for ages 3 years plus (1000 t) 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 non-evolutionary model. The historic scenario predicts age and length at maturation to fall to between age 6-7, and 60-70 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 even more so if fishing mortality is high.

Fig. 3. Eco-evolutionary dynamics and age-truncation. The optimal HCR scenario is shown by green bars, while high fishing mortality is indicated with red bars. The evolutionary model outcome is shown in the full bars, while the non-evolutionary one is shown by grey inner bars. **(A)** the mean size is larger for all age-classes if evolution occurs, **(B)** the numbers 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. The evolutionary model (black) predicts higher TAC than the non-evolutionary model (grey) when selection also acts on very young fish. For a minimum size limit of 85 cm, the two models are not different. 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.


A
Biological model
Phenotypic expression
Growth
Maturation
Reproduction
Mortality
Selection pressure
Genetic response
Harvest control rule
SSB
TAC
Realized catch
Economic model
Yield
Costs
Supply
Number of vessels
Quota per vessel
Demand
Sales price
Fleet profit
B
Fishing mortality (yr-1)
Fmax
Bmax
Spawning stock biomass


A
Optimal harvest control rule
Historic fishing pressure
Total biomass from age 3 (1000 t)
4000
3000
2000
1000
0
B
Age at maturation (yr)
9
8
7
6
5
C
Length at maturation (cm)
80
75
70
65
60
D
Stock productivity
0.105
0.1
0.095
0.09
0.085
1960
2000
2040
2080
Year
1960
2000
2040
2080
Year


A
120
90
60
30
0
Size
3
4
5
6
7
8
9
10
11
12
B
400
300
200
100
0
Number of individuals
3
4
5
6
7
8
9
10
11
12
Age

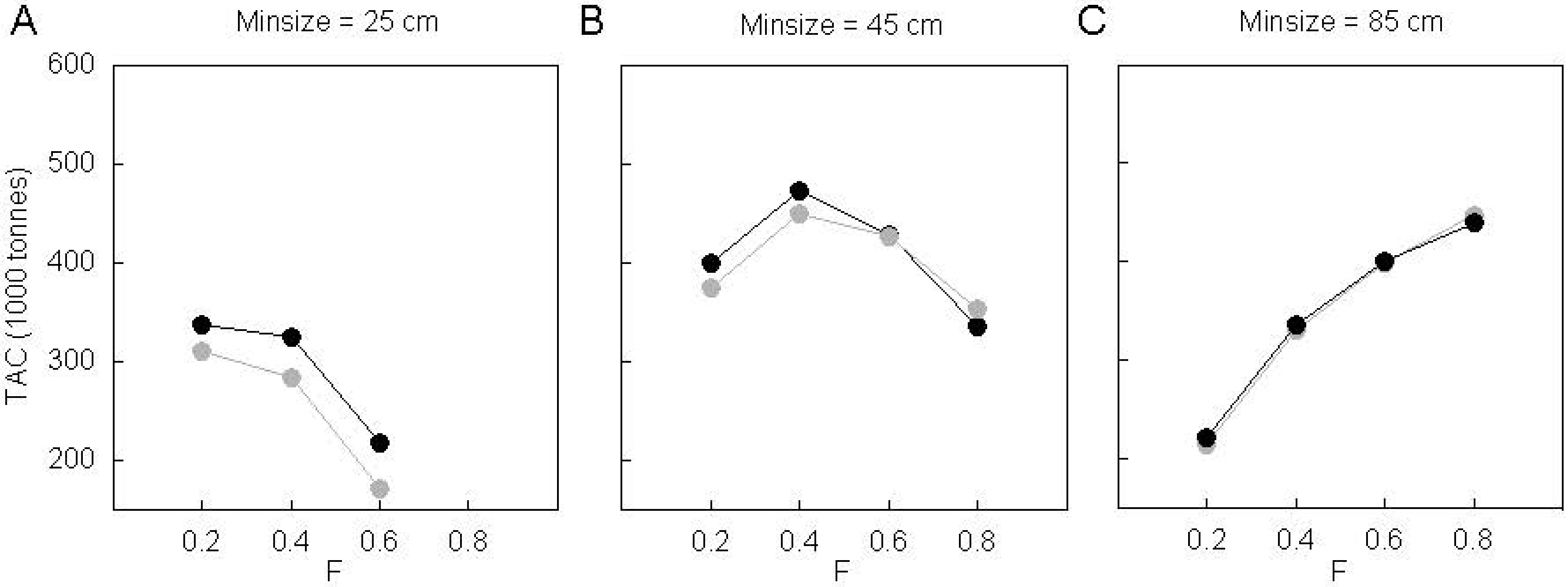

A
Minsize = 25 cm
B
Minsize = 45 cm
C
Minsize = 85 cm
TAC (1000 tonnes)
600
500
400
300
200
0.2
0.4
0.6
0.8
F

Table 1. Optimal harvest control rule (HCR) for an evolutionary model ("Evolution") and non-evolutionary model ("Ecology"). Values shown are averages for 1932-2100 on fishing mortality (*F*), catch (TAC), spawning stock biomass (SSB), with temporal standard deviation in parentheses, and NPV with a discount rate of 2%. "Evolution ignored" uses an evolutionary model with the ecologically optimal HCR.

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

Units: *F* (inst. rate), TAC, SSB (1000 tonnes); NPV (billion USD).

Supporting Information

The economic repercussions of fisheries-induced evolution

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SI text

The Supporting Information consists of two main sections: (i) SI Materials and Methods and (ii) SI Results. In the methods section, we describe the biological and economic component in the bio-economic model, including a description of the data used to parameterize the model (Table S1). At the end of the SI Materials and Methods, we discuss model limitations. In the 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. Furthermore, we probe into the robustness of our results. Simulating different levels of constant fishing mortality rates (0.2-0.8 yr^{-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 individual-based and based upon the framework developed by ref. (1). It 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 the individuals to adapt to the selection pressure brought about by harvesting. The individual-based model follows about 50,000 super-individuals (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) and the

Fisheries Directorate, 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 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, secondly, 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 z_{G} (denoted by subscript G) has a corresponding phenotypic trait value z_{P} (denoted by subscript P), with a genetic variance $\sigma^2_{\mathrm{z,G}}$ and phenotypic variance $\sigma^2_{\mathrm{z,P}}$. At the population level, we assume phenotypic variance to be the sum of the genetic and environmental variance $(\sigma^2_{\mathrm{z,P}} = \sigma^2_{\mathrm{z,G}} + \sigma^2_{\mathrm{z,E}})$. Based on quantitative genetics (6) each trait has a heritability, $h_z^2 = \sigma^2_{\mathrm{z,G}} / \sigma^2_{\mathrm{z,P}}$, which allows us to calculate the environmental variance $\sigma^2_{\mathrm{z,E}} = \sigma^2_{\mathrm{z,G}} \left(h_z^{-2} - 1 \right)$ for each trait in the initial population (where $\sigma^2_{\mathrm{z,G}}$ 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 $z_G = s_{\mathrm{G}}$ and (ii) intercept $z_G = i_{\mathrm{G}}$; (iii) growth capacity $z_G = g_{\mathrm{G}}$; and (iv) reproductive investment given by the gonado-somatic index $z_G = \mathrm{GSI}_{\mathrm{G}}$. 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 $\mathrm{CV}_{\mathrm{z,G}}$, 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_E^2. We made an evolutionary and a non-evolutionary version of the model, each modeling their respective population of individuals in order to compare a population that has the propensity to evolve, with a population that does not evolve. First, the non-evolutionary model was calibrated to accomplish a match with data on Northeast arctic (NEA) cod phenotypic growth, biomass, and age and length at maturation for the period 1932-1950 (4). For the non-evolving population, which is only driven by ecological processes, the coefficient of genetic variation ($\mathrm{CV}_{z,G}$) equals zero. In the evolving population, $\mathrm{CV}_{z,G}$ was determined by matching trends in age and length at maturation over a 74 year period (i.e., 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. The range of evaluated coefficients of genetic variation, $\mathrm{CV}_{z,G}$ was between 0% and 12% and based on previous models (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 $\mathrm{CV}_{z,G}$ values for each trait.

Offspring inherited genetic trait values from their parents by drawing randomly from normal distributions with means equal to the mid-parental 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; see ref. (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 natural mortality

Each year, the probability p_m that an immature individual will mature is described by a probabilistic maturation reaction norm, PMRN (11, 12). This is a function of the individual's length l and age a and given by $p_\mathrm{m} = \left[1+\exp\left(-\left(l-l_{\mathrm{p}50,a}\right)/v\right)\right]^{-1}$. The length $l_{p50,a}$ is where the maturation probability p_m is equal to 50% at age a, as given by $l_{\mathrm{P}50,a} = i_\mathrm{P} + s_\mathrm{P}a$, with a phenotypic intercept i_P and slope s_P. The parameter v is determined by the lower bound probability p_u (25%) and the upper bound probability p_l (75%) of the maturation envelope (1, 4), together with the PMRN width, 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 $g_{\mathrm{P,D},t} = g_{\mathrm{P},t}\exp(-xB_t)$ 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 and stock assessment (4, 13). The parameters were estimated by regressing log-transformed mean annual growth increments for ages 0 to 5 years in the winter survey against total biomass and other co-variates (R^2= 73 %), see ref. (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, $l_t^\mathrm{I} = l_{t-1}^\mathrm{I} + g_{P,\mathrm{D},t-1}$. Mature individuals, denoted by a superscript M, also allocate resources to reproduction, depending on the reproductive investment. This is given by the phenotypic gonado-somatic 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 $l_t^{\mathrm{M}} = 3(l_{t-1}^{\mathrm{M}} + g_{\mathrm{P,D},t-1}) / (3+\gamma\mathrm{GSI}_{\mathrm{P},t-1})$. An individual female's fecundity f is determined by its length l and gonado-somatic index phenotype $\mathrm{GSI}_{\mathrm{P}}$ and given by $f = kl^j\mathrm{GSI}_{\mathrm{P}}D,$ 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 gonado-somatic 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 modelled by using an estimated Beverton-Holt stock-recruitment relationship (19) from VPA-data (20, 21). Recruitment depends on spawning stock biomass 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 Northeast Arctic cod (22-25). The expected number $\mathrm{R}_{3,t}$ of recruits at age 3 is then given by $\mathrm{R}_{3,t+3} = c_0\mathrm{SST}_t + \left(c_1\mathrm{SSB}_t / \left(1+c_2\mathrm{SSB}_t\right)\right),$ 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 1932-2005 was fed into the modelled stock-recruitment relationship and after 2006 we used the average from 1995-2005. 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 $\mathrm{R}_{0,t}$ of newborn recruits by back-calculating the predicted number of 3-year olds, assuming an annual total natural mortality probability equal to 0.2 yr^{-1} as conventionally done for this stock in assessment (21). The survival probability of the offspring of a given spawning pair was equal to $\mathrm{R}_{0,t}$ divided by the total fecundity of the spawning population.

The second source of mortality, the growth-survival trade-off, accounts for less energy available for maintenance (27, 28) and lower survival as growth increases. This may be a result of, for example, risky foraging behavior (29, 30). We therefore included a trade-off between an individual's survival and genetic growth capacity g_{G} through the extra mortality probability $m_{\mathrm{g}} = g_{\mathrm{G}} / g_{\max}$, where $g_{\max}$ is the maximal genetic growth increment at which the survival probability drops to zero, and determines the strength of this trade-off. The parameter $g_{\max}$ is *a priori* unknown and has been determined in a non-evolutionary model to imitate the stock demographically from 1932-1950 (4), by varying $g_{\max}$ from 50-200 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 trade-off 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 onwards (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 ground at about ¼ 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 specify first the harvest function, second, 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 harvest control rule.

The harvest function

Following ref. (33) and ref. (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 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.

The 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”; see also ref. (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 $C_{i,t} = \left(D_{i8,t} \sum_{k=1}^{11} c_{ik,t}\right) / \left(\mathrm{PPI}_t \sum_{j=1}^{8} D_{ij,t}\right)$.

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, while 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 (see 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 TAC and total stock biomass (for details see ref. (32)), where $n_t^* = H_t q^{-1} e^{*-\beta} B_t^{-\alpha}$.

The 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 kg price in the period 1998-2007 (in 2000 NOK) of 12.59 NOK, and the average landing of 527.8 thousand tonnes, allows us to solve for b_0 and b_1 (see Table S1).

The objective function and the harvest control rule

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 net present value (NPV) of the fishery over *T* years, as given by $\mathrm{NPV} = \sum_{t=0}^{T} \Pi_t \left(1/\left(1+\delta\right)\right)^t$, 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 of 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 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) that 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 $F_{\max}\mathrm{SSB}/B_{\max}$. 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 $B_{\max}=B_{\mathrm{pa}}$ and $F_{\max}=F_{\mathrm{pa}}$. 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 profit) and identify those as optima. The grid size for the parameters gave a grid of 4141 different HCRs. The parameters $B_{\max}$ were varied from 0-800 thousand tonnes in steps of 20, and the instantaneous fishing mortality $F_{\max}$ varied from 0.2-1.2 yr^{-1} in steps of 0.01 yr^{-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 modelled mature “super-individuals”), see ref. (3, 4). The computations were completed on Abel, the computer cluster with 10000+ cores at the Research Computing Services at the University of Oslo.

Model limitations

As with all models, our bioeconomic model has limitations and 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, though 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 sensitivity analysis on 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 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.

Supplementary Results

Historic fishing pressure

Table S2 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 total allowable catch (TAC), total biomass from age 3 onwards and also lower net present value (NPV), while the spawning stock biomass (SSB) is slightly higher compared to the non-evolutionary 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. S2). This may have implications for stock assessment and the target reference points that are used for management.

Alternative discount rates

Table S3 presents optimal harvest control rules (HCR) derived for alternative discount rates. As expected, higher discount rates lead to slightly higher fishing mortality, even though only marginally. This 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; see also ref. (5).

Alternative scenarios with constant fishing mortalities

Constant and weight-dependent prices

We probe into 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 kg 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 kg 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/kg. Cod that weighs between 2.5 and 6.5 kg yields 14.25 NOK/kg, while cod that weighs between 1.0 and 2.5 kg yields 12.25 NOK/kg, and all cod that weighs less than 1.0 kg yields 9.25 NOK/kg. Table S4 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, while 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 total allowable catch (TAC), total biomass above the age of 3, and net present value (NPV) that complement Fig. 4. For a fishing mortality of *F* = 0.8 and a minimum size limit equal to 25 cm, both the evolutionary and the non-evolutionary model population goes 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 non-evolutionary 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. S4 shows the final genetic trait values (year 2100) for different fishing mortalities (F=0.4, 0.8 yr^{-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. S4).

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 year period (i.e. from 1932-2005), ref. (4). The genetic changes emerging from this study are found to be lower than what has been predicted in comparable studies, such as ref. (1, 7) and ref. (8, 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 1932-2100 we compare the simulation endpoints for age at maturation and TAC with our calibrated evolutionary model (see Table S1) and non-evolutionary model (all coefficients of genetic variation are equal to 0). As expected, we find that an assumed $\mathrm{CV}_{z,G}$ of 6% and 8% predicts stronger evolutionary responses, expressed in much lower age at maturation in year 2100 (see Fig. S3A). As genetic variance increases, the fish mature at a younger age and at a smaller size, and grow also faster. As fishing mortality increases, age at maturation also declines for the non-evolutionary 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 to 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. This corraborates our earlier finding that evolution towards higher growth tends to have rather positive effects on the fishery.

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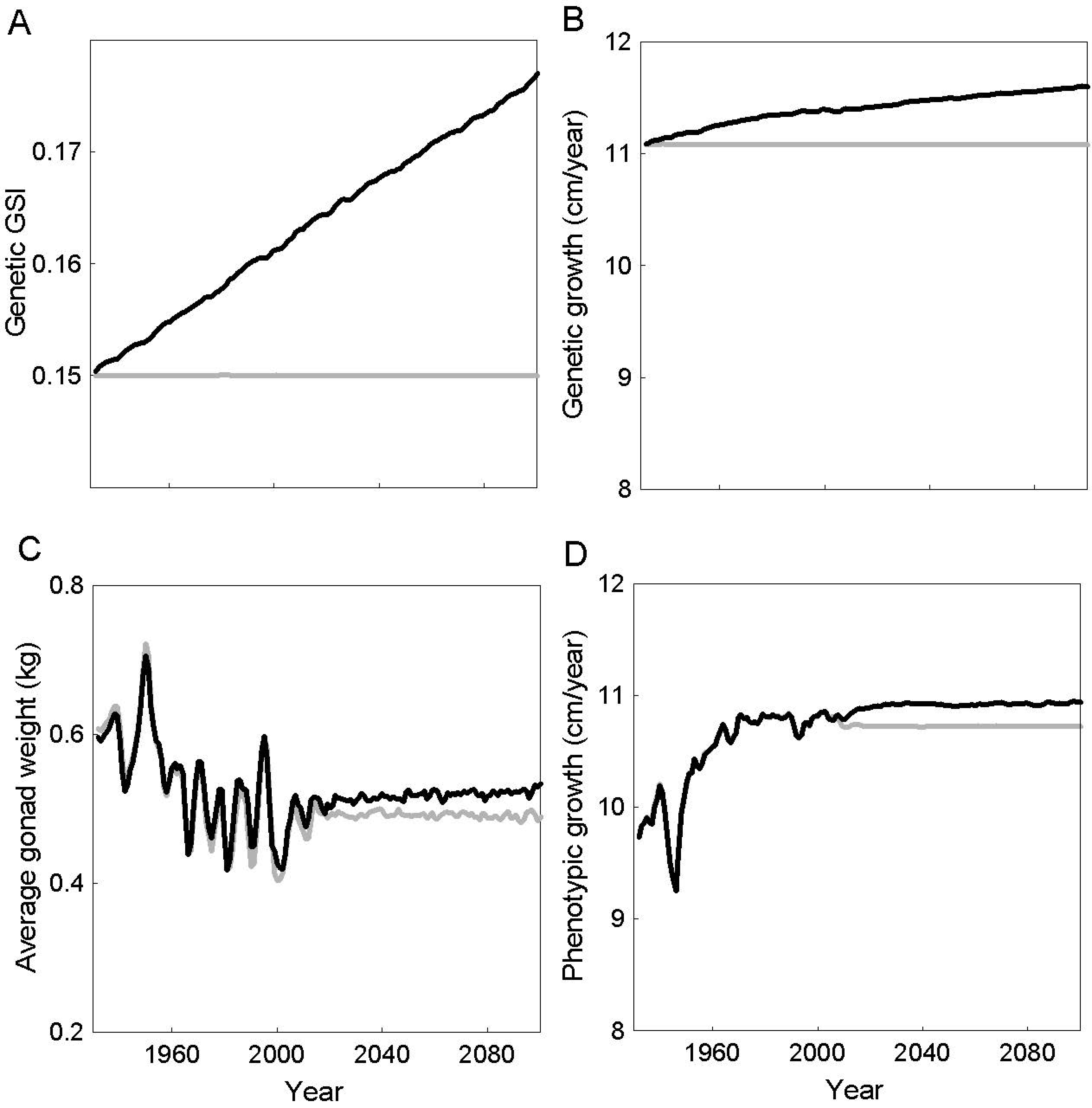
Figure legends

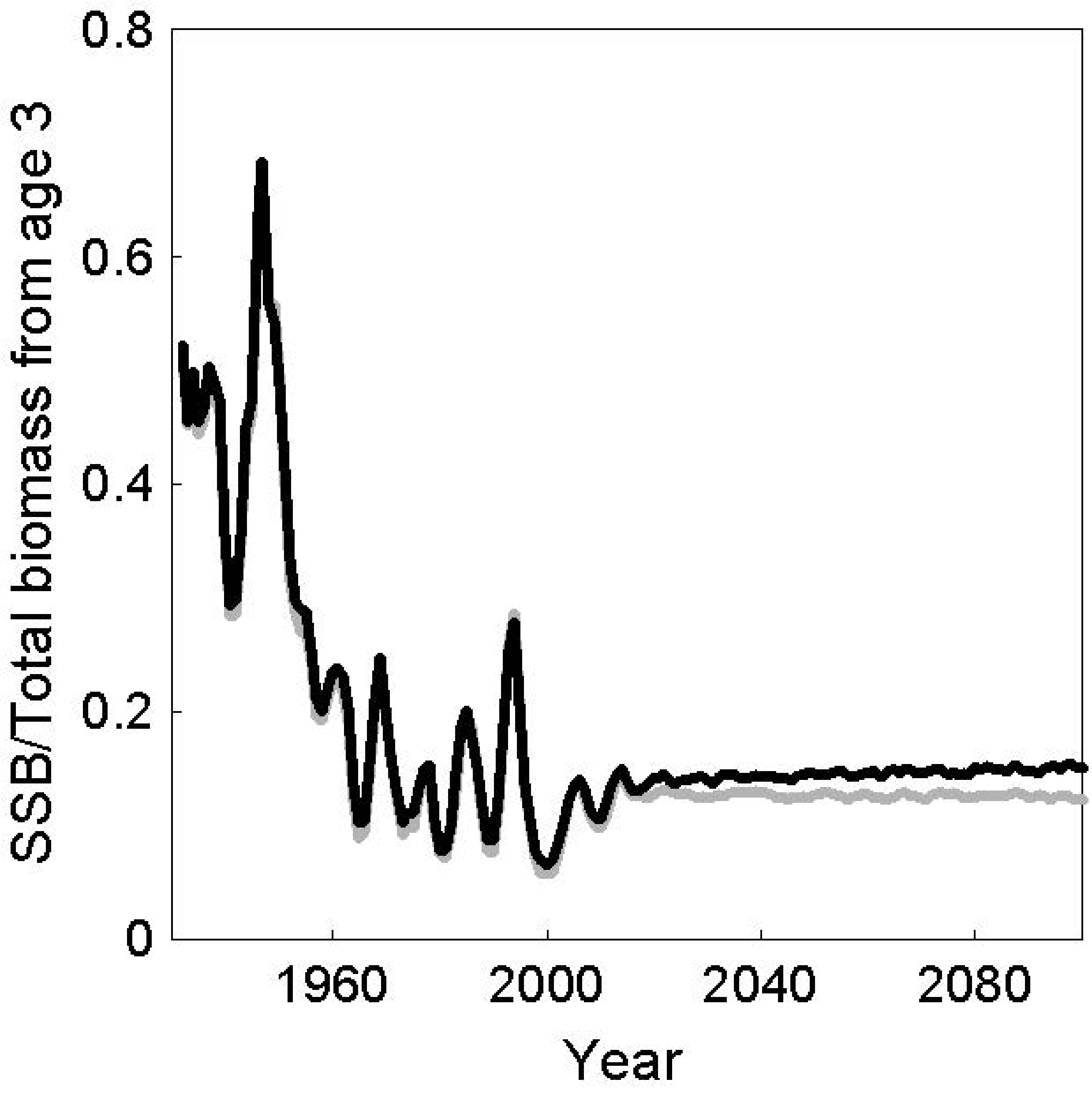
Fig. S1. Life-history changes from 1932-2100 in the scenario for “historic fishing pressure” in the evolutionary (black line) and non-evolutionary model (grey line), corresponding to Fig. 2 and 3 in the main text. **(A)** Genetic GSI (gonado-somatic index), **(B)** genetic growth (cm/year), **(C)** average gonad weight (kg), and **(D)** phenotypic growth (cm/year).

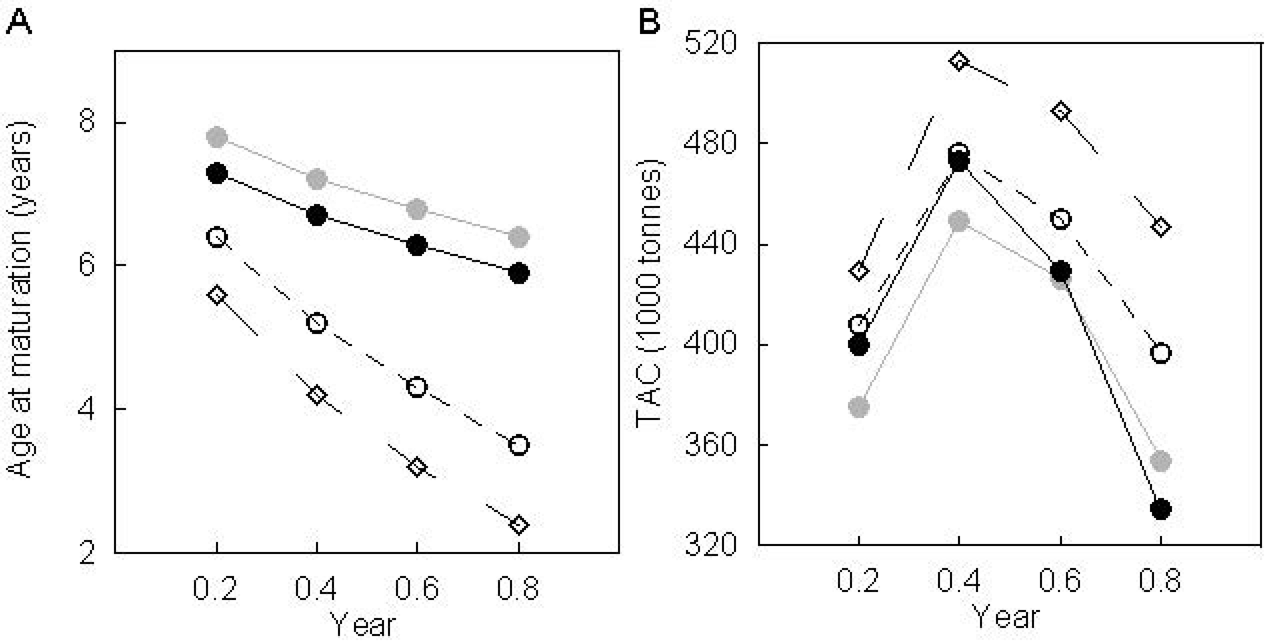
Fig. S2. Ratio between spawning stock biomass and total biomass from age 3 onwards for the scenario “historic fishing pressure” in the evolutionary (black line) and non-evolutionary model (grey line).

Fig. S3. Simulation endpoints (year 2100) for different coefficients of genetic variation (CV) and different fishing mortalities. Fishing mortalities were applied from 1932-2100. Open circles are for CV=6% for all traits and open squares are for CV=8% for all traits, while grey circles are the non-evolutionary model and black circles are the evolutionary model used in the main text (Table S1). **(A)** Age at maturation (years) and **(B)** total allowable catch, TAC (1000 tonnes).

Fig. S4. Simulation endpoints (year=2100) in the evolving life-history traits for different minimum size limits and different fishing mortalities. Fishing mortalities were applied from 1932-2100. Results apply to the evolutionary model. Coefficients of genetic variance 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. Black lines and circles are for F=0.4 yr^{-1} and grey dashed lines and circles are for F=0.8 yr^{-1}. **(A)** Probabilistic maturation reaction norm, PMRN intercept (cm), **(B)** PMRN slope (cm/year), **(C)** genetic gonado-somatic index, GSI, and **(D)** genetic growth capacity (cm/year).


A
Genetic GSI
0.17
0.16
0.15
B
Genetic growth (cm/year)
12
11
10
9
8
C
Average gonad weight (kg)
0.8
0.6
0.4
0.2
1960
2000
2040
2080
Year
D
Phenotypic growth (cm/year)
12
11
10
9
8
1960
2000
2040
2080
Year


SSB/Total biomass from age 3
0.8
0.6
0.4
0.2
0
1960
2000
2040
2080
Year


A
Age at maturation (years)
8
6
4
2
0.2
0.4
0.6
0.8
Year
B
TAC (1000 tonnes)
520
480
440
400
360
320
0.2
0.4
0.6
0.8
Year

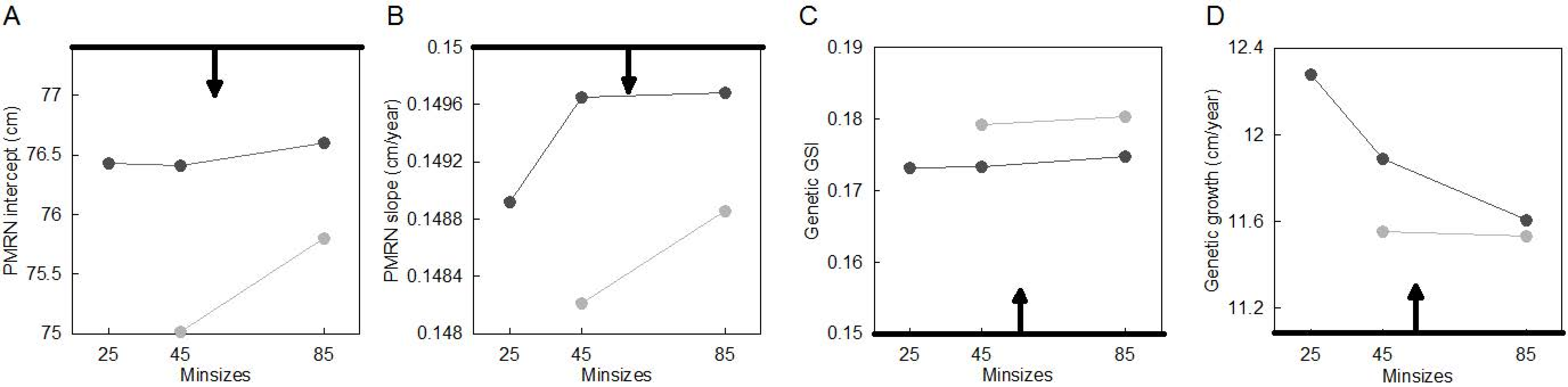

A
PMRN intercept (cm)
77
76.5
76
75.5
75
25
45
85
Minsizes
B
PMRN slope (cm/year)
0.15
0.1496
0.1492
0.1488
0.1484
0.148
25
45
85
Minsizes
C
Genetic GSI
0.19
0.18
0.17
0.16
0.15
25
45
85
Minsizes
D
Genetic growth (cm/year)
12.4
12
11.6
11.2
25
45
85
Minsizes

Table S1. Parameter values and data sources for the bio-economic model.

Parameters	Value	Source
Biological model		
Initial mean PMRN slope, $\overline{s}_{\mathrm{G}}$	0.15 cm yr^{-1}	1
Initial mean PMRN intercept, $\overline{i}_{\mathrm{G}}$	77.4 cm	1
Initial mean reproductive investment, $\overline{\mathrm{GSI}}_{\mathrm{G}}$	0.15	2
Initial mean growth capacity, $\overline{g}_{\mathrm{G}}$	11.08 cm	3,4
PMRN width, w	12.88 cm	1
Coefficient of genetic variation in PMRN slope, $\mathrm{CV}_{\mathrm{s,G}}$	10 %	3
Coefficient of genetic variation in PMRN intercept, $\mathrm{CV}_{\mathrm{i,G}}$	2 %	3
Coefficient of genetic variation in reproductive investment, $\mathrm{CV}_{\mathrm{GSI,G}}$	12 %	3
Coefficient of genetic variation in genetic growth, $\mathrm{CV}_{\mathrm{g,G}}$	4 %	3
Initial heritability, h_z^2	0.2	5
Strength of density dependence in growth, x	2.08 10^{-5} kg^{-1}	3,4
Reproductive investment conversion factor, γ	0.60241	6
Allometric constant, k	3.2 10^{-6} kg cm^{-j}	4
Allometric exponent, j	3.24	4
Weight-specific oocyte density, D	4.45 10^{6} kg^{-1}	7
Maximal growth capacity, $g_{\max}$	105 cm	3
Stock-recruitment constant, c_1	0.7549 kg^{-1}	3,8
Density-dependent stock-recruitment constant, c_2	-6.0633 kg^{-1}	3,8
Temperature coefficient in stock-recruitment, c_0	0.4241 °C^{-1}	9
Natural mortality probability, m	0.18	8
Immature fishing probability in spawning-ground pre-1932	0.38	4
Immature fishing probability in feeding-ground pre-1932	0.09	4
Minimum-size limit on feeding grounds	45 cm	4,8
Economic model		
Intercept of the demand function, b_0	18.88 NOK kg^{-1}	10
Slope of the demand function, b_1	1.19 10^{-8} NOK kg^{-2}	10
Stock-output elasticity α	0.58	10
Effort-output elasticity β	0.85	10
Catchability coefficient q	6.17 10^{-4} tonnes^{-1}days^{-1}	10
Fixed costs per boat c_f	*1.55 10^{6}* NOK	10
Variable costs per boat c_v	*131.6* NOK tonnes^{-1}days^{-1}	10
Optimal number of tonnage days, e^*	66,712 tonnes days	10

Sources: 1= (4, 12); 2= (17); 3= (4); 4= IMR data for NEA cod. Survey data on growth from 1932-2009, provided by M.Heino; allometric data from survey 1999–2007, provided by O. R. Kjesbu; data on fishing mortality and minimum size limit provided by O.R. Godø; 5= (6); 6= (14); 7= (16); 8= (21); 9=12 = PINRO, Murmansk and (22, 23); 10 = (32). Data for the economics: costs and harvests from the Norwegian Directorate of Fisheries, provided by P. Sandberg; biomass and total landings from ICES (21); demand function from Statistics Norway and Directories of fisheries. Economic values have been inflation corrected using the producer price index from the OECD, with year 2000 as a baseline. The exchange rate is 1 USD = 5.6 NOK.

Table S2. Mean values corresponding to the historic fishing pressure corresponding to Figure 2. Averages of fishing mortality (*F*), total allowable catch (TAC), total biomass from age 3, spawning stock biomass (SSB) are shown with temporal standard deviation in parentheses. The NPV is discounted at 2%.

Model	*F*	TAC	SSB	Biomass	NPV
Evolution	0.68	360 (95)	267 (365)	1103 (562)	17.8
Ecology	0.68	370 (93)	260 (356)	1167 (526)	18.6

Units: *F* (inst. rate); TAC, biomass and SSB (1000 tonnes); NPV (billion USD).

Table S3. Optimal harvest control rule (HCR) with parameters $F_{\max}$, $B_{\max}$, and corresponding net present value (NPV) for different discount rates (δ), 0, 2 and 4%. Averages of fishing mortality (F), total allowable catch (TAC), spawning stock biomass (SSB) are shown with temporal standard deviation in parentheses.

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

Units: $F_{\max}$ and F (inst. rate); $B_{\max}$, TAC, SSB (1000 tonnes); NPV (billion USD).

Table S4. Averages for different constant fishing mortalities (*F*) from 1932-2100, showing total allowable catch, TAC (1000 tonnes), total biomass from age 3 (1000 tonnes), and net present value, NPV (bill USD) for a discount rate of 2% assuming a constant price (NPV_{CP}) and weight-dependent prices (NPV_{WP}). For comparison we also show the NPV derived from the model used in the main text. Temporal standard deviation for TAC and biomass is given in parentheses.

F	Model	TAC	Biomass	NPV_{CP}	NPV_{WP}	NPV
0.2	Evolution	400 (55)	2686 (375)	25.7	30.5	23.1
0.2	Non-evolutionary	375 (42)	2503 (277)	24.6	29.2	23.0
0.4	Evolution	473 (60)	1779 (216)	27.3	31.5	25.2
0.4	Non-evolutionary	449 (51)	1711 (178)	26.47	30.8	25.1
0.6	Evolution	429 (70)	1208 (176)	21.41	23.8	21.6
0.6	Non-evolutionary	427 (66)	1246 (164)	22.1	24.8	22.3
0.8	Evolution	335 (90)	800 (191)	13.0	13.9	14.7
0.8	Non-evolutionary	354 (85)	889 (176)	15.1	16.6	16.7

Units: *F* (inst. rate); TAC and total biomass (1000 tonnes); NPV (billion USD).

Table S5. Net present value (NPV), total allowable catch (TAC), and total biomass for the minimum size limits 25, 45 and 85 cm across different constant fishing mortalities (*F*). Values shown for TAC and total biomass (1000 tonnes) are averages for 1932-2100 with temporal standard deviation in parentheses. The NPV (bill USD) is given for a discount rate of 2%.

	Minimum size limit (cm)					
	25		45		85	
F	Evolution	Ecology	Evolution	Ecology	Evolution	Ecology
			TAC			
0.2	337 (48)	310 (34)	400 (154)	375 (42)	222 (50)	215 (54)
0.4	325 (58)	283 (49)	473 (60)	449 (51)	336 (65)	331 (55)
0.6	217 (79)	170 (79)	429 (69)	426 (66)	401 (70)	398 (60)
0.8	-	-	335 (91)	354 (86)	441 (71)	446 (67)
			NPV			
0.2	20.7	20.2	23.1	23	13.4	12.9
0.4	16.9	15.5	25.2	25.1	19.1	19.7
0.6	6.4	4.51	21.6	22.3	22.0	22.8
0.8	-	-	14.7	16.7	23.6	24.5
			Biomass			
0.2	2026 (309)	1852 (221)	2689 (374)	2505 (276)	3914 (535)	3833 (479)
0.4	1034 (191)	896 (159)	1778 (216)	1709 (178)	3639 (446)	3590 (446)
0.6	487 (183)	385 (184)	1208 (176)	1245 (165)	3464 (395)	3438 (423)
0.8	-	-	798 (193)	888 (178)	3341 (365)	3324 (382)

Units: *F* (inst. rate), TAC and total biomass (1000 tonnes), NPV (billion USD).