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IIASA Interim Report
2012

Heino, M., Baulier, L. and Dieckmann, U. (2012) Can fisheries-induced evolution shift reference points for fisheries management? IIASA Interim Report. IR-12-041 Copyright © 2012 by the author(s). http://pure.iiasa.ac.at/10234/

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February 2015

# Can fisheries-induced evolution shift reference points for fisheries management?

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## Abstract

Biological reference points are important tools for fisheries management. Reference points are not static, but may change when a population's environment or the population itself changes. Fisheries-induced evolution is one mechanism that can alter population characteristics, leading to "shifting" reference points by modifying the underlying biological processes or by changing the perception of a fishery system. The former causes changes in "true" reference points, whereas the latter is caused by changes in the yardsticks used to quantify a system's status. Unaccounted shifts of either kind imply that reference points gradually lose their intended meaning. This can lead to increased

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[1] This article has been prepared jointly by participants of the Study Group on Fisheries-Induced Adaptive Change (SGFIAC) of the International Council for the Exploration of the Sea (ICES). MH and UD coordinated preparations and integrated the writing. LB, DSB, UD, BE, MH, FJ, FM, HP, ADR, NOT, SUH, and AV wrote and reviewed sections. RA, DJD, ESD, AME, KE, GHE, CJ, ATL, SM, SN, DU, and RW contributed suggestions and comments. In the meanwhile, SGFIAC has become the Working Group on Fisheries-induced Evolution (WGEVO). For further information about the working group, please contact the WGEVO chairs UD, MH, or ADR.

precaution, which is safe, but potentially costly. Shifts can also occur in more perilous directions, such that actual risks are greater than anticipated. Our qualitative analysis suggests that all commonly used reference points are susceptible to shifting through fisheries-induced evolution, including the limit and "precautionary" reference points for spawning-stock biomass, $B_{\mathrm{lim}}$ and $B_{\mathrm{pa}}$, and the target reference point for fishing mortality, $F_{0.1}$. Our findings call for increased awareness of fisheries-induced changes and highlight the value of always basing reference points on adequately updated information, to capture all changes in the biological processes that drive fish population dynamics.

Keywords: biological reference points, fisheries-induced evolution, fisheries management, population dynamics, precautionary approach, uncertainty.

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## Introduction

Reference points are tools that facilitate assessing the status of a fishery system in relation to management objectives (Table 1). Over the last two decades, reference points have become established as important tools for fisheries management (FAO, 1996; Gabriel and Mace, 1999; ICES, 2007a). Fishery reference points are expressed as targets that management should aim to reach, or as limits beyond which a system should not pass (Caddy and Mahon, 1995; Mace, 2001). Reference points are most commonly based on stock-recruitment relationships, yield-per-recruit relationships, or production models. Inherent to these models are the influences of growth, reproduction, and survival on population dynamics. If these underlying processes change over time, the "true" values of reference points that depend on them change accordingly. In particular, any trend in a stock's life-history traits will have demographic repercussions that could lead to a gradual change in their true values. Similarly, a trend in life-history traits can lead to a gradual change in our perception of a system's state relative to its reference points. We refer to both types of gradual change collectively as "shifting" reference points. Such shifts should be accounted for if reference points are to maintain their intended interpretation and utility for management.

Fisheries-induced evolution (FIE, Table 1) is a mechanism that can alter life-history traits and resultant stock properties directionally, causing reference points to shift. Starting from the seminal articles by Silliman (1975), Ricker (1981), Law and Grey (1989), and Rijnsdorp (1993), there is an increasing body of observational studies, experiments, and theoretical work supporting the hypothesis that fishing causes contemporary evolution in traits related to growth, maturation, and fecundity (for reviews, see Jørgensen *et al.*, 2007; Kuparinen and Merilä, 2007; Conover and Baumann, 2009; Dieckmann *et al.*, 2009; Dunlop *et al.*, 2009b; Sharpe and Hendry, 2009). FIE is therefore likely contributing to many of the ubiquitous phenotypic changes in fish life histories (e.g., Trippel, 1995; Hutchings and Baum, 2005; Hsieh *et al.*, 2010), even though phenotypic field studies alone can never conclusively prove that an observed phenotypic change has a genetic component or a particular cause (e.g., Dieckmann and Heino, 2007; Kuparinen and Merilä, 2007).

FIE is not the only source of concern regarding directional changes in reference points. Fishing also changes life histories through phenotypic plasticity, and these changes often occur in the same direction as the effects of evolution (e.g., Trippel, 1995). For example, a well-documented compensatory response to fishing is earlier maturation due to the faster body growth that may occur when population density is reduced by fishing (Trippel, 1995). The term fisheries-induced adaptive change (Table 1) covers such plastic changes together with evolutionary changes. Furthermore, factors that are exogenous to fishery systems (e.g., regime shifts, eutrophication or other changes in productivity, climate change) alter fish population dynamics, and consequently may cause shifts in reference points (e.g., Cook and Heath, 2005; Kell *et al.*, 2005; Köster *et al.*, 2009).

Management decisions based on reference points that do not account for directional changes in life histories may become either more or less precautious than originally intended. As a concrete example, ICES continues to use a maturity ogive from the early 1980s in their stock assessment of North Sea plaice (Enberg *et al.*, 2010), despite evidence for significant changes in life-history traits (van Walraven *et al.*, 2010, and references therein). Since not all reference points utilize the same biological information (Gabriel and Mace, 1999; Hall and Mainprize, 2004), the robustness of any particular reference point to FIE will depend on which data are used to establish it, which traits are affected by FIE, and how large the resultant changes are.

The objective of this article is to assess how currently used reference points are expected to shift as a result of FIE and to draw attention to possible management implications. We restrict the analysis to situations in which a fish population with an iteroparous life history is adapting to ongoing exploitation of both immature and mature fish. We compare how reference points based on the current life history differ from those estimated in the past, when no or less FIE had occurred. Specifically, we do not consider consequences of future FIE in this assessment (which is the remit of evolutionary impact assessments or EvoIAs; Jørgensen *et al.*, 2007; Laugen *et al.*, 2013). We first review the possible influences of FIE on life-history traits, stock dynamics, and productivity, and then examine how such changes are expected to affect various types of reference points.

## Fisheries-induced evolution and its consequences for the dynamics and productivity of fish stocks

The potential for sustainably exploiting a fish stock depends on stock renewal through recruitment and on how existing individuals grow and die. These processes are influenced by life-history traits such as those governing maturation, reproductive effort, and somatic growth. As the basis for understanding how reference points are influenced by FIE, this section provides an overview of how FIE might influence these life-history traits, and how these changes then influence fish population dynamics and the fishery (Fig. 1). We focus on the evolution of growth rates, maturation schedules, and reproductive efforts because FIE in these traits is theoretically best understood and empirically most widely documented, and also because such changes have direct consequences for stock dynamics and productivity (Law and Grey, 1989; Kaitala and Getz, 1995; Heino, 1998; Ernande *et al.*, 2004; de Roos *et al.*, 2006; Andersen and Brander, 2009; Dunlop *et al.*, 2009a; Enberg *et al.*, 2009, 2010; Jørgensen *et al.*, 2009; Okamoto *et al.*, 2009; Matsumura *et al.*, 2011; Vainikka and Hyvärinen, 2012).

## Individual-level consequences of FIE

In general terms, fishing, like any other factor reducing life expectancy, can be expected to lead to the evolution of "faster" life histories: under many fishing regimes, fish improve their lifetime reproductive success by reaping fitness gains early in life, even if this trades off with their survival and reproduction later on. Such an acceleration of life histories can result from changes in a number of traits (for a general discussion, see Jeschke and Kokko, 2009).

When fishing increases the mortality of both immature and mature fish, evolution towards earlier maturation is expected (Law, 2000). All else being equal, earlier maturation increases the abundance of potential spawners (Enberg *et al.*, 2010). An average spawner will be younger and smaller; the latter because of the younger age, but also because encountering the trade-off between growth and reproduction earlier in life leads to smaller body size at age (Enberg *et al.*, 2012). Average per capita fecundity will be reduced, because gonad size and fecundity show an isometric or positively allometric relationship with body weight (Roff, 1983). Moreover, the duration of spawning can decline with female body size or age, as shown for some batch spawners (Rijnsdorp, 1989; Kjesbu *et al.*, 1996). Furthermore, size-dependent maternal effects have been observed in several fish species, with smaller and younger females producing offspring that suffer from lower viability compared to offspring of larger and older females (Birkeland and Dayton, 2005; but see Marshall *et al.*, 2010). When present, such maternal effects may aggravate the negative impacts of FIE on per capita reproductive capacity.

Theory also suggests that FIE will increase reproductive effort among mature individuals, leading not only to elevated fecundity in relation to body size, but also to a reduced frequency of skipped spawning (Jørgensen *et al.*, 2006). Increased energy allocated to reproduction will lessen somatic growth and therefore negatively impact fecundity later in life (Roff, 1983). Furthermore, increased reproductive effort might reduce survival (Gunderson, 1997; Kuparinen and Hutchings, 2012). Current models (Andersen and Brander, 2009; Dunlop *et al.*, 2009a, c; Enberg *et al.*, 2009; Matsumura *et al.*, 2011) suggest that the FIE of reproductive effort might be relatively slow, and only of modest magnitude. In line with these expectations, empirical studies of exploited stocks have so far reported little or no change in reproductive effort (Yoneda and Wright, 2004; Rijnsdorp *et al.*, 2005; Baulier, 2009; Nusslé *et al.*, 2009; Thomas *et al.*, 2009; van Walraven *et al.*, 2010; Wright *et al.*, 2011). It thus appears that earlier maturation, rather than elevated reproductive effort, more readily absorbs the selection for a faster life history.

For adult fish, the aforementioned changes in maturation and reproductive effort cause somatic growth to decrease. Positively size-selective fishing mortality may further favour evolution towards smaller adult size. For juvenile fish, the situation is more complex (Enberg *et al.*, 2012): current models show that evolution towards either faster or slower growth is possible (Andersen and Brander, 2009; Dunlop *et al.*, 2009c; Enberg *et al.*, 2009; Wang and Höök, 2009; Matsumura *et al.*, 2011). This is because, under conditions of positively size-selective fishing, reduced somatic growth lessens an individual's cumulative exposure to fishing mortality, but this fitness benefit comes at a cost: cumulative energy intake is reduced, time to reach maturation size is prolonged, and individuals maturating at smaller sizes will have reduced fecundity, implying three types of fitness cost of reduced somatic growth (Bodin *et al.* 2012; Enberg *et al.*, 2012). Furthermore, smaller size usually leads to higher predation mortality, amounting to a fourth type of fitness cost. The balance among all resultant selection pressures needs to be addressed on a case-by-case basis; an expectation of slower growth based on the widely recognized laboratory experiment by Conover and Munch (2002) is not readily generalized (Enberg *et al.*, 2012).

The aforementioned life-history adaptations caused by fishing may result in increased natural mortality (Jørgensen and Fiksen, 2010). This is a compound effect of several potential mechanisms. First, as already mentioned, decreased growth can result in increased mortality from predation because the latter usually declines with body size (Heino and Godø, 2002; Jørgensen and Fiksen, 2010). Second, increased fishing mortality, by devaluing future, favours more risky behaviours (e.g., foraging and mating behaviours), in turn implying higher natural mortality. Third, increased investment in reproduction may elevate the mortality costs of reproduction (Jørgensen and Fiksen, 2010). While there is empirical evidence for increased natural mortality in some fish stocks, in accordance with these predications, the observed effects could alternatively be explained by non-evolutionary changes (Jørgensen and Holt, 2013).

## Population-level consequences of FIE

Any evolutionary changes in individual traits that affect recruitment or mortality will have population-level consequences. Combining insights from life-history theory and models of FIE, we are now beginning to understand the generalities that apply to population-level consequences of FIE. Synthesizing current knowledge, we derive two main predictions. First, we can often expect that a population that adapts to fishing can maintain higher population biomass under fishing than a population not adapted to fishing would under the same conditions; conversely, if fishing is stopped after a population has been adapting to fishing, it will usually recover to a lower equilibrium biomass (i.e., carrying capacity) than observed before fishing started. Second, when fishing drives evolution towards faster life histories, the consequence is that, at least initially, maximum population growth rate will often increase. The reasoning behind these predictions is given below. The predictions are not fully general, but we argue that they are general enough to guide us further in understanding how FIE may change reference points.

To understand the reasoning behind the predicted population-level consequences of FIE, we need to review life-history theory that is somewhat technical and little known outside of theoretical biology. Below we first introduce the general theory underlying the predictions, discuss the specific predictions and the conditions under which they apply, and finally, review the supporting evidence.

A population's equilibrium biomass in the absence of fishing is a measure of its carrying capacity $K$. This metric is jointly determined by the environment in which a population lives and by its current life history. Consequences of FIE on population biomass can be assessed based on so-called pessimization principles derived from life-history theory (Mylius and Diekmann, 1995; Metz *et al.*, 2008). These principles generalize the earlier, less general predictions that evolution maximizes a population's equilibrium size (Roughgarden, 1976), or more specifically, the equilibrium size of the population's age group that is critical for its density regulation (Charlesworth, 1994). In general, pessimization principles state that the life-history trait that allows a population to persist under the worst environmental condition cannot be invaded by any other such trait (Mylius and Diekmann, 1995; Metz *et al.*, 2008). This implies that the biomass is maximized of the life stage that is critical for the population's density regulation. It must be noted, however, that this general prediction only holds for populations regulated by a single source of density dependence (in which the strength of density regulation depends on just a single quantitative feature of the population or its environment).

The pessimization principle has interesting implications. For example, for a population in which density regulation occurs only at the newborn stage, theory predicts that evolution maximizes newborn abundance, and thus, spawning-stock biomass (as the former usually requires the latter), provided that the stock-recruitment relationship is not overcompensatory. Thus, the life history that is best adapted to the current conditions is also the one that has the highest spawning-stock biomass under these conditions. This implies that a population that is adapted to fishing is able to maintain a higher equilibrium spawning-stock biomass in the presence of fishing than a hypothetical population that is exposed to the same fishing pressure without being adapted to it. Likewise, a population adapted to fishing will have a lower equilibrium spawning-stock biomass in the absence of fishing, and thus a reduced carrying capacity $K$, than its hypothetical counterpart best adapted to the fishing-free environment.

A more heuristic argument as to why FIE reduces $K$ can be made by noting that in general, better adaptation to one particular set of conditions trades off against adaptedness under other conditions. Thus, good performance under fishing occurs at the expense of good performance in the absence of fishing (Conover, 2000; Heino and Dieckmann, 2008; Jørgensen *et al.*, 2008). When equilibrium population biomass is a relevant metric of performance (which it is under a suitable pessimization principle), the equilibrium population biomass a population would reach in the absence of fishing (that is, $K$) is expected to decline under FIE. This effect is readily seen in evolutionary fish population models (Enberg *et al.*, 2009; Kuparinen and Hutchings, 2012).

In populations in which density regulation comes from multiple sources—for example, through density-dependent survival among newborns and from density-dependent somatic growth during later life stages—the pessimization principle no longer holds.

Nevertheless, when there is a single dominant source of density regulation, the corresponding pessimization principle can still serve as an approximation, although it is difficult to assess how accurate such an approximation will be. For example, in a model including density regulation in recruitment (pre-recruit survival declines as population egg production increases) and in somatic growth (growth declines as total population biomass increases), Enberg *et al.* (2009) showed that FIE causes total population biomass to increase relative to the hypothetical non-adapted population. When fishing ceases, the adapted population recovers to a lower *total population biomass* than the non-adapted population. Thus, the model shows behaviour that is in agreement with the expectations based on the pessimization principle for populations in which density regulation depends solely on total population biomass. In other words, from an evolutionary perspective, growth regulation dominates recruitment regulation in the analysed model. In line with this conclusion, the model also shows that a population adapted to fishing recovers to a higher *spawning-stock biomass* than the non-adapted population, which, as expected, contradicts what would apply to a purely recruitment-regulated population.

The result that populations adapted to fishing can maintain higher population biomass under fishing than those with the original, non-adapted life history has now been reported in several models (Enberg *et al.*, 2009, 2010), the most extreme case being that the non-adapted population goes extinct (Kaitala and Getz, 1995; Heino, 1998). That a population adapted to fishing recovers to a lower equilibrium total biomass under a fishing moratorium has been found in models by Enberg *et al.* (2009) and Kuparinen and Hutchings (2012). Recovery to a lower equilibrium spawning-stock biomass under a fishing moratorium could also occur, in the special case that previous fishing has led to an evolutionary regime shift (de Roos *et al.*, 2006).

Consequences of FIE on maximum population growth rate ($r_{\max}$) can be predicted by combining insights from life-history theory with fundamentals of population demography. The rate $r_{\max}$ is defined by the Euler-Lotka equation and measures a population's instantaneous growth rate at low density (i.e., in the absence of negative effects of density dependence) and in the absence of fishing. Another metric, the basic reproduction ratio ($R_0$, also called the expected lifetime reproductive success), measures relative population growth on a generational time scale; like for $r_{\max}$, we assume that $R_0$ is evaluated at low density and in the absence of fishing. Despite their ignoring of population regulation, these measures are useful in determining evolutionary outcomes in density-regulated populations, but, as already discussed above, only in those that are regulated by a single source of density dependence (Mylius and Diekmann, 1995; Metz *et al.*, 2008). Specifically, when density dependence reduces the expected lifetime production of offspring in a multiplicative manner—like in fish populations that are recruitment-regulated—the life history maximizing $R_0$ corresponds to an evolutionary optimum in that environment. In this case, a fish population adapted to its natural environment possesses the maximum possible $R_0$, so any change in its life history lowers $R_0$. A change caused by FIE is no exception to this rule, and thereby will necessarily decrease $R_0$ in the environment without fishing (Fig. 2). When such a life-history change occurs in the direction of faster life histories (e.g., through earlier maturation), $r_{\max}$ will simultaneously increase, at least as an initial response. This somewhat counterintuitive result is obtained because in viable populations (with $r_{\max} > 0$), $r_{\max}$ is maximized for a life history that is "faster" than the one maximizing $R_0$, barring some artificial examples (J. A. J. Metz, pers. comm.). A heuristic explanation is that in viable populations an offspring produced late in life counts less towards determining $r_{\max}$ than one produced early in life, whereas offspring produced early and late in life are equally valuable for determining $R_0$. Therefore, it is possible to increase $r_{max}$ while decreasing $R_0$.

The prediction of increased $r_{max}$ is supported by models showing that populations adapted to fishing can tolerate higher fishing pressures than non-adapted populations (Kaitala and Getz, 1995; Heino, 1998; Enberg *et al.*, 2009), and that the slope at the origin in their stock-recruitment relationships increases (Enberg *et al.*, 2010). The limitations to the generality of this prediction is that it may not apply to populations that are not recruitment-regulated, and that it may not apply after the early phases of FIE. Nevertheless we know of no example showing a significant deviation from this prediction. A slight decrease in population growth rate was observed by Kuparinen and Hutchings (2012) in a model population that was regulated through both somatic growth and recruitment, and for which the prediction based on recruitment-regulated populations does not apply. A larger effect was reported by Hutchings (2005), who showed that in a model of cod a reduction in the age at maturation from 6 to 4 years could result in a reduced $r_{max}$ (or more precisely, in a reduction of the proxy for $r_{max}$ considered in that study). However, reduced age at maturation was an assumption, not an outcome of evolution. Consequently, what Hutchings (2005) showed was that a reduced age at maturation can reduce $r_{max}$, but not that FIE reduces $r_{max}$. Thus, we consider the prediction that FIE increases maximum population growth rate as a good working hypothesis, in the absence of evidence to the contrary.

## Fishery-level consequences of FIE

FIE can have important implications for fisheries. The most dramatic consequence is that FIE might allow a population to avoid extinction caused by excessive fishing (Kaitala and Getz, 1995; Heino, 1998; Ernande *et al.*, 2004; Enberg *et al.*, 2009). Other effects, however, are often negative from a human perspective. Spawning stock consisting of young and small individuals may reduce a population's resilience to low-frequency environmental perturbations (Longhurst, 2002; Jørgensen *et al.*, 2008). FIE will usually lead to smaller average adult size (Heino, 1998; Matsumura *et al.*, 2011), while consumers, recreational anglers, and the fishing industry tend to prefer large fish and are willing to pay a price premium for such fish (Hilborn and Walters, 1992; Oh *et al.*, 2005; Zimmermann *et al.*, 2011). Models also suggest that FIE leads to reduced sustainable yield (Law and Grey, 1989; Heino, 1998; Andersen and Brander, 2009; Matsumura *et al.*, 2011; Vainikka and Hyvärinen, 2012), and experimental work supports these results (Edley and Law, 1988; Conover and Munch, 2002). Moreover, FIE may also result in reduced overall catchability when the vulnerability to capture is a heritable trait (Philipp *et al.*, 2009).

Finally, FIE will influence fishery advice, even when it is not explicitly accounted for. Management advice is based on estimating the past and predicting the future. The advice is therefore influenced by changing stock parameters, with FIE being one of the drivers of such change. An important avenue through which FIE will influence advice is that reference points for fisheries management are likely to change, as we shall show below.

## Consequences of fisheries-induced evolution for reference points

In this section we review how FIE might influence reference points that are often used in fisheries management. We start with reference points based on stock-recruitment relationships and yield-per-recruit analyses that focus on certain parts of the life cycle. In contrast, production models cover the whole life cycle but in much less detail. Finally, we briefly discuss reference points based on virgin biomass.

## Reference points based on stock-recruitment relationships

Stock-recruitment relationships describe the average relationship between the size of a stock's spawning component and its offspring production (e.g., Quinn and Deriso, 1999). The spawning component is typically characterized by its spawning-stock biomass (*SSB*). Offspring production is often measured as the mean number of recruits (*R*), defined as members of the first age class for which effective abundance estimation becomes possible (because such individuals appear either in catches or in surveys). Typically, stock-recruitment relationships are not meant to account for variations in *R* through other important factors, including environmental conditions and spawning-stock composition (for exceptions, see e.g. Marshall *et al.*, 2000; Mantzouni *et al.*, 2010). Stock-recruitment relationships thus mainly capture two biological processes: spawning limitation (when few fish spawn, *R* increases with *SSB*) and survival limitation (when many fish spawn, pre-recruit survival is diminished through density regulation).

The most commonly used stock-recruitment models are the Ricker model and the Beverton-Holt model (Quinn and Deriso, 1999). These specify, respectively, humped (over-compensatory) and monotonically increasing (compensatory) dependences of *R* on *SSB*. However, for many fish stocks, stochasticity in *R* overwhelms the average effect of *SSB* on *R* across a large range of *SSB*. Stock-recruitment relationships can then be approximated in a piecewise fashion by two linear parts: (i) *R* is proportional to *SSB* when *SSB* is low, and (ii) *R* is constant, and thus independent of *SSB*, when *SSB* is high (Fig. 3). When fisheries management aims to avoid recruitment overfishing, *SSB* must be prevented from falling below the range across which *R* is thought to be constant. The lower boundary $B_{\mathrm{lim}}$ of that range thus assumes the role of a limit reference point, operationally defined through the simplistic "hockey-stick" stock-recruitment relationship just described (ICES, 2007a). By analyzing how FIE may affect stock-recruitment relationships and estimations of *SSB*, we can assess its impacts on $B_{\text{lim}}$, as well as on the reference points whose values depend on $B_{\text{lim}}$ by definition: the precautionary reference point $B_{\text{pa}}$, and the corresponding fishing-mortality reference points $F_{\text{lim}}$ and $F_{\text{pa}}$ (Table 1).

Stock-recruitment relationships of the simple form described above are determined by two variables: at low *SSB*, by the mean number of recruits per spawning-stock biomass (the slope of the relationship when *R* is proportional to *SSB*), and at high *SSB*, by the mean number of recruits (the ceiling attained when *R* is constant). FIE can affect both values. When recruitment at a given *SSB* is higher ($R_+$) or lower ($R_-$) than before, the relationship's slope is, respectively, increased or decreased (Fig. 3a). This may occur when FIE changes a species' reproductive investment (either in egg number or size), or the survival of its pre-recruits. Figure 3a shows that $R_+$ lowers $B_{\text{lim}}$, whereas $R_-$ shifts $B_{\text{lim}}$ to a higher value. Shifts of this kind are particularly likely when FIE causes earlier maturation, because skewing spawning-stock composition towards younger and smaller fish can lower pre-recruit survival (e.g., Kjesbu *et al.*, 1991; Trippel *et al.*, 1997; Marteinsdóttir and Steinarsson, 1998; Brunel, 2010). Such evolutionary changes thus raise $B_{\text{lim}}$. If undetected, implications of a raised $B_{\text{lim}}$ for the sustainable exploitation of a stock are potentially serious: fishing at levels based on the lower $B_{\text{lim}}$ (uncorrected for FIE) could diminish *SSB* below the actual threshold $B_{\text{lim}}$, and thus impair the stock's reproductive potential.

Shifts in the ceiling of a stock-recruitment relationship can also be caused by FIE ($R_+$ and $R_-$ in Fig. 3b). Reflecting the density-dependent survival of pre-recruits, such a ceiling describes a stock's carrying capacity for pre-recruits expressed in the resultant number *R* of recruits. For example, if FIE caused slower pre-recruit growth, without prolonging the pre-recruit stage, each pre-recruit would require fewer resources, and the ceiling might increase accordingly ($R_+$). By contrast, if FIE causes lower pre-recruit survival after the early density-dependent phase, the ceiling might decrease ($R_–$). The ecological mechanisms underlying changes in the ceiling's position could be manifold and naturally become more involved when pre-recruits undergo ontogenetic niche shifts; generalized predictions are therefore difficult to make. However, any changes in the ceiling that do occur will alter $B_{\text{lim}}$. Figure 3b shows that $R_+$ raises $B_{\text{lim}}$, whereas $R_–$ reduces $B_{\text{lim}}$. This suggests that FIE towards slower pre-recruit growth could be most problematic, since it may lead to the underestimation of $B_{\text{lim}}$, and thus to the stock's exploitation beyond safe biological limits.

FIE not only alters stock-recruitment relationships, but may also bias estimations of *SSB* (Enberg *et al.*, 2010; Rijnsdorp *et al.*, 2010). In practice, *SSB* is often estimated in two steps. First, a stock's observed abundance-at-age structure is multiplied by the stock's maturity ogive to determine the population size of its spawning component. Second, the result is translated into *SSB* by multiplication with the stock's weight-at-age key and summing this product over all mature ages. Because FIE can affect the maturity ogive as well as the weight-at-age key, and because the former may not be updated in every assessment cycle, FIE will interfere with such estimations of *SSB*. Naturally, the resultant bias depends on the degree to which the maturity ogive used, and potentially the weight-at-age key used, are determined by old data. For example, when FIE has shifted maturation to younger ages, using an old ogive will underestimate *SSB* ($SSB_–$ in Fig. 3c). The same may happen if skipped spawning negatively biases maturity-at-age andf FIE has reduced the frequency of skipped spawning and thereby the bias (Jørgensen *et al.*, 2006). Conversely, when FIE has diminished the weight-at-age of mature fish, using an old weight-at-age key would result in an overestimation of $SSB$ ($SSB_+$ in Fig. 3c). In terms of comparing $SSB$ with $B_{\mathrm{lim}}$, a systematic under- or overestimation of $SSB$ bears the same risks for sustainable exploitation as if $B_{\mathrm{lim}}$ were, respectively, increased or decreased. In particular, when $SSB$ is overestimated, recruitment overfishing becomes more likely.

Finally, FIE can affect stock-recruitment relationships beyond the simplified piecewise linear shapes assumed so far. In particular, FIE could lead to, or aggravate, the effects of depensation, that is, declining per capita reproductive success at low abundances. For example, once fishing has removed large fish and FIE has caused maturation at younger ages and smaller sizes, Allee effects (Myers *et al.*, 1995; Frank and Brickman, 2000) in the remaining spawning population of small fish may result in impaired reproduction. Given that stock-recruitment data tend to be scarce and highly variable at low $SSB$, reliable detection of depensation tends to be difficult (Shelton and Healey, 1999). This means that FIE not only changes limit reference points for recruitment overfishing, but can also elevate the risk of collapse once such limits are violated.

## Reference points based on yield-per-recruit analyses

Yield-per-recruit analysis is a tool to study how the yield $Y$ from a cohort, divided by the number of recruits $R$, depends on the fishing mortality rate $F$ (age-unspecific, describing overall fishing intensity) and on the age-specific vulnerability to fishing, captured by the so-called selection pattern. Usually, the goal is to find a combination of fishing mortality rate and selection pattern that confers a high yield. Such analyses assume growth rates and natural mortalities to be constant and independent of changes in recruitment (Fig. 4a). The challenge is to find an exploitation regime that avoids harvesting fish too early, when they have not yet realised much of their growth potential (growth overfishing; Table 1), but also not too late, when too much of potential harvest is lost to natural mortality (Fig. 4b). A standard result derived from simple models (Beverton and Holt, 1957; Quinn and Deriso, 1999) is that the maximum yield from a single cohort is obtained by harvesting all fish at the age $a_{\mathrm{opt}}$ (Fig. 4b) at which a cohort's biomass reaches its maximum.

The selection pattern of an exploitation regime is assumed to be fixed and often has a logistic shape (Fig. 4c) that can be summarized by the age $a_{50}$ at which half of the maximal selectivity is reached. If the selection pattern is such that harvesting starts late relative to a cohort's peak biomass ($a_{50} > a_{\mathrm{opt}}$), $Y/R$ increases monotonically with $F$. In the more typical alternative case (which we will focus on here) in which harvesting starts early relative to a cohort's peak biomass ($a_{50} < a_{\mathrm{opt}}$), the relationship between $Y/R$ and $F$ is humped, and a finite fishing mortality rate, known as $F_{\mathrm{max}}$, maximizes the yield from a cohort (Fig. 5). Situations with $F > F_{\mathrm{max}}$ will then lead to growth overfishing.

Yield-per-recruit relationships are the basis for defining two commonly used reference points (e.g., Caddy and Mahon, 1995). The goal of maximizing yield and avoiding growth overfishing suggests $F_{\mathrm{max}}$ as a biological reference point. However, because $F_{\mathrm{max}}$ can be very sensitive to changes in growth, natural mortality, and selection pattern, its use as a target reference point is discouraged (Quinn and Deriso, 1999). Moreover, fishing at the rate $F_{\mathrm{max}}$, even when accurately estimated and implemented, could still result in recruitment overfishing (Hilborn and Walters, 1992; Table 1). Therefore, $F_{\mathrm{max}}$ has largely been replaced by the more conservative reference point $F_{0.1}$, which is defined as the fishing mortality rate for which the slope of the yield-per-recruit curve is 10% (rather than 0%) of its value at the origin (Table 1, Fig. 5).

As discussed above, FIE typically favours “fast” life histories characterized by an earlier onset of maturation and an increased reproductive effort. Both effects occur at the expense of somatic growth after maturation, and may also entail riskier behaviours (Jørgensen and Fiksen, 2010) and reduced investments into maintenance, leading to diminished survival. All else being equal, these life-history changes therefore imply a lower expected size after maturation and lower survival. Under these conditions, we can predict how FIE changes the dynamics of a cohort: owing to the “fast” life histories, the cohort’s biomass will reach its peak earlier than in the absence of FIE (Fig. 4b). And for a selection pattern that has fixed size selectivity, age-specific selectivity is reduced (Fig. 4c). These changes translate into changes in yield-per-recruit curves (Fig. 5). As more of a cohort’s biomass production is realized earlier in that cohort’s lifespan, it would be optimal to increase fishing mortality on those early ages. However, when the selection pattern is fixed, this can only be achieved through elevating the overall fishing intensity $F$, which means that $F_{\max}$ shifts to higher fishing mortalities (Fig. 5). Because $F_{0.1}$ is correlated with $F_{\max}$, we can usually expect that $F_{0.1}$ follows this shift and thereby increases too.

These changes can be amplified when selection is primarily size-specific and only secondarily age-specific, which is almost always the case. When FIE reduces size-at-age, a fixed size-specific selection pattern means that selectivity-at-age is effectively lowered, so the resultant age-specific selection pattern shifts to older ages (Fig. 4c), which in turn shifts $F_{\max}$ and $F_{0.1}$ to even higher values.

In summary, we thus expect FIE to shift the “true” reference points $F_{\max}$ and $F_{0.1}$ to higher values. This implies that managers failing to account for FIE would allow to less intensive harvesting than those who do.

## Reference points based on production models

The Johannesburg Declaration's goal (United Nations, 2002) to "maintain or restore stocks to levels that can produce the maximum sustainable yield" has considerably raised the profile of the time-honored concept of maximum sustainable yield (MSY), and consequently, of the corresponding reference points for stock biomass, $B_{\mathrm{MSY}}$, and for fishing mortality, $F_{\mathrm{MSY}}$, despite criticisms and uncertainties associated with the MSY concept (Larkin, 1977; Hilborn and Walters, 1992; Caddy and Mahon, 1995; Mace, 2001; ICES, 2007a). Estimating $B_{\mathrm{MSY}}$ and $F_{\mathrm{MSY}}$ requires models that cover a population's full life cycle, i.e., from spawning stock to recruitment and from recruitment back to spawning stock. The simplest full-life-cycle models are surplus-production models (Schaefer, 1954; Pella and Tomlinson, 1969). These are also known as biomass-dynamic models (Hilborn and Walters, 1992) and can be used to estimate *MSY*, $B_{\mathrm{MSY}}$, and $F_{\mathrm{MSY}}$. Despite their relative simplicity (e.g., lack of age structure), production models are still in use for the assessment of several fish stocks, in particular when age-specific data are unavailable. Production models therefore provide a useful starting point for understanding the possible effects of FIE on $B_{\mathrm{MSY}}$ and $F_{\mathrm{MSY}}$.

The simplest production model, known as the Schaefer (1954) model, is based on the logistic population model and predicts the well-known parabolic dependence of equilibrium yield on fishing effort. Our argument in what follows below is readily extended to the more general Pella-Tomlinson (1969) model, but we nevertheless use the Schaefer model for the sake of greater clarity. The aforementioned parabolic relationship arises from the assumption of two underlying linear relationships (Fig. 6): when fishing mortality increases from zero to $F_{\mathrm{crash}}$, the (lowest) fishing mortality that brings the stock to a collapse, total population abundance linearly decreases from its carrying capacity $K$

to zero (Fig. 6a), whereas an individual's biomass growth rate linearly increases from zero to its maximum (Fig. 6b). Surplus production, corresponding to equilibrium yield, is defined in terms of population-level growth rate, and is therefore obtained as the product of the biomass growth rate of each individual with total population abundance. Because in this model $F_{\mathrm{crash}}$ is equal to the maximum growth rate $r_{\mathrm{max}}$, the assumed linear dependences, and thus the effort-yield relationship, are determined by just two parameters: the carrying capacity $K$ and the maximum growth rate $r_{\mathrm{max}}$.

The principles of life-history theory we have reviewed above provide relevant indications as to how $K$ and $r_{\mathrm{max}}$ are expected to be influenced by FIE. As explained, fish populations adapted to fishing can tolerate higher fishing pressures (Kaitala and Getz, 1995; Heino 1998; Enberg *et al.*, 2009), because evolution towards faster life histories increases $r_{\mathrm{max}}$; consequently $F_{\mathrm{crash}}$ increases too. As explained, predictions regarding $K$ are more ambiguous, but when density regulation has a single source such that a pessimization principle applies, we can expect $K$ to decline.

In the Schaefer model, the parabolic effort-yield relationship implies $F_{\mathrm{MSY}} = F_{\mathrm{crash}}/2$, so $F_{\mathrm{MSY}}$ is expected to increase through FIE (Fig. 6c). Analogously, $B_{\mathrm{MSY}} = K/2$, so $B_{\mathrm{MSY}}$ is expected to decrease through FIE. Both predictions are supported by an age-structured model (Heino, 1998) that is considerably more realistic than the simple Schaefer model. The effect of FIE on MSY is qualitatively ambiguous, because $MSY = r_{\mathrm{max}}K/4$, so that the net change resulting from the increase of $r_{\mathrm{max}}$ and the decrease of $K$ depends on which of these two quantities is changing more as the result of FIE. Models that are more realistic than the simple Schaefer model suggest that FIE usually reduces MSY (Law and Grey, 1989; Heino, 1998; Andersen and Brander, 2009; Matsumura *et al.*, 2011; Vainikka and Hyvärinen, 2012).

A problem associated with production models is their aggregate nature, which does not distinguish between the various processes affecting a stock's dynamics. However, even in more complex models, yield can still be determined as the product of per capita growth rate with population abundance. The dependence of these two factors on fishing mortality will remain qualitatively similar, with the former being an increasing function of fishing mortality, and the latter a decreasing function (as long as Allee effects do not come into play). For this reason, we can expect that the predictions provided by the simple Schaefer model provide a valuable indication of how more complex models will behave.

## Reference points based on virgin biomass

Biomass reference points are sometimes defined in terms of a stock's virgin biomass $B_0$ (Beddington and Cooke, 1983; Caddy and Mahon, 1995; Hilborn, 2002; ICCAT, 2009), where $B_0$ describes a stock's pristine, unfished equilibrium biomass and thus equals its carrying capacity $K$. The objective is usually to secure a spawning-stock biomass that is sufficiently large to ensure that recruitment is not impaired, without specific knowledge about the stock-recruitment relationship. The reference point $pB_0$ is therefore expressed as a fraction of the virgin biomass, with $p$ usually set to 20% or 30%.

A stock's virgin biomass is often inferred from the earliest available observations and corresponding stock assessments. Thus, $pB_0$ is expressed in terms of a static quantity $B_0$ that describes past conditions, when fishing pressure was low and the stock's biomass might therefore have been closer to its $K$. As a result, $B_0$ reflects the properties the stock had then and, by definition, is unaffected by FIE.

Yet, accounting for FIE might change our perception of what a stock's virgin biomass was, or currently is. First, as explained above, ongoing FIE will gradually erode the hypothetical $K$ characterizing the current stock. Using the reference point $pB_0$ to prevent recruitment overfishing can then lead to harvest policies that are more conservative than intended. A second effect is more worrisome. If the stock had already been exposed to significant fishing pressure by the time observations underlying $B_0$ were taken, and had already been adapting to fishing, the reference point $pB_0$ will be affected by past, undocumented FIE. Because FIE is typically expected to reduce a stock's $K$, this is likely to result in an underestimate of the "true" $B_0$, defined for a hypothetical stock not yet adapted to fishing.

## Discussion

Reference points for fisheries management are not static quantities, but instead may shift when the environment in which a population is living is altering, or when the population itself is changing (Murawski *et al.*, 2001; ICES, 2007c). Here we have argued that fisheries-induced evolution (FIE) is one mechanism that can drive trends in population characteristics, leading to the shifting of reference points either by changing their "true" values or by confounding their estimation. If unaccounted for, such shifting means that reference points can become systematically biased, gradually losing their intended meaning, and hence, their utility as reliable tools for fisheries management (Enberg *et al.*, 2010).

Our qualitative analysis suggests that the biomass reference point $B_{\text{lim}}$ derived from stock-recruitment relationships, together with its precautionary counterpart $B_{\text{pa}}$, will shift under FIE. These shifts will influence the associated fishing-mortality reference points, $F_{\text{lim}}$ and $F_{\text{pa}}$, denoting the fishing mortalities that would drive a stock to the respective biomass reference point. These reference points currently form an important part of many fisheries-management frameworks, including the advice provided by ICES for northeast

Atlantic fish stocks (ICES, 2007a, 2012). When populations evolve to mature earlier, the resultant younger spawning stock might, at least initially, produce less viable pre-recruits, which will increase the “true” $B_{\mathrm{lim}}$. If undetected, this shift can have detrimental consequences. At the same time, maturation evolution can cause a population’s “true” spawning-stock biomass to be underestimated, which could counteract the aforementioned negative effect of FIE. Similarly, gradual erosion of a population’s carrying capacity undermines the meaning of the static limit reference point $pB_0$, expressed relative to the stock’s estimated virgin biomass $B_0$. Also reference points based on yield-per-recruit analyses—including $F_{0.1}$, a widely used fishing-mortality reference point also serving as a proxy for $F_{\mathrm{MSY}}$ (ICES, 2007a)—are predicted to increase through FIE. The same applies to $F_{\mathrm{MSY}}$ itself, at least when derived from the Schaefer model. The corresponding biomass reference point $B_{\mathrm{MSY}}$ is predicted to decrease. Curiously, these changes imply that management ignoring the shifting of these reference points would act more cautiously than when accounting for FIE. However, this might not apply in the longer term, as MSY itself is likely to erode under FIE (Law and Grey, 1989; Kaitala and Getz, 1995; Heino, 1998). In the long run, accounting for FIE is thus likely to pay off.

FIE is one of several mechanisms that can lead to shifting reference points. More generally, all fisheries-induced adaptive changes (Table 1), whether plastic or genetic, can shift reference points. Factors extraneous to fishery systems can have similar effects. For example, if a stock’s productivity changes because of a regime shift, eutrophication, or other environmental fluctuations, precautionary reference points need to be adjusted (King and McFarlane, 2006; ICES, 2007c; Kell and Fromentin, 2007; Köster *et al.*, 2009). Climate change is another potential driver of changes in the “true” values of reference points (Cook and Heath, 2005; Kell *et al.*, 2005; Perry *et al.*, 2010). In some respects, the way climate change affects reference points is akin to the influence of FIE: both kinds of change typically accrue slowly and become prominent only at decadal timescales. Thus, while the effects of climate change and FIE may appear insignificant in the short term, their cumulative effects can be significant, warranting timely attention by fisheries managers.

Our analyses here are based on qualitative insights arising from general life-history theory and from models specifically addressing FIE. To date, only one quantitative study has focused on the influence of FIE on reference points (Enberg *et al.*, 2010). We therefore highlight that our qualitative analyses may be subject to important limitations. In particular, the considerations presented here do not address how rapidly, or how much, FIE is expected to shift reference points. Such information can only be obtained by studying quantitative models that are sufficiently detailed biologically and calibrated to specific systems. For example, eco-genetic models (Dunlop *et al.*, 2009c) have been specifically designed for addressing such tasks. Several stock-specific eco-genetic models have recently been developed (Dunlop *et al.*, 2007; Thériault *et al.*, 2008; Okamoto *et al.*, 2009; Pardoe, 2009; Eikeset, 2010; Mollet, 2010), enhancing the scientific basis for making reliable quantitative predictions. A second limitation concerns the generality of our qualitative analyses. Our investigations of FIE effects on reference points have deliberately focused on "typical" fishery systems, featuring iteroparous fish populations with several age classes and harvesting regimes that do not discriminate between immature and mature fish. The selection pressures underlying FIE, and therefore the implications of FIE for reference points, are different for those few stocks in which harvesting primarily targets mature fish (Law and Grey, 1989; Heino, 1998; Ernande *et al.*, 2004; Andersen and Brander, 2009; Dunlop *et al.*, 2009a), as well as for semelparous species (Heino and Godø, 2002) and sequential hermaphrodites (Sattar *et al.*, 2008). Populations undergoing important ontogenetic niche shifts or migrations may also show responses deviating from our general predictions. Furthermore, we emphasize that, in a changing environment, it cannot be taken for granted that FIE makes fish populations more robust to exploitation, as models so far have suggested (Kaitala and Getz, 1995; Heino, 1998; Ernande *et al.*, 2004; Enberg *et al.*, 2009). Instead, general theoretical arguments lead us to expect that FIE might reduce a population's resilience to low-frequency environmental perturbations (Longhurst, 2002; Jørgensen *et al.*, 2008; Hsieh *et al.*, 2010). Ultimately, no natural system is ever truly typical, and care must always to be taken to assess whether its special characteristics may invalidate the general qualitative predictions presented here.

While existing reference points are subject to changes caused by FIE, new reference points can (and should) be devised to monitor and manage FIE. For example, Olsen *et al.* (2005) suggested the use of a reference point based on monitoring trends in a stock's maturation schedule (as quantified through its probabilistic maturation reaction norm). Another, simpler, option is to define limit reference points relative to estimated or assumed pre-fishing trait values, considering as undesirable those changes that exceed a certain percentage. Moreover, Hutchings (2009) suggested a reference point $F_{\mathrm{evol}}$, defined as the highest fishing mortality for which evolution in the considered traits is avoided. However, this fishing mortality will usually be very low or equal to zero (Matsumura *et al.*, 2011), unless a stock has already significantly adapted to fishing.

While FIE has been suggested to have occurred in many fish stocks, unequivocal evidence for its occurrence in the wild is still lacking. Nevertheless, in qualitative terms, it is difficult to argue against the position that some FIE is likely occurring. However, there is considerable uncertainty, and no scientific consensus, regarding rates of FIE (is FIE slow or fast?) as well as the relative contributions of evolutionary and plastic processes in documented long-term changes in life histories (are they mostly genetic or mostly plastic?). This uncertainty has led to differing conclusions regarding the importance of considering FIE in fisheries management (e.g., Jørgensen *et al.*, 2007; Andersen and Brander, 2009). We have highlighted a new angle in this discussion by showing how reference points for fisheries management can be impacted by FIE.

Whether reference points shift because of FIE, climate change, or other drivers, our work emphasizes that their intended meaning can only be relied upon if the biological information underlying their estimation is scrupulously kept up to date. In this context, we must also bear in mind that estimates of reference points and of the metrics they are based on can be highly uncertain, which implies that distinguishing between trends and noise often is challenging. This applies in particular to reference points based on stock-recruitment relationships, which by their very nature require the integration of information over many years. In practice, stochasticity and lack of contrast in the data may result in insufficient statistical power to discern changes caused by FIE. Nonetheless, the potential for significant recruitment decline if changes are undetected calls for an acknowledgement of, and heightened attention to, the additional model uncertainty caused by FIE, i.e., uncertainty in structural assumptions and parameter values in models of stock dynamics (Francis and Shotton, 1997). Similarly, natural mortality estimates, which are notoriously difficult to obtain, are needed when calculating reference points based on yield-per-recruit analyses, or when age-structured models are used to estimate reference points related to spawning-stock biomass and MSY. On the positive side, maturity ogives and weight-at-age keys, which are crucial for estimating spawning-stock biomass and for process-based assessments of MSY and yield-per-recruit, are more readily estimated. Such estimates can therefore be updated annually, which can help reduce undetected shifts in the corresponding reference points. Furthermore, the general qualitative insights laid out in this paper, particularly when accompanied by quantitative predictions derived from stock-specific models, should help guard against unpleasant surprises caused by shifting reference points.

## Acknowledgements

We thank Hans Metz for his insightful comments on fitness measures. Preparation of this article was supported by the Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks; contract number MRTN-CT-2004-005578) and by the Specific Targeted Research Programme FinE (Fisheries-induced Evolution; contract number SSP-2006-044276), funded through the European Community's Sixth Framework Programme (LB, DSB, DJD, UD, ESD, BE, ATL, FM, MH, HP, ADR, DU, AV, RW). The article does not necessarily reflect the views of the European Commission and does not anticipate the Commission's future policy in this area. The authors gratefully acknowledge additional financial support by the Research Council of Norway (MH, ESD, CJ), the Bergen Research Foundation (MH, KE, CJ, LB), the European Science Foundation (UD), the Austrian Science Fund (UD), the Austrian Ministry for Science and Transport (UD), the Vienna Science and Technology Fund (UD), the Adaptfish Programme funded by the Leibniz-Community (RA, UD, FJ, SM, SUH), the Besatzfisch Project funded by the Federal Ministry of Education and Research (RA), and the strategic research programme "Sustainable spatial development of ecosystems, landscapes, seas and regions” funded by the Dutch Ministry of Agriculture, Nature Conservation and Food Quality (AR).

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# Tables

Table 1. Terms and definitions.

| Term | Definition |
|---|---|
| Biological reference points | Quantitative benchmarks against which fish biomass, fishing mortality rate, or other stock properties can be compared to determine stock status and provide management advice (Caddy and Mahon, 1995; Gabriel and Mace, 1999). Reference points can be used either as limits or targets (e.g., Caddy and Mahon, 1995; Mace, 2001). |
| Target reference points | Desirable levels of stock properties such as biomass or fishing mortality that a management regime should aim to achieve on average (Hall and Mainprize, 2004). For example, these could be values that allow for the largest possible catch, while ensuring sustainable exploitation over the long-term (Cadima, 2003). |
| Limit or threshold reference points | Benchmark values of stock properties that, if passed, indicate that a stock is being over-exploited and that its capacity for self-renewal and its long-term sustainability may be impaired (Caddy and Mahon, 1995; Cadima, 2003). Biomass levels below, and/or fishing mortality rates above, limit reference points are considered undesirable and should be avoided by management actions (Caddy and Mahon, 1995). |

| | |
|---|---|
| $B_{\mathrm{lim}}$ and $F_{\mathrm{lim}}$ | Limit reference points based on spawning-stock biomass $SSB$ and fishing mortality $F$, respectively. $B_{\mathrm{lim}}$ is defined by ICES (2007a) such that if $SSB$ is depressed below this level, there is a high risk that recruitment will be impaired (i.e., that, on average, it will be significantly lower than at higher $SSB$), or alternatively, $B_{\mathrm{lim}}$ is defined as the lowest observed $SSB$, below which the stock dynamics are unknown. $F_{\mathrm{lim}}$ is the fishing mortality that, if maintained, will drive the stock to $B_{\mathrm{lim}}$ (ICES, 2007a). |
| $B_{\mathrm{pa}}$ and $F_{\mathrm{pa}}$ | So-called precautionary reference points (ICES, 2007a). These reference points provide a buffer zone relative to $B_{\mathrm{lim}}$ and $F_{\mathrm{lim}}$, and were established to account for the uncertainty associated with estimating fishing mortality and spawning-stock biomass. $B_{\mathrm{pa}}$ is defined such that if the estimated $SSB$ exceeds this benchmark, then the true $SSB$ exceeds $B_{\mathrm{lim}}$ with a high probability (usually 95%). $F_{\mathrm{pa}}$ is defined analogously. |
| $B_{\mathrm{MSY}}$ and $F_{\mathrm{MSY}}$ | Reference points that describe, respectively, the biomass and fishing mortality that enable maximum sustainable yield (MSY). Reference points based on MSY can be used either as targets or as limits (Mace, 2001; ICES, 2007a). $B_{\mathrm{MSY}}$ and $F_{\mathrm{MSY}}$ are usually estimated using a production model or an age-based model coupled with a stock-recruitment model (Gabriel and Mace, 1999). |

| | |
|---|---|
| $F_{\max}$ and $F_{0.1}$ | Reference points based on yield-per-recruit relationships. $F_{\max}$ is the level of fishing mortality that maximizes the average fishing yield from a recruit, given a constant selection pattern of the fishery (Caddy and Mahon, 1995). $F_{0.1}$ is defined as the fishing mortality at which the slope of the yield-per-recruit relationship equals 10% of its value at the origin. Even though this choice of slope is somewhat arbitrary, it guarantees that $F_{0.1}$ is more conservative than $F_{\max}$ (Caddy and Mahon, 1995). |
| Recruitment overfishing | A situation in which the rate of fishing is so high that recruitment to the stock becomes significantly reduced, characterized by greatly reduced $SSB$ (e.g., ICCAT, 2009). |
| Growth overfishing | A situation in which fish are harvested too early in their life, before they have realized most of their growth potential. Usually defined relative to $F_{\max}$, with fishing mortalities in excess of $F_{\max}$ implying growth overfishing (e.g., ICCAT, 2009). |
| Phenotypic plasticity | Dependence of an individual's phenotype on the environmental conditions it encounters. For example, conditions allowing for rapid growth usually facilitate maturation (Trippel, 1995). |
| Fisheries-induced evolution (FIE) | Defined by ICES (2007b) as a genetic change in a population with fishing serving as the driving force of evolution. |

| | |
|---|---|
| Fisheries-induced adaptive change | Defined as genetic and phenotypically plastic individual-level changes that increase the fitness of phenotypes in an exploited system (see also ICES 2007b). |

# Figure captions

**Figure 1.** Fisheries-induced evolution impacts life-history traits and other individual-level properties (a), with repercussions for the demography of fish stocks (b) and for fisheries (c). Impacts and interdependencies exist also within each group, e.g., maturation influences growth and reproduction, and changes in age structure influence spawning-stock biomass.

**Figure 2.** Evolution towards a faster life history can result in an increased maximum population growth rate ($r_{\max}$; black curve), here illustrated for an evolving age at maturation. In populations that are recruitment-limited (recruitment success declines as population density increases), selection favours an age at maturation that corresponds to the maximum of the basic reproduction ratio ($R_0$; grey curve). Both metrics describe a population's capacity to grow ($r_{\max}$ measures its absolute instantaneous rate of increase, while $R_0$ measures its relative increase per generation) under standard environmental conditions, usually in the absence of fishing and without density dependence. Because $R_0$ is blind to changes in generation length, whereas a shorter generation length increases $r_{\max}$, in a viable population $r_{\max}$ almost always reaches its maximum for a lower age at maturation than $R_0$. Under these conditions, acceleration of the life history results in increased $r_{\max}$ and decreased $R_0$, at least as an initial response. However, such acceleration might not stop near the maximal $r_{\max}$ (upper arrow), but may continue beyond this maximum and thus result in an $r_{\max}$ that again decreases (middle arrow) and eventually may even fall below its original value (lower arrow). See text for a detailed explanation.

**Figure 3.** Potential effects of fisheries-induced evolution (FIE) on reference points based on stock-recruitment relationships (a and b) and on the estimation of spawning-stock biomass *SSB* (c). Recruitment is measured by the mean number *R* of offspring reaching the age of recruitment. FIE may increase reproductive effort ($R_+$ in a), decrease pre-recruit survival ($R_-$ in a and b), or decrease pre-recruit growth ($R_+$ in b), resulting in corresponding shifts of the limit reference point $B_{\mathrm{lim}}$ for avoiding recruitment overfishing. FIE may also bias the estimation of *SSB*, resulting in the underestimation of *SSB* ($SSB_-$ in c) when FIE causes earlier maturation and old maturity ogives are used, or in the overestimation of *SSB* ($SSB_+$ in c) when FIE lowers weight-at-age and old weight-at-age keys are used.

**Figure 4.** Potential effects of fisheries-induced evolution (FIE) on the optimal age at harvest (a and b) and on the age-specific selection pattern (c). The illustrative example shown here is based on a quantitative model for trawl fisheries of North Sea plaice in which FIE results in earlier maturation, slower growth, and increased reproductive effort (Mollet, 2010). The development of a cohort's abundance (left black curve in a) and of the mean weight of its individuals (right black curve in a) as the cohort ages determine its biomass in dependence on its age (black curve in b). The yield from a single cohort can be maximized by harvesting all fish at the age $a_{\mathrm{opt}}$ at which the cohort's biomass peaks. Because FIE typically results in lower weight-at-age and lower survival-to-age, we expect that a cohort's biomass peaks at an earlier age ($a_{\mathrm{opt}-}$) after evolution (grey curves). However, in a typical fishery's selection pattern (black curve in c), fishing starts earlier than the optimum, so the age $a_{50}$ at which selectivity equals 50% is less than optimal ($a_{50} < a_{\mathrm{opt}}$). When selectivity is size-dependent, slower somatic growth caused by FIE leads

to a rightward shift of the age-dependent selectivity curve (grey curve in c), and thus to an increased age at 50% selectivity ($a_{50+}$). Consequently, the distance between $a_{\mathrm{opt}}$ and $a_{50}$ diminishes ($a_{\mathrm{opt}-} - a_{50+} < a_{\mathrm{opt}} - a_{50}$, as highlighted by the arrows in c).

**Figure 5.** Potential effects of fisheries-induced evolution (FIE) on reference points based on yield-per-recruit models. When fishing starts before the age of maximum biomass ($a_{50} < a_{\mathrm{opt}}$), yield-per-recruit is a humped function of fishing mortality $F$ (continuous thick black curve). The reference point $F_{\mathrm{max}}$ (right dashed black line) is defined as the fishing mortality that maximizes yield-per-recruit. As explained in the text, FIE is expected to change the yield-per-recruit curve (continuous grey curve) so as to shift this reference point to the right ($F_{\mathrm{max}+}$, right dashed grey line). The reference point $F_{0.1}$ (left dashed black line) is defined as the fishing mortality for which the slope of the yield-per-recruit curve equals 10% (dotted black line) of its value at the origin (thin continuous black line). Also this reference point is expected to shift to the right ($F_{0.1+}$, left dashed grey line). The shown curves are based on the same quantitative analysis as Figure 4.

**Figure 6.** Potential effects of fisheries-induced evolution (FIE) on reference points based on production models. The Schaefer production model describes how fishing mortality $F$ affects population abundance (black curve in a) and per capita growth rate $r_{\mathrm{max}}$ (black curve in b), and thus sustainable yield (black curve in c). The maximum sustainable yield *MSY* occurs at an intermediate level of $F$, where the product of abundance and per capita growth rate is maximized (c). Under FIE, carrying capacity $K$ is often expected to decline ($K_{-}$, grey curve in a), whereas $F_{\mathrm{crash}}$, which is equal to the maximum per capita growth rate $r_{\mathrm{max}}$, is expected to increase ($F_{\mathrm{crash}+}$, grey curve in b). Depending on whether the

decline in $K$ is larger or smaller than the increase in $r_{\mathrm{max}}$, $MSY$ is expected to decline ($MSY_{-}$, for the lower grey curve in c) or increase ($MSY_{+}$, for the upper grey curve in c), respectively. Either way, the reference point defined by the fishing mortality corresponding to MSY is expected to increase ($F_{\mathrm{MSY}+}$, for both grey curves in c).

Figure 1

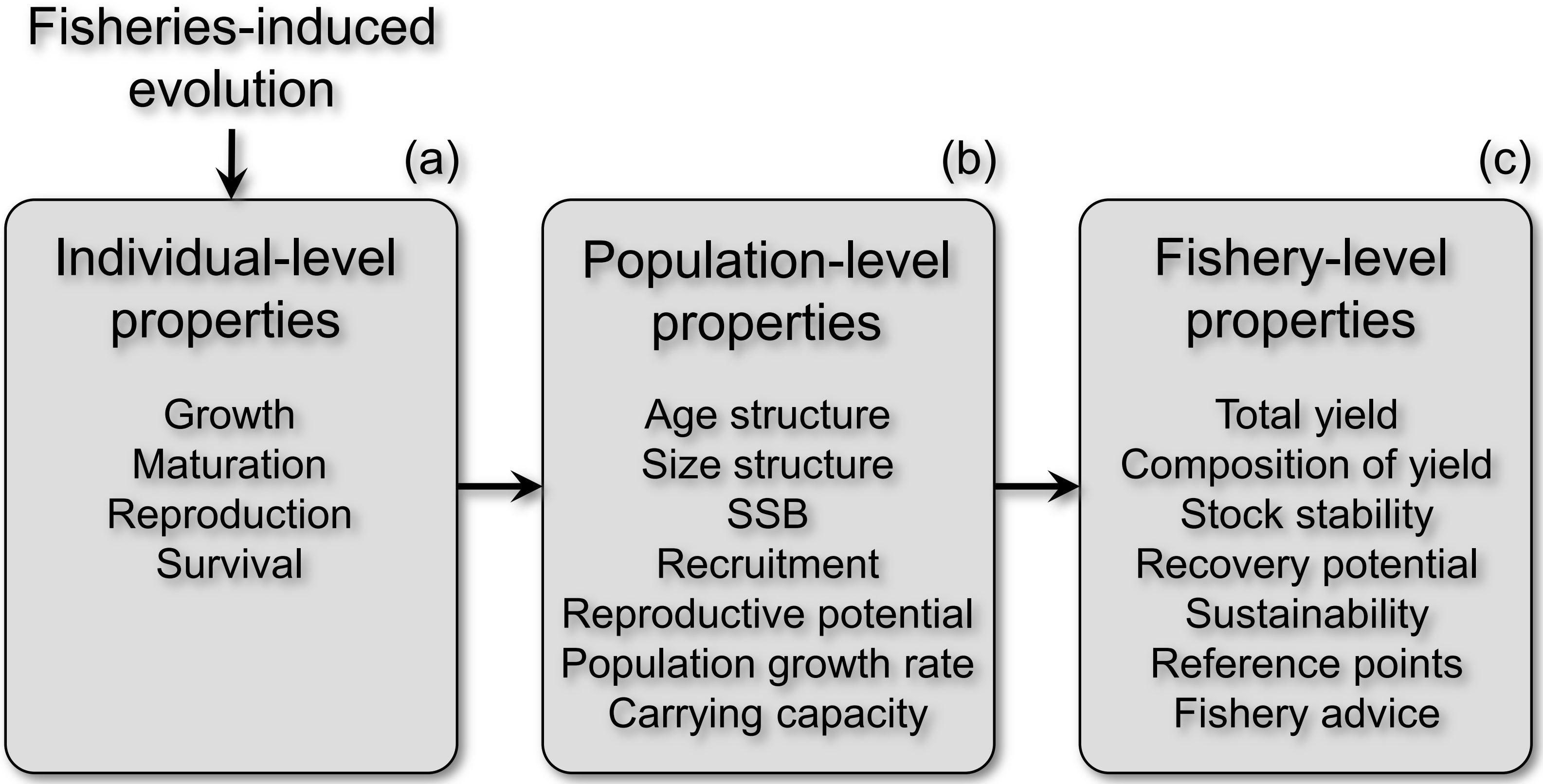

Fisheries-induced evolution
(a)
Individual-level properties
Growth
Maturation
Reproduction
Survival
(b)
Population-level properties
Age structure
Size structure
SSB
Recruitment
Reproductive potential
Population growth rate
Carrying capacity
(c)
Fishery-level properties
Total yield
Composition of yield
Stock stability
Recovery potential
Sustainability
Reference points
Fishery advice

Figure 2

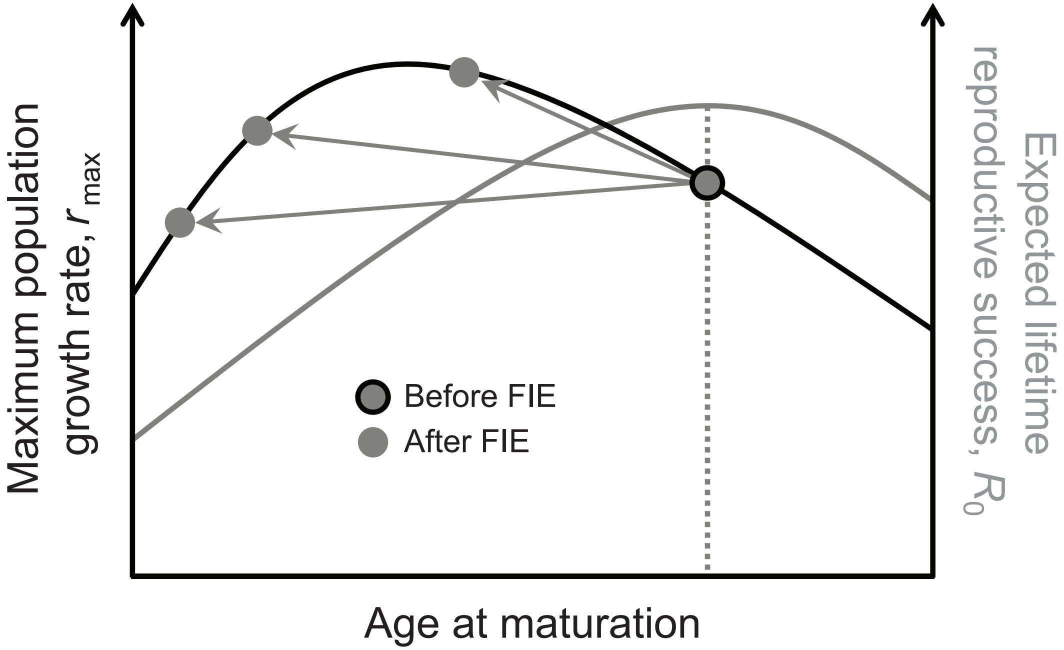

Maximum population growth rate, $r_{max}$
Expected lifetime reproductive success, $R_0$
Before FIE
After FIE
Age at maturation

Figure 3

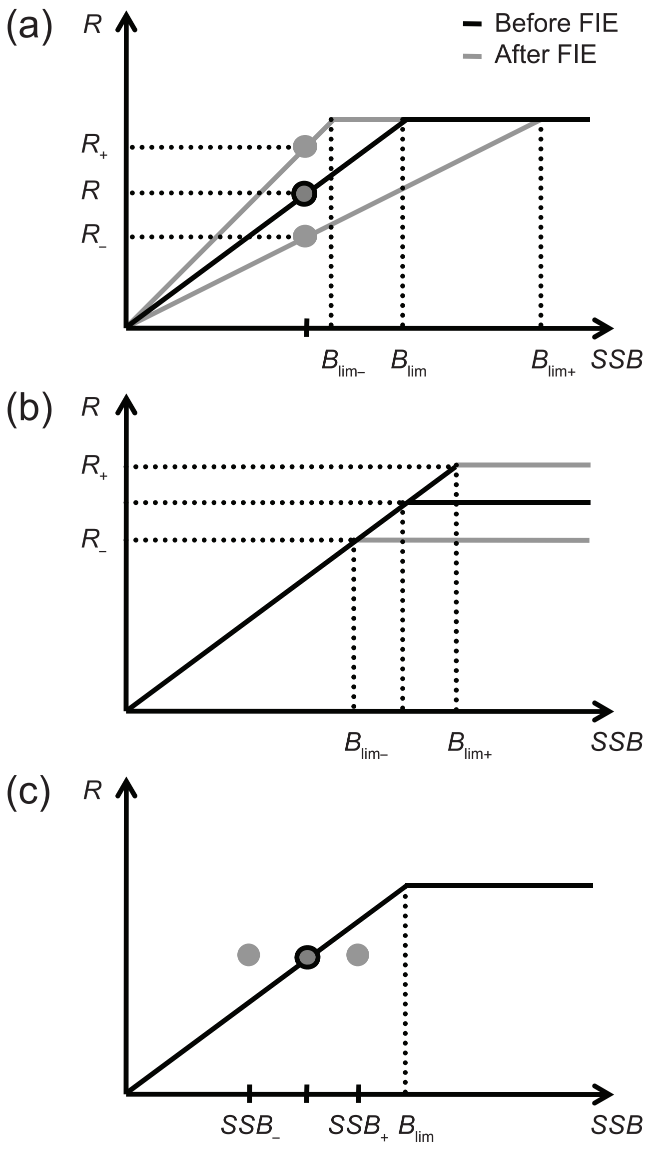

(a)
R
Before FIE
After FIE
R+
R
R−
B lim−
B lim
B lim+
SSB
(b)
R
R+
R−
B lim−
B lim+
SSB
(c)
R
SSB−
SSB+
B lim
SSB

Figure 4

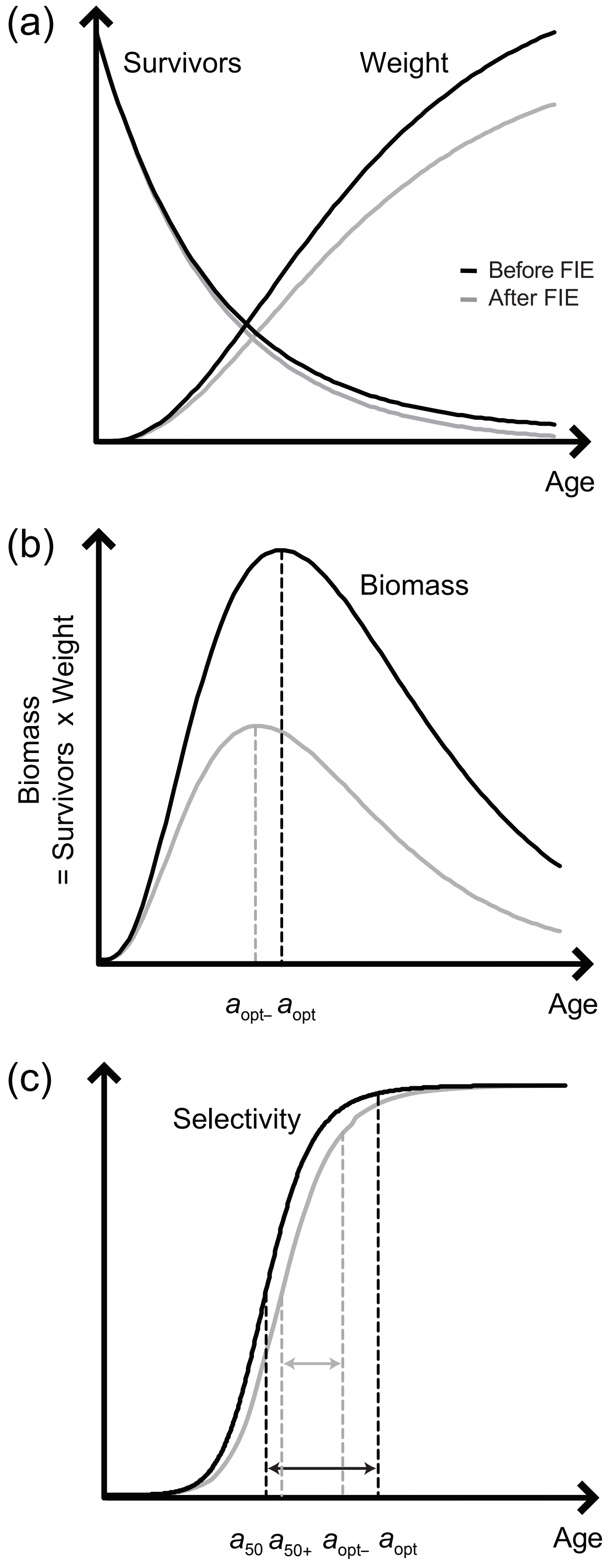

(a)
Survivors
Weight
Before FIE
After FIE
Age
(b)
Biomass
Biomass = Survivors x Weight
$a_{opt-}$ $a_{opt}$
Age
(c)
Selectivity
$a_{50}$ $a_{50+}$ $a_{opt-}$ $a_{opt}$
Age

Figure 5

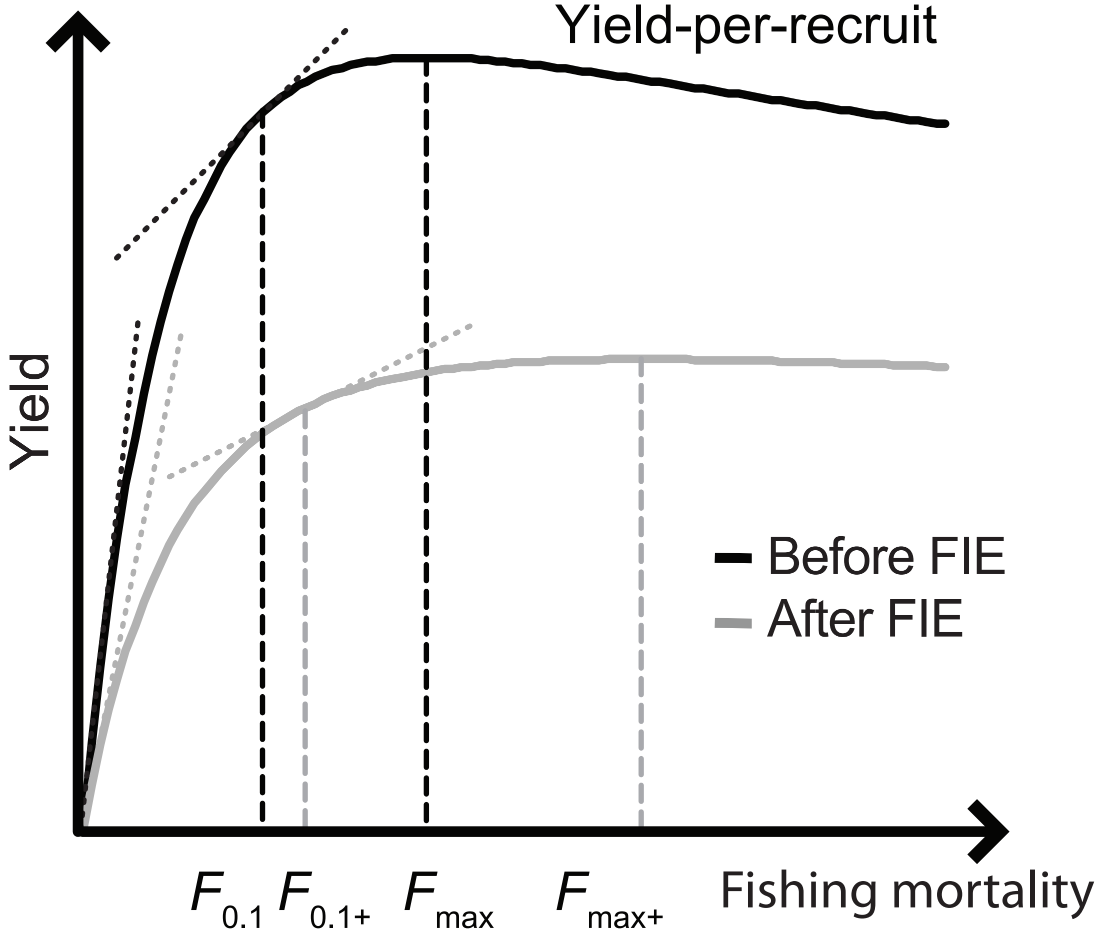
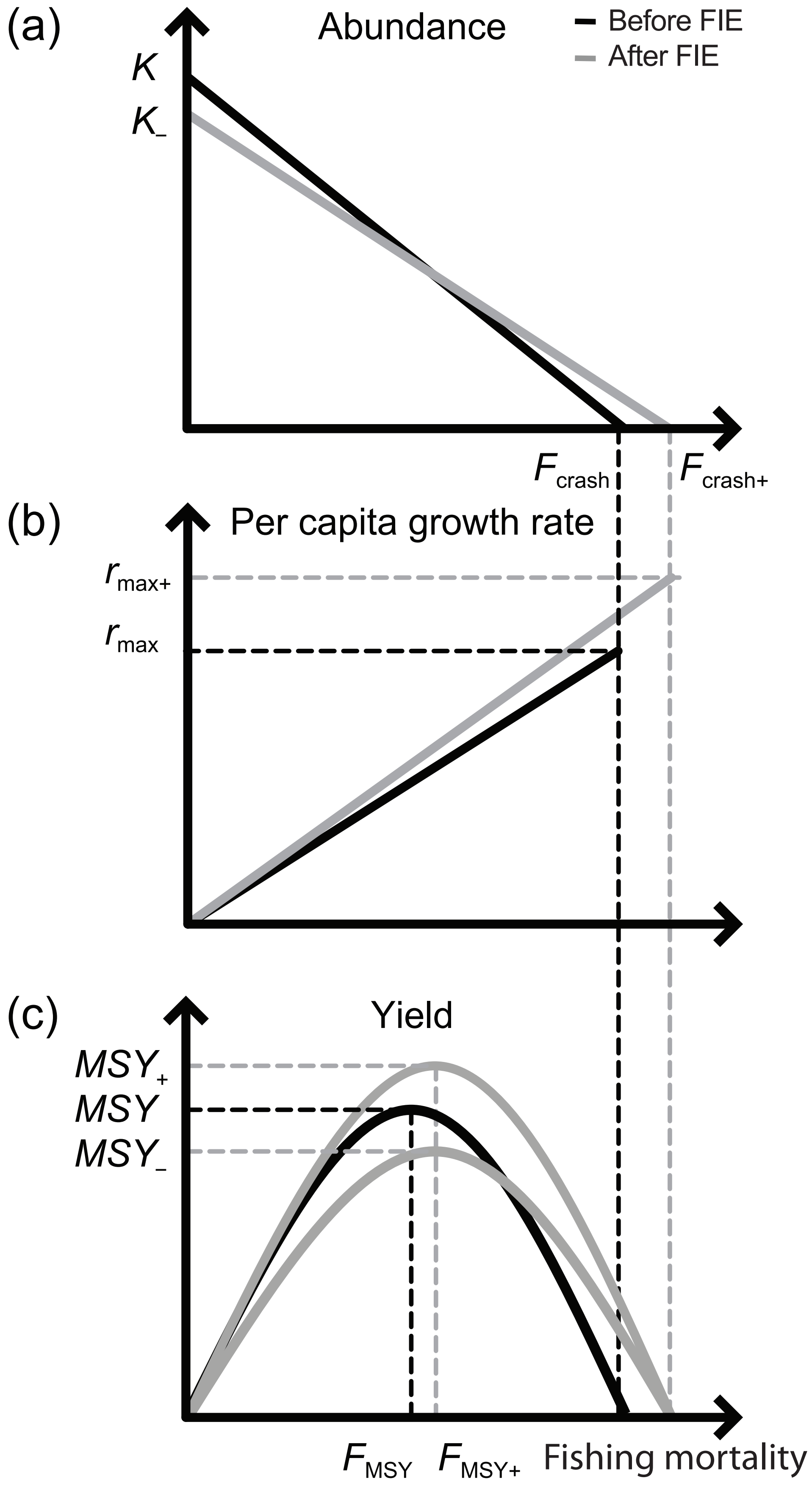

Yield-per-recruit
Yield
Before FIE
After FIE
$F_{0.1}$
$F_{0.1+}$
$F_{max}$
$F_{max+}$
Fishing mortality

Figure 6


(a)
Abundance
Before FIE
After FIE
$K$
$K_-$
$F_{crash}$
$F_{crash+}$
(b)
Per capita growth rate
$r_{max+}$
$r_{max}$
(c)
Yield
$MSY_+$
$MSY$
$MSY_-$
$F_{MSY}$
$F_{MSY+}$
Fishing mortality