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Economic repercussions of fisheries-induced evolution

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Economic repercussions of fisheries-induced evolution

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1 Classification:
2 - SOCIAL SCIENCES: Environmental Sciences
3 - BIOLOGICAL SCIENCES: Evolution
4

5 **The economic repercussions of fisheries-induced evolution**

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24 **Abstract**

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

42

43 \body

44

45 **Introduction**

46 Life-history theory, experiments, and field-based studies strongly suggest that fishing is capable
47 of inducing genetic adaptations, especially when it removes individuals with characteristics
48 such as large body size (1-5). Even if fishing is not size-selective, high fishing mortality may
49 be sufficient to induce genetic change (6, 7). It is difficult to predict how genetic changes at the
50 individual level affect population-level properties. Genetic adaptations may, in principle, be
51 beneficial for the state of a stock, by enabling individuals to invest more into reproduction and
52 growth (1, 8). As a consequence, the stock may become more productive, allowing exploited
53 populations to withstand higher fishing mortalities than they could in the absence of such
54 adaptation, possibly permitting higher yields. However, while an individual's increased
55 reproductive investment leads to larger gonads, this happens at the expense of slower post-
56 maturation growth. Maturing earlier may also reduce fecundity, because individuals are smaller
57 when they reproduce (9). Moreover, adapting to fishing may bear a cost of maladaptation
58 resulting in increased natural mortality (10, 11). Therefore, fisheries-induced evolution (FIE)
59 may reduce yield (2, 4, 12, 13) and may even imply a "Darwinian debt" (14) to be paid back by
60 future generations, at least if genetic changes are difficult to reverse (1, 15, 16). Clearly, FIE
61 has the potential for causing positive and negative effects on key stock properties such as
62 spawning stock biomass (SSB) and yield, making the economic effect ambiguous. It is also an
63 open question whether the expected size of the economic effects are substantial, largely because
64 any evolutionary changes are closely intertwined with ecological effects. For example, the
65 release of density dependence when population biomass is fished down, could be an important
66 driver of phenotypic change (1, 17, 18), and might override effects of FIE on yield. To our
67 knowledge, no study has yet to empirically investigate the economic consequences of FIE in

68 wild populations, and how these alter optimal fishing mortalities. Here, we ask how
69 evolutionarily informed management differs from classical fisheries management. First, we
70 determine how an evolving fish population should be optimally managed. Second, we analyze
71 how these management strategies differ compared to optimal management derived for a
72 population whose development is purely determined by ecological processes. Third, we ask
73 how substantial the losses are if a fishery's manager – unaware of any evolutionary changes –
74 manages an evolving population as if it were not evolving. Fourth, we analyze how FIE affects
75 the performance of the fishery that is not optimally managed, but heavily exploited.

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

86 We develop a bio-economic model to investigate if and how FIE affects economic yield
87 (Fig. 1). Our model is a comprehensive compilation of a life-history model for a harvested
88 species, and the economic components rely on individual vessel data, making this, as far as we
89 are aware, the first empirically bio-economic model for investigating genetic adaptations to
90 harvesting. It has been specifically built for NEA cod to investigate the ecological and
91 evolutionary effects of exploitation on the changes in maturation that occurred after fishing
92 mortality was intensified in the 1930s in the feeding grounds (17). To match the observed trends

93 in the biological model as closely as possible, we recreated the historical selection pressure to
94 determine the evolvability (i.e., the coefficient of genetic variation) in the life-history traits (17).
95 While we focus on the feeding grounds fishery in the Barents Sea, we also included fishing in
96 the spawning grounds at the historic levels between 1932 until 2005, and at a constant rate after
97 2006. Hence, we consider the spawning ground fishery to be beyond the control of the manager.
98 The biological model component is built upon the individual-based eco-genetic model
99 framework developed by ref. (1), describing four evolving life-history traits capturing key
100 aspects of growth, maturation, and reproduction. Changes in life-history traits may be driven
101 by both ecological processes, like phenotypic plasticity and density-dependence, and through
102 genetic processes. To evaluate whether accounting for FIE requires a special harvest strategy,
103 we also analyze a non-evolutionary version of the biological model in which the genetic traits
104 cannot evolve. We therefore compare a non-evolutionary model, in which changes in
105 populations are driven only by phenotypic plasticity, with an evolutionary model that allows,
106 in addition, for genetic adaptations. The economic model component consists of production and
107 cost functions estimated specifically for the Norwegian cod trawler fleet. We incorporate a
108 demand function, also estimated from empirical data, to account for how total catch affects the
109 price of landings (21). Our model incorporates feedbacks between the stock development and
110 the economic gains through an optimal harvest control rule (HCR), which is constrained by the
111 two parameters B_{\max} and F_{\max} (Fig. 1). Such shape makes it directly comparable to the HCR
112 that was implemented for NEA cod in 2004 (22, 23). We search for the parameter combination
113 that gives the highest net present value (NPV) for the objective fleet profits. We derive HCRs
114 that are either optimized in the evolutionary or non-evolutionary version of the model.

115

116 **Results**

117 We first compare the emerging properties of the evolutionary model with the non-evolutionary
118 model, when both are managed according to what an HCR recommends that has been optimized
119 for fleet profits (see Table 1, “Evolution” vs. “Ecology”). We find that the optimal fishing
120 mortality is almost identical for the evolutionary and non-evolutionary model and substantially
121 lower than what it has been historically. In spite of this, the emerging biomass levels and the
122 total allowable catch (TAC) are higher in the evolutionary model, indicating that evolution
123 indeed makes the stock more productive, permitting higher yields for the same fishing
124 mortality. Overall, the NPV of the fishery is higher when evolution occurs, even though the
125 total effect is very small. Given that the recommended fishing mortalities are almost identical,
126 the loss of disregarding any evolutionary effects is negligible and the NPV is still higher if
127 evolution occurs and ignored by managers (Table 1, “Evolution ignored”). The key message
128 here is that a low fishing mortality is optimal, no matter whether genetic changes occur or not.
129 This prediction holds for different discount rates (Table S3), when sales prices are assumed
130 independent of the total catch, and when the price that can be obtained per kg of cod rises with
131 the weight of the fish (Table S4).

132 Given that fishing mortality has not been low for the NEA cod fishery in the past, and
133 worldwide most fisheries are still far from being managed optimally, we also investigate how
134 evolution affects the stock when it is overexploited. To do so, we use historic fishing mortalities
135 between 1932 and 2006 and the average fishing mortality afterwards to simulate a scenario of
136 high fishing pressure. This is then contrasted with a counterfactual scenario that analyzes how
137 the fate of the fishery would have developed if an optimal HCR had been already introduced in
138 1932 (as given in Table 1, “Evolution”). We find that using an optimal HCR leads to higher
139 biomass levels in the evolutionary model, compared to the case where only ecological effects
140 are present. The opposite is true for the scenario of historically high fishing mortality, where
141 biomass is actually slightly lower in the evolutionary model (Fig. 2A). As a result, the

142 corresponding TAC and NPV are also slightly lower when evolution occurs and fishing
143 mortality is high (Table S2).

144 It is not immediately obvious why evolution has a positive effect on the fishery if fishing
145 mortality is set optimally, but a negative effect if fishing mortality is high. Inspecting key life
146 history traits reveal that age at maturation declines over time in all scenarios (Fig. 2B). While
147 this occurs in the non-evolutionary model (solely as a result of phenotypic plasticity), the
148 decline is even more severe when evolution takes place. A decline in length at maturation occurs
149 in all scenarios as well, and is even more pronounced if fishing mortality is high (Fig. 2C). In
150 spite of reduced age and length at maturation, the reproductive output per unit of SSB, a
151 measure of the stock's productivity, is increasing over time when evolution occurs (Fig. 2D).
152 In order to better understand the population structure, we take a closer look at the age
153 composition at the simulation endpoints (Fig. 3). We find that in spite of individual fish being
154 smaller at maturation, the size at a given age is consistently larger for the evolutionary model
155 compared to the non-evolutionary model, irrespective of the fishing mortality being optimal or
156 high (Fig. 3A). Indeed, the underlying genetic trait changes show that the evolving population
157 invests more in intrinsic somatic growth capacity and reproductive investment, with the end
158 result being overall larger body sizes and higher reproductive output (Fig. 3A, S1). Looking
159 closer at the age structure of the fish makes it immediately clear that the evolutionary loss occurs
160 because the number of individuals in each age-class is much lower if fishing mortality is high
161 and evolution occurs (Fig. 3B). The fish grow quicker and mature earlier in the evolutionary
162 scenario when fishing pressure is high, but these genetic changes do not pay off in terms of
163 population biomass, TAC or NPV, because fish are also younger (and still immature) when
164 they are potentially caught by trawlers, which spare all fish below the minimum size limit of
165 45 cm. It might seem surprising that these genetic changes towards faster growth occur, given
166 that this makes the fish more vulnerable to fishing at an earlier age. However, faster growth

167 also means maturing earlier, which enables individuals to have a higher probability to reproduce
168 and pass on genes before being captured by the fishery.

169 If interactions with the environment are responsible for the evolutionary loss, it may be
170 sufficient to tweak the environment to avoid or reverse these losses. Indeed, we find that
171 changing the minimum size limit is sufficient to avoid any evolutionary costs (Fig. 4). With a
172 very low minimum size limit, evolution is unambiguously good for the fishery, because it leads
173 to individual growth that is fast enough to negate any detrimental effects of early maturation on
174 TACs (Fig. 4A). As expected, evolution has little effect on the TAC when the minimum size
175 limit is high because selection acting on maturation and growth is weaker and there is little
176 difference between the evolutionary and non-evolutionary predictions (Fig. 4C and S4).
177 Therefore, the loss in NPV due to evolution only occurs for intermediate minimum size limits,
178 where the beneficial effects of growing faster are swamped out by making those fish more
179 vulnerable who are larger, but also younger and still immature (Table S5).

180 In this study, the coefficient of genetic variation was set at a level that resulted in the
181 best fit to empirical observations in age and length at maturation (Table S1), but we nonetheless
182 investigated the effect of this parameter (the evolvability of traits) on model predictions. As
183 expected (1, 16, 24, 25), higher genetic variance resulted in fish maturing at even younger ages
184 and smaller sizes, while also growing faster. Consequently, higher TACs can be obtained when
185 the evolvability is high, predicting that stronger evolutionary forces can have a positive effect
186 on the fishery (Fig. S3).

187

188 **Discussion**

189 Our model predicts that evolutionary change occurs even if fishing mortality is low, which
190 implies that a management strategy aimed at avoiding genetic change might not be feasible. At
191 the same time, we find that fisheries-induced evolution is not necessarily bad for the fishery,

192 and most of the time even beneficial. Especially a fishery that is managed according to what is
193 ecologically optimal can safely ignore any evolutionary effects – at least for the stock and under
194 the conditions that we are considering. This finding is very surprising and in contrast to much
195 of the existing literature, which tends to sketch a gloomy picture of the potential consequences
196 of FIE. It is also comforting that fishing can cause evolution of faster growth, allowing the
197 population to withstand higher harvest pressure and prevent stock collapse (Fig S3).
198 Nonetheless, the life-history changes we predict could have management implications because
199 they affect important indicators that are commonly used to assess the state of the stock.
200 Evolution tends to increase the ratio between SSB and total biomass (Fig. S2), which could
201 mask a decreasing trend in total biomass and affect the stock-recruitment relationship with
202 associated accuracy of predictions (25). This may furthermore have important management
203 implications when biomass levels approach SSB-based limit reference points (26). Even more
204 worrisome is our finding that evolutionary effects tend to be more important when a fish stock
205 is overexploited and the fishery is intermediately size selective. Admittedly, such institutional
206 setting is a special case, but unfortunately the one that worldwide most fisheries are facing.
207 Surprisingly, an economic cost of evolution under these conditions does not materialize because
208 of a drop in reproductive output or as many might expect because of a reduction in growth or
209 size-at-age (27). To the contrary, evolution here promoted faster growth, yet still could exact
210 an economic cost. These results underscore the importance of management taking into account
211 the detailed age and size-structure of the stock (28-30).

212 While we find that removing selectively individuals of intermediate size may result in
213 economic losses due to evolutionary change, we do not find any evidence that targeting only
214 large fish results in evolutionary loss (Fig. 4). These findings may shed new light on the
215 discussion whether harvesting should be balanced or selective (31). While we assume a knife-
216 edge selectivity in our model (32, 33), different gear types with selectivity patterns remain to

217 be explored for further research. While gear regulation can – in principle – be easily changed,
218 our findings may also hint at broader problems. If predation is size selective, evolutionary
219 changes may affect natural mortality which may lead to similar consequences as fishing
220 mortality (10, 11). Investigating how FIE acts in concert with natural mortality, climatic
221 changes, or other driving forces remains to be explored, especially in the light of recovery
222 potential (16).

223 While our biological model is very complex, the optimal HCR was constrained by two
224 parameters, resembling the shape of the HCR currently adopted for NEA cod. It would be
225 interesting to see to what extent our results carry over to a simpler biological model that could
226 then be used for more flexible optimization routines treating the minimum size limit, for
227 example, as a choice variable. Another interesting avenue is to separately optimize harvest
228 control rules for the NEA cod's feeding and spawning grounds. Previous research has found
229 predictions for fisheries-induced evolution to differ depending on whether management actions
230 target feeding or spawning grounds (34). Here, we focused on the fishery in the stock's feeding
231 grounds and kept the fishing mortality at observed levels in the stock's spawning grounds to
232 mimic the historic selection pressure on mature fish, while parsimoniously asking what can be
233 changed for the trawler fleet in the Barents Sea.

234 Altogether, our results show that the economic consequences of FIE are rather small, and mostly
235 beneficial. This is largely because of the positive effects of fishing on growth. This prediction
236 is made possible because of the crucial eco-evolutionary feedbacks between biomass, growth
237 and maturation and because of the inclusion of growth as an evolving trait. Models that don't
238 include these crucial factors might incorrectly predict a larger economic cost of evolution.
239 Regardless, low fishing mortality is the key for successful management. Today, many fish
240 stocks are still far away from being managed in an ecologically optimal way. In such a case,
241 our model predicts that FIE enables the stock to withstand higher harvests, but only if fishing

242 mortality is not intermediately selective. Otherwise, FIE may reduce economic yield and make
243 the stock actually less viable. Admittedly, these evolutionary costs are very small, but they may
244 just be enough to push a fish stock from the state of overexploitation into collapse.

245

246 **Materials and methods**

247 Our bio-economic model consists of two sub-models: “the biological model” which is a
248 description of the life-cycle of NEA cod, and “the economic model” describing details such as
249 cost and demand for the NEA cod trawl fishery. Each of the sub-models have been specifically
250 estimated and calibrated for this stock by using data from the time period 1932-2007 (Table
251 S1). A more extensive model description can be found in SI Materials and Methods.

252

253 **The biological model**

254 The biological model is individual-based and has been developed in ref. (17) building upon the
255 “eco-genetic” modeling framework derived in ref. (1). The model describes each individual’s
256 growth, maturation, reproduction and mortality in each year and follows the fate of about
257 50,000 super-individuals (34, 35). If a fish reproduces, genetic traits are inherited by offspring
258 and expressed phenotypically. Mortality acts on these phenotypic traits, resulting in selection
259 that may cause a genetic response in the life-history traits (Fig. 1A). We made two versions of
260 our model, an evolutionary and a non-evolutionary version, each modeling their respective
261 population of individuals in order to compare a population that has the propensity to evolve,
262 with a population that does not evolve. We consider the evolution of four quantitative life-
263 history traits: maturation tendency given by the (i) slope and (ii) intercept of a probabilistic
264 maturation reaction norm (20), (iii) growth capacity and (iv) reproductive investment. The
265 genetic traits evolve independently, and we therefore do not account for pleiotropy or genetic
266 linkage between traits. Our model has limitations, but thanks to the data availability for NEA

267 cod, we are able to include estimates of the initial mean life-history trait values and annual
268 exploitation rates, as well as parameters specifying the stock-recruitment relationship (i.e.,
269 newborn mortality) and the density dependence of growth on stock biomass (17). Furthermore,
270 a growth-survival tradeoff is included and the strength of this trade-off was determined by
271 matching the ecological properties for data on age and length at maturation, phenotypic growth
272 and biomass from 1932-1950 in the non-evolutionary version of the model to reach
273 demographic equilibrium (17). In the evolving population, the coefficient of genetic variation
274 (CV) has been determined empirically for each trait (17) by matching trends in age and length
275 at maturation over a 74 year period (i.e. from 1932-2005). In this calibration, the historic
276 selection pressure was mimicked by using annual harvest probabilities in the feeding and
277 spawning ground from 1932 until 2005. The resultant CV has been found to be lower than what
278 was assumed in previous studies using the same modeling framework but not based on specific
279 stocks (1, 16, 24, 25), as was the case here. For the non-evolving population, which is only
280 driven by ecological processes, the CV is equal to zero.

281

282 **The economic model and harvest control rule**

283 The economic model (i) specifies the harvest function, (ii) specifies the profit function, (iii)
284 derives a procedure for allocating fishing quotas, and (iv) derives the demand function. All of
285 these functions have been estimated and derived in detail in ref. (36) and used in ref. (21). We
286 assume a knife-edge selectivity (32, 33) that targets all fish above the size of 45 cm (17, 37).
287 The biological and economic models are linked together through an annual feedback loop:
288 spawning stock biomass (SSB) is fed into the economic model where ultimately the total
289 allowable catch (TAC) is determined by a harvest control rule (HCR). The derived TAC feeds
290 back into the biological model and affects the stock size (Fig. 1, “realized catch”). The shape
291 of the HCR is based on the one that was implemented for NEA cod in 2004 (22, 23): the

292 maximum fishing mortality F_{\max} is allowed above a certain SSB level, given by the parameter
293 B_{\max} . Below B_{\max} , fishing mortality decreases linearly to the origin (Fig. 1B). We explore model
294 simulations over a large grid of combinations of F_{\max} and B_{\max} , searching for those
295 combinations that maximize the economic objective, fleet profit. All results, such as those for
296 SSB and TAC, are given for a population that has been scaled up by a factor of 100,000. As
297 the model is stochastic, we ran each scenario for 15 independent replicates, and then averaged
298 across these, presenting the mean in the tables and figures.

299

300 **Historic fishing pressure**

301 The observed harvest pressure in the feeding ground increased steadily from the 1930s to the
302 middle of the 1960s and remained high until the mid- 2000. In the “historic fishing” scenarios,
303 we use observed fishing mortalities from 1932-2005 and then assume a constant fishing
304 mortality in the feeding ground (0.68 year^{-1}) being maintained from 2006 and into the future.
305 This constant (0.68 year^{-1}) is an average of the historic fishing mortality between 1946-2005
306 and is higher than what is considered to be precautionary for the NEA cod (0.4 year^{-1}) (37).

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417

418

419

420 **Figure legends**

421 **Fig. 1.** An overview of the bio-economic model. **(A)** The biological and economic models are
422 coupled by the harvest control rule (HCR). The individual-based biological model describes the
423 evolution of key life-history traits if genetic changes are allowed to occur in the model. The
424 economic model accounts for the supply and demand side of the fishery, as well as fleet profit
425 generated. **(B)** The shape of the HCR depends on two parameters: above the level B_{\max} of
426 spawning stock biomass the maximum fishing mortality F_{\max} is allowed. Between B_{\max} and a
427 biomass level of zero, fishing mortality linearly decreases from F_{\max} to zero. The structure of
428 this HCR is in agreement with that advised in 2004 by ICES (The International Council for the
429 Exploration of the Sea) for the NEA cod fishery.

430

431 **Fig. 2.** The first scenario is based on an optimal harvest control rule (HCR) maximizing fleet
432 profit (green shading shows the period for which we have data), and the second scenario of
433 historic fishing mortality is based on the observed fishing mortalities for 1932-2005 (red
434 shading), and from 2006 onwards follows the average fishing mortality for 1946-2005. For each
435 scenario, the emerging properties from an evolutionary model (black) are compared with those
436 of the corresponding non-evolutionary model (grey). **(A)** Total biomass for ages 3 years plus
437 (1000 t) is lower in the evolutionary model when fishing mortality is high, but higher in the
438 evolutionary model when the optimal HCR is used. **(B)** Predicted age at maturation and **(C)**
439 length at maturation is lower in the evolutionary model than in the non-evolutionary model.
440 The historic scenario predicts age and length at maturation to fall to between age 6-7, and 60-
441 70 cm in 2005, in agreement with the observed data. **(D)** Stock productivity, i.e. mean gonad
442 mass divided by total spawning stock biomass, increases when evolution occurs, and even more
443 so if fishing mortality is high.

444

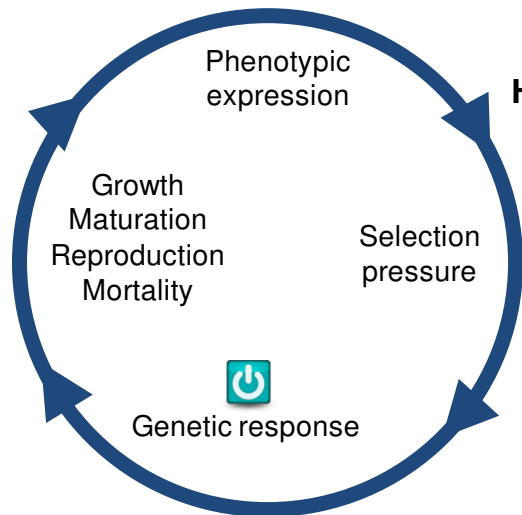
445 **Fig. 3.** Eco-evolutionary dynamics and age-truncation. The optimal HCR scenario is shown by
446 green bars, while high fishing mortality is indicated with red bars. The evolutionary model
447 outcome is shown in the full bars, while the non-evolutionary one is shown by grey inner bars.
448 **(A)** the mean size is larger for all age-classes if evolution occurs, **(B)** the numbers of individuals
449 in each age class is much lower if evolution occurs, but only if fishing mortality is high.

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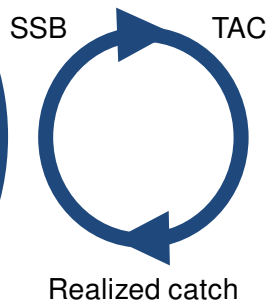
451 **Fig. 4. (A-C)** Total allowable catch (TAC) under different minimum size limits and for different
452 constant fishing mortalities. The evolutionary model (black) predicts higher TAC than the non-
453 evolutionary model (grey) when selection also acts on very young fish. For a minimum size
454 limit of 85 cm, the two models are not different. At the intermediate minimum size limit of 45
455 cm, the TAC is highest for the evolutionary model when fishing mortality is low, but as fishing
456 intensity increases, the TAC is smaller for the evolutionary model.

A

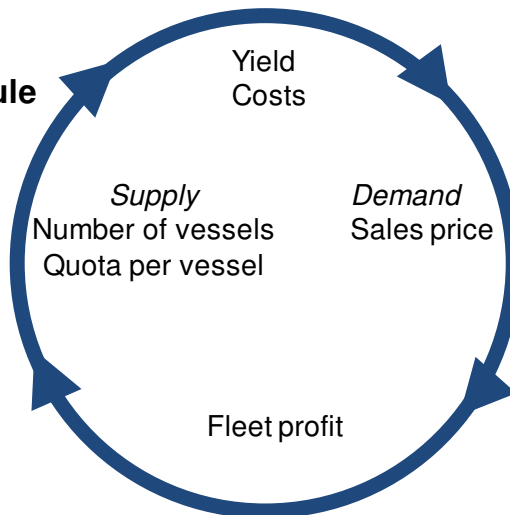
Biological model



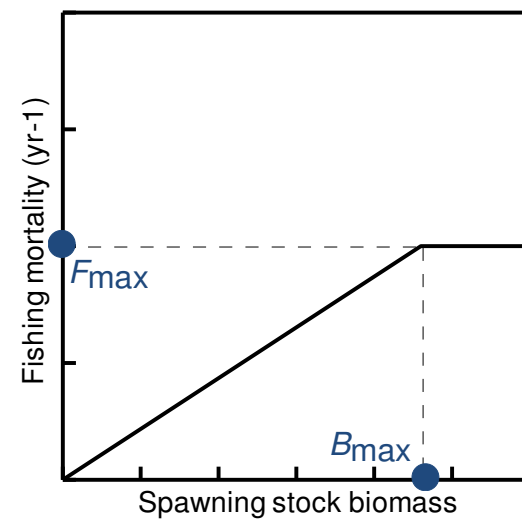
Harvest control rule

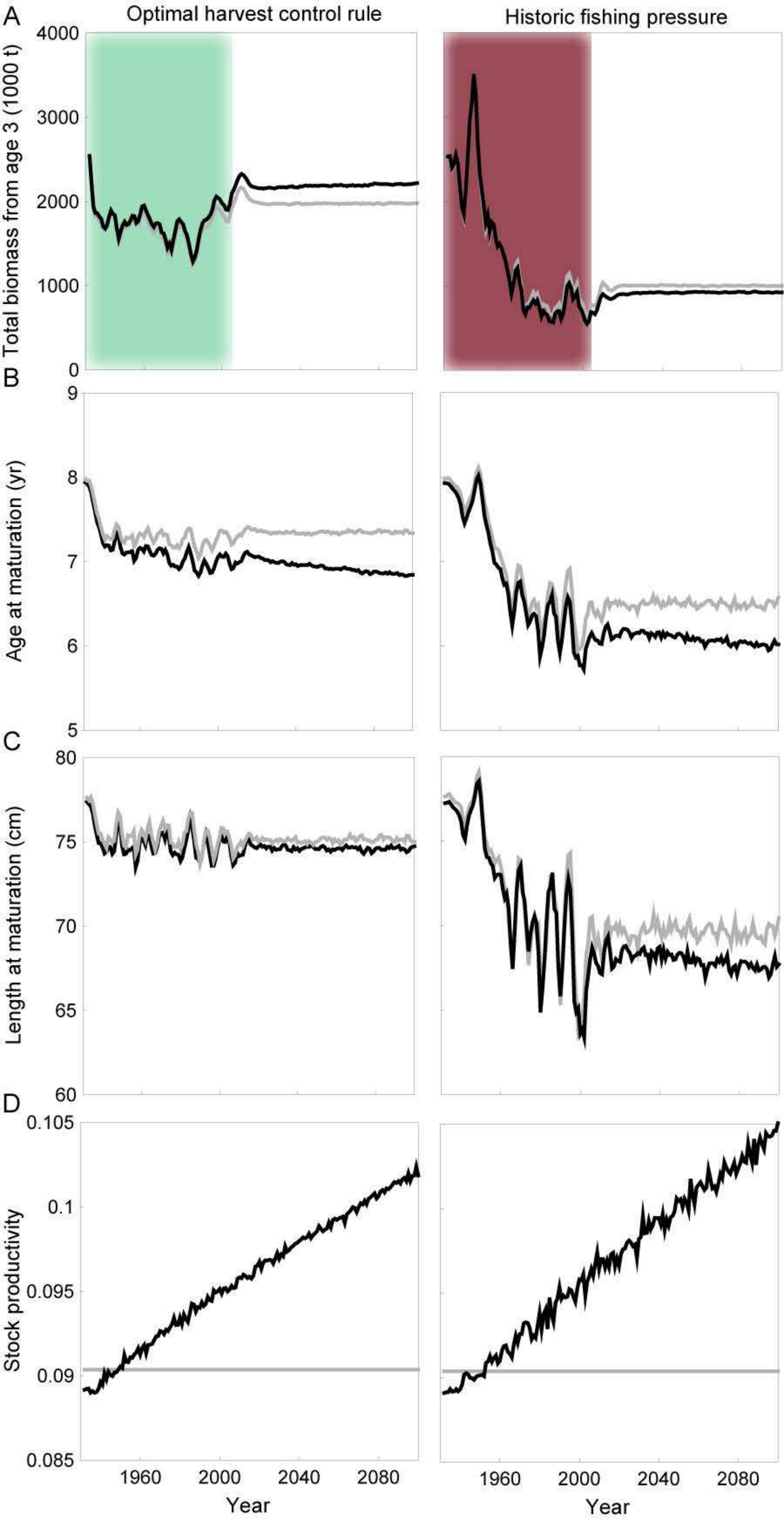


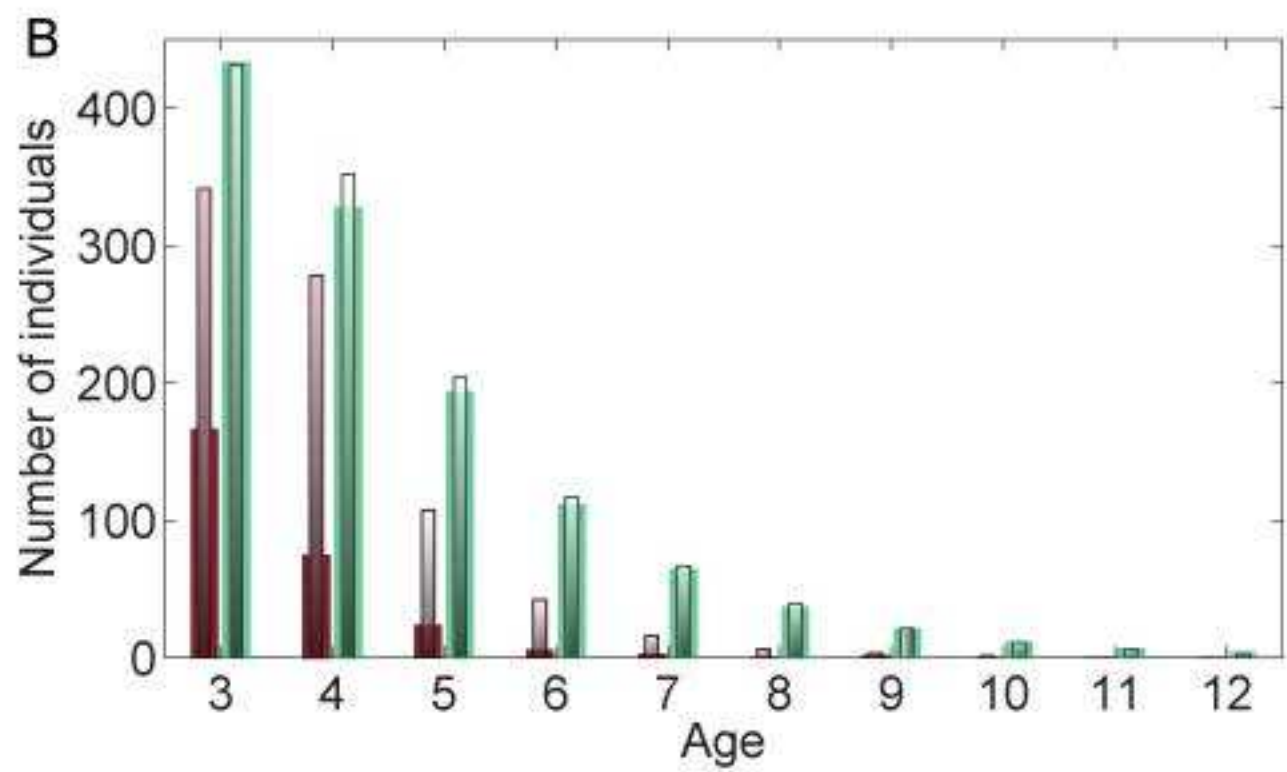
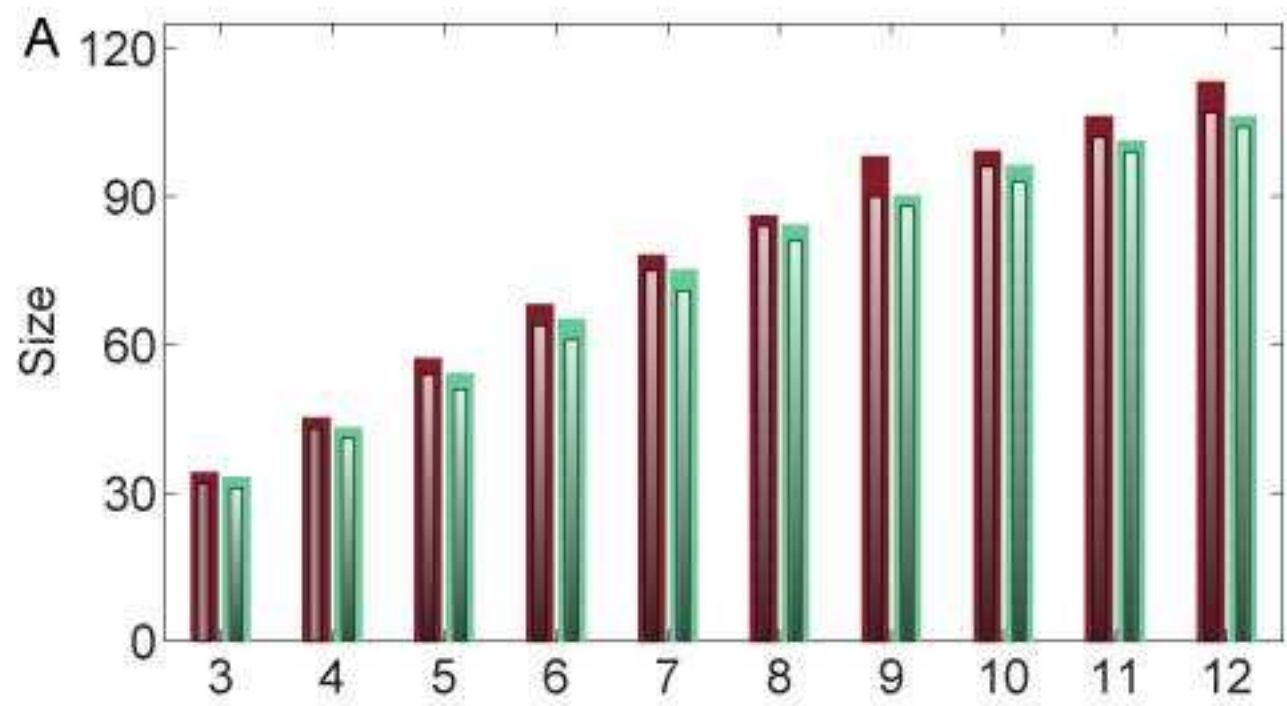
Economic model



B







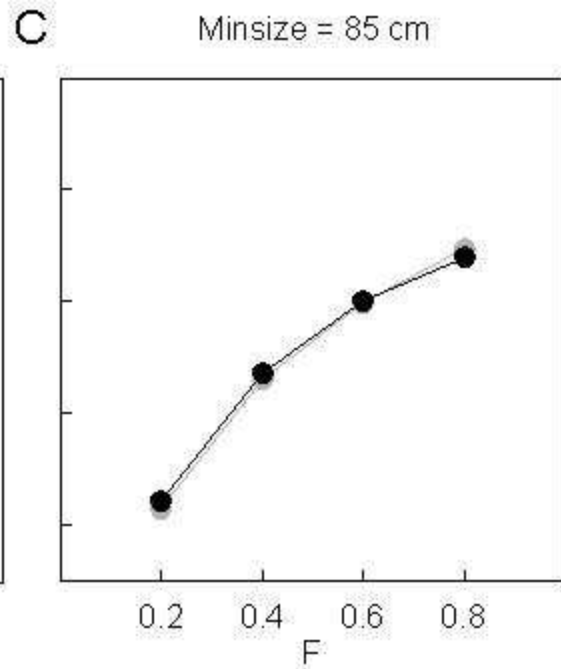
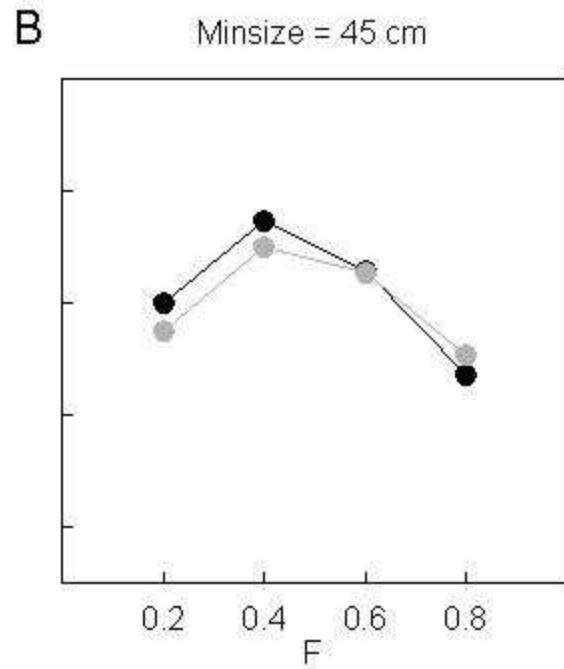
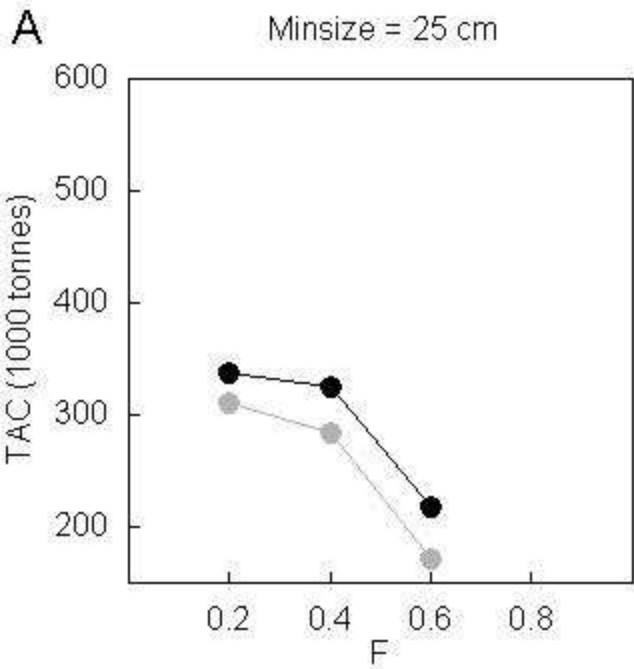


Table 1. Optimal harvest control rule (HCR) for an evolutionary model (“Evolution”) and non-evolutionary model (“Ecology”). Values shown are averages for 1932-2100 on fishing mortality (F), catch (TAC), spawning stock biomass (SSB), with temporal standard deviation in parentheses, and NPV with a discount 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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23 **SI text**

24 The Supporting Information consists of two main sections: (i) SI Materials and Methods and
25 (ii) SI Results. In the methods section, we describe the biological and economic component in
26 the bio-economic model, including a description of the data used to parameterize the model
27 (Table S1). At the end of the SI Materials and Methods, we discuss model limitations. In the
28 SI Results, we show in greater depth the emerging properties of the “historic fishing” scenario
29 that may give rise to an evolutionary cost. Also, we investigate the implications of alternative
30 discount rates for deriving optimal harvest control rules. Furthermore, we probe into the
31 robustness of our results. Simulating different levels of constant fishing mortality rates (0.2-
32 0.8 yr⁻¹), we evaluate the impact of changing the minimum size limit, assuming a constant
33 price, weight-dependent price, and finally, changing the coefficient of genetic variation (i.e.,
34 evolvability) of the genetic life-history traits.

35

36 **SI Materials and Methods: Model and data description**

37 **Biological model**

38 The biological model is individual-based and based upon the framework developed by ref.
39 (1). It combines quantitative genetics with ecological processes taking place at the individual
40 level to derive knowledge on how fishing pressure progressively affects the stock at the
41 population level. The genetic component of this model allows the individuals to adapt to the
42 selection pressure brought about by harvesting. The individual-based model follows about
43 50,000 super-individuals (2, 3). All models results, such as spawning stock biomass (SSB)
44 and catch, are given for a population that has been scaled up by a factor of 100,000 to recreate
45 realistic stock levels. Parameter values for our model (Table S1) are based on published
46 sources, data collected by the Norwegian Institute of Marine Research (IMR) and the

47 Fisheries Directorate, and survey data made available through the International Council for
48 the Exploration of the Sea (ICES). This model has been developed and calibrated for the NEA
49 cod stock in ref. (4). A similar model was used in ref. (5) for the same stock, without
50 considering any evolutionary dynamics.

51 **Evolutionary dynamics**

52 This section describes first how we model the phenotypic expression of the genetic traits for
53 individual maturation tendency, growth, and reproductive investment, secondly, how we
54 introduce the distribution of the evolving genetic traits in the initial population, and finally,
55 how the traits are inherited by offspring. Each genetic trait z_G (denoted by subscript G) has a
56 corresponding phenotypic trait value z_P (denoted by subscript P), with a genetic variance
57 $\sigma_{z,G}^2$ and phenotypic variance $\sigma_{z,P}^2$. At the population level, we assume phenotypic variance
58 to be the sum of the genetic and environmental variance ($\sigma_{z,P}^2 = \sigma_{z,G}^2 + \sigma_{z,E}^2$). Based on
59 quantitative genetics (6) each trait has a heritability, $h_z^2 = \sigma_{z,G}^2 / \sigma_{z,P}^2$, which allows us to
60 calculate the environmental variance $\sigma_{z,E}^2 = \sigma_{z,G}^2 (h_z^{-2} - 1)$ for each trait in the initial
61 population (where $\sigma_{z,G}^2$ is empirically determined for each trait, see below). This
62 environmental variance was then subsequently kept constant through time. The four
63 considered quantitative genetic traits are the maturation tendency by a probabilistic
64 maturation reaction norm (PMRN) (i) slope $z_G = s_G$ and (ii) intercept $z_G = i_G$; (iii) growth
65 capacity $z_G = g_G$; and (iv) reproductive investment given by the gonado-somatic index
66 $z_G = \text{GSI}_G$. In the initial population, the genetic traits are assumed to be normally distributed
67 with mean initial trait values and genetic variances determined by the coefficient of genetic
68 variation $\text{CV}_{z,G}$, both based on empirical data (Table S1). The genetic traits are expressed
69 phenotypically by random draws from a normal distribution with means equal to the

70 respective genetic trait (see Table S1 for initial values), with the corresponding environmental
71 variances σ_E^2 . We made an evolutionary and a non-evolutionary version of the model, each
72 modeling their respective population of individuals in order to compare a population that has
73 the propensity to evolve, with a population that does not evolve. First, the non-evolutionary
74 model was calibrated to accomplish a match with data on Northeast arctic (NEA) cod
75 phenotypic growth, biomass, and age and length at maturation for the period 1932-1950 (4).
76 For the non-evolving population, which is only driven by ecological processes, the coefficient
77 of genetic variation ($CV_{z,G}$) equals zero. In the evolving population, $CV_{z,G}$ was determined
78 by matching trends in age and length at maturation over a 74 year period (i.e., 1932-2005).
79 For all four evolving traits these were then varied to determine the amount of evolution
80 needed to match the maturation trends for 1932-2005. The range of evaluated coefficients of
81 genetic variation, $CV_{z,G}$ was between 0% and 12% and based on previous models (1, 7-9). All
82 possible combinations were systematically evaluated and ranked by log likelihood. The
83 combination that ranked best was consequently selected and used to define the $CV_{z,G}$ values
84 for each trait.

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

94 **Maturation, growth, reproduction and natural mortality**

95 Each year, the probability p_m that an immature individual will mature is described by a
96 probabilistic maturation reaction norm, PMRN (11, 12). This is a function of the individual's
97 length l and age a and given by $p_m = \left[1 + \exp\left(-\frac{l - l_{p50,a}}{v}\right)\right]^{-1}$. The length $l_{p50,a}$ is where
98 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
99 phenotypic intercept i_p and slope s_p . The parameter v is determined by the lower bound
100 probability p_u (25%) and the upper bound probability p_l (75%) of the maturation envelope
101 (1, 4), together with the PMRN width, as given by $v = w / \ln \frac{p_l^{-1} - 1}{p_u^{-1} - 1}$.

102 To reflect density-dependence in growth brought about by changes in abundance, and
103 consequently competition and resource availability, we used an estimated relationship of
104 phenotypic growth $g_{P,D,t} = g_{P,t} \exp(-xB_t)$ depending on total stock biomass B_t in year t . The
105 hypothetical length increment where biomass B_t is zero is referred to as the maximum growth
106 increment, and x is the strength of density dependence reducing growth relative to this
107 maximum. For this estimation (Table S1), derived in detail in ref. (4) and used in ref. (5), we
108 used data on annual growth increments and biomass for the period 1978-2009, obtained from
109 survey and stock assessment (4, 13). The parameters were estimated by regressing log-
110 transformed mean annual growth increments for ages 0 to 5 years in the winter survey against
111 total biomass and other co-variates ($R^2 = 73\%$), see ref. (4). For the immature individuals,
112 denoted by a superscript I, the body length in a given year depends on the length in the
113 previous year and the growth increment in that year, $l_t^I = l_{t-1}^I + g_{P,D,t-1}$. Mature individuals,
114 denoted by a superscript M, also allocate resources to reproduction, depending on the
115 reproductive investment. This is given by the phenotypic gonado-somatic index GSI_p and a
116 conversion factor, γ , needed to account for the higher energy content of gonadic tissue

117 relative to somatic tissue (14, 15). Consequently, the length of a mature individual is given by
118 $l_t^M = 3(l_{t-1}^M - g_{P,D,t-1}) / (3 - \gamma \text{GSI}_{P,t-1})$. An individual female's fecundity f is determined by its
119 length l and gonado-somatic index phenotype GSI_p and given by $f = kl^j \text{GSI}_p D$, where D
120 is the weight-specific packing density of oocytes (16), and k and j are allometric constants
121 relating body length to body mass. The gonad weight at a given age can be calculated from
122 fecundity by dividing it by the weight-specific packing density (shown in Fig. S1). An
123 individual's probability to mate is proportional to its gonad mass, where large gonads due to
124 larger body size and/or gonado-somatic index result in a higher production of gametes (eggs
125 and sperm), and therefore in the production of more offspring. In our model, sex was assigned
126 randomly at birth at a 1:1 primary sex ratio. Atlantic cod are batch spawners and so may mate
127 with several different partners (17, 18). We therefore assumed mating to be random with
128 replacement.

129 The individuals can die from natural or fishing mortality. In our model, natural
130 mortality originated from three sources: newborn mortality, cost of growth, and a constant
131 background natural mortality. The density-dependent newborn mortality was modelled by
132 using an estimated Beverton-Holt stock-recruitment relationship (19) from VPA-data (20, 21).
133 Recruitment depends on spawning stock biomass SSB_t in year t and sea surface temperature
134 SST_t , reflecting the impact of climate. The sea surface temperature stretches from the Kola
135 meridian transect (33°50' E, 70°50' N to 72°50' N) and has been shown to be a good
136 indicator for recruitment for Northeast Arctic cod (22-25). The expected number $R_{3,t}$ of
137 recruits at age 3 is then given by $R_{3,t+3} = c_0 \text{SST}_t (c_1 \text{SSB}_t + (1 - c_2 \text{SSB}_t))$, where c_0 , c_1 and c_2
138 are statistically estimated parameters ($R^2 = 58.9\%$). The two density-dependent parameters
139 c_1 and c_2 were scaled to the modeled population (Table S1). Annual temperature data from
140 1932-2005 was fed into the modelled stock-recruitment relationship and after 2006 we used

141 the average from 1995-2005. In this stock-recruitment model, we ignore cannibalism, even
142 though it has been shown to be important for natural mortality in young age-classes (24, 26).
143 We found the expected number $R_{0,t}$ of newborn recruits by back-calculating the predicted
144 number of 3-year olds, assuming an annual total natural mortality probability equal to 0.2 yr^{-1}
145 as conventionally done for this stock in assessment (21). The survival probability of the
146 offspring of a given spawning pair was equal to $R_{0,t}$ divided by the total fecundity of the
147 spawning population.

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

163 As is the case for NEA cod, harvesting was implemented in the model separately in
164 the feeding grounds and spawning grounds. In the feeding grounds, harvesting was size-

165 selective with minimum-size limits within the range recorded for NEA cod from the 1980s
166 onwards (31). In the spawning grounds, only mature individuals were harvested and there was
167 no minimum-size limit. Due to annual spawning migration out of the feeding ground at about
168 $\frac{1}{4}$ of the year, the harvest probability of mature fish on the feeding grounds was $1 - (1 - p_0)^{3/4}$,
169 where p_0 is the harvest probability for the immature fish.

170

171 **Economic model**

172 To calculate the welfare effects of harvesting, we specify first the harvest function, second,
173 the profit function, third, derive a procedure for allocating fishing quotas, and fourth, derive
174 the demand function. All of these functions have been estimated and derived in detail in ref.
175 (32) and used in ref. (5). Furthermore, we specify the objective functions to derive an optimal
176 harvest control rule.

177 **The harvest function**

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

184 **The profit function**

185 The cost data for each vessel contains expenses made for “labor wages and shares to crew”,
186 “social expenses” (i.e. payroll-related expenses, such as employer contributions to pension
187 and the employer portion of social security tax), “fuel and lubrication oil”, “bait, ice, salt, and

188 packaging“, “food expenses to crew”, as well as “maintenance on vessel”, “maintenance and
 189 investment on gear”, “insurance on vessel”, “other insurances”, “depreciation on vessel” and
 190 “other operating expenses”; see also ref. (35). In total, there are 11 cost components, which
 191 are indexed $k = 1 \dots 11$. Total costs incurred by vessel i in year t are given by the vector of
 192 nominal cost components, $C_{ik,t}$ which are subsequently corrected for inflation using the
 193 Producer Price Index, PPI. We calculate the part of the total costs incurred for catching cod by
 194 the share of days vessel i spends on catching cod in the total number of days vessel i is fishing
 195 at sea. Using index j to enumerate all eight fish species caught (with cod being $j = 8$) and
 196 denoting the number of days in year t that vessel i catches species j by $D_{ij,t}$, the total number
 197 of days vessel i spends catching fish in year t is equal to $\sum_{j=1}^8 D_{ij,t}$. Therefore, the costs
 198 attributed to catching cod by vessel i in year t are $C_{i,t} = \left(D_{i8,t} \sum_{k=8}^{11} c_{ik,t} \right) / \left(\text{PPI}_t \sum_{j=1}^8 D_{ij,t} \right)$.

199 We empirically determine which fraction of the costs of fishing per boat $C_{i,t}$ comprise
 200 fixed and variable costs by estimating $C_{i,t} = c_f + c_v e_{i,t}$, where c_f can be interpreted as fixed
 201 costs, while c_v are variable costs. Multiplying the catch $h_{i,t}$ of vessel i with the price of cod
 202 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
 203 this revenue with the costs of vessel i and given by $\pi_{i,t} = P_t h_{i,t} - c_f - c_v e_{i,t}$.

204 **Issuing individual quotas**

205 Harvest quotas could in principle be allocated through a market mechanism, such as an
 206 auction or handed out by the government to the boat owners. It is not clear *a priori* what the
 207 most efficient allocation (or market outcome) is, because the size of the quota and number of
 208 quotas can vary. Each boat faces a fixed cost, but is harvesting less efficiently when the size
 209 of the quota per boat increases, determined by the estimated effort-output elasticity (see

210 parameter β in Table S1). For each year t , we identify an optimal number n_t^* of vessels
211 harvesting an optimal number e^* of tonnage days for a given TAC and total stock biomass (for
212 details see ref. (32)), where $n_t^* = H_t q^{-1} e^{*-\beta} B_t^{-\alpha}$.

213 **The demand function**

214 The NEA cod fishery contributes a large part of the world's cod landings and therefore affects
215 the international market price for cod. To describe this relationship, we use a linear demand
216 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
217 biomass in year t (as determined by the TAC), and b_0 and b_1 are parameters. The inverse
218 price elasticity is estimated to be 0.5, i.e. if the supply of cod increases by 1%, the world price
219 drops by 0.5% (32). Using the average kg price in the period 1998-2007 (in 2000 NOK) of
220 12.59 NOK, and the average landing of 527.8 thousand tonnes, allows us to solve for b_0 and
221 b_1 (see Table S1).

222 **The objective function and the harvest control rule**

223 Each year, the NEA cod fishery generates economic profits for the fishing fleet, given by Π_t .
224 Finding the maximum economic yield requires us to maximize the net present value (NPV) of
225 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.

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

231 fishing mortality decreases linearly to the origin, i.e. fishing mortality is zero at a biomass
232 level of zero.

233 Here, we generalize a HCR with two parameters (Fig. 1b) that can be compared with
234 the implemented management plan. If the SSB is between zero and B_{\max} , the instantaneous
235 fishing mortality for the given year is given by $F_{\max} \text{SSB} / B_{\max}$. If the SSB is larger than B_{\max} ,
236 the fishing mortality is equal to F_{\max} . The current HCR is therefore recovered as a special
237 case when $B_{\max}=B_{\text{pa}}$ and $F_{\max}=F_{\text{pa}}$. In our model, we vary the parameters in the HCR over a
238 wide range of values, not constraining them to existing precautionary reference points. We
239 search for the combination of parameter values B_{\max} and F_{\max} that deliver the best results for
240 the objective function (maximize profit) and identify those as optima. The grid size for the
241 parameters gave a grid of 4141 different HCRs. The parameters B_{\max} were varied from 0-800
242 thousand tonnes in steps of 20, and the instantaneous fishing mortality F_{\max} varied from 0.2-
243 1.2 yr^{-1} in steps of 0.01 yr^{-1} . Our model is individual-based, and for some of these HCRs,
244 fishing could make the abundance very low. To avoid stochastic effects at low abundances,
245 we therefore set a threshold below which the population was classified as extinct (at 20
246 modelled mature “super-individuals”), see ref. (3, 4). The computations were completed on
247 Abel, the computer cluster with 10000+ cores at the Research Computing Services at the
248 University of Oslo.

249

250 **Model limitations**

251 As with all models, our bioeconomic model has limitations and simplifications. A few
252 assumptions merit special attention here. First, we assume an initial 1:1 sex ratio although it
253 has been shown that the sex ratio has fluctuated over time in this cod stock (39). Second, we
254 assume no sexual selection, though it is possible that sexual selection may influence the
255 evolutionary changes in life-history traits (40-42). Third, we do not include genetic

256 correlations between the life-history traits describing maturation tendency, growth capacity,
257 and reproductive investment (4). Fourth, we assume a constant minimum size limit that
258 determines the harvestable biomass (Table S1), implicitly assuming knife-edge selectivity
259 (19, 43), which may not be fully realistic. Although our size limit is based on data, the size
260 selectivity has varied over the considered time period and across vessels since 1932 (for
261 sensitivity analysis on minimum size limit, see Table S5). Fifth, the shape of the HCR we are
262 considering is constrained by two parameters, reflecting the current management plan.
263 Investigating completely different shapes or considering parameters that change over time is
264 an interesting avenue for further research. Sixth, we focused on the fishery in the stock's
265 feeding grounds and kept the fishing mortality at observed levels in the stock's spawning
266 grounds. We did this because we wanted to mimic the historic selection pressure on the
267 mature fish, while parsimoniously asking what can be changed for the trawler fleet in the
268 Barents Sea. This assumption could be changed, and the next step would be to derive an
269 optimal HCR for each of these fisheries.

270

271 **Supplementary Results**

272 **Historic fishing pressure**

273 Table S2 shows the harvesting properties for the scenario of historic fishing pressure (i.e., high
274 fishing mortality) presented in Fig. 2. The evolutionary model delivers lower total allowable catch
275 (TAC), total biomass from age 3 onwards and also lower net present value (NPV), while the
276 spawning stock biomass (SSB) is slightly higher compared to the non-evolutionary model.

277 In Fig. S1 we show the life-history changes in the scenario of “historic fishing
278 pressure”, corresponding to Figs. 2 and 3. Genetic adaptations caused by fishing pressure lead
279 to higher reproductive investment (Fig. S1A) and genetic growth (Fig. S1B). As a result, the
280 evolving population has consistently larger gonad weight (Fig. S1C) and higher phenotypic
281 growth (Fig. S1D). Due to evolutionary changes, the ratio between spawning stock biomass and
282 total biomass changes over time because of a change in maturation schedule (Fig. S2). This may
283 have implications for stock assessment and the target reference points that are used for
284 management.

285

286 **Alternative discount rates**

287 Table S3 presents optimal harvest control rules (HCR) derived for alternative discount rates.
288 As expected, higher discount rates lead to slightly higher fishing mortality, even though only
289 marginally. This may seem surprising, but happens because larger catches result in lower
290 prices, and hence profits. At a certain point, the resulting profit loss from lower prices
291 outweighs the profit gain resulting from catching more fish – irrespective of the discount rate;
292 see also ref. (5).

293

294

295

296 **Alternative scenarios with constant fishing mortalities**

297 **Constant and weight-dependent prices**

298 We probe into the robustness of our results by varying the fishing mortality under
299 alternative assumptions and investigating how this influences the effects of
300 evolutionary changes. First, as a theoretical exercise, we assume that sales prices are
301 independent of the total catch and the price is constant. This is clearly not realistic
302 for the NEA cod fishery, but certainly the case for many other fisheries. As a
303 constant price we use the inflation-corrected average kg price in the period 1998-
304 2007 of 12.59 NOK. Second, in addition, we assume that sales prices are weight-
305 dependent, i.e. the price that can be obtained per kg of cod rises with the weight of
306 the fish. We found little evidence that this is actually the case for the fleet of trawlers
307 we are considering here, but it may be relevant for other vessel types, notably
308 smaller coastal vessels. As a theoretical benchmark we can rely on the minimum
309 prices from the Norwegian fishermen's sales organization (44). The prices for the
310 different weight-classes are as follows. Cod that is heavier than 6.5 kg yields 17
311 NOK/kg. Cod that weighs between 2.5 and 6.5 kg yields 14.25 NOK/kg, while cod
312 that weighs between 1.0 and 2.5 kg yields 12.25 NOK/kg, and all cod that weighs
313 less than 1.0 kg yields 9.25 NOK/kg. Table S4 shows the emerging properties of
314 different fishing mortalities and the NPV for a constant price (NPV_{CP}) and for
315 weight-dependent prices (NPV_{WP}). For comparison, we also show the NPV derived
316 from the model used in the main text. We find that our earlier results presented in
317 Table 1 fully carry over to the case where the price is constant or weight-dependent.
318 Still, evolution increases the NPV of a fishery if fishing mortality is low, while it
319 decreases the NPV of a fishery if fishing mortality is high (Table S4).

320

321 **Emerging properties for minimum size limits of 25, 45 and 85 cm**

322 Table S5 shows the emerging properties of total allowable catch (TAC), total biomass above
323 the age of 3, and net present value (NPV) that complement Fig. 4. For a fishing mortality of F
324 = 0.8 and a minimum size limit equal to 25 cm, both the evolutionary and the non-
325 evolutionary model population goes extinct. When harvest pressure is high and the size limit
326 is low (=25 cm), the economic losses due to evolution that we see at a size limit of 45 cm,
327 disappear. The NPV values are overall lower, however, for the 25 cm size limit than for the
328 45 cm size limit. At a very high minimum size of 85 cm the non-evolutionary model performs
329 insignificantly better than the evolutionary model, suggesting that economic losses from
330 evolutionary change are not increasing as minimum sizes increase. Instead, those evolutionary
331 costs are highest (albeit still small) for a minimum size of 45 cm, a size that is based on
332 historic values for the Norwegian and Russian cod fisheries (4, 21) and very close to the size
333 currently used as a legal minimum size (45). Fig. S4 shows the final genetic trait values (year
334 2100) for different fishing mortalities ($F=0.4, 0.8 \text{ yr}^{-1}$) and for different minimum size limits.
335 We find here that the evolutionary change is larger as fishing mortality increases for all traits
336 except for growth and that higher minimum size limits result in lower selective pressure and
337 less evolution (Fig. S4).

338

339 **Varying the coefficients of genetic variation and fishing mortality**

340 In the evolutionary version of our model, the coefficient of genetic variation (Table S1) has
341 been determined empirically by matching trends in age and length at maturation over a 74
342 year period (i.e. from 1932-2005), ref. (4). The genetic changes emerging from this study are
343 found to be lower than what has been predicted in comparable studies, such as ref. (1, 7) and
344 ref. (8, 9). These studies assumed a coefficient of genetic variation for all traits equal to 8%
345 and 6%, respectively. As a robustness check, we therefore used these higher coefficients of

346 genetic variation (6% and 8%), and performed simulations for different fishing mortalities.
347 After fishing with a particular fishing mortality from 1932-2100 we compare the simulation
348 endpoints for age at maturation and TAC with our calibrated evolutionary model (see Table
349 S1) and non-evolutionary model (all coefficients of genetic variation are equal to 0). As
350 expected, we find that an assumed $CV_{z,G}$ of 6% and 8% predicts stronger evolutionary
351 responses, expressed in much lower age at maturation in year 2100 (see Fig. S3A). As genetic
352 variance increases, the fish mature at a younger age and at a smaller size, and grow also
353 faster. As fishing mortality increases, age at maturation also declines for the non-evolutionary
354 model, which is entirely due to phenotypic plasticity and density dependence in response to a
355 lower abundance of the stock. For the case where the coefficients of genetic variation are set
356 to 6% and 8 %, we find that for a given fishing mortality higher TACs can be obtained
357 compared to the models where evolutionary change is weaker or even absent. This finding
358 indicates that stronger evolutionary forces tend to have a positive effect on the TAC. This
359 corroborates our earlier finding that evolution towards higher growth tends to have rather
360 positive effects on the fishery.

361

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- 476
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478 **Figure legends**

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

483

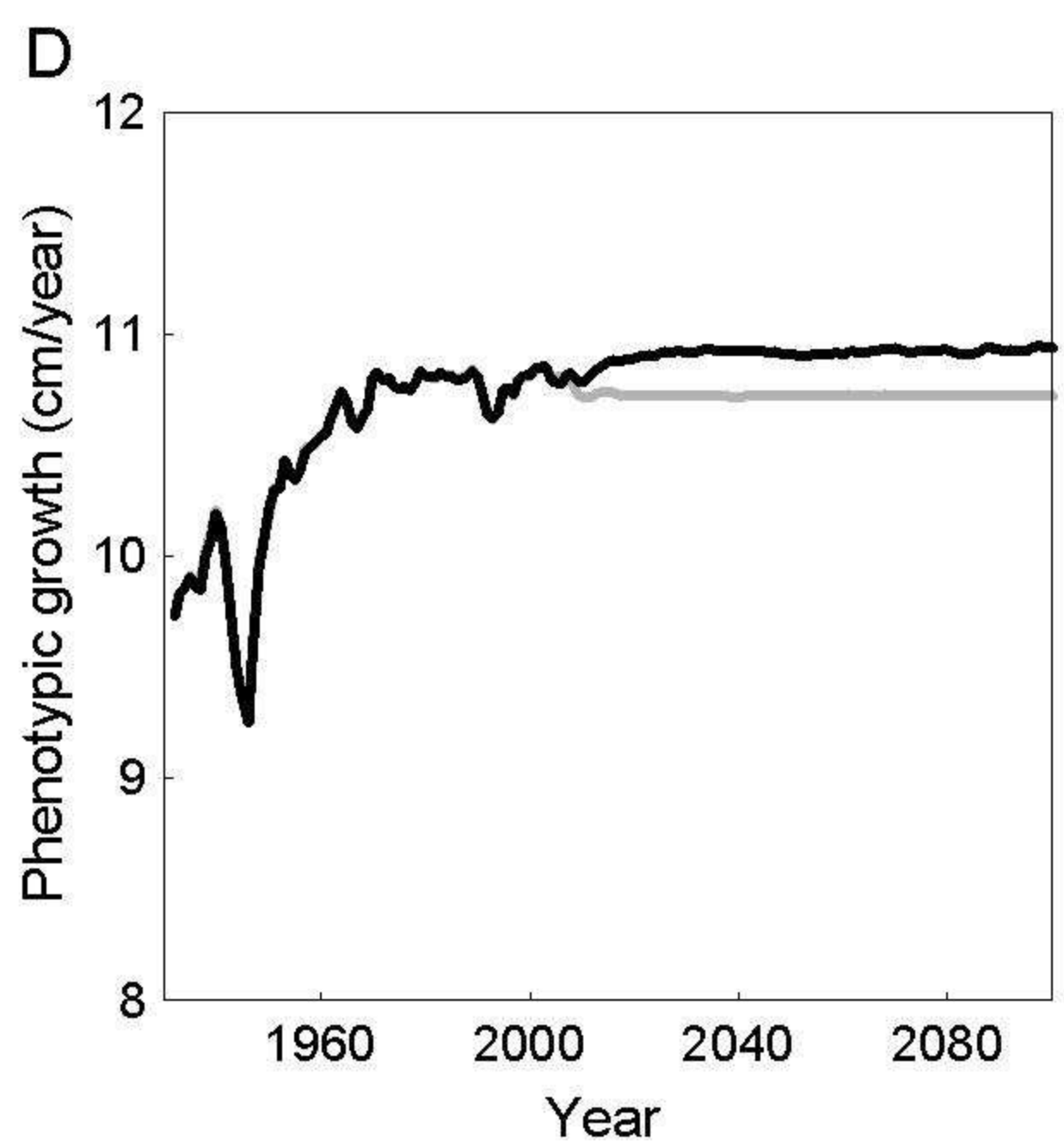
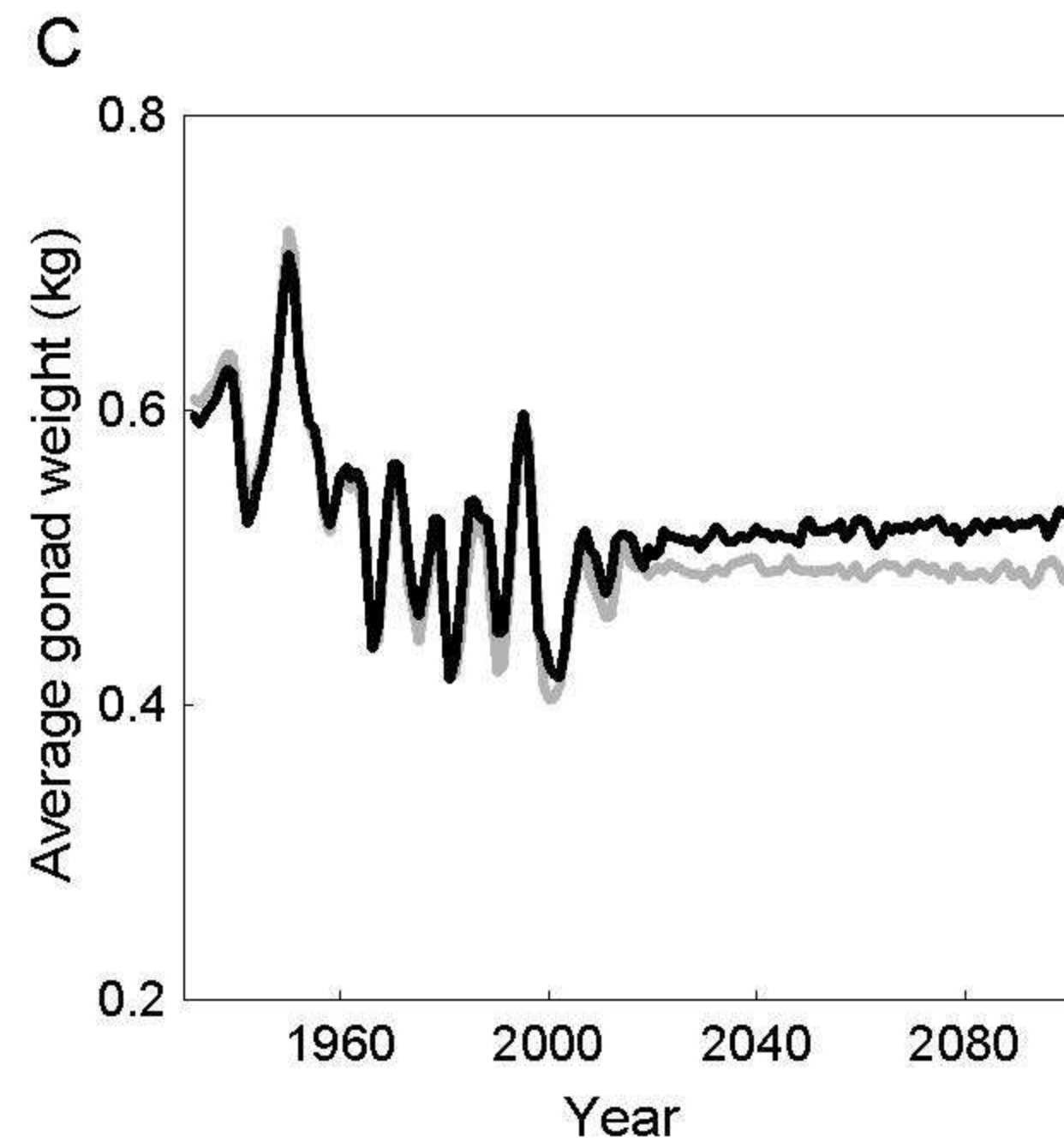
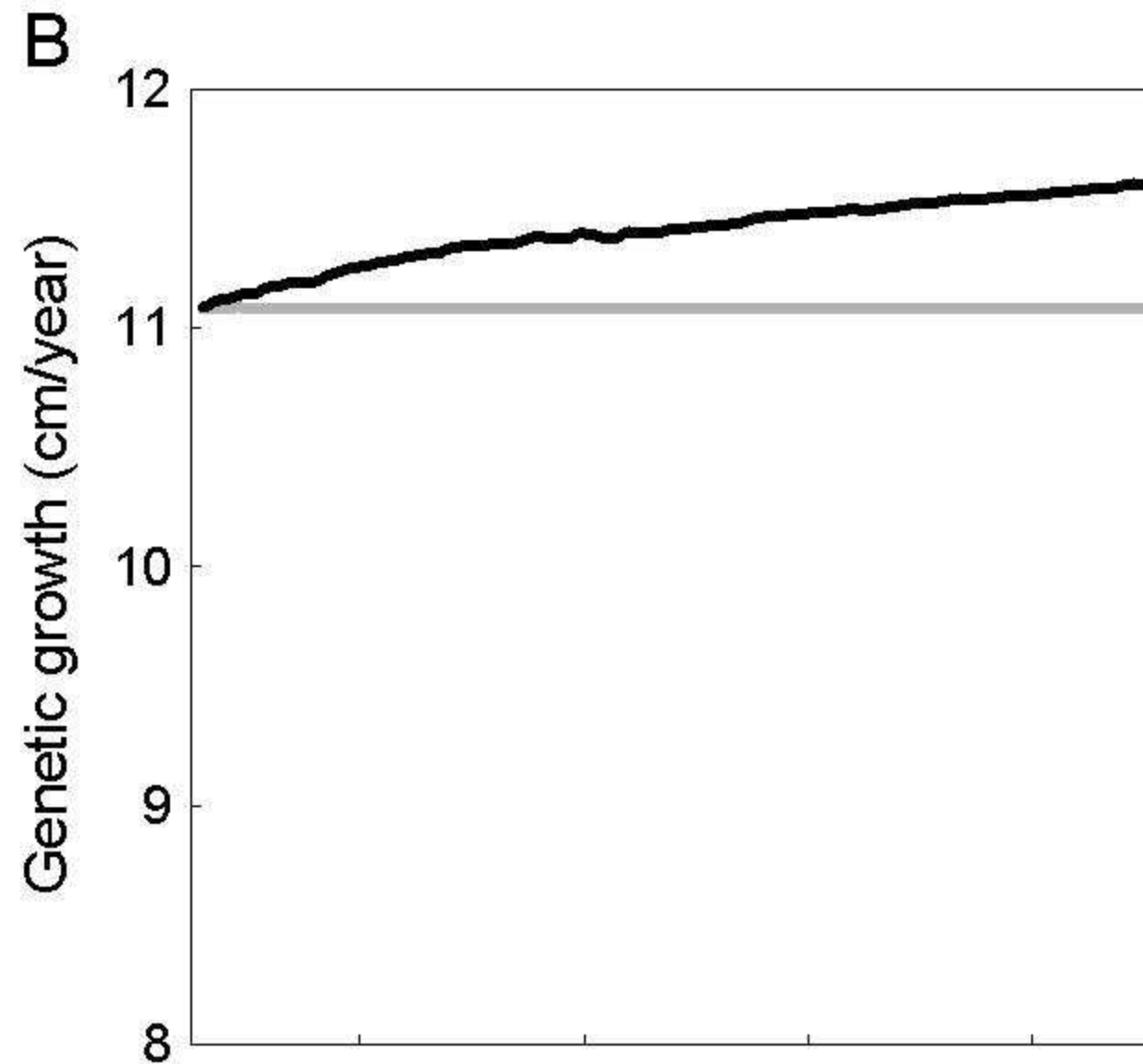
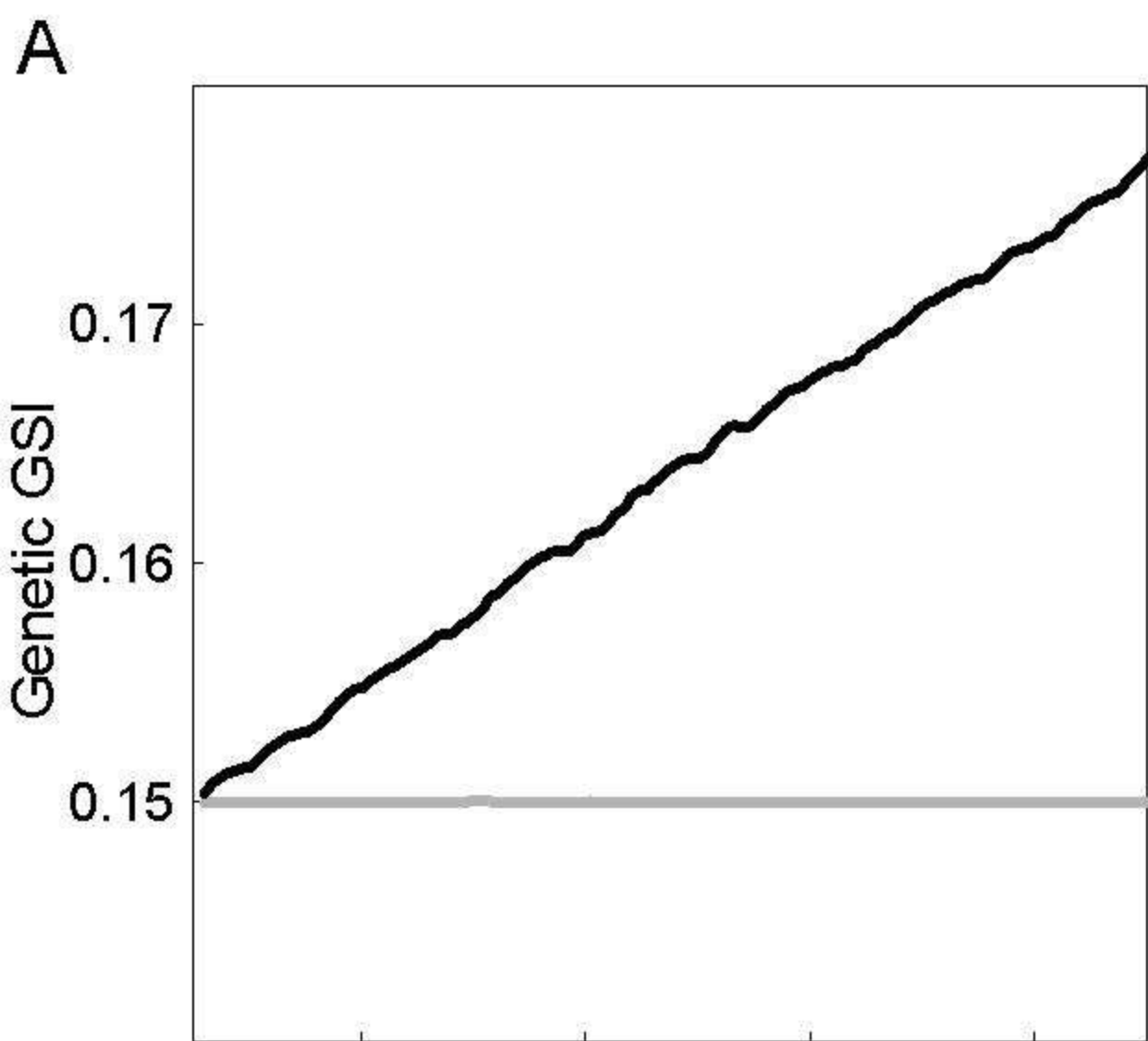
484 **Fig. S2.** Ratio between spawning stock biomass and total biomass from age 3 onwards for the
485 scenario “historic fishing pressure” in the evolutionary (black line) and non-evolutionary model
486 (grey line).

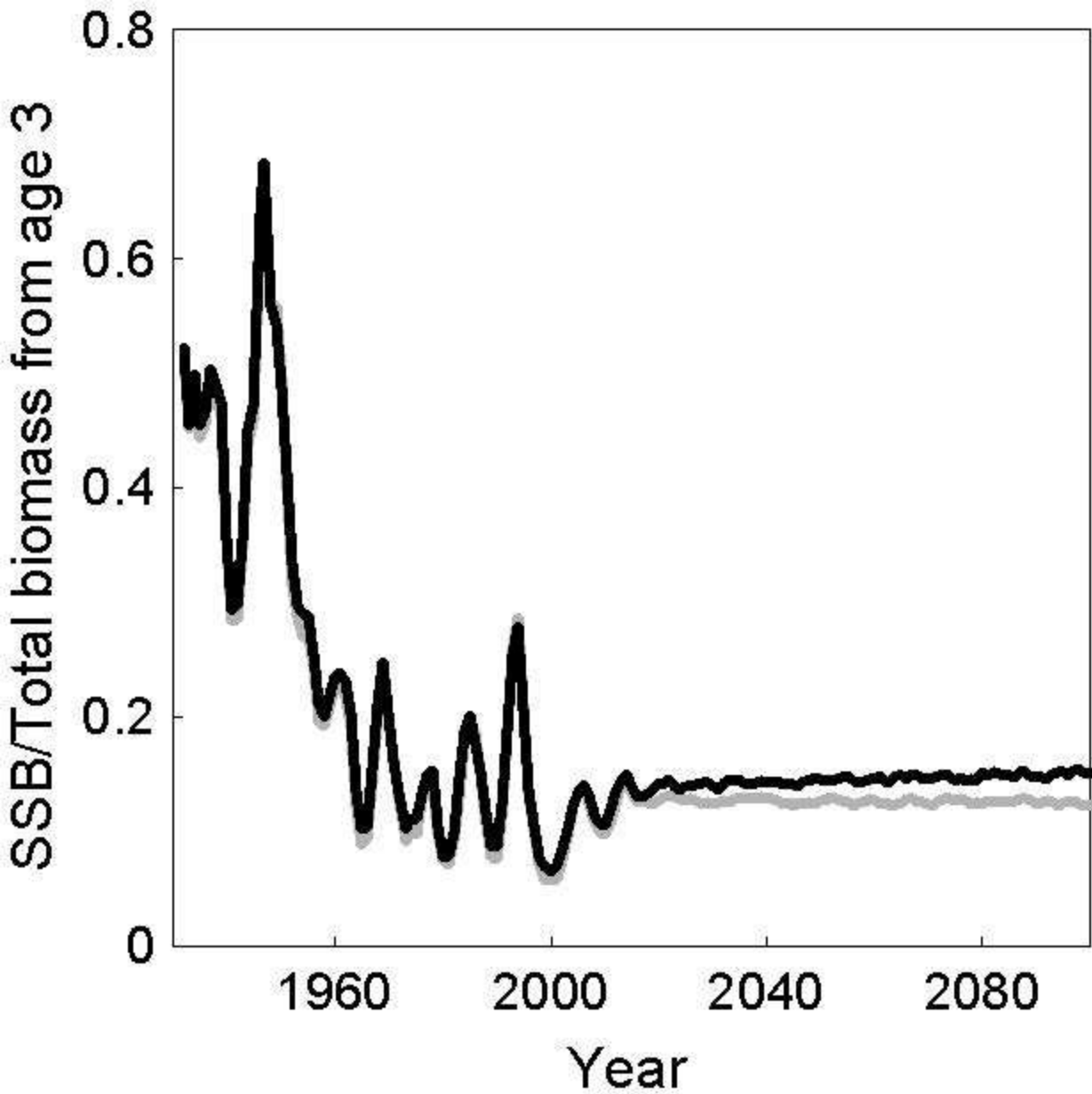
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488 **Fig. S3.** Simulation endpoints (year 2100) for different coefficients of genetic variation (CV)
489 and different fishing mortalities. Fishing mortalities were applied from 1932-2100. Open
490 circles are for CV=6% for all traits and open squares are for CV=8% for all traits, while grey
491 circles are the non-evolutionary model and black circles are the evolutionary model used in
492 the main text (Table S1). **(A)** Age at maturation (years) and **(B)** total allowable catch, TAC
493 (1000 tonnes).

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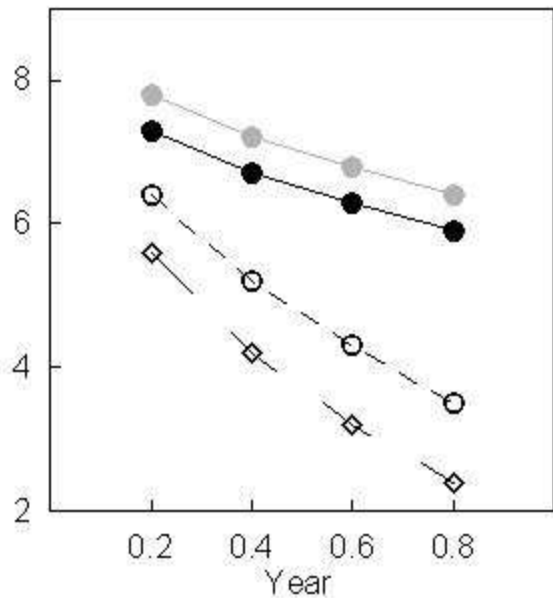
495 **Fig. S4.** Simulation endpoints (year=2100) in the evolving life-history traits for different
496 minimum size limits and different fishing mortalities. Fishing mortalities were applied from
497 1932-2100. Results apply to the evolutionary model. Coefficients of genetic variance are the
498 same as those used in the main text. Initial trait values are shown by the horizontal bold line,
499 and the arrow shows the direction of evolution. Black lines and circles are for $F=0.4 \text{ yr}^{-1}$ and
500 grey dashed lines and circles are for $F=0.8 \text{ yr}^{-1}$. **(A)** Probabilistic maturation reaction norm,
501 PMRN intercept (cm), **(B)** PMRN slope (cm/year), **(C)** genetic gonado-somatic index, GSI,
502 and **(D)** genetic growth capacity (cm/year).



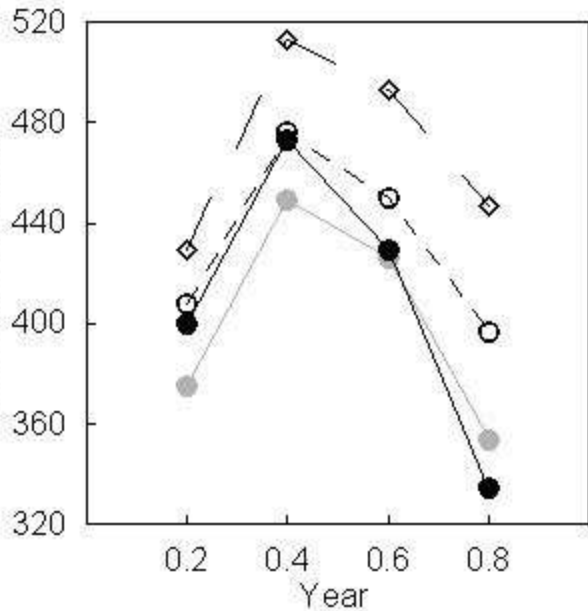


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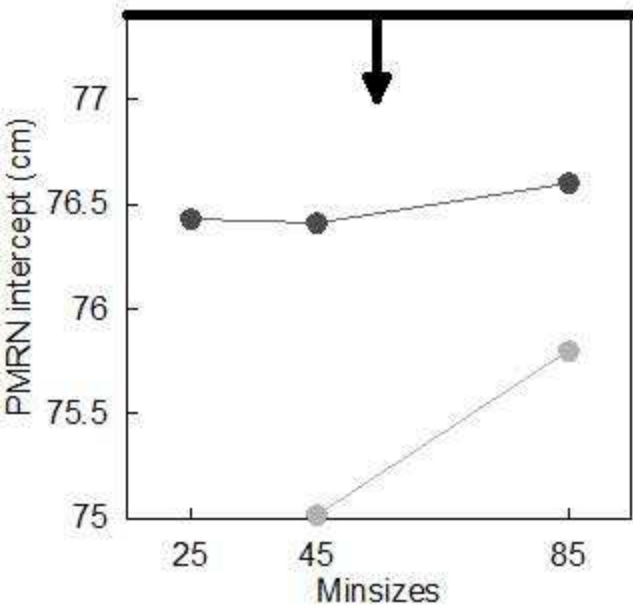
Age at maturation (years)

**B**

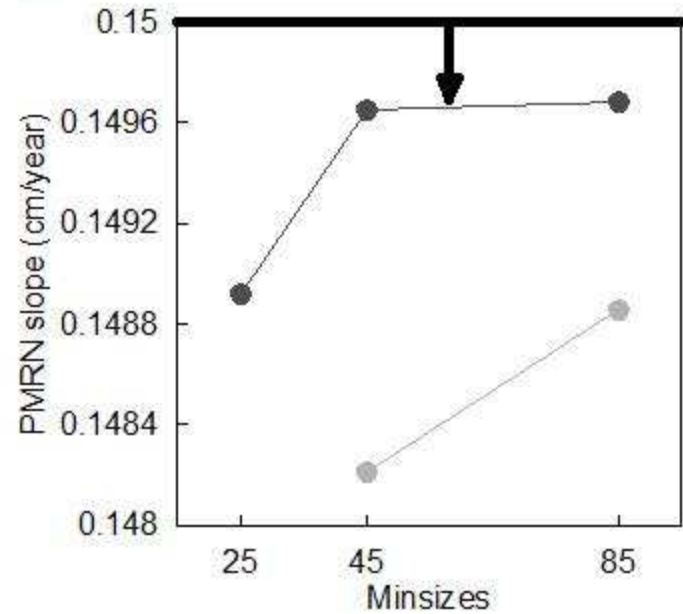
TAC (1000 tonnes)



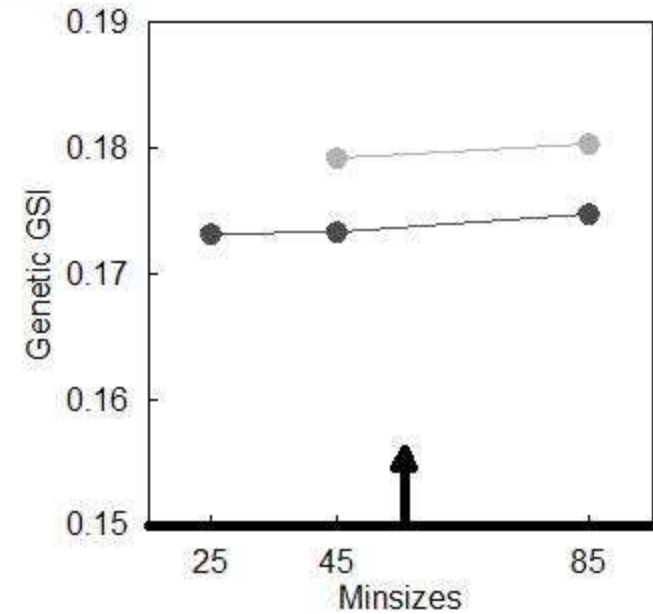
A



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C



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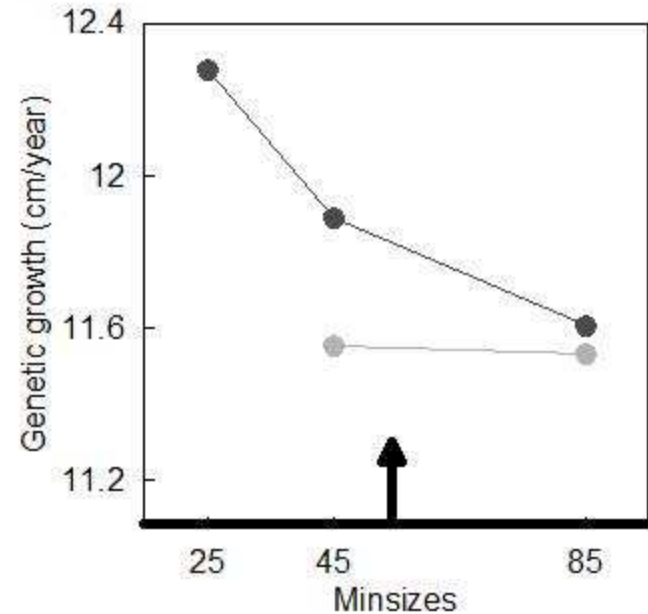


Table S1. Parameter values and data sources for the bio-economic model.

Parameters	Value	Source
Biological model		
Initial mean PMRN slope, \bar{s}_G	0.15 cm yr ⁻¹	1
Initial mean PMRN intercept, \bar{l}_G	77.4 cm	1
Initial mean reproductive investment, \overline{GSI}_G	0.15	2
Initial mean growth capacity, \bar{g}_G	11.08 cm	3,4
PMRN width, w	12.88 cm	1
Coefficient of genetic variation in PMRN slope, $CV_{s,G}$	10 %	3
Coefficient of genetic variation in PMRN intercept, $CV_{l,G}$	2 %	3
Coefficient of genetic variation in reproductive investment, $CV_{GSI,G}$	12 %	3
Coefficient of genetic variation in genetic growth, $CV_{g,G}$	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).