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Bioeconomic consequences of fishing-induced evolution: a model predicts limited impact on net present value

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Abstract: Fishing reduces stock size and shifts demographics, and selective mortality may also lead to evolutionary changes. Previous studies suggest that traits may change evolutionarily because of fishing on decadal time scales. Here we examine the potential bioeconomic impacts of fishing-induced evolutionary change. We used a life-history model with stock dynamics based on evolving maturation age, which has consequences for size-at-age, coupled with a fishing module that describes costs and economic yield. Size-dependent natural mortality and trawl-like fishing mortality are drivers of selection, and in the analysis we varied fishing mortality and size-selectivity of the fishing gear to determine trait evolution as well as economic yield. Comparison of two scenarios — allowing for evolution and assuming no evolution — shows that under current size selectivity, the fishing regimes generating maximum economic yield are not different when evolution is accounted for. However, ignoring evolution overestimates long-term yield under optimal fishing regimes and underestimates resilience to overfishing. Whether fishing-induced evolution matters for management strategies depends on size selectivity, stock state, how it acts on specific traits, and its sensitivity to the assumed discount rate, calling for a cautious use of net present value as sole criterion for management of evolving resources.

Résumé : La pêche réduit la taille des stocks et produit des changements au sein des populations, et la mortalité sélective pourrait également mener à des changements évolutionnaires. Des études antérieures donnent à penser que des caractères pourraient évoluer en raison de la pêche à l'échelle décennale. Nous examinons les possibles impacts bioéconomiques des changements évolutifs induits par la pêche. Nous avons utilisé un modèle de cycle biologique intégrant la dynamique des stocks basé sur l'évolution de l'âge à la maturation, ce qui a des conséquences pour la taille selon l'âge, jumelé à un module de pêche qui décrit les coûts et le rendement économique. La mortalité naturelle selon la taille et la mortalité par pêche de type chalut sont des moteurs de sélection et, dans notre analyse, nous avons modulé la mortalité par pêche et la sélectivité selon la taille des engins afin de déterminer l'évolution des caractères, ainsi que le rendement économique. La comparaison de deux scénarios, un qui permet l'évolution et l'autre non, montre que, dans les conditions actuelles de sélectivité selon la taille, les régimes de pêche qui engendrent le rendement économique maximum ne diffèrent pas selon que l'évolution est prise ou non en considération. Cela dit, la non prise en considération de l'évolution se traduit par la surestimation du rendement à long terme dans des régimes de pêche optimaux et sous-estime la résilience à la surpêche. L'importance de l'évolution induite par la pêche pour les stratégies de gestion dépend de la sélectivité selon la taille, de l'état des stocks et de son effet sur des caractères précis et elle est sensible au taux d'actualisation présumé, ce qui nécessite une certaine prudence dans l'utilisation de la valeur actualisée nette comme seul critère pour la gestion de ressources en évolution. [Traduit par la Rédaction]

Introduction

Management of living resources relies heavily on models that predict future consequences of natural dynamics and management actions. These models range from being conceptual and simple to being complex and data-hungry, but all depend on assumptions about how the real world works. These assumptions constrain the conclusions one can draw from a model and may therefore bias the manager's view of the world, in particular when the manager is not aware of the underlying assumptions or their relevance. As a consequence, the predictive power of model projections is often overestimated (Brander et al. 2013). This applies for uncertainty arising from the use of data or the lack of data, as well as from the properties of the mechanisms included (or ignored) in a model. In fisheries management, this leads to ignorance towards ecological, environmental, or evolutionary processes that either are unknown or are known but deemed irrelevant or too complex to be included in the model. Conse-

quently, a systematic bias may be introduced, particularly in long-term reference points like maximum sustainable yield (MSY) or maximum economic yield (MEY).

In this paper we investigate the consequences of ignoring evolutionary responses to fishing, which is still common practice in fisheries management today. There is widespread scientific awareness that fishing can cause evolutionary changes in exploited fish stocks (Law and Grey 1989; Conover and Munch 2002; Hutchings and Fraser 2008). This process of nature is not incorporated in management models, and current models may thus introduce a systematic bias because they ignore evolutionary trait changes over time and their consequences. We attempted to quantify this bias for bioeconomic predictions and optimal management strategies by asking whether the bias is of such numerical importance that current management models would need to be improved. We also discuss how assumptions regarding specific evolutionary processes may influence this bias and its relevance.

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Fishing-induced evolution is corroborated by several lines of evidence, including time-series analysis of fisheries data (Ricker 1981; Swain et al. 2007; Heino and Dieckmann 2008), evidence of reduced heterozygosity in exploited populations (Smith et al. 1991), and analyses of genetic change over time (Therkildsen et al. 2013). These findings are underlined by experimental evolution under controlled conditions (Reznick and Ghalambor 2005; Conover and Baumann 2009) and theoretical work (e.g., Dunlop et al. 2009).

Conceptually, fishing acts in the same way as predation mortality, by changing survival probabilities, which alters fitness. In commercially important stocks, fishing mortality may be four to five times as high as the natural mortality (Mertz and Myers 1998). This alters the selection landscape and may lead to adaptation of life-history traits such as age at maturation or growth. In this context, age at maturation is a key trait and particularly well studied (Dieckmann and Heino 2007), and selective harvesting has been clearly linked to changes in body size (Conover et al. 2009). Selection may be further intensified by fishing selectivity on size or other traits, though it remains controversial how rapidly evolutionary responses take place in the wild (Andersen and Brander 2009; Darimont et al. 2009) and to what extent observed phenotypic trends are caused by evolutionary changes (Belgrano and Fowler 2013).

If fishing-induced evolution occurs, it becomes crucial to assess its potential consequences. Existing life-history models predict that fishing-induced evolution may impair stock biomass and yield (Law and Grey 1989), cause smaller body size (Heino 1998), and increase natural mortality rates (Jørgensen and Fiksen 2010). The potential reversal of such evolutionary changes might be slow (Law and Grey 1989; Enberg et al. 2009). On the other hand, models also predict that fishing-induced evolution may cause an increase in some measures of recruitment (Enberg et al. 2010; Heino et al. 2013) and spawning-stock biomass in populations where harvesting continues (Enberg et al. 2009). It may also increase the short-term recovery potential of depleted stocks but decrease the long-term ability to fully recover (Enberg et al. 2009) and increase resilience towards high fishing pressures (Heino et al. 2013). Hence, it has been suggested broadly that fisheries management should address fishing-induced evolution and its consequences, at least by quantifying potential impacts for sustainability, ecological services, yield, and resource economics (Heino 1998, Ashley et al. 2003). Despite its key role for fisheries management, only a few studies have focussed on potential bioeconomic impacts of fishing-induced evolution (Guttormsen et al. 2008; Eikeset et al. 2013; Laugen et al. 2014).

The goal of this work was therefore to explore the economic consequences of fishing-induced evolution in a generic bioeconomic model that includes trait evolution, using parameter values of the well-studied Northeast Arctic (NEA) stock of Atlantic cod (*Gadus morhua*). To analyse the consequences of fishing-induced evolution, we compared a model incorporating evolution of age at maturation with a model that allows no evolutionary change and thus quantified potential systematic bias introduced by fisheries managers were they to ignore evolution.

Model description

We have strived to make a generic and tractable tool for studying the bioeconomic impacts of fishing-induced evolution. The evolving trait in the model is age at maturation that affects growth, survival, and reproduction, which in turn have consequences for population dynamics, fisheries yield, and bioeconomics. For the parameterization, we used information from the NEA stock of Atlantic cod, a long-lived and slow-growing species with late maturation, typical for many gadoids and rockfishes in

Table 1. Table of model variables.

Variable	Symbol	Unit
Age	a	Years
Maturation age	m	Years
Abundance	$N_t(a,m)$	Individuals
Individual length	$L(a,m)$	cm
Individual mass	$W(a,m)$	kg
Individual gonadosomatic index	$G(a,m)$	kg·kg^{-1}
Natural mortality	$M(a,m)$	Year^{-1}
Fishing mortality	$f(a,m)$	Year^{-1}
Total mortality	$Z(a,m)$	Year^{-1}
Fishing selectivity	$k(a,m)$	—
Fishing selectivity input variable	L_{50}	cm
Fishing mortality input variable	F	Year^{-1}
Catch	$H_t(a,m)$	Individuals
Total annual yield	Y_t	kg
Total annual revenue	R_t	NOK
Catchability	q_t	—
Effort	E_t	Year^{-1}
Total annual costs	C_t	NOK
Discount rate	d	—
Net present value (NPV)	V	NOK

temperate to Arctic waters. At maturation, growth slows down as resources are channelled towards gonads for reproduction (Rijnsdorp 1993), resulting in small fish with low fecundity if maturation is early and bigger more fecund fish if maturation occurs late in life. As a consequence, maturation age plays a central role in determining the lifetime trajectories of growth, survival, and reproduction. We describe age at maturation as a quantitative trait that is inherited from parents to offspring and also affects population dynamics, which is described by age-dependent equations, where we in addition to the abundance at each age also keep track of their genetically determined maturation age. Because of its key role, we chose age at maturation as the only evolving trait that determines growth trajectories and thus fecundity as well as survival. As a consequence, changes in age at maturation alter the growth trajectory and therefore size-at-age (Fig. S1[1]). Theory has shown that early maturation is generally favoured when fishing mortality increases (Law and Grey 1989), and mortality, including fishing, represents the driving force of selection and adaption over time in this model. Fishing costs and effort are based on total yield, biomass, and catchability, and revenue is determined by yield and constant price. By setting a fishing rate and a size-selectivity curve, we could compare and analyse different fishing strategies and their impacts on trait evolution, bioeconomics, and net present value (NPV). Model parameters and variables are listed in Tables 1 and 2.

Growth and maturation

The model we used contains genetic and phenotypic structure. Phenotypes were tracked by age class a, with $0 \leq a \leq a_{\max}$. At $a_{\max}$ all individuals die, but the value of $a_{\max}$ is chosen so high that it does not influence population dynamics or evolutionary trajectories. Within each cohort we tracked the frequency of genotype g, which codes for maturation age. For the translation from genotype to phenotype we used the theory of quantitative trait inheritance, which assumes that a trait is determined by infinitely many loci each with a small additive effect (Lynch and Walsh 1998). With g being the additive component of the genetic trait, the expressed phenotypic maturation age m will have a normal distribution around g where the deviance δ_{DE} is due to nonadditive genetic effects such as dominance (indicated by D) and all environmental effects (indicated by E):

Table 2. Table of model parameters.

Parameter	Symbol	Unit	Value
Maximum age	a_{max}	Years	25
Genotype	g	—	
Standard deviation of nonadditive effects	δ_{DE}	—	3
Growth coefficient[a]	h	—	3.8
Exponent of allometric mass–length relationship[a]	b_1	—	3.0
Exponent of allometric relationship between resource-acquisition rate and mass[a]	b_2	—	0.75
Constant in allometric mass–length relationship[a]	b_3	—	0.01
Coefficient in allometric mass–length relationship[a]	c_1	—	0.01
Target gonadosomatic index[a]	Q	—	0.3
Length at age 0[a]	L_0	cm	12.5
Base natural mortality	M_0	Year^{-1}	0.15
Natural mortality coefficient[b]	M_1	Year^{-1}	72.5
Exponent of relationship between individual length and natural mortality[b]	M_2	cm	1.61
Steepness of fishing selectivity curve	s	cm^{-1}	0.15
Beverton–Holt recruitment parameter	λ	—	10
Beverton–Holt recruitment parameter	ϕ	—	0.1
Price	p	NOK·kg^{-1}	17
Cost coefficient	c	NOK	8.71
Yield exponent of cost function	z_1	—	1
Biomass exponent of cost function	z_2	—	1

[a]Enberg et al. (2009).
[b]Gislason et al. (2010).

(1) $m = \text{round}(g + \delta_{DE})$

Here, deviance δ_{DE} is modelled as a random noise term with zero mean and normal distribution, and round() is a function that finds the nearest integer value (as maturation only can take place in discrete annual steps). From this, the conditional probability $P_m(m|g)$ of having maturation age m given genotype g was calculated. Note that this refers to the distribution of m given g at birth; thereafter, demographic processes may cause differential survival (and growth and reproduction) among different phenotypes produced from the same genotype.

Growth and hence individual length-at-age follow a biphasic growth model (Quince et al. 2008) with the formulation used by Boukal et al. (2014). This growth model is consistent with how energy and resources can be allocated either to growth or to reproduction, so that length growth slows down in individuals that have become sexually mature[2]. Length-at-age L is deterministically given by the following recursive equation for a given age at maturation:

(2) $L(a, m) = \sqrt[b_1 \cdot b_2]{\dfrac{L(a-1,m)^{b_1 \cdot b_2} + b_2 \cdot h \cdot c_1^{-b_2}}{1 + b_2 \cdot Q(a,m)}}$

Here, h is a growth coefficient, and parameters b_1 and c_1 come from the allometric relationship between somatic mass W and length, $W = b_3 \cdot L^{b_1}$. Reproductive investment is given as the gonadosomatic index $Q(a,m)$, which is zero for $a < m$ and ρ above that unless constrained by the maximum value $h \cdot L(a,m)^{-b_1 \cdot b_2} \cdot c_1^{-b_2}$. The gonadosomatic index is the mass of the gonads relative to somatic mass, such that gonad mass can be found by

(3) $G(a, m) = Q(a,m) \cdot W(a,m)$

We assumed that fecundity is proportional to gonad mass.

Natural and fishing mortality

Mortality is a crucial life-history process, and in this model mortality comes from two sources: natural processes and fishing. To account for the large difference in natural mortality between very early and later life stages, we used size-dependent natural mortality with a base natural mortality M_0, adapted from Gislason et al. (2010):

(4) $M(a, m) = M_0 + M_1 \cdot \left[\dfrac{L(a-1,m) + L(a,m)}{2} \right]^{-M_2}$

Parameters M_1 and M_2 describe the level and scaling of the size-dependent component, and we used the mean length in a year to determine natural mortality. The underlying natural mortality model (Gislason et al. 2010) was adapted by condensing all constant parameters, including values for von Bertalanffy asymptotic length and growth rate (Froese and Pauly 2013), into M_1 and adding M_0 to adjust natural mortality for adult fish to a range that corresponds to the values used in stock assessments (ICES 2013). This approach allows for substantial mortality rates in the youngest age classes and low values of M for age classes above age 3 (Fig. 1).

The equation for size-selective fishing was based on a sigmoid function to emulate a trawl-like fishing pattern, corresponding to empirical selectivity curves in the Norwegian cod fishery (Huse et al. 2000, Kvamme and Isaksen 2004):

(5) $k(a, m) = \left(1 + e^{-s \cdot \left[\frac{L(a-1,m)+L(a,m)}{2} - L_{50} \right]} \right)^{-1}$

The parameter L_{50} defines the size at which fishing mortality reaches 50% of maximum fishing mortality, i.e., the midpoint of the sigmoid selectivity curve. In short, we will refer to this as the minimum size limit of the fishery, and it will be varied systematically. Additionally, s determines the steepness of the sigmoid curve around the midpoint and is assumed constant in all simu-

[2]Possible growth trajectories are shown in Fig. S1[1].

Fig. 1. Natural mortality M and size selectivity of fishing for $L_{50} =$ 40, 60, and 80 cm as functions of individual length.
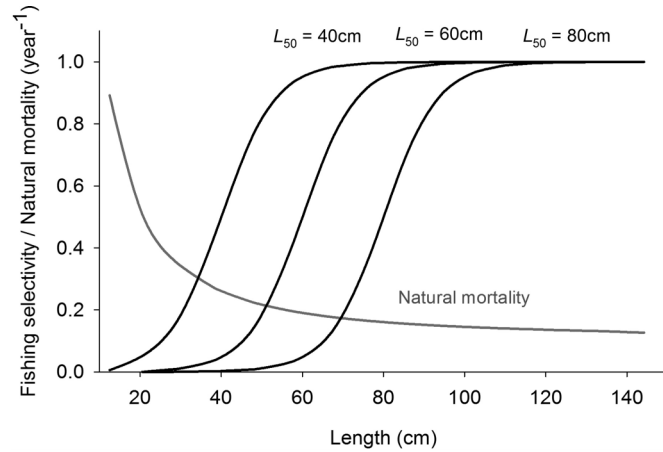
lations. A second parameter we vary is the maximum annual fishing mortality F for sizes fully recruited to the fishery. Fishing mortality for fish of a given age and maturation age is thus described as the product of the overall fishing mortality rate and selectivity at age:

$$(6) \qquad f(a, m) = F \cdot k(a, m)$$

Denoting total mortality rate per year

$$(7) \qquad Z(a, m) = f(a, m) + M(a, m)$$

annual survival is given by

$$(8) \qquad S(a, m) = e^{-Z(a,m)}$$

Population dynamics, reproduction, and trait evolution

We kept track of population dynamics of a population structured by age, phenotypic maturation age, and genotype; abundance at time t was thus denoted as $N_t(a,m,g)$. Only survival changes abundance for ages $a \geq 1$, thus:

$$(9) \qquad N_{t+1}(a + 1, m, g) = N_t(a, m, g) \cdot S(a, m)$$

Reproduction required slightly more tracking, as we needed to be careful how to distribute the recruiting cohort over genotypes g and phenotypic maturation ages m. We began by finding the total number of recruits in the next time step, based on an assumed density-dependent survival of recruits to balance the population dynamics. This takes as input the total amount of gonads invested in reproduction in a given year, G_t. As reproduction takes place at the end of the year, we first calculated the survivors; for these we summed gonad size to find total contribution to reproduction, and this was summed over all genotypes by taking the integral over g:

$$(10) \qquad G_t = \sum_a \sum_m \int N_t(a, m, g) dg \cdot S(a, m) \cdot Q(a, m) \cdot W(a, m)$$

The number of recruits is then given by a Beverton–Holt function:

$$(11) \qquad N_{0,t+1} = \frac{\lambda \cdot G_t}{1 + \varphi \cdot G_t}$$

To find the genotypic composition of the new cohort, we began by describing the probability density function $P_{G,t}(g)$ for gametes produced by the adult population:

$$(12) \qquad P_{G,t}(g) = \frac{\sum_a \sum_m \int N_t(a, m, g) dg \cdot S(a, m) \cdot Q(a, m) \cdot W(a, m)}{G_t}$$

We did not differentiate between males and females, so the gamete distribution is the same for each sex. Reproduction was assumed to be sexual and based on random mating. The distribution of mid-parental trait values is thus given as

$$(13) \qquad P_{M,t}(g) = \int P_{G,t}(g + g') \cdot P_{G,t}(g - g') dg'$$

The rationale for this equation is that a mid-parental value of g is obtained if both parents differ from g in equal amounts g' but in opposite directions, and the integral is taken over all possible values of g'.

The genotype distribution in the new cohort $P_{N,t}(g)$ now only depends on mutation, segregation, and recombination, and we assumed these can be described as one process based on a noise term δ_{MSR} that has a normal distribution with zero mean described by the probability density function $P_{\delta_{MSR}}$. Thus:

$$(14) \qquad P_{N,t+1}(g) = \int_{-\infty}^{+\infty} P_{\delta_{MSR}}(\delta_{MSR}) \cdot P_{M,t}(g - \delta_{MSR}) d\delta_{MSR}$$

The composition of the new cohort is thus given as

$$(15) \qquad N_{t+1}(0, m, g) = N_{0,t+1} \cdot P_{N,t+1}(g) \cdot P_m(m|g)$$

Economics

Harvestable biomass is given as

$$(16) \qquad B_t = \sum_a \sum_m \int N_t(a, m, g) dg \cdot W(a, m) \cdot k(a, m)$$

Harvestable biomass is the biomass of fish that is vulnerable to fishing at the beginning of the fishing season, as defined by the size selectivity of the gear (based on a and m). This assumes that gear selectivity is the only factor that influences the catchability of fish of a given length. Knowing fishing mortality f and natural mortality M, the Baranov catch equation (Beverton and Holt 1957; Branch 2009) was extended to incorporate the population structure by age, phenotypic maturation age, and genotype and used to calculate total annual catch:

$$(17) \qquad H_t(a, m) = \int N_t(a, m, g) dg \cdot [1 - e^{-Z(a,m)}] \cdot \frac{f(a, m)}{Z(a, m)}$$

The continuous formulation of catch assumes that fishing and natural mortality occur simultaneously and are specific for age and phenotypic maturation age. Total yield is achieved by multiplying catch with individual mass and summing over maturation ages, age classes (for $a \geq 3$; recruitment to the fishery was considered to take place at age 3; ICES 2013), and genotypes:

$$(18) \qquad Y_t = \sum_a \sum_m H_t(a, m) \cdot W(a, m)$$

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Revenue R_t at time t is the product of annual yield and an assumed constant price p:

$$(19) \qquad R_t = p \cdot Y_t$$

Given the common assumption that yield equates to the product of fishing effort, catchability, and biomass, we could calculate effort from yield, biomass, and catchability:

$$(20) \qquad E_t = \frac{Y_t^{z_1}}{q_t \cdot B_t^{z_2}}$$

where catchability q_t is the proportion of total biomass (for $a \geq 3$) that is harvestable given demography and size selectivity, and the exponents z_1 and z_2 determine the yield and biomass effect on effort (Béné et al. 2001; Grafton et al. 2007). In the main analysis the exponents z_1 and z_2 are set to 1, a common assumption based on the economic extension of the Schaefer model (Gordon 1954). The results were compared with a nonlinear parameterization as well as empirical cost functions (Figs. S4, S5[1]), but these changes had little effect on the results.

Total fishing costs are the product of effort multiplied with a cost coefficient c:

$$(21) \qquad C_t = c \cdot E_t$$

To calibrate c, a simulation was run starting from a pristine population and with input fishing mortality equal to the mean Fbar = 0.53 (mean F for age classes 5–10 as used by ICES) in NEA cod between 2000 and 2010 (ICES 2013) using $L_{50} = 60$ cm. Given that mean maturation age was between 7 and 8 in this period in NEA cod, we could use the corresponding maturation ages in our simulation model to estimate values for effort and revenue. From these, we calculated c so that the profitability is equal to the mean profit margin of 7% in the Norwegian demersal fishery from 2000 to 2010 (Norwegian Fisheries Directorate 2012). As an alternative, we also tested a cost equation with total costs at the fleet level, in form of output-regulated costs with empirical parameter estimates (see online supplementary material[1]).

Net revenue Π_t is then total revenue minus total costs:

$$(22) \qquad \Pi_t = R_t - C_t$$

and from net revenue one can find net present value (NPV) V under discount rate d:

$$(23) \qquad V = \sum_{t=0}^{\infty} \frac{\Pi_t}{(1 + d)^t}$$

Implementation and simulations

In the numerical implementation of the model, we used age in discrete steps of 1 year, we divided g into 100 segments, and the model was run with annual time steps.

How population dynamics and bioeconomics unfold depends on the stock's initial state as well as whether traits are evolving or assumed constant. We therefore provide results for two cases of interest to evaluate how awareness versus ignorance of evolution would bias projections of stock characteristics and net present value: a "pristine stock" with high mean age at maturation representative of an emerging fishery; and an "overfished stock" with low mean age at maturation representative of a fishery with a long history of exploitation. The pristine stock represents the NEA cod stock at the onset of industrial exploitation, while the overfished stock is similar to the state of the NEA cod in early 2000s before its

recent recovery. From these two different starting points, we then ran two simulations: one allowing for trait evolution and one assuming no evolution. During these simulations, performance was recorded both in terms of biology and economics. If total mature biomass fell below 0.1% of its initial size, the stock was considered collapsed and the simulation stopped.

Results

Our model predicts that evolution of age at maturation will affect yield and profit and therefore has bioeconomic consequences, but the quantitative bias introduced by ignoring evolution depends on the stock's initial state and fishing strategy and is small for most parameter values even at low discount rates.

Biases in optimal harvesting regimes and the resulting yield and profit were more pronounced in lightly exploited stocks compared with stocks that have adapted to fishing throughout a long history of exploitation (Fig. 2). Models that ignore evolution tended to overestimate yield and profit for stocks managed near their maximum economic yield (MEY, defined as maximum NPV). In contrast, the nonevolutionary model underestimated yield and profit in overfished stocks, mainly because evolutionary adaptation helped sustain populations, at least temporarily, or enhanced the recovery potential when fishing mortality was reduced to very low levels.

In the model, evolutionary adaptation of maturation age changed stock structure and yield. This evolutionary impact is revealed when comparing total cumulative yield (the sum of yield over the whole simulation period) and NPV as a function of F under fixed gear selectivity L_{50} (Fig. 2). In the pristine stock, ignoring evolution overestimated total cumulative yield and NPV for all fishing mortalities around optimal F; in addition, optimal F itself was slightly overestimated. This effect was more pronounced for yield than for NPV. Only under high fishing pressures did a non-evolutionary model underestimate total cumulative yield and NPV and more so when size selectivity was high. This implies that at intense exploitation, the stock may evolve properties that result in an economic benefit, given that everything else is held constant. The benefits of a maturation age adapted to fishing could also be seen for total cumulative yield and NPV when an overfished stock was assumed as starting point (Figs. 2b, 2d).

The underlying mechanisms are visualized by the evolutionarily stable endpoints (Fig. 3) and how changes play out over time (Fig. 4). Because fishing mortality adds to total mortality and is size-selective, age at maturation generally tended to decrease as a response to fishing (Figs. 3a, 4a, 4b). A stronger fishing pressure caused a faster decrease in maturation age and a lower evolutionary equilibrium. Only when the initial value of age at maturation was low as a consequence of previous fishing could a low fishing mortality allow for increasing maturation ages (Fig. 4b), which in turn caused a long-term increase of yield and NPV (Fig. 4f). This happens because fish evolve towards earlier maturation and thus lower length-at-age, which leaves a bigger proportion of the mature biomass unaffected by the selectivity range of the fishing gear (Figs. 4d–4f). Remaining below the minimum size limit provides a size refuge and allowed the stock to sustain higher F than when maturation age is nonevolving, but it also led to lower harvestable biomass and less yield. Additionally, fecundity and natural mortality are size-dependent, so lower age at maturation reduces the per capita productivity, as a smaller-sized adult has lower fecundity and higher natural mortality.

The bias of ignoring evolutionary trait changes on yield and NPV varied with the initial age at maturation (Fig. 5). While for high initial maturation ages maximum cumulative yield and NPV were lower with evolution, the deviation became smaller with decreasing age at maturation and eventually became positive. Lower initial maturation age and corresponding length-at-age implies less potential to adapt to fishing, hence the gradually

Fig. 2. Total cumulative yield (*a*, *b*) and net present value (NPV) *V* (*c*, *d*) as a function of fishing mortality *F*. Two scenarios are shown: simulations starting with a stock in pristine state (*a*, *c*) and in an overfished state (*b*, *d*). Discount rate is *d* = 0.01, and the lines illustrate three different size selectivities (light grey: L_{50} = 40 cm; dark grey: L_{50} = 60 cm; black: L_{50} = 80 cm), with solid lines allowing life-history evolution, while broken lines assume no evolution. The scales of yield and NPV were normalized to their maximum value for L_{50} = 60 cm in the model run that allowed no life-history evolution and started from a pristine stock.
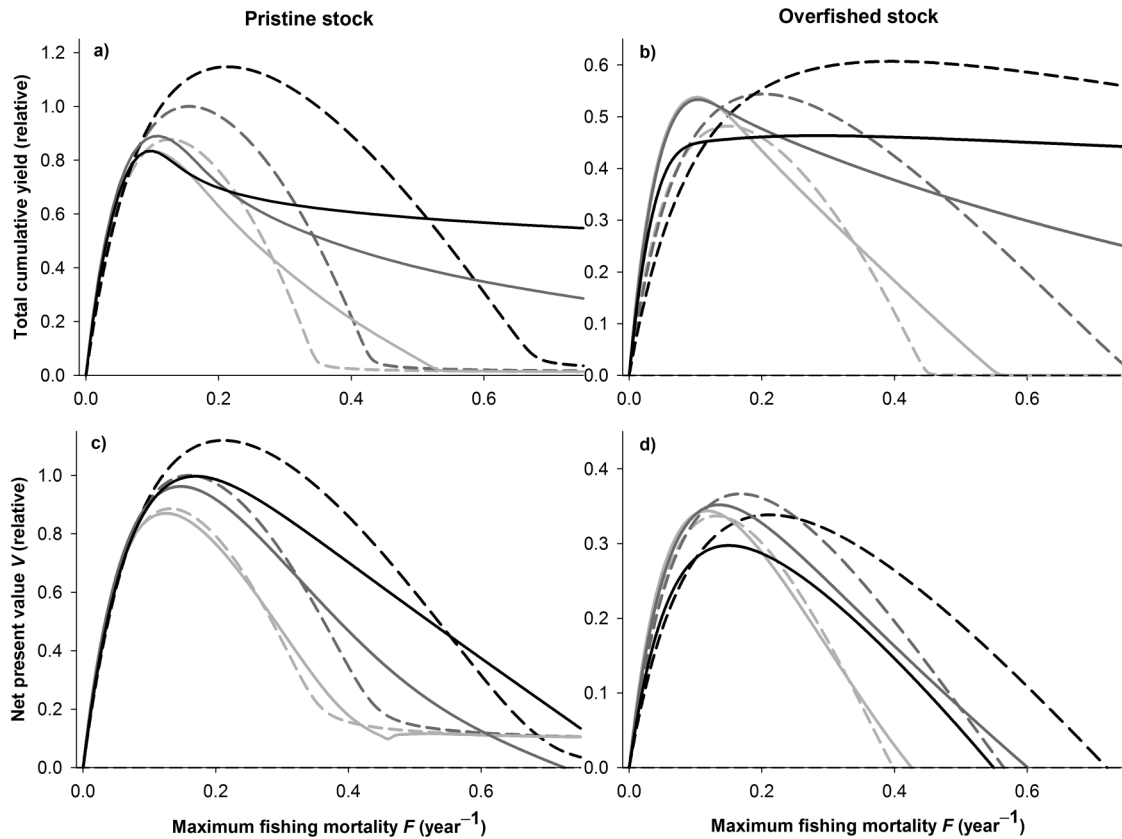
decreasing differences between the nonevolutionary and evolutionary model. Only at very low initial maturation ages did the model that includes evolution result in slightly higher yield and NPV. This happened because the optimal *F* was lower than the value that would cause such a low maturation age, and the relaxed selection pressure then led to increasing maturation ages and higher harvestable biomass. Consequently, the fishing mortality that maximizes yield and NPV was, regardless of initial maturation age, substantially lower in the evolving model than in the nonevolving model. For a fisheries manager, this implies that fishing should be less intense than prescribed by a nonevolving model (Fig. 5, grey lines).

The higher the L_{50}, the larger the bias introduced by ignoring evolution (Fig. 6). Assuming no evolution suggests maximization of NPV for higher values of L_{50} and *F* than when evolution is considered. This applies independently of initial stock state, although the bias was stronger for a less exploited stock at the onset of simulations. Ignoring the adaptive potential led to an overestimation of the fishing mortality that maximizes NPV F_{MEY} as well as the corresponding L_{50} and NPV.

The choice of discount rate dictates how much NPV and optimal harvest patterns are biased by ignoring evolution (Fig. 7). NPV became indistinguishable between models with and without evolution at discount rates above 5%. With the pristine starting conditions, there was no bias in optimal L_{50} for discount rates above 5%, whereas optimal *F* was lower in the nonevolving model. Only at very low discount rates was there an overestimation of F_{MEY} and the corresponding L_{50} when evolution was ignored.

Discussion

With increasing indications that fishing could cause evolutionary changes in fish stocks (Law and Grey 1989; Conover and Munch 2002; Hutchings and Fraser 2008), calls for considering evolution in fisheries management have gained relevance (Heino 1998; Ashley et al. 2003; Jørgensen et al. 2007). Although the overall relevance of evolutionary changes for fisheries management is still debated (Borrell 2013), shifts in management reference points due to fishing-induced evolution (Enberg et al. 2010; Heino et al. 2013) and a framework for evolutionary impact assessments have been suggested (Jørgensen et al. 2007; Laugen et al. 2014). However, despite their importance for successful fisheries management, few studies have considered socioeconomic consequences of fishing-induced evolution (in an analytical model, Guttormsen et al. (2008); for specific fisheries, Rijnsdorp et al. (2012); Eikeset et al. (2013)). Of these, Eikeset et al. (2013) studied the same population as this study but reached different conclusions.

According to our model, ignoring fishing-induced evolution of age at maturation introduces a systematic bias when estimating biological yield and economic consequences, but the quantitative impact depends on the choice of discount rate, size selectivity, and the stock's initial state. Firstly, the economic relevance of fishing-induced evolution depends on the specific fishing regime and stock state. The bias of not including evolution may be negative, insignificant, or even positive. The latter occurred in our study for scenarios with historical overfishing owing to evolution of increased resilience against fishing. In the range of intermediate fishing mortalities that maximize yield and NPV, evolutionary

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Fig. 3. Evolutionarily stable endpoints of mean age at maturation (*a*), mature biomass (*b*), and total yield (*c*) as a function of maximum fishing mortality *F*. The lines illustrate three different size selectivities (light grey: L_{50} = 40 cm; dark grey: L_{50} = 60 cm; black: L_{50} = 80 cm), with solid lines allowing life-history evolution, while broken lines assume no evolution. The scales of mature biomass and total yield were normalized to the pristine mature biomass and the maximum total yield for L_{50} = 60 cm in the model run that allowed no life-history evolution, respectively. Discontinued lines indicate that the stock goes extinct before reaching a stable age at maturation.
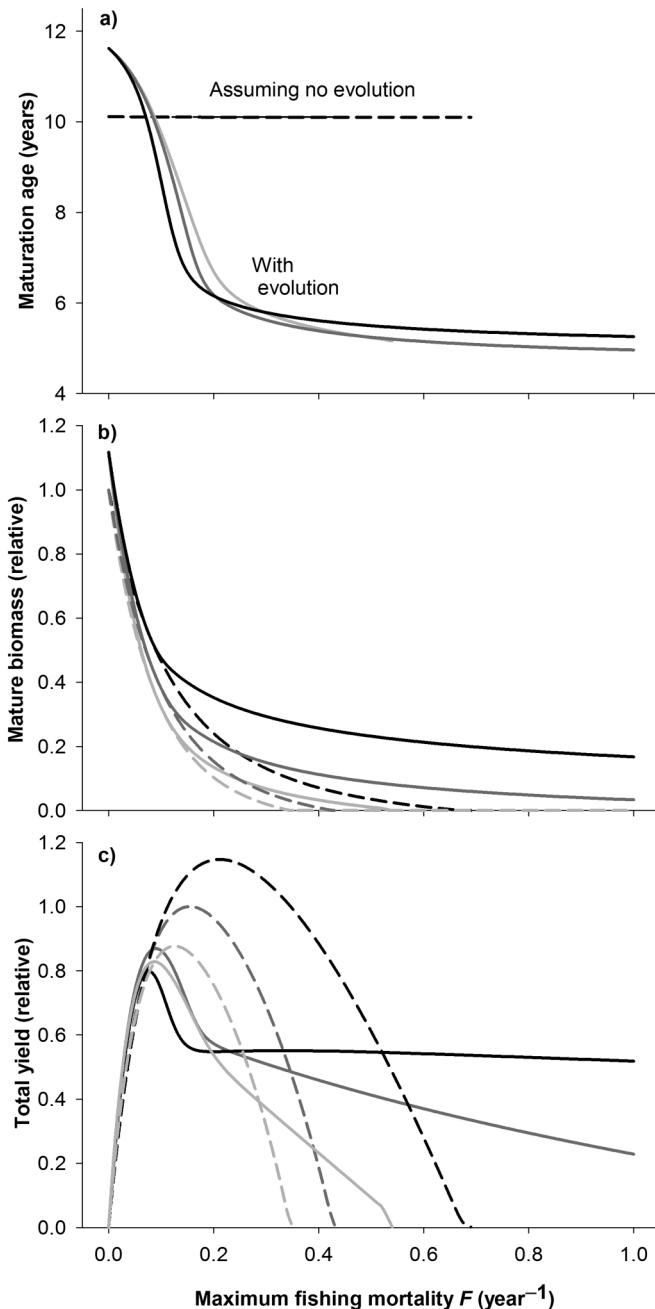
adaptations to fishing may increase mature biomass but decrease fish size and lead to a long-term decline in harvestable biomass and yield. Thus, when aiming for an optimal utilization of fish stocks, ignoring evolution could lead to an overestimation of optimal *F* and size selectivity as well as the resulting NPV. This effect is more pronounced for unexploited stocks; however, the same

trends are seen in stocks that have adapted to fishing throughout a history of exploitation.

The key mechanism is the adaptation of fish to harvesting by maturing earlier and stopping growth at smaller sizes, potentially remaining below the minimum size limit for a longer portion of their life. Because postmature size-at-age is directly linked to age at maturation, evolutionary changes in maturation age will alter the mean growth trajectory and resulting length-at-age (Figs. S2, S3[1]). Since early-maturing fish are smaller, they are less susceptible to fishing gear but suffer higher rates of natural mortality. When fishing was substantial, the overall effect was increased survival, allowing them a higher reproductive contribution and thus a decrease of inherited mean age and length at maturation in the next generation. This adaptation caused a reduction in harvestable fraction of the stock but also a concomitant increase in reproduction, and the balance between these two processes determined whether the effect on yield is positive or negative. For most parameters, evolutionary adaptation reduced harvestable biomass and yield but increased the abundance of mature fish below harvestable size, which allowed the stock to sustain itself despite intense fishing pressure.
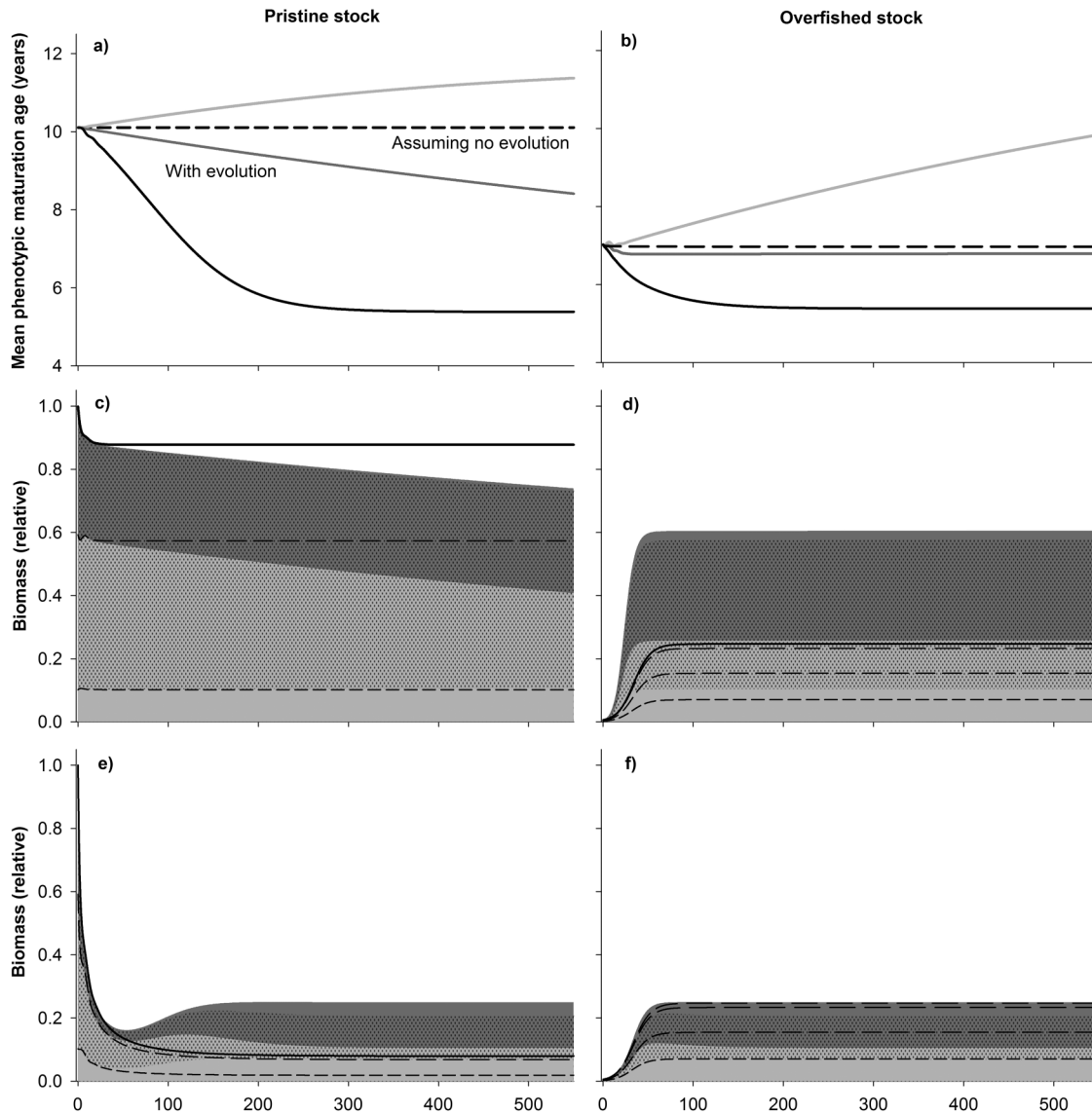
The selectivity of fishing gear strongly influenced the potential evolutionary consequences of fishing and their gravity. Size selectivity, as in our model, is an essential attribute of most fisheries and defines how fishing mortality acts on the structured stock. Fishing selectivity may shift the selection pressure on specific traits and also create size refuges where there is little risk of mortality. This mechanism drove the result of this study, because mean length-at-age decreased with age at maturation, reducing vulnerability to size-selective fishing and thus providing an evolutionary advantage to early-maturing fish that remained small. For practical purposes, there was relatively little impact on F_{MEY} and NPV within the range of current size selectivity in the NEA cod fishery, should evolution be ignored. The evolutionary bias became stronger when looking at higher size selectivity of L_{50} = 80 cm and above, which would enlarge the potential size refuge and therefore make it more advantageous to mature early at a small size. Because the model without evolution did not allow an evolutionary adaptation towards earlier maturation, it suggests a higher optimal size selectivity. For optimal harvest strategies, this indicates that potential evolutionary changes are of particular relevance in the context of size selectivity and may lead to results that can deviate from similar models with static traits (Diekert et al. 2010; Diekert 2013). Another factor to consider is the shape of the selectivity curve. In our study we focused on trawl-like selectivity curves because bottom-trawling is dominating in cod fisheries, yet dome-shaped selectivity curves may better conserve desirable values for life-history traits because they may create size refuges for large fish too (Law 2007; Jørgensen et al. 2009).

The economic impact of evolutionary change is highly sensitive to discounting. Generally, the quantitative economic bias of ignoring fishing-induced evolution was relatively small and accumulated over long time spans. This had the consequence that the economic relevance of fishing-induced evolution diminished rapidly with discount rate and became negligible at or above a discount rate of 5%. Thus, the choice of discount rate determines directly whether there are any significant bioeconomic consequences of fishing-induced evolution. This situation is analogous to other examples of anthropogenic impacts on the environment and subsequent societal costs that accrue slowly over long time spans, most notably climate change (Stern 2008).

Bioeconomics submodel

The model we used had a single-stock, single-market framework and assumed a steady state for the economic domain. It further ignored fluctuations and uncertainty due to climate, ecosystem, or market effects. The lack of fleet and market dynamics contrasts reality, and there was no feedback from state of stock to

Fig. 4. Temporal development of stock characteristics. Two scenarios are shown: simulations starting with the stock in a pristine state (left column) and an overfished state (right column) for L_{50} = 60 cm and F = 0.15 (*a–d*) and 0.4 year^{-1} (*a, b, e, f*) as well as F = 0.0 (*a, b*). The panels show the evolution of maturation age over time (*a, b*) for F = 0.0 (light grey lines), 0.15 (dark grey lines), and 0.4 year^{-1} (black lines), and the changes in biomass (*c–f*) subdivided in mature (dark grey area) and immature (light grey area) as well as harvestable biomass (dotted area) of the evolutionary model. The corresponding trajectories of the model without evolution are indicated with lines (solid line = nonharvestable mature biomass; long dashed line = harvestable mature biomass; medium dashed line = harvestable immature biomass; short dashed line = nonharvestable immature biomass; solid and long dashed lines overlap completely in panel *c*). Biomass values were standardized to total biomass at time 0 in the pristine stock.

fishing, e.g., by using harvest control rules. The inevitable adjustment of fishing effort and gear selectivity that would continuously adapt to the current state of the stock was left out from our model to allow for a clear analysis of the isolated effect of evolutionary change. In real fisheries, a gradual adaptation of management policies and fishermen behaviour to changes in the stock and its traits may lessen or exacerbate the potential evolutionary impacts over time. Furthermore, we did not account for size-structured pricing or price elasticity based on consumer demand and seasonal availability, although price dynamics can substantially influence economically optimal fishing (Loannides and Whitmarsh 1987; Sandal and Steinshamn 2001; Zimmermann et al. 2011). In particular, size-dependent pricing is common in many fisheries (Carroll et al. 2001; Asche and Guillen 2012; Zimmermann and Heino 2013) and could interact with shifts in

stock and catch composition towards lower sizes, typically increasing the bias of ignoring evolution. Our model furthermore has no spatial distribution, and practical challenges in balancing stakeholder interests or implementing and enforcing management policies are ignored (Beddington et al. 2007; Agnew et al. 2009; Mora et al. 2009).

The validity of the cost formulation in our model is constrained by simplifying assumptions. The link among biomass, catchability, yield, and effort is a classic concept but may insufficiently reflect the true costs of fishing. Empirical estimates of cost parameters (Sandberg 2006) may provide much more precise information on costs for the specific historic state of NEA cod stock and fishery; however, applying such an empirical cost function to the large range of fishing mortality and size selectivity, across completely different stock states and very long time spans, may

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Fig. 5. Influence of initial age at maturation on maximum cumulative yield (*a*) and net present value (NPV) V_{MEY} (*b*) as well as corresponding optimal *F* (grey lines) for $L_{50} = 60$ cm and *d* = 0.01. Values of cumulative yield and NPV were standardized to their maximum levels at age at maturation of 11.
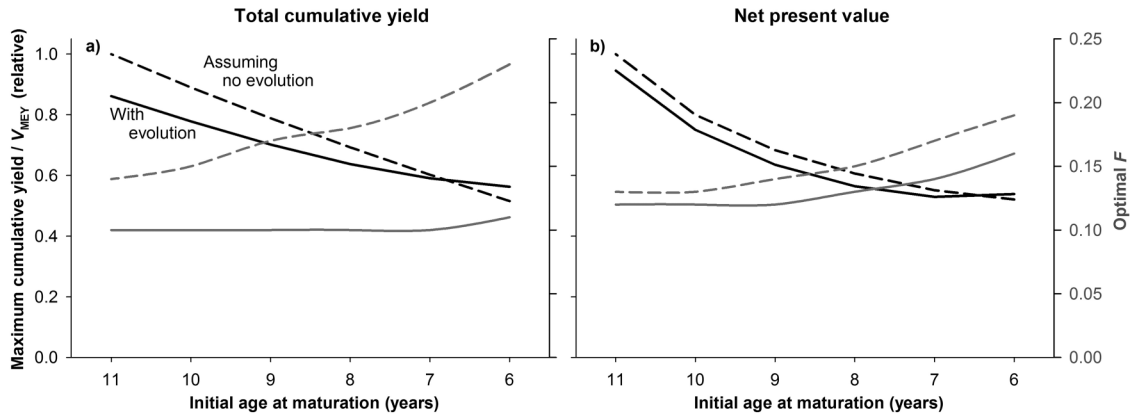

Fig. 6. Net present value (NPV) *V* as a function of maximum fishing mortality *F* and size selectivity L_{50}. The greyscale gradient represents *V* from zero (dark) to maximum (light) for stocks in a pristine (left) or overfished (right) state and simulations assuming no evolution (top) or including evolution (bottom). The scale of NPV was normalized to the maximum of *V* for $L_{50} = 60$ cm in the simulation that started with a pristine stock and allowed no life-history evolution, and contour lines are shown for each increment of 0.05.
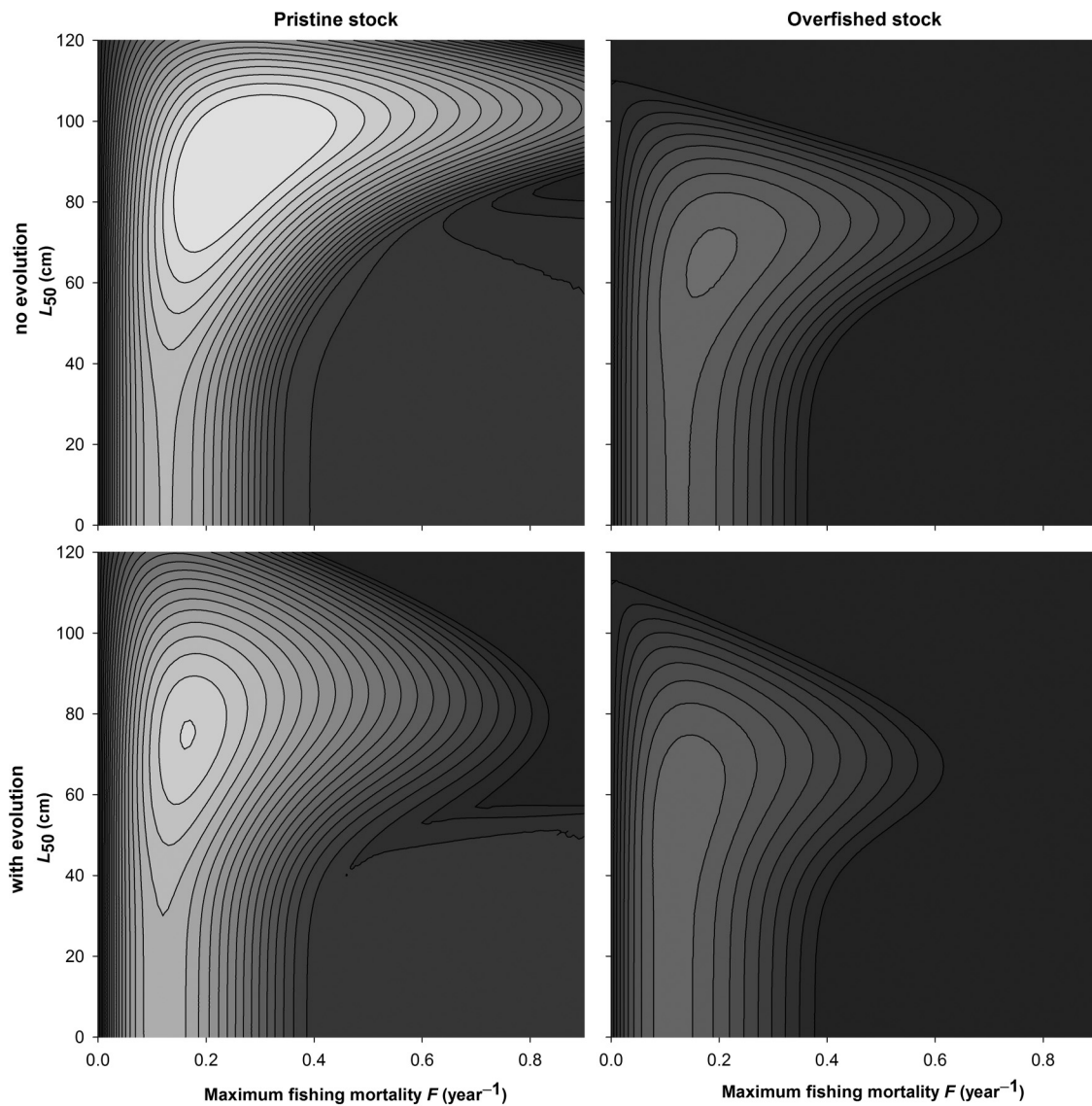
Fig. 7. Influence of discount rate on net present value (NPV) and optimal fishing regime. The bias of ignoring evolution on maximum NPV for varying discount rates for pristine (*a*) and overfished (*b*) stock. Values larger than 0 indicate higher NPV in simulations without evolution. The corresponding optimal fishing regimes (*c*, *d*) are shown as L_{50} (black lines, left axis) and *F* (grey lines, right axis) as a function of discount rates. Simulations that allowed life-history evolution are shown with solid lines, and simulations without evolution are shown with dashed lines. Simulations were run with a pristine (*a*, *c*) and overfished (*b*, *d*) state of the stock as starting point.
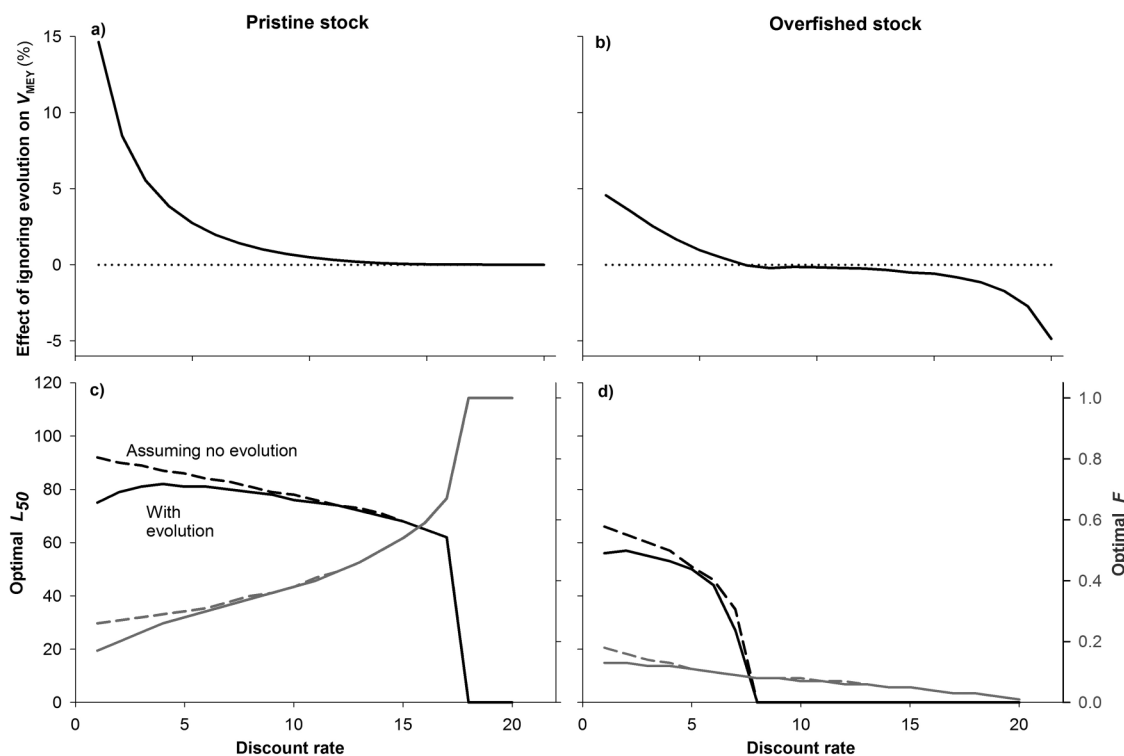
extrapolate too far and weaken the results. Our cost equation was therefore highly simplified to remain applicable in our generic model and implied the flexibility of the fleet to adjust to an efficient size. Capital cost and other fixed costs were not explicitly considered. Also, for the time span we considered, an absence of major changes in fuel or labour costs or fishing technology is rather unrealistic. On the other hand, external economic fluctuations are hardly predictable and are outside of our scope. Our goal was rather a generic impact assessment of what bioeconomic consequences fishing-induced evolution might have. Furthermore, our results remained qualitatively the same when our simplified cost equation was replaced with an empirical cost equation or when cost parameters were varied, demonstrating that substituting the cost function with alternatives has no consequences for our conclusions.

Biological submodel

The biological submodel is constrained by the assumptions we made regarding population dynamics and life-history evolution, in particular using age at maturation as the only evolving trait with direct consequences for growth trajectories and thus fecundity and natural mortality. Age at maturation is a key life-history trait in species like cod and is shown to be sensitive to fishing-induced evolution (Law and Grey 1989; Dieckmann and Heino 2007). However, the extent to which observed changes in phenotypic maturation age and length are caused by genetic changes has yet to be fully determined. Our model did not include density-dependent growth, which likely is an important contributor to phenotypic plasticity (Beverton and Holt 1957; Lorenzen and Enberg 2002). Additionally, when age at maturation approaches its lower boundary under severe overfishing, it can be assumed that other traits like growth (Enberg et al. 2012), spawning migration (Jørgensen et al. 2008), or other behavioural traits (Jørgensen

and Fiksen 2010; Jørgensen and Holt 2013) become more relevant. Evolutionary and plastic changes in growth could also lead to compensatory responses in maturation age (see e.g., Marshall and Browman 2007). These concerns relate mostly to overfishing scenarios, not in the area of lower, optimal harvest pressures. Furthermore, evolution may also cause higher natural mortality, as has been suggested in some models (Jørgensen and Fiksen 2010; Jørgensen and Holt 2013) and which corresponds to observed trends in some important harvested cod stocks (Swain and Chouinard 2008). This is reflected in our model through size-dependent natural mortality causing higher natural mortality when length-at-age decreases. Limiting evolutionary changes to age at maturation alone and relating size-at-age directly to maturation age were therefore potentially problematic simplifications, but did on the other hand provide clear tractability and underpinned the model with a well-studied key trait.

Comparisons with similar studies

The differences in approach and results between our study and the work of Eikeset et al. (2013) underline the sensitivity to specific model assumptions and highlight the need for further mechanistic as well as applied studies to contribute to a thorough bioeconomic impact assessment of fishing-induced evolution. Our study and that of Eikeset et al. (2013) share a very similar scope but reach different main results and conclusions, suggesting that predictions are sensitive to model assumptions. Where Eikeset et al. (2013) found that the impact of fishing-induced evolution was negligible or even beneficial under optimal fishing mortalities and became negative under high historic fishing mortalities, we found the opposite. These contrasting results may be caused by substantial differences in modelling approach and the mechanisms included. Major differences are that Eikeset et al. (2013) used several evolving traits (maturation age and size, reproduc-

tive investment, and growth rate), included density-dependent growth, assumed constant natural mortality across all sizes, used knife-edge size selectivity in the fishery, and incorporated an economic module with higher complexity (demand- and size-dependent price, empirical cost function).

It is challenging to point to the single most important factor that could explain the discrepancy between their study and ours. While Eikeset et al. (2013) used time series data to fit the parameters of their individual-based model and then analysed individual-based simulations for effects of harvesting strategies, we have assumed parameter values based on the literature. It seems that one implication of these diverging modelling strategies is that evolution of maturation age happens much faster in our model than in Eikeset et al. (2013). Inspecting their figure 2b, the historic fishing regime with $F = 0.68$ year^{-1} causes a reduction of maturation age of about 0.2 years between 2000 and 2100 when fluctuations in density dependence are minimal, which is very slow compared with the rates our model predicted and also previous empirical studies on the NEA stock (Jørgensen 1990; Heino et al. 2002). Looking further into the assumptions they made about genetic versus environmental variance in maturation, it seems that heritability of length (age) at maturation is roughly (slightly higher than) $h^2 = 0.02$, which is a lot lower than the $h^2 = 0.2$ quantified in breeding experiments on other Atlantic cod stocks (Kolstad et al. 2006) and the range $h^2 = 0.09–0.67$ found in salmonids (Gjedrem 1983). Eikeset et al. (2013) chose model parameters to fit observed time series of mean age and length at maturation as well as biomass, so it may very well be that their findings reflect the actual evolutionary dynamics of the NEA cod stock and that other cod stocks differ. If so, our results are an inadequate representation of this actual cod stock and would be more informative for other long-lived stocks where heritability is closer to the common value of $h^2 = 0.2$. At the same time, we know of no other studies that have quantified heritability from wild population-level data in this way; the closest method we are aware of is the more rigorous approach taken by Swain et al. (2007).

A consequence of the slow evolution of maturation dynamics is that the density dependence acting on individual growth rate is strong, and probably together with growth evolution is the main driver of the effects on yield and productivity in Eikeset et al. (2013). In contrast, our model assumed growth trajectories based on age at maturation; therefore, size-at-age decreased with higher fishing mortalities and only in the evolutionary model. These opposite effects on size-at-age together with their effects on fecundity, natural mortality, and susceptibility to fishing can likely explain a large part of the differences relative to our study. In our model, early maturation caused small size and allowed fish to stay below mesh size. In Eikeset et al. (2013), the slow response of maturation age and size left the fish only with the option of accelerating reproduction by growing fast and with large gonads, but there was no size refuge from fishing. This could explain their prediction of lower biomass at high fishing mortality and intermediate size selectivity, which has the consequence that fishing-induced evolution may decrease the stock's resilience to high fishing pressure, in contrast with what has been found in this study and earlier studies (Enberg et al. 2009, 2010).

Overall, Eikeset et al. (2013) and our study chose very distinct approaches to the same problem. Eikeset et al. (2013) used a data-heavy, highly stock-specific model to look at fishing-induced evolution in a historic context, while we evaluated a more generic model to explore the mechanism in a broader context. The different results due to contrasting approaches and assumptions highlight the particular sensitivity of bioeconomic models to evolutionary dynamics and the important interplay with density dependence and plasticity effects that our model omits. Future studies will therefore require a careful evaluation of model design and choice of mechanisms and parameter values that describe genotypic and phenotypic change.

Choice of discount rate

Our results show that the bias of ignoring fishing-induced evolution is highly sensitive to the choice of discount rate, and differences between the evolutionary and nonevolutionary model become insignificant under low discount rates. Discounting is essential to determine the dynamic solution of cost–benefit analyses and, accordingly, the optimal utilization for resources like fish stocks (Clark 1990; Tietenberg and Lewis 2008). Reasonably low discount rates commonly ensure a modest exploitation and high stock abundance (Grafton et al. 2007), but in specific cases even low discount rates favour overexploitation or extinction to maximize profit (Clark 1973). In general, a higher discount rate implies that future dynamics are considered less important, and the exponential decay of present value over time often makes NPV calculations indifferent to small changes that accrue over long periods, like a gradual erosion of yield or slow increases in costs. This raises ethical questions (Ainsworth and Sumaila 2005) and calls for low or zero discount rates for environmental impacts or under stochastic uncertainty (Lande et al. 1994; Weitzman 1998). The characteristics of evolutionary change demand, therefore, a prudent approach to discounting and, potentially, concepts like a decreasing discount rate over time (Weitzman 2001), otherwise the economic consequences of fishing-induced evolution and the impact on optimal harvest strategies could be deemed insignificant.

Management implications

Our study does not support an increased awareness of evolution in fisheries management purely for economic reasons, but reveals that the details of model assumptions may cause highly variable consequences. In our case, we found that ignoring evolution may bias predictions for optimal harvesting strategies so that a higher fishing mortality and size selectivity would be chosen than if evolution was accounted for. If fishing-induced evolution occurs but is ignored when reference points like MSY and MEY are calculated, then long-term management plans may implement flawed targets (see also Heino et al. 2013). However, in our study the differences were mostly small when considering current size selectivity, and they were minor in view of other management challenges such as natural fluctuations, climate change, or overcapacity. Fisheries are also not managed through static inputs as in our model, but regulations adjust to current changes in stock size and structure and therefore indirectly and partly account for evolutionary changes in real time, albeit in a nonoptimal manner. Furthermore, the precise impact of fishing-induced evolution on observed phenotypic changes in fish stocks is still debated, adding uncertainty to any predictions on potential consequences. For all these reasons, it has been argued that management of fishing-induced evolution will be most successful if it aligns with the objectives of traditional fisheries management (Law 2007); hence, standard management approaches like MEY or precautionary approach may provide a sufficient response to fishing-induced maturation evolution even without incorporating it explicitly. To achieve MSY with maturation evolution, our results suggest that fishing mortality should be roughly one-third lower than predictions made without considering evolution. For NEA cod, the (nonevolutionary) MSY reference point is a fishing mortality of 0.4 year^{-1} (ICES 2013), but recent exploitation levels have been lower: 0.27 and 0.23 year^{-1} in 2011 and 2012, respectively. These reduced values correspond to optimal harvest rates as predicted by our evolutionary model and, if maintained, imply an evolutionary sustainable harvest in recent years. This demonstrates that with implementation of established concepts to optimize resource rent and minimize risks, the error made by using models that ignore evolutionary change may become small and the biological impact reduced to modest levels. This also corresponds to the main conclusion of Eikeset et al. (2013), yet distinct differences

in the detailed results call for a cautious consideration of assumptions made in evolutionary models.

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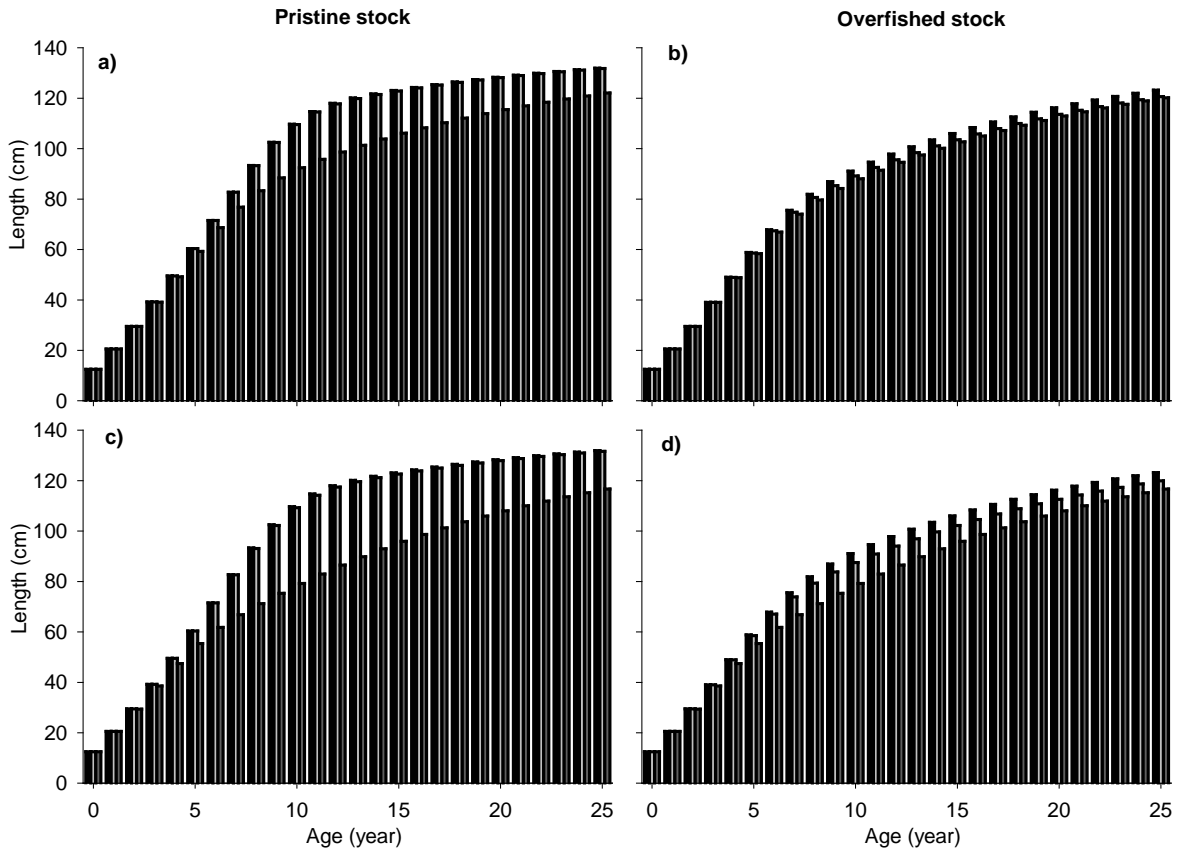
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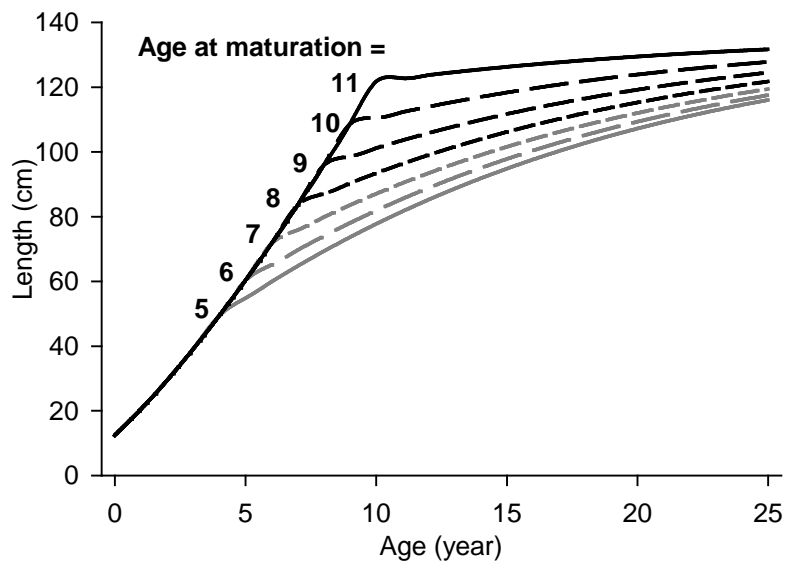
3 Fig. S1: Length at age for all maturation ages from 5 to 11. The lines represent the growth

4 trajectories based on a biphasic growth function with reduced growth rates after the age at

5 maturation.

6

Fig. S2: Length at age at the beginning ($t = 0$, black bars) and end ($t = 1000$, light and dark grey bars) of the simulation with and without evolution for four different scenarios: Starting from a pristine stock with $F = 0.15$ (a) and $F = 0.4$ (c), and starting from an overfished stock with $F = 0.15$ (b) and $F = 0.4$ (d). Black bars show initial length at age while length at age at the end of the simulations is shown for the models without evolution (light grey bars) and with evolution (dark grey bars).

2
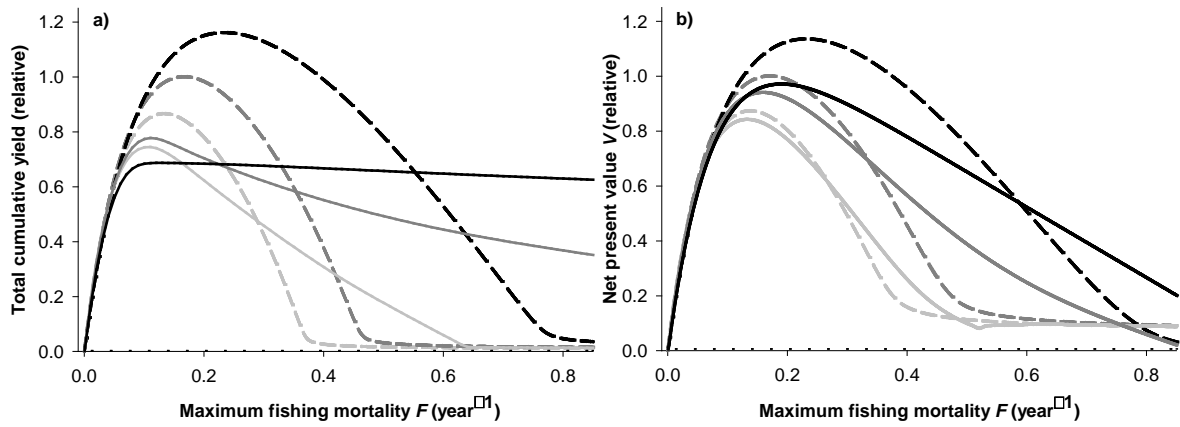
15

16   Fig. S3: Effects of assuming constant natural mortality. Total cumulative yield (a) and net

17   present value (NPV) V (b) as a function of fishing mortality F when assuming a constant

18   natural mortality of $M = 0.2$ for all ages $a \geq 3$ and starting from a pristine stock state.

19   Discount rate is $d = 0.01$, and the lines illustrate three different size selectivities (light grey:

20   $L_{50} = 40$cm; dark grey: $L_{50} = 60$cm; black: $L_{50} = 80$cm), with solid lines allowing life-history

21   evolution while broken lines assume no evolution. The scales of yield and NPV were

22   normalized to their maximum value for $L_{50} = 60$cm in the model run that allowed no life-

23   history evolution and started from a pristine stock.

24

3

25   **Alternative cost function**

26   To check sensitivity to the cost function used we re-ran model simulations with an alternative

27   cost function:

$$C_t = c \cdot \frac{Y_t^{1-z_1}}{q_t \cdot B_t^{z_2}}$$

28   where we relied on empirical studies from vessel costs in the Norwegian cod fishery for

29   values of c, z_1 *and* z_2 (Sandberg 2006) and $q = 1$, using parameter values from two distinct

30   components of the fleet: factory trawlers ($c = 20.33$, $z_1 = 0.22$ *and* $z_2 = 0.59$) and small coastal

31   vessels ($c = 17.14$, $z_1 = 0.48$ *and* $z_2 = 0.21$). The parameter values imply that unit costs

32   decrease when total yield Y_t or total harvestable biomass B_t go up, indicating economies of

33   scale and overcapacities in the fishery.
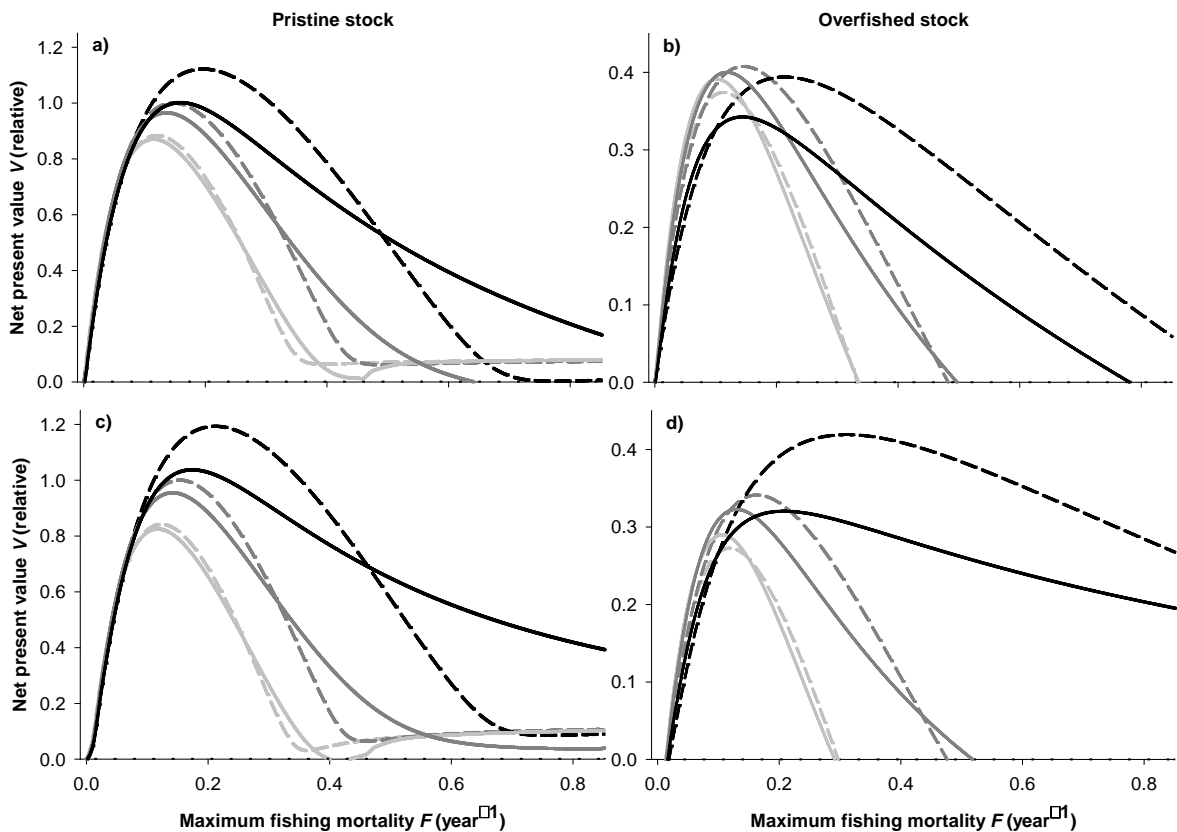
34

35   Fig. S4: Net present value (NPV) V as a function of fishing mortality F in the model with

36   alternative cost equation and parameterization based on factory trawlers (a,b) and small

4

37   coastal vessels (c,d). Discount rate is $d = 0.01$, and the lines illustrate three different size

38   selectivities (light grey: $L_{50} = 40$cm; dark grey: $L_{50} = 60$cm; black: $L_{50} = 80$cm), with solid

39   lines allowing life-history evolution while broken lines assume no evolution. The scale of

40   NPV was normalized to the maximum of V for $L_{50} = 60$cm in the model run that allowed no

41   life-history evolution and started from a pristine stock.
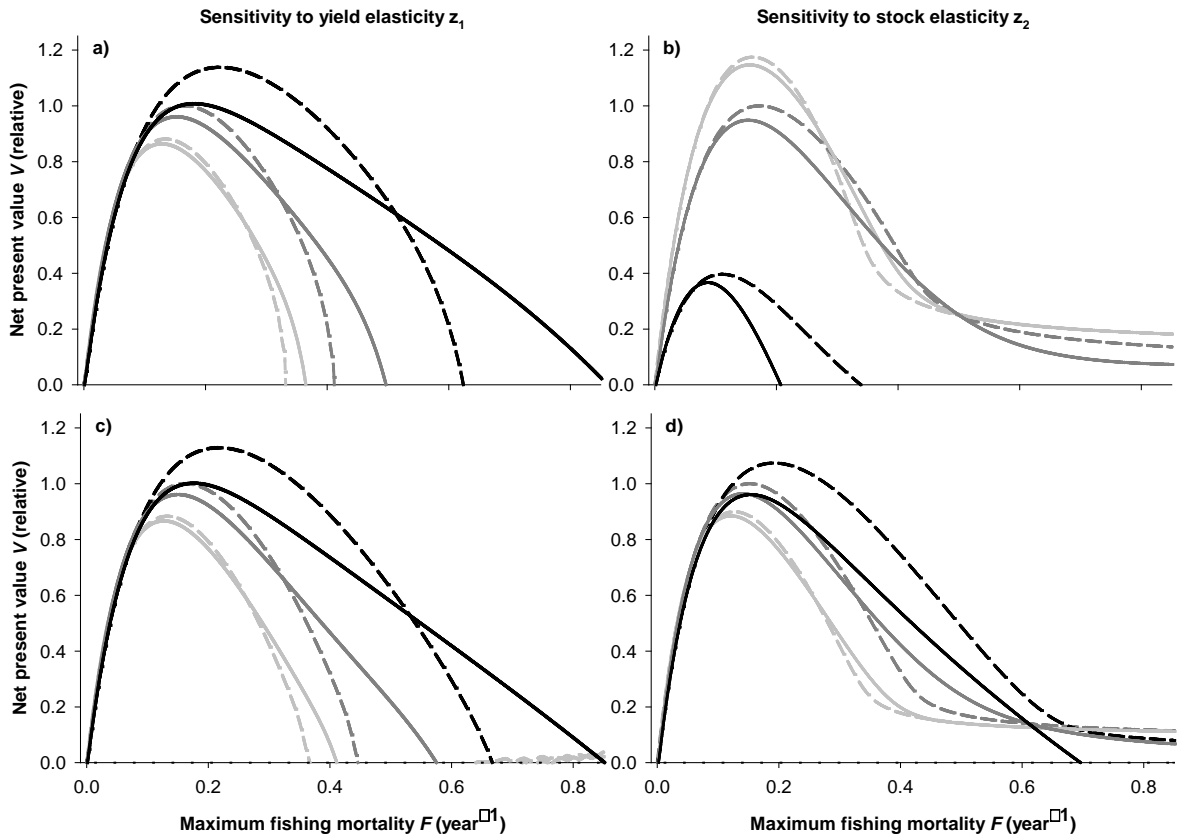
42

43   Fig. S5: Net present value (NPV) V as a function of fishing mortality F in the model with

44   varying cost exponents z_1 (a,c) and z_2 (b,d). The specific combinations are: $z_1=-0.5$ and $z_2=1$

45   (a), $z_1=-0.5$ and $z_2=-0.1$ (b), $z_1=0.5$ and $z_2=1$ (c), and $z_1=-1$ and $z_2=0.5$ (d). Discount rate is $d =$

46   0.01, and the lines illustrate three different size selectivities (light grey: $L_{50} = 40$cm; dark

47   grey: $L_{50} = 60$cm; black: $L_{50} = 80$cm), with solid lines allowing life-history evolution while

48   broken lines assume no evolution. The scale of NPV was normalized to the maximum of V for

49    $L_{50} = 60$cm in the model run that allowed no life-history evolution.

50