



Minimizing the impact of fishing

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Abstract

Minimizing the impact of fishing is an explicit goal in international agreements as well as in regional directives and national laws. To assist in practical implementation, three simple rules for fisheries management are proposed in this study: 1) take less than nature by ensuring that mortality caused by fishing is less than the natural rate of mortality; 2) maintain population sizes above half of natural abundance, at levels where populations are still likely to be able to fulfil their ecosystem functions as prey or predator; and 3) let fish grow and reproduce, by adjusting the size at first capture such that the mean length in the catch equals the length where the biomass of an unexploited cohort would be maximum (L_{opt}). For rule 3), the basic equations describing growth in age-structured populations are re-examined and a new optimum length for first capture (L_{c_opt}) is established. For a given rate of fishing mortality, L_{c_opt} keeps catch and profit near their theoretical optima while maintaining large population sizes. Application of the three rules would not only minimize the impact of fishing on commercial species, it may also achieve several goals of ecosystem-based fisheries management, such as rebuilding the biomass of prey and predator species in the system and reducing collateral impact of fishing, because with more fish in the water, shorter duration of gear deployment is needed for a given catch. The study also addresses typical criticisms of these common sense rules for fisheries management.

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Introduction	2
Rule 1: Take less than nature	2
Rule 2: Maintain populations above half of natural abundance	3
Rule 3: Let fish grow and reproduce	3
Material and Methods	3
Results	4
Importance of length at first capture	4
Yield per recruit analysis	4
Biomass per recruit analysis	6

Discussion	6
Criticism of single-species models is overstated	6
Influence of stock-recruitment models on fisheries reference points	7
The evolutionary M/K ratio 1.5	7
Minimizing the impact of fishing	9
Economic considerations	9
Towards ecosystem-based fisheries management	11
Refuting calls for unselective fishing	11
Caveats associated with the proposed rules	12
Conclusion	13
Acknowledgements	13
References	13
Appendix	16

Introduction

A reduction of the impact of fishing on ecosystems is called for in international forums such as the Rio+20 summit of June 2012 (UN 2012), meetings on responsible fishing at the international level (FAO 2012), and in regional directives and laws such as the European Marine Strategy Framework Directive (MSFD 2008) and the recently reformed Common Fisheries Policy of Europe (CFP 2013). For example, in addition to the legal requirement of rebuilding stocks above the level that can produce the maximum sustainable yield, the CFP demands in Article 2.3 that ‘...negative impacts of fishing activities on the marine ecosystem are minimized...’ and the MSFD requires in commercially exploited stocks a ‘[...] population age and size distribution that is indicative of a healthy stock’. Here it is proposed that three simple management rules can help in meeting these requirements.

Rule 1: Take less than nature

The first rule states that humans should not take more than nature, that is human-induced mortality shall not exceed the instantaneous rate of natural mortality (M), so that total mortality in exploited populations is not higher than twice the rate that populations have evolved to withstand. M has long been used in fisheries science as a proxy for the upper limit of the instantaneous rate of sustainable fishing mortality F_{MSY} (Gulland 1971; Shepherd 1981; Beddington and Cooke 1983; Clark *et al.* 1985; Beverton 1990; Patterson 1992; Thompson 1993; Walters and Martell

2002, 2004; MacCall 2009; Pikitch *et al.* 2012). For example, the U.S. National Oceanographic and Atmospheric Agency uses M as proxy for F_{MSY} in assessments of data-limited stocks (NOAA 2013). Here it is argued that to minimize impact of fishing on the age and size distribution in a population, fishing mortality (F) may not exceed the average M of adults in any size or age class. A meta-analysis of 245 fish species worldwide suggested that $F_{MSY} = 0.87 \cdot M$ was a reasonable target for teleosts and $F_{MSY} = 0.41 \cdot M$ for chondrichthyans (Zhou *et al.* 2012). To avoid the widespread collapse of shoaling pelagic species (Essington *et al.* 2015) such as herring (*Clupea* spp., Clupeidae), sprat (*Sprattus* spp., Clupeidae) or anchovies (Engraulidae), F must be smaller than $2/3$ of M (Patterson 1992). A large study of population dynamics of forage fish concluded that ‘to ensure a high probability (75–95%) that forage fishing will not place dependent predators (fish, birds, marine mammals) at jeopardy of extinction’, F should not exceed $0.5 \cdot F_{MSY}$ or $0.5 \cdot M$ (Pikitch *et al.* 2014). An examination of stock assessment failures (Walters and Martell 2002) concluded that ‘...any assessment that results in $F \gg 0.5 \cdot M$ must be very carefully justified...’. Setting F to about half of M also takes care of the large uncertainties associated with the estimation of these parameters (Punt 2006; MacCall 2009; Punt *et al.* 2014), because the precautionary principle, which is a key ingredient of basically all legal systems, demands that in the face of uncertainty, policy-makers should implement policies that reduce the probability of harm to the resource (FEU 2009). These considerations make it clear that $F = M$ is

the upper, to-be-avoided limit of sustainable fishing mortality and that $F \approx 0.5 \cdot M$ may be a precautionary target.

Rule 2: Maintain populations above half of natural abundance

The second rule states that fishing should not reduce populations below half of their natural unexploited abundance. Production models such as those of Fox (1970) or Schaefer (1954) show that maximum sustainable yields can be obtained at stock sizes between 37% and 50% of unexploited biomass (B_0), respectively. Beverton and Holt (1957) yield per recruit models demonstrate that, for a given fishing mortality, higher catch and biomass can be obtained by increasing the length at first capture. A study of seabird populations (Cury et al. 2011) showed that about $1/3 B_0$ of forage fish is needed to prevent the collapse of dependent seabirds. These models and empirical data suggest that populations may be unable to fulfil their respective roles as prey and predator if fishing reduces them below half of their natural abundance. Therefore, in accordance with the more conservative (Cadima 2003) Schaefer model and keeping in mind the insights from yield per recruit analysis, $1/2 B_0$ is proposed as a lower-limit reference point for stock size.

Rule 3: Let fish grow and reproduce

The third rule states that individuals of exploited populations should be allowed to reproduce and realize their growth potential before being caught. Fish grow throughout their lives, and it is long known 'that it would pay to give the fish a chance to grow' before being caught (Graham 1935), that is that larger catches can be obtained with the same effort if the onset of fishing is postponed to older ages and greater sizes (Beverton and Holt 1957; Garcia and Demetropoulos 1986; Vasilakopoulos et al. 2015). In fact, catches and profits near the theoretical maximum can be obtained together with a strongly reduced impact of fishing on biomass and age-structure if the allowed catch is taken around an optimum size of individuals (around $2/3$ of maximum length, L_∞) where cohort biomass is a maximum (Froese et al. 2008).

Arguably, the body length L_{opt} , where the biomass of a cohort and its fecundity are maximum (see Discussion of M/K ratio below), is the most important point in the life of adult fish. Semelparous

fish such as lampreys (Petromyzontiformes), eels (Anguillidae) or salmon (Salmonidae) maximize the output of their single reproductive event at L_{opt} (Roff 1984). Iteroparous species maximize their lifetime fecundity, if they mature such that their multiple spawning events cluster around L_{opt} (Froese and Pauly 2013). For a given allowed catch, starting fishing at L_{opt} leads to greater stock sizes and greater profits, albeit with a slightly increased cost of fishing (Froese et al. 2008, 2015b). Instead, gear selectivity can be regulated such that L_{opt} is not the smallest but the average length in the catch, thus avoiding an unusually large size at first capture (Cardinale and Hjelm 2012) which may be difficult to enforce. For strongly size-selective gears such as gill nets or traps, this can be performed by adjusting selectivity such that the peak of the selection curve occurs at L_{opt} . For gears that retain fish beyond a certain size, such as trawls and seines, a new optimum length at first capture L_{c_opt} is presented, that is a target length for the start of fishing which results in yields and catch per unit effort that are practically identical with the maximum that can be achieved with a certain fishing mortality. At the same time, starting fishing at L_{c_opt} maintains large stock sizes and leads to a mean length of L_{opt} in the catch and in the exploited part of the population.

The purpose of this study was to present support for the three rules from analytical yield per recruit and economic modelling perspectives and to contrast them with current fisheries management, using North Sea cod (*Gadus morhua* Gadidae) as an example (ICES 2015).

Material and methods

The equations and assumptions underlying the results and conclusions of this study are presented in the Appendix 1. Some of these equations have been published in heterogeneous documents and are poorly known. Here, all the equations are presented in a unique and homogeneous framework. A completely new equation to determine the optimal length at first capture L_{c_opt} is also presented. Starting fishing at this length results in a mean length of L_{opt} for the catch and the exploited part of the population.

$$L_{(c_opt)} = \frac{L_\infty(2 + 3F/M)}{(1 + F/M)(3 + M/K)} \quad (1)$$

where L_∞ and K are parameters of the von Bertalanffy growth equation, and other variables are as defined in the text above.

Some of the equations in Appendix 1 are very long and prone to typing errors. The spreadsheets behind Figs 1–5 (YpR_generic_5.xlsx, YpR_cod_3.xlsx) are therefore provided as online material for download from <http://oceanrep.geomar.de/30244/>.

Based on the equations in Appendix 1, and building on the evolutionary M/K ratio of 1.5, generic yield- and biomass per recruit curves could be calculated and were used to explore the performance of the proposed three simple rules for fisheries management. Sensitivity analyses were performed for other values of the M/K ratio. Performance of the simple rules was also tested with a conventional age-structured dynamic pool model (Clark 1991), including a realistic range of Beverton and Holt (Beverton and Holt 1957) spawner–recruitment curves (Myers *et al.* 1999; Rose *et al.* 2001) and a wide range of life history parameters. The corresponding results and graphs are part of the online material and can be generated with the R-script Age-structured-simulation_2.R. Data for North Sea cod were obtained from stock assessment documents (ICES 2015).

Results

Importance of length at first capture

For every fishing mortality, there is a corresponding length at first capture L_{c_max} that will maximize yield typically within a few years in stocks

with medium resilience (Beverton and Holt 1957, 1966) (Fig. 1). Similarly, there is a slightly larger length L_{c_opt} resulting in a mean length of L_{opt} in catch (see Equations A7, A12 and A13 in Appendix 1). In the area of sustainable fishing mortalities from $0.5 \cdot M$ to M , L_{c_opt} exceeds L_{c_max} by 8–19%, respectively, with the difference decreasing as F increases. At the maximum fishing pressure $F = M$ allowed under rule 1, the value of the length at first capture L_{c_opt} suggested by rule 3 is equal to 56% of L_{∞} . For the proposed target of $F = 0.5 M$, the corresponding L_{c_opt} is 52% of L_{∞} . Note that L_{c_opt} remains well above the length where, for example, 90% of North Sea cod reach maturity (Fig. 1). The minimum legal landing size for North Sea cod of 35 cm would maximize yield only for a very low fishing mortality of $F = 0.1 \cdot M$. Instead, the actual fishing mortality of cod in 2014 was $1.9 \cdot M$. The L_{c_opt} for a fishing mortality of $1.9 M$ is 76 cm, while it would be 72 cm for $F = M$ and 67 cm for $F = 0.5 M$.

Yield per recruit analysis

To facilitate comparison between stocks, yield is expressed relative to the theoretical maximum yield (Holt 1958) that would result from fishing with infinite effort and capturing all fish at the length L_{opt} where cohort biomass is at its maximum (Fig. 2a). Fishing starting at L_{c_max} or L_{c_opt} results in practically the same maximum yield for

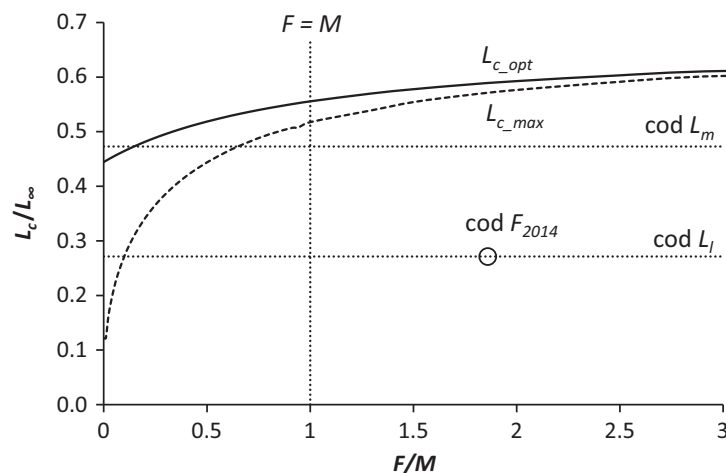


Figure 1 Relative length at first capture (L_c/L_{∞}) as a function of fishing mortality F relative to natural mortality M . The dashed curve (L_{c_max}) results in the maximum yield per recruit, and the solid curve (L_{c_opt}) results in a mean length of L_{opt} in the catch. Using North Sea cod as an example, L_m indicates the length where 90% of the individuals reach maturity, L_l indicates the minimum legal landing size, and F_{2014} marks the actual fishing mortality in 2014.

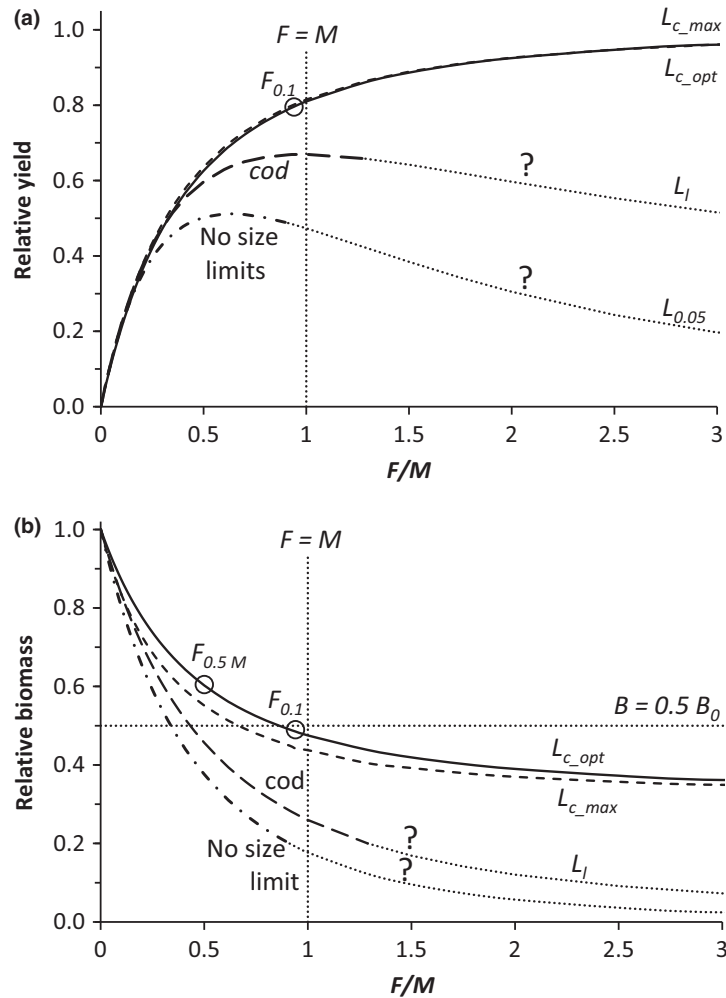


Figure 2 a) Yield per recruit relative to the theoretical maximum yield and b) Biomass per recruit relative to unexploited biomass, as a function of the F/M ratio, for different lengths at first capture. L_{c_opt} (solid curve) indicates the length that results in L_{opt} as mean length in the catch and L_{c_max} (short dashed curve) indicates the length that results in maximum yield for a given F/M ratio. $F_{0.1}$ marks a widely-used precautionary level of fishing mortality. The long-dashed curve is an example of yield or biomass per recruit for North Sea cod, caught from the legal minimum landing size $L_I = 35$ cm onward with a fishing mortality of nearly $2 M$ in 2014. The lowest yields and biomass are obtained by fishing without lower size limits, as indicated by the dot-dashed line, which assumes an onset of fishing at 5% of asymptotic length. The curves for cod and the no-size-limit scenario are dotted and marked with question marks once biomass falls below 20% of unexploited biomass B_0 level, where recruitment may be impaired and absolute biomass and yield may be much reduced.

a given F . The respective yield curves approach the theoretical maximum yield asymptotically with increasing F , thus illustrating the historical difficulty of deriving guidance on maximum sustainable fishing from yield per recruit analyses. Only if the length at first capture is suboptimal, as in the curve for North Sea cod or in the curve without size limits (Fig. 2a), the yield per recruit as a function of F shows a humped curve – and thus an indication of F_{max} at the peak. To deal with this

lack of guidance, arbitrary precautionary levels for F have been introduced, such as $F_{0.1}$ (Gulland and Boerema 1973), which has been used widely in fisheries management, and which marks the fishing mortality where the slope of the yield per recruit curve is 1/10th of its value at the origin (Pauly 1984; Cadima 2003). As Shepherd and Pope (2002, p. 175) have put it, $F_{0.1}$ is a ‘common sense rule for determining when future increases in F lead to little extra yield’. $F_{0.1}$ falls

below the level where F equals M and results in an equilibrium stock size of nearly half of unexploited biomass (Fig. 2b); in other words, $F_{0.1}$ is a high but still precautionary management target if combined with the appropriate length at first capture (L_{c_opt} for $F = F_{0.1}$ is 55% of L_{∞} , leading to a catch of 80% of the theoretical maximum). A less arbitrary upper-limit reference point suggested by the simple rules is $F = M$, which, if combined with $L_{c_opt} = 56\%$ of L_{∞} , leads to a catch of 81% of the theoretical maximum. Note that the target of $F = 0.5 M$ does not reduce this catch by half, but rather gives 77% of the yield at $F = M$, that is a decrease in effort (and associated cost) of 50% results in a decrease in catch (and income) of only 23%.

The 2014 exploitation pattern of North Sea cod with $F = 1.9 M$ and $L_c = 35$ cm is suboptimal and leads to poor yield per recruit. Having no size limits on fishing leads to the lowest yield per recruit of all scenarios (Fig. 2a). Note that for the cod and the 'no-size-limit' scenarios, yields at F values associated with low biomass may be much lower than suggested by the yield per recruit curves (thin dotted curve extensions in Fig. 2a), because above $F = M$, biomass per recruit is strongly reduced ($B \leq 0.2 \times B_0$, Fig. 2b), suggesting increased probability of impaired recruitment.

Biomass per recruit analysis

To evaluate the impact of fishing, biomass is shown relative to unexploited biomass, with $B = 0.5 \cdot B_0$ indicating the lower limit of acceptable stock sizes (Rule 2) and $F = M$ indicating the upper limit of fishing mortality (Rule 1) (Fig. 2b). Within these limits, the best compromise between high yield, high biomass and a low cost of fishing is found at fishing starting at L_{c_opt} (bold line indicated in Fig. 2b). Note that this fishing strategy results in $B = 0.5 \cdot B_0$ when $F = 0.86 \cdot M$. Thus, a fishing pressure equal to 86% of the rate of natural mortality marks the highest theoretical fishing pressure that still fulfils all three proposed rules.

Using again the example of the North Sea cod with fishing starting at $L_l = 35$ cm, the actual fishing mortality $1.9 \cdot M$ of 2014 would keep the stock below 13% of unexploited biomass-per-recruit, that is outside of safe biological limits. Instead, reducing F to half of M and starting fishing at L_{c_opt} would result in about 60% of the

unexploited biomass, with higher yields and substantially lower cost of fishing (Fig. 2).

Having no size limits results in the lowest possible biomass per recruit for any fishing pressure. When fishing mortality equals the natural mortality of adults, the resulting biomass per recruit is less than 18% of the unexploited biomass, that is within the range where successful production of offspring may be compromised (Beddington and Cooke 1983) and thus outside of safe biological limits (Common Fisheries Policy 2013; Froese et al. 2014).

Discussion

In discussing the implications of the three proposed rules for fisheries management, typical criticisms of the models and assumptions used in support of the three rules are addressed first. Then the biological and economic implications of the rules and their potential contribution to ecosystem-based fisheries management are discussed. Then recent calls for fishing all species at all sizes are refuted, caveats associated with the three rules are acknowledged, and conclusions summarize the findings.

Criticism of single-species models is overstated

The call for ecosystem-based fisheries management has led to criticism of single-species models as used in this study, which are said to ignore species interactions and trophic relationships (e.g. ICES 2013a). Such criticism may be overstated. Typical single-species stock assessment models such as presented in this paper contain three parameters that link the stock in question with its prey and predators and its environment: the first parameter is the rate of natural mortality M , which is the sum of mortality rates caused by predation, disease, environmental harshness and hazards, competition, and old age. While each of these causes of mortality may fluctuate strongly between years and size-classes, the overall sum appears to be reasonably stable during the average duration of the adult phase (Kenchington 2014) and thus is a reasonable representation of the fraction of observed total mortality that has natural causes. The second parameter is K , which determines how fast maximum body size is approached, and hence quantifies somatic growth, as influenced by the availability of food, the energy spent on hunting

and grazing, the inter- and intraspecific competition for food resources, the impact of environmental temperature and oxygen on assimilation of food (Pauly 2010), and the composition of individual genetic growth potentials present in the population in a certain year. Again, while all these impacts on somatic growth will vary between years and cohorts, using an average K estimated across cohorts in recent years provides a reasonable representation of the range of ecological and environmental impacts on the stock. The third parameter is the number of recruits R that join the exploited part of the population. This number is influenced by the number and fecundity of their parents, by environmental conditions (temperature, oxygen, salinity, currents and wind stress) during the early development stages, and by the abundance and small-scale co-occurrence of predators and suitable prey. Unless there are strong changes in the overall ecosystem, M and K can be expected to be reasonably stable over the average adult lifetime. In contrast, R may fluctuate strongly due to short-term environmental conditions, or exhibit marked trends, such as the long-term decrease recently shown for many European stocks in relation to overfishing and global change (Gascuel *et al.* 2014). Thus, because R is difficult to predict, the pertinent equations in this study are expressed on a per-recruit basis (Beverton and Holt 1957).

In summary, the criticism that single-species models do not take into account species interactions and environmental variability is overstated because assessments are carried out on real-world stocks interacting with other species through growth and natural mortality and responding to environmental variability with highly variable recruitment.

Influence of stock-recruitment models on fisheries reference points

Yield per recruit analysis as applied in this study has been criticized for not taking into account the relationship between number of recruits and the corresponding spawning stock size (Sparre and Venema 1998), in other words the claim is that curves for yield and biomass would look different if stock–recruitment (S-R) relationships had been considered. Widely-used S-R models are those of Beverton and Holt (Beverton and Holt 1957) and Ricker (Ricker 1975). More parsimonious S-R

models are simple hockey-stick functions which assume log-normal fluctuations around a constant recruit-per-spawner ratio at low population sizes and around constant mean recruitment at large population sizes (Clark *et al.* 1985; Barrowman and Myers 2000). A decline in recruitment is typically assumed at stock sizes below 20% of unexploited biomass B_0 (Beddington and Cooke 1983; Myers *et al.* 1994; Gabriel and Mace 1999). However, starting fishing at L_{c_opt} does not reduce equilibrium biomass below 1/3 of B_0 , even if F is very high (Fig. 2b). Thus, the decline in recruitment at low biomass does not affect the predicted yield and biomass curves associated with the three rules. Similarly, with hockey-stick recruitment, no change to the predictions from yield and biomass per recruit is expected for high biomass (ICES 2013b).

For good measure, the predictions of the yield-per-recruit analyses as used in this study were compared with those from a conventional age-structured dynamic pool model (Clark 1991), including a realistic range of Beverton and Holt (Beverton and Holt 1957) spawner–recruitment curves (Myers *et al.* 1999; Rose *et al.* 2001) and a wide range of life history parameters. Starting fishing at L_{c_opt} with $F = 0.5 M$ consistently produced equilibrium spawning biomass levels of 40 to 60% of pristine spawning biomass with equilibrium yields typically ranging from 75 to 80% of the theoretical maximum yield. These results lead to the same conclusions as the yield per recruit results shown in Fig. 2 and are therefore not presented in detail. They can be reproduced with an R script that is part of the online material.

In summary, the conclusions presented in this study with respect to fishing at $F < M$ and starting fishing at L_{c_opt} do not change if realistic assumptions about stock–recruitment relationships are included in the models.

The evolutionary M/K ratio 1.5

Using the M/K ratio instead of the individual parameters M and K is advantageous because the ratio is known to vary less than the parameters themselves (Beverton and Holt 1959), and the ratio can be approximated from life history theory (Jensen 1996; Hordyk *et al.* 2015; Prince *et al.* 2015). The curves shown in this study refer to populations with an M/K ratio of 1.5, where the peak in cohort biomass coincides with maximum

growth in body weight. With other M/K ratios, the shape of, for example, the yield curve would change slightly (Fig. 3). Typical M/K ratios for species with indeterminate growth fall between 1.0 and 2.0 (Beverton and Holt 1959) with extreme values around 0.5 and 3.0, and with 1.5 representing a median of observed values (Prince *et al.* 2015). But why do M/K ratios cluster around the 1.5 ratio? This question can be answered by exploring the relation between peak cohort biomass and cohort age at that peak. Because fecundity is proportional to body weight in most fish (Gunderson 1997) and because most fish mature at or before the peak in cohort biomass (Froese and Pauly 2013), the height of this peak can be understood as a proxy for the lifetime reproductive output (LRO), and the corresponding age can be understood as a proxy for generation time, which itself is an inverse proxy for r_{max} , the intrinsic rate of population increase (Charnov 1993; Roff 2002). If the M/K ratio is smaller than 1.5, then mortality is low relative to growth and the peak in cohort biomass occurs at a later age and increases in height, thus increasing fitness as measured by LRO. However, as the peak in biomass and reproductive output appears at a later age, generation time increases, thus reducing r_{max} , the other measure of fitness (Charnov 1993; Roff 2002). In the opposite way, if the M/K ratio is larger than 1.5, then mortality is high relative to growth and the peak in cohort biomass occurs at

an earlier age with decreased height, thus increasing fitness as measured by r_{max} but decreasing fitness as measured by LRO. In other words, there is a trade-off between amount and timing of reproductive output, with no obvious optimum, and other life history traits are needed to determine the best combination of LRO and r_{max} .

One such trait is the net production of body mass dW/dt , which reaches a peak at about 30% of maximum body weight. It can be demonstrated that the peak in cohort biomass coincides with this body weight if the ratio M/K is equal to 1.5 (Jensen 1996; Jennings *et al.* 2007). In that case, net tissue production of parents would be maximum at the time when most of their gametes are produced and a given reproductive output would take the least fraction of net tissue production. Thus, from an evolutionary perspective, maximum growth performance including the production of gonad tissue is combined with the peak in expected offspring production if $M/K = 1.5$ (Froese and Pauly 2013). This provides a fitness advantage because with this ratio, natural selection has ‘economize[d ...] the organization’ of reproduction (Darwin 1859). In conclusion, Figs 1–3 can be seen as representing key population traits under an evolutionary optimized scenario with respect to growth performance and production of offspring.

With $M/K = 1.5$, the equation for L_{opt} simplifies to $L_{opt}/L_{inf} = 2/3$ and the equation for the age at the peak in biomass simplifies to $t_{opt} \cdot M = 1.65$.

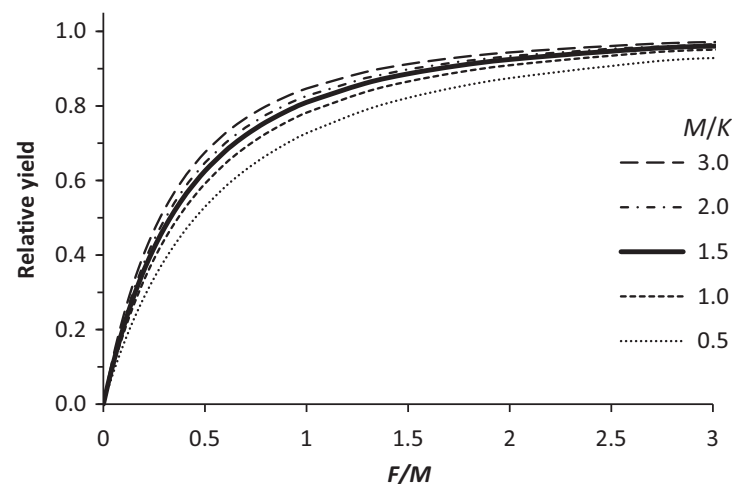


Figure 3 Relative yield if fishing starts at $L_{c, opt}$, for different M/K ratios, where 1.0 and 2.0 represent the typical range and 0.5 and 3.0 represent extreme bounds of observed ratios. $M/K = 1.5$ is proposed as an evolutionary ratio, providing a fitness advantage because the peak in gamete production coincides with the peak in the production of new tissue.

These three numbers are known as 'Beverton and Holt life history invariants' (Jensen 1996; Prince *et al.* 2015) and were derived from optimization of age at first maturity (Roff 1984) with the assumption that all species mature around $L_{\text{opt}}/L_{\text{inf}} = 2/3$, which is clearly not the case (Froese and Pauly 2013). As argued above, it suffices to assume that fecundity is proportional to body weight (Gunderson 1997) and that individuals are reproductively active at the peak of cohort biomass (Froese and Pauly 2013), which then becomes the peak of cohort fecundity and the peak of offspring production. A fitness advantage is then derived from the fact that with $M/K = 1.5$, the peak in cohort reproduction coincides with the average peak in somatic growth rate of cohort members, meaning that at the time when most offspring are produced, their parents are capable of producing the highest amount of extra tissue per unit time.

In summary, it can be argued that the M/K ratio, which is a key component of the equations used in this study, provides an evolutionary advantageous alignment of fecundity with somatic growth at a value of 1.5.

Minimizing the impact of fishing

Minimizing the impact of fishing on a population means that close-to-natural numbers of individuals should participate in important life history events. One such event is maturation, and the rules proposed here would ensure that in species with multiple spawning events, the number of individuals reaching maturation is not reduced by fishing. A second such event is reaching the size and age where the somatic growth rate is maximum and where a fitness advantage is gained if the peak of expected offspring production happens at this stage. The rules proposed here ensure that the individuals in the exploited part of the population reach that age and size on average. But there are two other important population traits that have not yet been used in fisheries management. The first is the average duration of the reproductive phase. If total mortality $Z = M + F$ is reasonably constant after the age where fish reach maturity, then the average duration of the reproductive phase is simply the inverse of Z (Charnov 1993). Thus, in the example for North Sea cod with $M = 0.21$, the average duration of the reproductive phase without fishing is 4.8 years. Fishing throughout the reproductive phase with the actual

fishing mortality of 2014 of $F = 0.39$ results in $1/Z = 1.7$ years or 35% of the natural duration. In contrast, starting fishing at L_{c_opt} with $F = 0.5 \cdot M$ results in a mean total mortality rate $Z_{\text{mean}} = 0.3$ and an average duration of the reproductive phase of 3.3 years or 69% of the natural duration, a substantial reduction of the impact of fishing.

The second population trait that has not been used in fisheries management is the mean body weight of spawners, which is related to mean fecundity by the gonadosomatic index (Gunderson 1997). In the example for North Sea cod, predicted mean body weight of spawners in the unexploited stock is about 8.0 kg (see Equation A23 in Appendix 1). For the exploitation scenario of 2014, predicted mean body weight of spawners is 4.4 kg or 55% of the natural weight and fecundity. In contrast, starting fishing at L_{c_opt} with $F = 0.5 \cdot M$ results in a predicted mean body weight of spawners of 6.5 kg or 81% of the natural weight and fecundity, again a substantial reduction of the impact of fishing (see Equation A22 in Appendix 1).

In summary, the proposed three rules would reduce the impact of fishing by ensuring that all fish reach maturation, that the age of maximum growth rate and natural generation time is reached on average in the exploited part of the population, that mean duration of the reproductive phase is not less than 69% of the natural duration, and that mean body weight and fecundity of spawners are not less than 81% of the unexploited levels.

Economic considerations

The main economic driver of commercial fishing is profitability, which is determined by the discounted value of the difference between the market value of the catch and the cost of fishing (Clark 1990; Sumaila *et al.* 2012). It is customary in the fisheries economics literature to assume that the variable cost of fishing increases about linearly with fishing effort (Clark 1990), which is itself proportional to fishing mortality F (Beverton and Holt 1966). A break-even point, known as the open access or bionomic equilibrium (Clark and Munro 1975), is reached when the value of the catch equals the cost of fishing. Here, four scenarios are explored, where the break-even points are reached at relative fishing mortalities from $F/M = 1$ to $F/M = 4$ (Fig. 4). For fishing with $F = M$ and

$L_c = L_{c_opt}$, these cost scenarios correspond to profit margins of 0%, 44%, 60% and 70%, respectively. The average profit margin of the European fleet in 2012 was 6.6% (STECF 2014) with an average fishing mortality of about $F/M = 1.75$, which would give a break-even point (i.e. no profit) near $F/M = 2$, that is close to the second scenario. Scenario 1 with break-even at $F/M = 1$ would represent a fishery with either low value of the catch, such as in mixed demersal fisheries for fish meal, or high cost of fishing, such as in deep-sea trawl fisheries, or both. Scenarios 3 and 4 would represent highly profitable fisheries on high-value fish at relatively low cost, such as in some tuna fisheries.

Notably, with fishing starting at L_{c_opt} , maximum profits are obtained in all scenarios at fishing mortalities below natural mortality. In contrast, fishing at $F = M$ without size limits results in large losses for scenario 1, zero profit for scenario 2 and much reduced profits for scenarios 3 and 4.

These simple economic considerations are consistent with a proxy for the biomass that can produce the maximum economic yield $B_{mey} = 1.2 \cdot B_{msy}$ used in Australian fisheries management (Punt et al. 2013). Studies across different Australian stocks have shown that a biomass that is about 20% higher than the one that can produce the maximum sustainable yield maximizes economic returns. Similarly, simulation testing of

proxies for B_{mey} suggests that depletion levels in the range $0.5\text{--}0.7 \times B_0$ typically maximize profit (Punt et al. 2013). The rules presented in this study ensure that biomass of exploited populations remains within that range.

Note that yield is the product of fishing mortality and annual exploitable biomass. To obtain the maximum yield for a given F , length at first capture can be increased to allow for a longer unexploited growth phase, until exploitable biomass and therefore catch per unit effort (CPUE) reach a maximum. Consequently, if exploitable biomass or CPUE was plotted as a function of F , the CPUE curves for L_{c_max} and L_{c_opt} would overlap similar to the yield curves shown in Fig. 2. In other words, the gain in cohort biomass when fishing starts at a slightly larger size than needed to maximize yield is not countered by a notable reduction in catch or increase in cost of fishing; these economic indicators both remain near their theoretical optimum for a given F . This surprising result stems from the fact that the yield isopleths in a yield per recruit diagram, at their intersection with L_{c_max} (see B' curve in Fig. 17.14 of Beverton and Holt 1957; p. 318), run nearly parallel to the length at first capture axis, and therefore a modest increase in L_c from L_{c_max} to L_{c_opt} (Fig. 1) results in about the same exploitable biomass, CPUE and yield, but in a larger total biomass (Fig. 2).

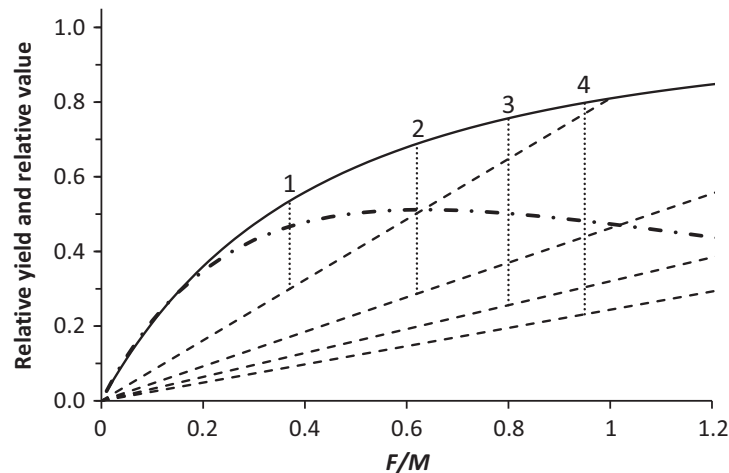


Figure 4 Relative yield and value as a function of fishing pressure F/M with fishing starting at L_{c_opt} . Illustrated are four different scenarios for the cost of fishing (dashed lines). The scenarios are differentiated by break-even points at $F/M = 1$ to $F/M = 4$, where the cost of fishing equals the value of the catch. The vertical dotted lines indicate the maximum profit that can be obtained under a given cost scenario. Note that in all cost scenarios, maximum economic yield is obtained at fishing mortality rates below the natural mortality rate. The dot-dashed curve indicates fishing without size limits, leading to much reduced or negative profit margins.

In conclusion, if fishing starts at L_{c_opt} and if realistic costs of fishing are assumed, profits are maximized at fishing mortality rates below natural mortality, with corresponding stock sizes above half of unexploited stock size.

Towards ecosystem-based fisheries management

One of the goals of ecosystem-based fisheries management is to minimize the impact of fishing on size and age-structure of exploited populations (Marine Strategy Framework Directive 2008). Life history data for North Sea cod were used to explore the impacts of different fishing regimes on cohort biomass (Fig. 5a). Under an L_{c_opt} fishing scenario with $F = M$, biomass is still unexploited at the length of maturity and reasonably high at L_{opt} (62% of unexploited biomass). In comparison, fishing North Sea cod with $F = M$ starting at the current legal length of $L_l = 35$ cm results in reduced biomass at maturity and a biomass of only 30% of unexploited biomass at L_{opt} . Fishing without size limits reduces biomass even further, especially if higher M and therefore also higher F values are applied to pre-recruits, as advocated in some recent publications (Garcia *et al.* 2012; Law *et al.* 2015; but see critique in Froese *et al.* 2015b), and as indicated in the 'no-size-limit' curve in Fig. 5a. With regard to size-structure of the population (Fig. 5b), the number of surviving individuals declines about linearly with length in the absence of fishing. Starting fishing at L_{c_opt} allows all fish to reproduce before capture, allows about two-third of the fish to reach full growth potential (at L_{opt}) and has an overall much reduced impact on size-structure compared to starting fishing at legal length or without size limits.

Note that while we have used cod as a convenient example of a highly commercial species, the same principles apply to other fish and to invertebrates. Application of the three rules to all exploited species may achieve several goals of ecosystem-based fisheries management (Pikitch *et al.* 2004), such as rebuilding the biomass of prey and predator species in the ecosystem and reducing collateral impacts of fishing, such as by-catch and habitat disturbance, because with larger stock sizes and higher catch per unit effort, less duration of gear deployment is needed for a given catch and more selective gears such as traps can replace unselective gears such as trawls. For example, medieval fishers have caught North Sea cod mostly at

sizes between 80 and 120 cm, that is roughly L_{c_opt} to L_{opt} for a fish that could get to 180 cm in length. The fishing mortality at the time was probably well below natural mortality. This historical application of the three rules resulted in a fishery that was sustained over hundreds of years, without a noticeable decline in mean length (Barrett *et al.* 1999; Harland and Parks 2008), suggesting a sustainable fishery with catches probably above current catches. More generally, ecosystem modeling shows that keeping exploited stocks above half of their unexploited level with exploitation rates of about half of the maximum sustainable level strongly reduces the impact on other ecosystem components while still achieving high catches (Eddy *et al.* 2015; Tyler *et al.* 2015).

In summary, while the three rules do not deal with all aspects of ecosystem-based fisheries management, such as discards, destructive gears, mixed fisheries, community structure, habitat restoration, system optimization or protection of threatened species, they go a long way in restoring ecosystem biomass and reducing human impact while maintaining highly profitable fisheries.

Refuting calls for unselective fishing

The proposed simple rules for fisheries management are in stark contrast to recent calls for unselective fishing or 'balanced harvesting' (Garcia *et al.* 2012; Kolding and Van Zwieten 2014; Law *et al.* 2015). The concept suggests fishing of all species and of all size-classes above larvae at their respective productivity levels. Such fishing without size limits is predicted to increase catches and reduce ecosystem impacts. However, fishing indiscriminately all species from worms to whales and from kelp to corals runs counter to global efforts and laws aiming at protection of threatened species and vulnerable ecosystems and avoidance of the capture of unwanted species (UN 1992; Marine Strategy Framework Directive 2008; Common Fisheries Policy 2013). More importantly, the proposed indiscriminate fishing of all size-classes ignores the fact that members of a small size-class consist of small species as well as of the young of all larger species (Froese *et al.* 2015a). As a result, 'balanced harvesting' would catch most fish well before they had a chance to grow and reproduce, at fishing intensities equal to the productivity level of the small size-classes that is well above adult mortality levels. The benefits of letting fish grow

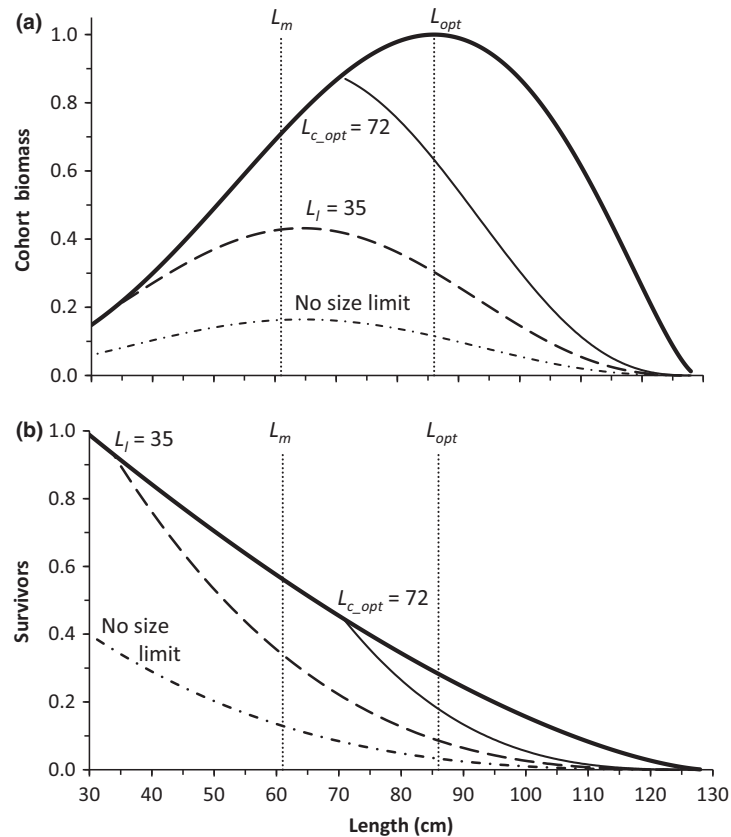


Figure 5 (a) Cohort biomass relative to maximum and (b) fraction of surviving recruits over body length, based on life history data for North Sea cod with recruitment at about 30 cm and mean natural mortality of 0.21. Included are indications of the length L_m where individuals reach maturity and the length L_{opt} where cohort biomass reaches a maximum. The bold curve indicates no fishing. The three other curves indicate fishing with $F = M$, but with fishing starting at different lengths. The solid curve results if fishing starts at $L_{c_opt} = 72$ cm, resulting in a mean length in the catch equal to L_{opt} and also in the highest catch (see Fig. 2). The long-dashed curve indicates biomass when fishing starts at the legal minimum landing length of 35 cm. The dot-dashed curve indicates fishing of the smallest possible size, here assumed at 6 cm, with natural and fishing mortality of pre-recruits at twice the adult level.

before they are caught have been demonstrated in countless studies (Beverton and Holt 1957; Garcia and Demetropoulos 1986; Froese 2004; Froese et al. 2008; Brunel and Piet 2013; Chávez et al. 2013; Maravelias et al. 2014). As the equations and figures in this study clearly show, starting fishing of large species such as cod at their early life stages leads to severely reduced recruitment, biomass and size-structure and may result in the extinction of slow-growing species such as sharks.

Caveats associated with the proposed rules

This section lists some of the cases where the proposed rules have to be applied with caution or with additional considerations.

For example, if there is strong sexual dimorphism in a species, such as in Greenland halibut (*Reinhardtius hippoglossoides* Pleuronectidae), then the rules shall be applied to the larger, or later maturing sex. The reasoning is that less fishing of the smaller sex may result in a distorted sex ratio, but applying the rules to the smaller sex would result in a distorted sex ratio as well as in over-fishing of the larger sex.

In semelparous species that die after spawning, such as salmon, squid or eels, postponing fishing until after maturity is of course not an option. But starting modest fishing shortly before the spawning event will still reduce impact on the stock while assuring high and profitable catches.

In some species, the gonadosomatic index is not more or less constant (Gunderson 1997) but increases with body weight. In such cases, the peak in cohort fecundity would occur after the peak in cohort biomass and management might consider postponing even further the onset of fishing than suggested by L_{c_opt} .

In species with alternating cycles of high and very low recruitment, such as Blue whiting (*Micromesistius poutassou* Gadidae), the assumption of average recruitment at large biomass does not hold. However, the build-up of a large spawning stock biomass and the improved size and age-structure resulting from the application of the three rules during periods of high recruitment will act as a buffer during periods of low recruitment and are likely to prevent the near-collapse scenarios visible under current management (Froese et al. 2011).

Application of the three rules in practical management requires knowledge of the M/K ratio, the current F/M ratio, the current B/B_0 ratio and the current L_c/L_∞ ratio. These ratios are typically known in fully assessed stocks or can be derived from the equations given in the Appendix 1. Also, in the context of a maximum sustainable yield framework, managers could decide to replace F/M with F/F_{msy} (if F_{msy} estimates are reasonably close to M) and $B/(0.5 \cdot B_0)$ with B/B_{msy} . For application in data-limited stocks, Equation A29 in Appendix 1 allows the estimation of the F/M ratio and Equation A30 can be used to estimate the mean length in the catch that would be indicative of $F = M$. In extreme data-poor situations, enforcing a minimum length of half the maximum length and regulating fishing effort such that the mean length in the catch is about 2/3 of maximum length may go a long way towards a sustainable and profitable fishery.

Conclusion

Shifting from the current approach of maximum acceptable ecological impact to the principle of minimizing impact is a major conceptual change with substantial consequences for fisheries research and management (Gascuel et al. 2011). Our results show that reducing impact and increasing catches are not mutually exclusive goals if size at first capture is adjusted properly. The proposed rules would also achieve some of the goals of ecosystem-based fisheries management, such as rebuilding biomass of prey and predator species and reducing capture of unwanted or threatened species and of collateral

damage to the ecosystem. It is hoped that the simple rules for fisheries management presented in this study will be accepted as a reminder of the basic concepts of fisheries science and will contribute to sustainable, high-quality food supply from a healthy future ocean.

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Appendix 1

This Appendix presents the equations and assumptions behind the results, graphs and conclusion of this study. References cited in this Appendix can be found in the References section of this study. Spreadsheet implementations of the equations can be found in the online material of this study.

Growth in body length follows the von Bertalanffy growth equation (Von Bertalanffy 1938):

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (A1)$$

where L_t is the length at age t , L_∞ is the asymptotic length, K is the rate by which L_∞ is approached, and t_0 is the theoretical age at zero length. The age t_L corresponding to a given length is obtained from

$$t_L = t_0 - \frac{\ln\left(1 - \frac{L_t}{L_\infty}\right)}{K} \quad (A2)$$

Growth in weight also follows the von Bertalanffy growth equation:

$$W_t = W_\infty(1 - e^{-K(t-t_0)})^b \quad (A3)$$

where W_t is the body weight at age t , W_∞ is the asymptotic body weight and b is the exponent of the length–weight relationship $W = a L^b$. This exponent is typically close to three (Froese 2006) and was set in the subsequent models to $b = 3$ to facilitate integration.

As derivative of Equation A3, the instantaneous growth rate dW/dt is given by

$$dW/dt = 3KW_\infty \left(\left(1 - e^{-K(t-t_0)}\right)^2 - \left(1 - e^{-K(t-t_0)}\right)^3 \right) \quad (A4)$$

This growth rate has a maximum at $0.296 W_\infty$ with a corresponding body length of $2/3 L_\infty$ if $b = 3$. The corresponding age at maximum growth rate is

$$t_{\max dW/dt} = \frac{\ln(3)}{K} + t_0 \quad (A5)$$

The body weight W_{opt} where unexploited cohort biomass reaches a maximum is given by Holt (1958) as

$$W_{\text{opt}} = W_\infty \left(\frac{K}{K + \frac{M}{3}} \right)^3 \quad (A6)$$

where M is the average rate of natural mortality. The length L_{opt} corresponding to W_{opt} is given by Beverton (1992) as

$$L_{\text{opt}} = L_\infty \frac{3}{3 + \frac{M}{K}} \quad (A7)$$

The age at the peak of unexploited cohort biomass t_{opt} is given by replacing L_t in Equation A2 with L_{opt} .

$$t_{\text{opt}} = \frac{\ln\left(\frac{3K+M}{M}\right)}{K} + t_0 \quad (\text{A8})$$

The mean age in the spawning stock is given by

$$t_{\text{mean}} = t_m + \frac{1}{Z_{\text{mean}}} \quad (\text{A9})$$

where t_m is the mean age at first maturity, and Z_{mean} is the mean total annual mortality rate experienced after reaching t_m . The inverse of Z_{mean} is the average life expectancy (Charnov 1993) after reaching t_m , or the mean duration of the reproductive phase. The mean age of spawners in the unexploited stock is obtained by setting $Z_{\text{mean}} = M$ in Equation A9. If fishing starts before or at maturity, then $Z_{\text{mean}} = M + F$, where F is the rate of mortality caused by fishing. If fishing starts after maturity, then Z_{mean} can be approximated from

$$Z_{\text{mean}} = F + M - FMt_c + FMt_m \quad (\text{A10})$$

where t_c is the age at first capture.

The mean length L_{mean} in the catch and in the exploited part of the population is corresponding to (Beverton and Holt 1957)

$$L_{\text{mean}} = L_{\infty} \left(1 - \frac{(F+M)e^{-K(t_c-t_0)}}{F+M+K} \right) \quad (\text{A11})$$

Replacing age t_c with length at first capture L_c , based on Equation A2, and using the ratios F/M and M/K gives

$$L_{\text{mean}} = L_{\infty} \left\{ 1 - \frac{F/M + 1}{F/M + 1 + \frac{1}{M/K}} \left(1 - \frac{L_c}{L_{\infty}} \right) \right\} \quad (\text{A12})$$

Setting $L_{\text{mean}} = L_{\text{opt}}$ and solving for L_c gives the length at first capture L_{c_opt} that results in the mean length of L_{opt} in the catch and in the exploited part of the population (solid curve in Fig. 1, with $M/K = 1.5$).

$$L_{c_opt} = L_{\infty} \frac{2 + 3F/M}{(1 + F/M)(3 + M/K)} \quad (\text{A13})$$

The age t_{c_opt} corresponding to L_{c_opt} is obtained by inserting Equation A13 into Equation A2

$$t_{c_opt} = \frac{\ln\left(\frac{(F+M)(3K+M)}{M(F+K+M)}\right)}{K} + t_0 \quad (\text{A14})$$

Equations A13 and A14 are new and can be used to implement rule 3 as proposed in this study.

An index of yield per recruit expressed as a function of the length at first capture L_c is given by Beverton and Holt (1966) as

$$\frac{Y'}{R} = \frac{F/M}{1 + F/M} (1 - L_c/L_{\infty})^{M/K} \left(1 - \frac{3(1 - L_c/L_{\infty})}{1 + \frac{1}{M/K(1+F/M)}} + \frac{3(1 - L_c/L_{\infty})^2}{1 + \frac{2}{M/K(1+F/M)}} - \frac{(1 - L_c/L_{\infty})^3}{1 + \frac{3}{M/K(1+F/M)}} \right) \quad (\text{A15})$$

The relative length at first capture L_c/L_{∞} that results in the maximum Y'/R for a given fishing intensity F/M can only be obtained iteratively from Equation A15 (dashed curve in Fig. 1).

The theoretical maximum yield per recruit can be obtained with infinite fishing mortality at $L_c = L_{\text{opt}}$. It was named potential yield Y_{pot}/R (Holt 1958). An index of the potential yield per recruit is given by Holt (1958) as

$$\frac{Y'_{\text{pot}}}{R} = \max \frac{Y'}{R} = \left(\frac{M/K}{3 + M/K} \right)^{M/K} \left(\frac{3}{3 + M/K} \right)^3 \quad (\text{A16})$$

The ratio Y'/Y'_{pot} is equal to Y/Y_{pot} and then indicates yield relative to the theoretical maximum yield Y_{pot} , that is the fact that both yields were indices need not be considered anymore. This ratio was used for drawing relative yield in Figs 2, 3 and 5.

An index of catch per unit of effort (CPUE'/R) is obtained by dividing Equation A15 by the fishing intensity F/M , assuming that F is directly proportional to effort. As CPUE is proportional to biomass in the exploited phase of the stock, Equation A17 represents relative CPUE'/R as well as an index of exploited biomass per recruit B'/R (Beverton and Holt 1966):

$$\frac{\text{CPUE}'}{R} = \frac{Y'/R}{F/M} = \frac{1}{1 + F/M} (1 - L_c/L_{\infty})^{M/K} \left(1 - \frac{3(1 - L_c/L_{\infty})}{1 + \frac{1}{M/K(1+F/M)}} + \frac{3(1 - L_c/L_{\infty})^2}{1 + \frac{2}{M/K(1+F/M)}} - \frac{(1 - L_c/L_{\infty})^3}{1 + \frac{3}{M/K(1+F/M)}} \right) \quad (\text{A17})$$

The relative biomass per recruit without fishing is a function of relative length at recruitment $r = L_r/L_{\infty}$ and M/K and is given by

$$\frac{B_0'}{R} = (1-r)^{\frac{M}{K}} \left(1 - \frac{3(1-r)}{1 + \frac{1}{M/K}} + \frac{3(1-r)^2}{1 + \frac{2}{M/K}} - \frac{(1-r)^3}{1 + \frac{3}{M/K}} \right) \quad (A18)$$

The relative biomass in the exploited phase of the population if no fishing takes place is given by

$$\frac{B_0' > L_c}{R} = (1 - L_c/L_\infty)^{M/K} \left(1 - \frac{3(1 - L_c/L_\infty)}{1 + \frac{1}{M/K}} + \frac{3(1 - L_c/L_\infty)^2}{1 + \frac{2}{M/K}} - \frac{(1 - L_c/L_\infty)^3}{1 + \frac{3}{M/K}} \right) \quad (A19)$$

The total biomass of the exploited population relative to the unexploited population B/B_0 can then be obtained from

$$\frac{B}{B_0} = \frac{\frac{B_0'}{R} - \frac{B_0' > L_c}{R} + \frac{CPUE'}{R}}{\frac{B_0'}{R}} \quad (A20)$$

Equation A20 was used to draw relative biomass in Fig. 2, assuming an M/K ratio of 1.5. The fishing mortality $F_{0.5B}$ that results in half of B_0 (Rule 2) when fishing starts at L_{c_opt} was obtained iteratively as $F_{0.5B} = 0.86 \cdot M$.

The slope at the origin of the yield per recruit curve Q/R is given by Holt (Holt 1958) as

$$Q/R = \frac{6W_\infty K^3}{M(M+K)(M+2K)(M+3K)} \quad (A21)$$

The value of F where the slope of the Y/R curve equals 0.1 Q/R or the value of F/M where the increase in Y/R is close to 1/10th of the increase near the origin is the arbitrary fisheries reference point $F_{0.1}$.

The relative mean body weight in the catch and in the exploited phase of the population is given by

$$\frac{W_{\text{mean}}}{W_\infty} = 1 - \frac{3(1 - L_c/L_\infty)}{1 + \frac{1}{M/K(1+F/M)}} + \frac{3(1 - L_c/L_\infty)^2}{1 + \frac{2}{M/K(1+F/M)}} - \frac{(1 - L_c/L_\infty)^3}{1 + \frac{3}{M/K(1+F/M)}} \quad (A22)$$

Mean body weight above a certain length L_c in the unexploited population is given by

$$\frac{W_{\text{mean}}}{W_\infty} = 1 - \frac{3(1 - L_c/L_\infty)}{1 + \frac{1}{M/K}} + \frac{3(1 - L_c/L_\infty)^2}{1 + \frac{2}{M/K}} - \frac{(1 - L_c/L_\infty)^3}{1 + \frac{3}{M/K}} \quad (A23)$$

It is argued in the main text that a value of 1.5 for the M/K ratio would increase fitness. Under this evolutionary M/K ratio, several equations simplify considerably.

$$L_{\text{opt}} = 0.67L_\infty \quad (A24)$$

$$W_{\text{opt}} = 0.296W_\infty \quad (A25)$$

$$t_{\text{opt}} = \frac{\ln(3)}{K} + t_0 = t_{\text{max } dW/dt} \approx \frac{1.1}{K} \approx \frac{1.65}{M} \quad (A26)$$

$$L_{c_opt} = L_\infty \frac{4 + 6F/M}{9 + 9F/M} \quad (A27)$$

$$t_{c_opt} = \frac{3 \ln\left(\frac{9(F/M+1)}{3F/M+5}\right)}{2} + t_0 \quad (A28)$$

In data-poor situations, the F/M ratio can then be approximated from the mean length in the catch.

$$\frac{F}{M} = \frac{2(L_\infty - L_{\text{mean}})}{3(L_{\text{mean}} - L_c)} - 1 \quad (A29)$$

The theoretical mean length in the catch where $F = M$ can be estimated from

$$L_{F=M} = \frac{3L_c + L_\infty}{4} \quad (A30)$$

[Correction added on 26 April, 2016, after first online publication: The equation (A29) has been modified].