# Does size matter? A bioeconomic perspective on optimal harvesting when price is size-dependent 

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#### Abstract

Body size is a key parameter influencing demographic characteristics of fish populations as well as market value of landed catch. Yet in bioeconomic modelling body size is often an overlooked biological and economic parameter. Here we evaluate how sizedependent pricing influences optimal harvest strategies in a model parameterized for two pelagic fisheries, those targeting Atlantic herring (Clupea harengus) and Atlantic mackerel (Scomber scombrus) in Norway. In our model, positively size-dependent pricing clearly shifts optimal harvest strategies towards lower harvest rates and higher mean body size of caught fish. The results are relatively insensitive to biological (e.g., natural mortality) and economic details of the model (e.g., discount rate or demand function). These findings show that size-dependent pricing influences optimal harvest strategies aiming at maximum economic yield, and hence, require more attention in resource economics and in fisheries management.


Keywords: Bioeconomic modelling, fisheries management, optimal harvest strategies, sizedependent pricing

## Introduction

It is common that price of fish depends on their size; typically, large individuals fetch a higher price per kilogram than small individuals of the same species. When present, such size dependence should be considered when evaluating harvest strategies (Hilborn and Walters 1992). While size-dependent pricing is occasionally included in bioeconomic models, it is very rare that the consequences of size-dependent pricing per se have been studied in any detail. We are aware of only few studies where this question has been touched: Gallagher et al. (2004) and Holland et al. (2005) showed that for Oregon ocean shrimp (Pandalus jordani) and rock lobster (Jasus edwardsii), respectively, size-related pricing indeed influences management strategies. Similarly, Tahvonen (2009) demonstrated in a generic age-structured model how equilibrium revenue and stock size are affected by size-dependent pricing. More typically, size-dependent pricing has been either overlooked, acknowledged but not analyzed (Anderson 1989), or taken as an extrinsically determined model component that is kept fixed in the analysis (e.g., Thunberg et al. 1998, De Leo and Gatto 2001, Katsukawa 2005). Some studies also acknowledge other biological factors influencing price, e.g., seasonal changes in fish quality (Larkin and Sylvia 1999). Sizedependent pricing is also important in aquaculture (Bjørndal 1988, Asche and Guttormsen 2001). Thus, we have all reasons to expect that the size dependency of the price is widespread and highly relevant for optimal utilization of fish stocks.

Here our aim is to quantify how size-dependent pricing influences optimal harvest strategies. We use Atlantic herring (Clupea harengus) and Atlantic mackerel (Scomber scombrus) as case studies. Specifically, we focus on the Norwegian spring spawning herring stock and the Northeast Atlantic mackerel stock, following the stock definitions used in the management (ICES 2010a). Herring and mackerel are of major importance for the fisheries of several European countries, with a total catch of respectively about 1.7 and 0.7 million
tonnes in 2009 (ICES 2010a). Moreover, herring and mackerel are key species in the northeast Atlantic pelagic ecosystem (Skjoldal et al. 2004), making their sustainable management even more important.

We utilize an age-structured, discrete-time population model with size-dependent harvesting. Price data are based on Norwegian market data for herring and mackerel. For simplicity we assume that the relationship between size and price is linear; this allows us to smoothly vary the strength of size dependency, in contrast to the earlier studies that only considered a limited set of fixed pricing scenarios (Gallagher, et al. 2004, Holland, et al. 2005) The cost of harvesting is output-regulated and depends on yield. In the optimization the main target is to maximize the net present value over a long time-scale with discount rates on an efficient market level, while high discount factors are used to emulate an openaccess situation. We show how optimal fishing mortality and resulting mean individual weight in the catch depends on the size dependency of pricing. We also estimate the shadow cost, i.e., the opportunity costs for applying a suboptimal harvest regime and the lost margin of benefit due to ignoring the size dependency of pricing.

## Methods

## Biological model

The biological model is based on an age-structured population dynamics model with annual time steps. Sexes are combined because male and female life histories are similar in herring and mackerel. The parameters and their values are listed in Table A1 (Appendix).

There are $n$ discrete age classes denoted by $N_{a}$ with $a=1,2, . ., n$, and there is no senescence. The last age class is so-called plus-group representing all fish $n$ years of age or older. Population dynamics is then described by

$$
N_{a}(t+1)=\left\{\begin{array} { c } 
{ r ( \operatorname { S S B } ( t ) ) } \\
{ s _ { a } N _ { a - 1 } ( t ) } \\
{ s _ { n } ( N _ { a - 1 } ( t ) + N _ { a } ( t ) ) }
\end{array} \quad \text { if } \left\{\begin{array}{c}
a=1 \\
1<a<n, \\
a=n
\end{array}\right.\right.
$$

where $S S B$ is the spawning stock biomass, $r(S S B)$ the stock-recruitment function and $s_{a}$ is age-specific survival probability defined below.

The connection between age and size is defined through the von Bertalanffy growth model $l(a)=L_{\infty}\left(1-e^{-k a}\right)$ where $L_{\infty}$ is the asymptotic length and $k$ the growth coefficient. Furthermore, we assume an allometric weight-length relationship $w(l)=v l^{u}$, where $v$ is the length-weight coefficient and $u$ is the allometric exponent.

Reaching maturity is based on the age of the individual and defined by the agematurity ogive $o(a)=\left(1+e^{-(a-a 50) / a_{\text {widh }}}\right)^{-1}$ with $a_{50}$ is the age where $50 \%$ of the individuals have reached maturity and $a_{\text {width }}$ is the coefficient describing width of the maturity envelope. Mature individuals constitute the spawning stock, and spawning stock biomass is defined as $S S B=\sum_{a} w_{a} o_{a} N_{a}(t)$. For herring recruitment follows the Beverton-Holt stock-recruitment model as defined by (Fiksen and Slotte 2002), $r(S S B)=\frac{b_{1} S S B}{b_{2}+S S B}$, where $b_{1}$ is asymptotic maximum recruitment and $b_{2}$ determines how fast the asymptote is approached. For mackerel we use the hockey-stick recruitment model estimated by ICES (2010) implying that below a threshold $S S B_{\max }$ recruitment is a linear, increasing function of $\operatorname{SSB}$, $r(S S B)=b_{3} S S B$, whereas above the threshold recruitment is assumed to be constant, $r(S S B)=r_{\text {max }}$.

The fishing mortality is assumed to be length-dependent. Catchability usually increases with size until levelling off at some intermediate size, a relationship usually
described by a sigmoid curve. However, in our study stocks, no such levelling-off can be detected between fishing mortality (mean fishing mortality at age from 1984-2009; ICES 2010) and length-at-age (from the growth model described above): for mackerel, the threeparameter sigmoid model fails to converge, whereas for herring the inflection point in the resulting fit is far outside the range of observed lengths. Within the range of observed lengths, a two-parameter power function and the sigmoid function predict similar fishing mortalities for mackerel, but the power function gives a lower AIC (difference 2.0) than the sigmoid function. The relationship between fishing mortality and length is therefore most parsimoniously described as a power function for both stocks. Here we normalize length relative to mean catch length $\bar{l}$, such that

$$
\begin{equation*}
F_{a}=F(l(a))=F_{0}(l / \bar{l})^{n}, \tag{1}
\end{equation*}
$$

where $F_{0}$ is fishing mortality at mean catch length and $\eta$ is a selectivity parameter that determines the strength of length dependency; the function is convex for $\eta>1$. The equation was fitted to fishing mortality at age data from (ICES 2010a), transforming age into length using the von Bertalanffy model described above. Mean catch length $\bar{l}$ used in the normalization was estimated through back calculation of mean catch weight based on weight at age in the ICES catch from 2009 (ICES 2010a).

The natural mortality $M$ is based on the values used in the stock assessment (ICES 2010). The survival probability $s$ is determined by the total mortality $Z$, which is the sum of fishing mortality $F$ and natural mortality $M: s_{a}=e^{-Z_{a}}=e^{-\left(F_{a}+M_{a}\right)}$

The link between the biological and economic part of the model is the catch equation, $H_{a}=N_{a}\left(1-e^{-Z_{a}}\right) F_{a} / Z_{a}$, where $H_{a}$ is catch numbers at age. Total catch in terms of
biomass, or yield, is catch numbers times the mean age-specific individual weight,

$$
Y=\sum_{a} H_{a} w_{a} .
$$

## Economics

We assume that the relationship between size and price can be expressed as a simple linear function of weight, such that we can easily change the strength of size dependence. To make the parameters easily interpretable, we standardize weight relative to the mean observed individual catch weight over all age classes, $\bar{w}$. Furthermore, we standardize the price-weight coefficient relative to the observed coefficient, $\beta_{0}$. The price function is then $p(w)=p_{\bar{w}}+\beta \beta_{0}\left(\frac{w-\bar{w}}{\bar{w}}\right)$, where the intercept $p_{\bar{w}}$ is the price per unit biomass for $\bar{w}$, the observed slope $\beta_{0}$ gives the price increase when individual weight is increased by $\bar{w}$, and $\beta$ is the relative deviation from the observed slope. $\bar{w}$ thus acts as the pivot point in this function. The parameters $p_{\bar{w}}$ and $\beta_{0}$ of the price function (Figure 1) were estimated with linear regression using data provided by the Norwegian Fisheries Directorate (Per Sandberg, personal communication). The data comprise of total annual yield and value per weight class in 2000-2010 as registered by the sales organizations. Average prices per weight class are derived from these data. To obtain mean weight for each weight class, we assumed that weight at age in the catch is normally distributed with mean taken from ICES (2010) and coefficient of variation of $30 \%$. We then multiplied the age-specific weight distributions with catch numbers at age (ICES 2010) to obtain total weight distribution in a given year, which allows estimating the mean weight for a certain weight class as well as the overall mean weight $\bar{w}$. Mean price $p_{\bar{w}}$ was derived from the data from the Norwegian Fisheries Directorate.

We also considered constraining the influence of size on price. As the minimum price we used the minimum price set by the Norwegian pelagic fish sales organisation, which was $0.60 \mathrm{NOK} \cdot \mathrm{kg}^{-1}$ for both herring and mackerel in 2010 (Norges Sildesalgslaget 2011). As the maximum we used the highest mean price in 2010 , which was $4.16 \mathrm{NOK} \cdot \mathrm{kg}^{-1}$ for herring and 11.7 NOK $\cdot \mathrm{kg}^{-1}$ for mackerel.

The total revenue is the sum of the annual yield times the weight-dependent price for each age class, $R_{t}=\sum_{a} p\left(w_{a}\right) Y_{a}$. The cost function is derived from the model of Touzeau et al. (2000). To avoid potential complications due to the nonlinearity of this cost curve, a simplified cost function with a linear relationship between yield and cost based on a linear regression of the cost function of Touzeau et al. (2000), $C_{t}=C_{0}+v Y_{t}$, has been used. Here the intercept $C_{0}$ represents fixed costs and the term $v Y_{t}$ variable costs. The net revenue is then $\Pi_{t}=R_{t}-C_{t}$. With $d$ denoting discount rate, the net present value is the sum of annual discounted net revenues:

$$
N P V=\sum_{0}^{t} \frac{\Pi_{t}}{(1+d)^{t}}
$$

We tested a demand function estimated from Norwegian yield and price data in 2000-2009. However, the resulting fit was poor because the lack of information about willingness to pay outside the narrow range of actual production volumes and because of other factors influencing the price. Sensitivity analysis showed no significant influence on the results, and therefore demand effects were not considered further in this study. However, because of this, and the simple cost function used, we emphasize that we do not expect the model to give precise quantitative predictions, even though the results shown are qualitatively robust.

## Simulations

The model was run over 1000 years, an essentially infinite time horizon unless discount rate is very low ( $d<0.01$ ). The first 200 years were used to establish pre-fishing equilibrium. Fishing started from the virgin stock at year 200, causing the stock to decline towards a new equilibrium.. It is assumed that size selectivity of the fisheries is fixed, but that the managers can adjust the overall level of fishing mortality such that net present value (NPV) of the stock is maximized. Harvest strategies in our model are therefore defined through the parameter $F_{0}$, fishing mortality at mean catch length. The optimal $F_{0}$ was identified using the function "optimize" in R (R Development Core Team 2010).

## Results

The effect of size-dependent pricing is to shift harvest maximizing net present value (NPV) towards lower values (Figure 2). Comparing the harvest strategy optimized for size dependency of the current pricing regime and one without any size dependency, the shadow cost of omitting the size dependency in the current pricing regime is found to be about $3.3 \%$ for herring and $3.8 \%$ for mackerel relative to the optimal NPV (discount rate $d=0.05$ ). Shadow costs define here the difference in NPV between the optimal harvest strategy with the current, size-dependent price regime and the one that would be optimal when we assume no size-dependent pricing, i.e., the opportunity cost of ignoring size dependency in price.

With increasing effect of size on price (increasing $\beta$ ), the mean fishing mortality that maximizes NPV decreases and the corresponding mean individual size increases (Figure 3); for herring the effect is almost linear within the considered range whereas for mackerel the effect is levelling off for strong size dependence. Mean fishing mortalities (age groups 48 for mackerel and 5-14 weighted by stock numbers for herring) yielding maximum NPV (with discount rate $d=0.05$ ) are 0.146 year $^{-1}$ in the current pricing regime $(\beta=1)$
compared to 0.189 year $^{-1}$ without size-dependent pricing for herring and 0.242 year $^{-1}$ compared to 0.357 year $^{-1}$ for mackerel. For reference, the latest stock assessments estimated fishing mortalities at 0.154 year $^{-1}$ for herring and 0.233 year $^{-1}$ for mackerel (ICES 2010a). In our model, the decrease in mean fishing mortality between no size dependency and a realistic size-dependent pricing is about $23 \%$ for herring and $32 \%$ for mackerel, and the mean catch weight increases by about $6 \%$ and $8 \%$, respectively. The patterns remain similar if the initial stock states are changed from the pristine levels to lower population abundances estimated in the latest stock assessments (ICES 2010a).

The discount rate has no influence on the qualitative effect that size-dependent pricing has on optimal fishing mortality and the corresponding mean size (Figure 3), even when very high discount rates emulating an open-access situation are considered (Figure 4). Nevertheless, the discount rate has a considerable quantitative effect on the optimal fishing mortality: the optimal value increases almost threefold between the extreme cases of no discounting and a very high discount rate of one, mimicking an open-access situation. As theory suggests, the biggest effect on optimal fishing mortality is found on low to intermediate discounting levels.

Because natural mortality is an important parameter in age-structured models, we investigate its influence further. For both species, changing natural mortality results in changes in optimal fishing mortality and, to somewhat lesser extent, in the resulting mean catch weight (Figure 5). These changes are opposite for the two species: higher natural mortality leads to higher optimal fishing mortality for mackerel but lower optimal fishing mortality for herring; these effects are slightly more pronounced for low $\beta$ : an increasing $\beta$ tends to dampen the influence of changing natural mortality. The qualitative difference between the species is caused by the age-dependent natural mortality in herring: assuming a constant natural mortality for herring leads to mackerel-like results. For catch weights, the
influence of changing natural mortality is qualitatively the same for both species: mean catch weight is increased (decreased) by higher (lower) natural mortality.

Comparing the continuous price function with the empirical step functions either in 2009 or 2010 given in Figure 1 shows that the differences are negligible: optimization with discrete price classes displays the same shift between constant price and size dependency and similar quantitative results. The same applies when applying minimum and/or maximum price caps. Additionally, optimal fishing mortality depends on the selectivity parameter $\eta$, but the effect is minor and does not influence the qualitative pattern (Figure 6).

## Discussion

The size of fish is a key parameter from biological as well as technical and economic perspectives. In terms of biology, size is closely linked with growth, maturation, reproductive output and survival. Avoidance of growth overfishing - catching fish too small, before a cohort has realized its growth potential - has been a crucial part of fisheries management since Beverton and Holt (1957). Using minimum size restrictions and mesh size regulations as management tools to protect the productivity of a fish stock reflects this idea. Likewise, the fishing industry has a strong interest in fish size both to optimize the industrial utilization and to serve consumer preferences. Ultimately, these market incentives are a key driver for size-dependent pricing. Yet the connection between price and body size is an understudied issue in fisheries economics. This is surprising given that size-dependent pricing is ubiquitous and that its role in rational harvest management has in theory been acknowledged for a long time (Hilborn and Walters 1992). While a number of studies on capture fisheries have included size-dependent pricing, the majority of these have only considered a single scenario, without studying the effects of size-dependent pricing per se (e.g., Helser, et al. 1996, Thunberg, et al. 1998, Katsukawa 2005). A few studies have included a small number of alternative size-dependent pricing scenarios when analysing
specific fisheries (Gallagher, et al. 2004, Holland, et al. 2005). There are also a few generic models that have included size-dependent pricing (Anderson 1989, Tahvonen 2009). While Anderson (1989) did not elaborate on the importance of size-dependent pricing, Tahvonen (2009) showed with a concrete example how positively (or negatively) size-dependent pricing leads to equilibrium revenues to be maximized at a higher (respectively lower) stock biomass level. The topic has also been discussed outside fisheries economics. For example, price of fish produced in aquaculture is size-dependent, and this has consequences for optimizing the production cycle (Bjørndal 1988, Asche and Guttormsen 2001).

Our goal here was to demonstrate the importance of size-dependent pricing for economically optimal harvest strategies using simple age-structured models parameterized for two important pelagic fish stocks. The results confirm our expectations: fishing pressure maximizing economic yield in terms of revenue and net present value depends on the applied size-based pricing regime, with implications for mean size of fish in the catches and equilibrium stock abundance. The results reveal potential for overestimation of future profits and rent dissipation due to the application of suboptimal harvest strategies when ignoring size-dependent pricing; the effect in the examples studied here is nevertheless quantitatively modest. However, the effect on the resultant harvest strategy is appreciable. Considering that in most commercially important fish stocks the price is size-dependent, the insights presented here call for broader utilization of size-dependent pricing in economic modelling.

When the size-price relationship is monotonic and positive, maximum economic yields are obtained through higher stock sizes and smaller catches than when such size dependence is absent. In other words, positive size-price relationships imply that lower fishing mortalities optimize the net present value. It is acknowledged that catches below MSY typically maximize the resource rent (Clark 2006a, Grafton, et al. 2007, Tietenberg and Lewis 2008). Our results suggest that this effect might even be stronger than MEY
estimates ignoring size-dependent pricing would suggest. Therefore, taking positively sizedependent pricing into account would result in lower harvest rates, which would not only ultimately increase society's direct economic benefits from fisheries, but also reduce the negative effects fisheries might have on the ecosystems. This is in accord with the precautionary approach to fisheries management, calling for more conservative harvest policies that lead to an increased overall stock abundance. This would enhance population resilience, harvest productivity and efficiency.

Our results resonate with the calls to save the big fish for the sake of improved biological sustainability (Birkeland and Dayton 2005, Francis et al. 2007, Diekert, et al. 2010). This statement may seem counterintuitive since we emphasize the high market value of large-sized fish. However, we have focused on a single-owner fishery where the manager adopts a long time perspective, avoiding the short-sighted temptation of targeting the large fish. In our model the opportunity cost of choosing a suboptimal harvest strategy can only be mitigated by reducing the overall fishing mortality, therefore allowing more fish to reach large sizes, and ultimately, leaving more big fish in the sea.

We emphasize that in general, mesh size regulations and other means of modifying size-dependent catchability can be important levers of optimizing the harvest, even though we did not consider them here. Our model applies to pelagic fisheries where effective regulation of size-dependent catchability is difficult; gears like purse seines are weakly sizeselective, and pelagic fish have low survival after slipping through meshes or being strangled in a net. However, demersal fish are often more robust and have better chances of surviving if slipping through meshes or sorting grids, or discarded after the capture. Mesh size regulations can therefore be a means to ensure that enough fish have chance to grow to most valuable size classes. In such cases, economic implications of considering size-dependent pricing are likely larger than what we have found for herring and mackerel here.

We have used the simplest possible price function, a linear relationship between price and weight, as the default price function. While this is a good approximation for herring and mackerel, more complex relationships occur in some fisheries (Thunberg et al. 1998). There is also some evidence that the price premium for larger size disappears for very large mackerel (Fig. 1), a situation which may not be uncommon if very large fish have lower flesh quality, higher concentrations of contaminants, or are less suited for industrial processing. Similarly, if small-sized fish are destined to fish meal production instead of human consumption, their precise size may become unimportant. We therefore also tried constraining the price between certain minimum and/or maximum levels, but this did not change the results in any essential way (the bulk of the harvest comes from medium-sized fish). Additionally, our price function implies continuously increasing effect of size on price, whereas real markets commonly operate with discrete weight classes. While using the real weight classes should give more precise results, our simulations suggest that a linear function is a good approximation. Moreover, market weight classes often vary over time and space. For these reasons we consider a linear approximation as justified here.

Our study has several general limitations. We rely on a single species approach and focus in the steady state scenario without environmental oscillations. Size structure in the model is determined by the age structure using a static age-length relationship. In reality, size structure of the harvestable stock is determined by intra- and inter-specific interactions (availability of resources, and presence of predators). In particular, density-dependent body growth (e.g., Lorenzen and Enberg 2002) might counter the increase in average size that is expected to occur when fishing is reduced and therefore influence management strategies (Helser and Brodziak 1998). A significant source of uncertainty is natural mortality. This is modelled as constant (mackerel) or age-dependent (herring); both assumptions are crude approximations of reality but unfortunately data for more realistic choices are not available.

Also our economic model is rather simplistic, apart from inclusion of size-dependent price. We assume a simple yield-determined cost function, and absence of market feedbacks on price. Our initial explorations suggested that considering effort-dependent costs or demand curves is not important for the questions addressed here. Moreover, developing a more detailed bioeconomic model for mackerel would have been a major task on its own, whereas for herring, more detailed information exists (e.g.,Touzeau, et al. 2000, Sandberg 2006). Finally, the model does not account for practical challenges in balancing stakeholder interests nor policy implementation and enforcement; in reality, suboptimal management due to political and social pressures and illegal fishing are more a rule than an exception (Beddington, et al. 2007, Agnew, et al. 2009, Mora, et al. 2009).

Another angle worth discussing is that of fisheries-induced adaptive changes. Statistical, experimental and modelling approaches are giving increasing support to the hypothesis that fishing causes evolutionary shifts in life-history traits (Jørgensen, et al. 2007, Dunlop, et al. 2009a, Sharpe and Hendry 2009). Because these changes typically involve reduced adult body size (Heino 1998, Enberg, et al. 2011), size-dependent pricing is relevant also when trying to estimate the possible economic impacts of fisheries-induced evolution.

To conclude, this study has highlighted that size-dependent pricing has important implications for fisheries management. Because markets usually value large fish more than small fish, harvest strategies should consider how the harvest influences size structure of the catch: the higher the harvest pressure, the lower the mean size of fish. Therefore, harvest policies that aim at maintaining harvest of large-sized fish lead to lower harvest levels than those that ignore the quality of the catch; ultimately, this might lead to more sustainable harvest and increased economic benefits from the fisheries. We encourage further explorations into consequences of size-dependent pricing on fisheries management, both in
the direction of further generalizations and towards more detailed studies on specific fish stocks and fisheries.

## Acknowledgements

We thank C. Jørgensen and Ø. Fiksen for discussions, P. Sandberg at the Norwegian Directorate of Fisheries for providing the price data, and the Norwegian Research Council for funding (184951/S40). MH and FZ also acknowledge funding from the Bergen Research Foundation.References

## References

Agnew, D.J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J.R., and Pitcher, T.J. 2009. Estimating the worldwide extent of illegal fishing. PLoS One 4(2): e4570 doi: 10.1371/journal.pone. 0004570

Anderson, L.G. 1989. Optimal intra-and interseasonal harvesting strategies when price varies with individual size. Mar. Resour. Econ. 6(2): 145-162

Asche, F., and Guttormsen, A.G. 2001. Patterns in the relative price for different sizes of farmed fish. Mar. Resour. Econ. 16(3): 235-248
Beddington, J.R., Agnew, D.J., and Clark, C.W. 2007. Current problems in the management of marine fisheries. Science 316(5832): 1713-1716 doi: 10.1126/science. 1137362

Beverton, R., and Holt, S. 1957. On the dynamics of exploited fish populations Ministry of Agriculture, Fisheries and Food, London 533
Birkeland, C., and Dayton, P. 2005. The importance in fishery management of leaving the big ones. Trends Ecol. Evol. 20(7): 356-358 doi: 10.1016/j.tree.2005.03.015

Bjørndal, T. 1988. Optimal harvesting of farmed fish. Mar. Resour. Econ. 5: 139-159
Clark, C. 2006. The worldwide crisis in fisheries: economic models and human behavior. Cambridge University Press, Cambridge, UK.
De Leo, G.A., and Gatto, M. 2001. A stochastic bioeconomic analysis of silver eel fisheries.
Ecol. Appl. 11(1): 281-294 doi: 10.1890/1051-
0761(2001)011[0281:ASBAOS]2.0.CO;2]

Diekert, F.K., Hjermann, D., Nævdal, E., and Stenseth, N.C. 2010. Spare the young fsh: Optimal harvesting policies for North-East Arctic cod. Environ. Resource Econ. 47(4): 455-475 doi: 10.1007/s10640-010-9388-z
Dunlop, E.S., Enberg, K., Jørgensen, C., and Heino, M. 2009. Toward Darwinian fisheries management. Evol. Appl. 2(3): 245-259 doi: 10.1111/j.1752-4571.2009.00087.x

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., and Heino, M. 2011. Fishing-induced evolution of growth: concepts, mechanisms, and the empirical evidence. Mar. Ecol. in press
Fiksen, O., and Slotte, A. 2002. Stock-environment recruitment models for Norwegian spring spawning herring (Clupea harengus). Can. J. Fish. Aquat. Sci. 59(2): 211-217 doi: 10.1139/f02-002

Francis, R., Hixon, M., Clarke, M., Murawski, S., and Ralston, S. 2007. Ten commandments for ecosystem-based fisheries scientists. Fisheries 32(5): 217-233
Froese, R., and Pauly, D. 2009. FishBase. Available from www.fishbase.org [accessed 14.03.2009].

Gallagher, C., Hannah, R., and Sylvia, G. 2004. A comparison of yield per recruit and revenue per recruit models for the Oregon ocean shrimp, Pandalus jordani, fishery. Fish. Res. 66(1): 71-84 doi: 10.1016/S0165-7836(03)00147-4

Grafton, R.Q., Kompas, T., and Hilborn, R.W. 2007. Economics of overexploitation revisited. Science 318(5856): 1601

Heino, M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. 55(8): 19711982 doi: 10.1139/cjfas-55-8-1971
Helser, T.E., and Brodziak, J.K.T. 1998. Impacts of density-dependent growth and maturation on assessment advice to rebuild depleted US silver hake (Merluccius bilinearis) stocks. Can. J. Fish. Aquat. Sci. 55(4): 882-892

Helser, T.E., Thunberg, E.M., and Mayo, R.K. 1996. An age-structured bioeconomic simulation of US silver hake fisheries. N. Am. J. Fish. Manage. 16(4): 783-794
Hilborn, R., and Walters, C. 1992. Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty. Chapman \& Hall, New York.

Holland, D.S., Bentley, N., and Lallemand, P. 2005. A bioeconomic analysis of management strategies for rebuilding and maintenance of the NSS rock lobster (Jasus edwardsii) stock in southern New Zealand. Can. J. Fish. Aquat. Sci. 62(7): 1553-1569

ICES. 2010. Report of the Working Group on Widely Distributed Stocks (WGWIDE) ICES CM 2010/ACOM:15, International Council for the Exploration of the Sea (ICES). Jennings, S., and Beverton, R. 1991. Intraspecific variation in the life history tactics of Atlantic herring (Clupea harengus L.) stocks. ICES J. Mar. Sci. 48(1): 117 doi: 10.1093/icesjms/48.1.117

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., and Rijnsdorp, A.D. 2007. Managing evolving fish stocks. Science 318(5854): 1247-1248 doi: 10.1126/science. 1148089
Katsukawa, T. 2005. Evaluation of current and alternative fisheries management scenarios based on spawning-per-recruit (SPR), revenue-per-recruit (RPR), and yield-perrecruit (YPR) diagrams. ICES J. Mar. Sci. 62(5): 841-846 doi: 10.1016/j.icesjms.2005.04.002

Larkin, S.L., and Sylvia, G. 1999. Intrinsic fish characteristics and intraseason production efficiency: a management-level bioeconomic analysis of a commercial fishery. Am. J. Agr. Econ.: 29-43

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. B 269(1486): 49-54

Mora, C., Myers, R.A., Coll, M., Libralato, S., Pitcher, T.J., Sumaila, R.U., Zeller, D., Watson, R., Gaston, K.J., and Worm, B. 2009. Management effectiveness of the world's marine fisheries. PLoS Biol. 7(6): e1000131 doi: 10.1371/journal.pbio. 1000131

Norges Sildesalgslaget. 2011. Available from http://www.sildelaget.no [accessed 20.04.2011].

R: Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sandberg, P. 2006. Variable unit costs in an output-regulated industry: The Fishery. Appl. Econ. 38(9): 1007-1018 doi: 10.1080/00036840500405912

Sharpe, D.M.T., and Hendry, A.P. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol. Appl. 2(3): 260-275

Skjoldal, H.R., Sætre, R., Fernø, A., Misund, O.A., and Røttingen, I. 2004. The Norwegian sea ecosystem. Tapir Forlag, Trondheim.

Tahvonen, O. 2009. Optimal harvesting of age-structured fish populations. Mar. Resour. Econ. 24(2): 281-299

Thunberg, E., Helser, T., and Mayo, R. 1998. Bioeconomic analysis of alternative selection patterns in the United States Atlantic Silver Hake Fishery. Mar. Resour. Econ. 13: 51-74

Tietenberg, T., and Lewis, L. 2008. Environmental and natural resource economics. Addison Wesley, Boston.
Touzeau, S., Lindroos, M., Kaitala, V., and Ylikarjula, J. 2000. Economic and biological risk analysis of the Norwegian spring-spawning herring fishery. Ann. Oper. Res. 94(1): 197-217 doi: 10.1023/A:1018973217951

## Appendix

Table A1: List of parameters and their values.


| $a_{50}$ | age at $50 \%$ maturity $^{2}$ | year | 4 | 3 |
| :---: | :---: | :---: | :---: | :---: |
| $a_{\text {width }}$ | width of maturity envelope | year | 0.2 | 0.2 |
| $\eta$ | selectivity parameter ${ }^{2}$ | - | 4.3 | 3.3 |
| $\beta_{0}$ | price function slope ${ }^{4}$ | NOK $\cdot \mathrm{kg}^{-1}$ | 2.47 | 8.65 |
| $\bar{w}$ | mean catch weight ${ }^{2,4}$ | kg | 0.235 | 0.454 |
| $C_{0}$ | fixed costs ${ }^{5}$ | NOK | $3.4 \cdot 10^{5}$ | $3.4 \cdot 10^{5}$ |
| $v$ | cost function slope ${ }^{6}$ | NOK $\cdot \mathrm{kg}^{-1}$ | 0.7 | 0.7 |

${ }^{1}$ Fiksen and Slotte (2002)
${ }^{2}$ ICES (2010a)
${ }^{3}$ Jennings and Beverton (1991)
${ }^{4}$ Norwegian Directorate of Fisheries (direct communication)
${ }^{5}$ Touzeau et al. (2000)
${ }^{6}$ Froese and Pauly (2009)


Figure 1: Linear weight-price functions (solid lines) estimated from real price data (dots) and step functions based on price per weight categories for herring $(a, c)$ and mackerel (b, d). The actual price slopes $\beta_{0}$ are 2.43 (herring) and $8.97 \mathrm{NOK} \cdot \mathrm{kg}^{-1}$ (mackerel). For reference, also the case with constant price ( $\beta=0$; grey line) is shown. The pivot point of these lines corresponds to the observed mean individual catch weight, $\bar{w}$ (dotted line), and price per kilogram for this weight, $p_{\bar{w}}$. The price data are annual mean prices per weight class from Norwegian spring-spawning herring and Northeast Atlantic mackerel in 20002010 provided by the Norwegian Fisheries Directorate (Per Sandberg, personal communication). We use annual catch weight distributions (ICES 2010) to transform weight classes into mean weight of each weight class ( $a, b$ ). Step functions ( $c, d$ ) represent prices per weight class in 2009 (dashed line) and 2010 (solid line).


Figure 2: Net present value (NPV) for herring (a) and mackerel (b) fisheries as a function of harvest proportion under the current pricing regime (solid line), no size-dependent pricing ( $\beta=0$; long dashed line) and a twofold price slope ( $\beta=2$; short dashed line). The distance between vertical grey lines illustrates the difference in the NPV-maximizing harvest strategies in the presence and absence of size-dependent pricing. Discount rate $d=0.05$. Harvest proportion is calculated from the mean fishing mortality over reference ages as defined by ICES (ages 5-14 years for herring, 4-8 years for mackerel; ICES 2010).


Figure 3: The influence of relative price slope $\beta$ on optimal fishing mortality (black) and the resulting mean individual weight (grey) in the catch of herring (a) and mackerel (b) with respect to different discount rates $d$. Discount rate takes values $d=0.05 \pm 0.05 \quad(d=0$ short dashed, $d=0.1$ long dashed line). Optimal strategy is the one maximizing the net present value of a pristine stock. Strength of size dependence of price is expressed as the
relative price slope $\beta$, with $\beta=1$ corresponding to the current price dependence shown in Figure 1 and $\beta=0$ to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5-14 years weighted by stock numbers for herring, 4-8 years for mackerel; ICES 2010).


Figure 4: Mean fishing mortality optimized for net present value in herring (a) and mackerel
(b) fisheries under the assumptions of discount rates between 0 and 1 . The continuous line shows results for the real size dependence of pricing. The envelope with dashed lines shows the case of no size dependency (short dashed) and doubled slope (long dashed). Optimal strategy is the one maximizing the net present value of a pristine stock. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5-14 years weighted by stock numbers for herring, 4-8 years for mackerel; ICES 2010).


Figure 5: Mean fishing mortality (black) that maximizes NPV in herring (a) and mackerel
(b) fisheries and the corresponding mean catch weight (grey) as functions of the relative price slope. The lines represent the default natural mortality $M_{a}$ (solid) and $M_{a}$ decreased (long dashed) or increased (short dashed) by $20 \%$. The discount rate is $d=0.05$. Optimal strategy is the one maximizing the net present value of a pristine stock. Strength of size dependence of price is expressed as the relative price slope $\beta$, with $\beta=1$ corresponding to the current price dependence shown in Figure 1 and $\beta=0$ to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5-14 years weighted by stock numbers for herring, 4-8 years for mackerel; ICES 2010).


Figure 6: Mean fishing mortality (black) optimized for NPV in herring (a) and mackerel (b) fisheries and the corresponding mean catch weight (grey) as functions of the relative price slope. The lines represent the default selectivity parameter $\eta$ (solid line) and $\eta$ decreased (long dashed line) or increased (short dashed line) by $20 \%$. The discount rate is $d=0.05$. Optimal strategy is the one maximizing the net present value of a pristine stock. Strength of size dependence of price is expressed as the relative price slope $\beta$, with $\beta=1$ corresponding to the current price dependence shown in Figure 1 and $\beta=0$ to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5-14 years weighted by stock numbers for herring, 4-8 years for mackerel; ICES 2010).

