Original Article

An alternative reference point in the context of ecosystem-based fisheries management: maximum sustainable dead biomass

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Under the 2013 Reform of the European Union’s Common Fisheries Policy (CFP), fisheries management aims to ensure that, within a reasonable time frame, the exploitation of marine biological resources restores and maintains populations of harvested stocks above levels that can produce the maximum sustainable yield (MSY). The CFP also calls for the implementation of an ecosystem-based approach to fisheries management (EBFM).

In this paper, we present the concept of maximum sustainable dead biomass (MSDB) and its associated management reference points for fishing mortality and spawning-stock biomass as alternatives to those associated with MSY. The concept of MSDB is illustrated by a dynamic pool production model of a virtual fish stock which takes into account variations in natural mortality (M), fishing mortality (F), and exploitation pattern. Our approach implies a compensatory mechanism whereby survivors may benefit from compensatory density dependence and is implemented through progressive substitution of M with F for varying rates of total mortality (Z). We demonstrate that the reference points for fishing mortality and spawning-stock biomass associated with MSDB are less sensitive to increasing compensation of M with F than those associated with MSY and more sensitive to changes in selection pattern. MSDB-based reference points, which are consistent with maximum stock productivity, are also associated with lower fishing mortality rates and higher stock biomasses than their MSY-based counterparts. Given that selection pattern can be influenced through fishery input measures (e.g. technical gear measures, decisions on areas, and/or times of fishing), whereas variations of M in response to F are not controllable (indeed poorly understood), that the results of many fish stock assessments are imprecise, that maximum stock productivity corresponds to MSDB and that MSY-based reference points may best be considered as limits, we propose that MSDB-based reference points provide a more appropriate basis for management under an EBFM.

Keywords: compensatory density effects, ecosystem-based fishery management reference points, MSY, sustainability.

Introduction

A primary aim of the European Union’s (EU) Common Fisheries Policy (CFP) is to ensure inter alia that fishing contributes to long-term environmental sustainability (EU, 2013). To this end, and in accordance with the obligations enshrined in the declaration of the UN Johannesburg Summit on Sustainable Development (UN, 2002), fisheries management in the EU aims to ensure that, within a reasonable time frame, the exploitation of marine biological resources restores and maintains populations of harvested stocks above levels that can produce the maximum sustainable yield (MSY) and that such exploitation rates should be achieved by 2015 where possible and in any event no later than 2020 (EU, 2013). The CFP also calls for the implementation of an ecosystem-based approach to fisheries management (EBFM) and achievement of sustainable exploitation of marine biological resources based on the precautionary approach.
EBFM is a new direction for fishery management, essentially reversing the order of management priorities so that rather than focusing on single species, sustainable management of the ecosystem is the overarching priority. Primarily, an EBFM aims to sustain healthy marine ecosystems including the fisheries they support (Pikitch et al., 2004). Keeping fishing mortality rates low enough to prevent ecosystem-wide overfishing, avoidance of bycatch and protecting habitats from destructive fishing practices can be considered a first phase of this approach (Hilborn, 2011).

In the context of fisheries management, care is needed when converting results from population dynamics into appropriate management advice to ensure that subsequent implementation of management measures is likely to achieve management objectives. Within single-species management oversimplified modelling of some fisheries in combination with data deficiency has resulted in the collapse of key stocks (Walters and Maguire, 1996; Shelton et al., 2006; Eero et al., 2012). Several authors have pointed out that managing fisheries according to single-species MSY may not be wholly appropriate in the context of an EBFM as the MSY concept requires management reference points based on single-species stock assessments (Larkin, 1977; Rosenberg et al., 2006; Leslie et al., 2008; Worm et al., 2009). Walters et al. (2005) showed that widespread application of single-species policies consistent with constant MSY catches which do not account for stock dynamics would in general cause severe deterioration in ecosystem structure, in particular the loss of top predator species.

Fisheries management reference points and related options to achieve them are typically based on major assumptions related to coverage and correctness of data used. For example, MSY is generally considered and implemented as a point estimate, although it is known to be sensitive to changes in exploitation pattern (Scott and Sampson, 2011) as lower selection of young fish grants higher MSY.

Natural mortality (M) is defined to cover mortal causes other than fisheries which can be encapsulated under the label "ecological effects", e.g. habitat degradation, disease, competition, inertia, and predation (Beverton and Holt, 1957). However, the estimation of M is known to be notoriously difficult (Vetter, 1988), which explains the commonly applied axiom of constant natural mortality (Caddy, 1991) in stock assessments.

Recent ecological research on laboratory populations (Hazlerigg et al., 2012), terrestrial and freshwater ecosystems indicated that natural mortality, together with other important parameters driving stock dynamics and production, e.g. growth (Ali et al., 2003), maturity (Engelhard and Heino, 2004), and condition (Rätz and Lloret, 2003), may react in a compensatory way to additional anthropogenic mortality created by activities such as hunting (Sandercock et al., 2011; Sparkman et al., 2011) or fishing (Allen et al., 1998; Hansen et al., 2011). Compensatory density-dependent processes in fish stocks can be critical for the sustainability of fisheries (Fromentin et al., 2001; Hixon and Jones, 2005), yet the implications of different mechanisms of density dependence in populations are seldom considered in the models and assessments to derive management advice regarding regulatory options (Rose et al., 2001; Bardos et al., 2006).

Based on calculations using a dynamic pool stock production model (Sinclair, 1999; Shepherd and Pope, 2002), the present paper compares the sensitivity of MSY-related fisheries management reference points for sustainable exploitation and stock size, to variations in fishing mortality (F) and exploitation pattern (F at age). In particular, we investigate the potential effects of an inverse relationship between F and M as a means to reflect possible density-dependent compensatory mechanisms. This is implemented by creating different scenarios in which M is progressively substituted by F. Such an approach prompted us to propose alternative management reference points based on the concept of maximum sustainable dead biomass (MSDB). We demonstrate that reference points for fishing mortality and stock biomass associated with MSDB are more precautionary (i.e. lower fishing mortality rates and higher biomass) than those associated with MSY and consider the related issue of stock productivity in the context of an EBFM.

Material and methods

Model used

All calculations are based on a single generalized virtual stock consisting of 7 ages groups (see Virtual stock and fishery data). Future recruitment is defined through a spawning stock–recruitment (S–R) relationship. From the many available S–R functions, we have chosen the commonly used Ricker (1975) function expressed as

\[ R = \alpha SSB \exp \left( -\frac{SSB}{\beta} \right), \]  

where R denotes the recruitment to the stock, spawning-stock biomass (SSB) the parental spawning-stock biomass in weight with \( \alpha \) and \( \beta \) as stock-specific parameters. The fitted S–R function describes a classic dome-shape with an intuitive depensation effect of reduced recruitment at high stock density (Figure 1).

The coefficients for the instantaneous rates for natural mortality (M) and fishing mortality (F) at age (Pope, 1972) are defined as

\[ M_a = -\ln \frac{N_{y+1,a+1}}{N_{y,a}} - F_a, \]

\[ F_a = -\ln \frac{N_{y+1,a+1}}{N_{y,a+1}} - M_a, \]

where \( N \) denotes the size of the population in numbers, \( y \) denotes the year, and \( a \) denotes the age group.

![Figure 1. Spawning stock–recruitment relationship (Ricker, 1975) of the virtual stock under equilibrium conditions (eq) as defined in the production model. The spawning-stock biomass SSB$_{eq}$ is given in tonnes while the recruitment R$_{eq}$ at age 1 is in numbers (thousands).](https://academic.oup.com/icesjms/article-abstract/72/8/2257/2458743)
The model estimates stock size and catch at different instantaneous mortality rates by applying Equations (2–3) and the following catch equation:

\[ C_a = F_aN_a \left( \frac{1 - \exp(-(F_a + M_a))}{F_a + M_a} \right), \]  

(4)

where \( C_a \) denotes catch \( C \) in numbers-at-age \( a \) (Baranov, 1918).

The dynamic pool model (Shepherd and Pope, 2002; Sinclair, 1999) allows for variation in \( R \) as a function of \( SSB \) [as in Equation (1)]. The following functions define the estimation of spawning stock size at equilibrium (Equation (1)]. The following functions define the estimation of spawning stock size at equilibrium (Equation (1)], recruitment at equilibrium \( (R_{eq}) \), yield at equilibrium \( (Y_{eq}) \) with varying natural and fishing mortality,

\[ SSB_{eq} = \beta \ln \frac{\alpha SSB}{R}, \]

(5)

\[ R_{eq} = \alpha SSB_{eq} \exp \frac{-SSB_{eq}}{\beta}, \]

(6)

\[ Y_{eq} = R_{eq} \times YpR, \]

(7)

where \( YpR \) denotes the yield per recruit (Thompson and Bell, 1934).

Implementation of the dynamic pool model permits the estimation of \( MSY \), which is obtained from the maximum of the yield curve (slope = 0), together with the corresponding reference point for maximum sustainable exploitation rate \( (F_{MSY}) \) and the associated spawning-stock biomass \( (SSB_{MSY}) \). In addition to the yield estimate at equilibrium, we also estimate the biomass of individuals dying through natural mortality \( (M_{eq}) \) by applying \( M \) in the yield functions of the \( YpR \) model resulting in an estimate of natural deaths per recruit \( (MpR) \), which is multiplied with recruitment at equilibrium \( (R_{eq}) \). The sum of the weights of individuals dying through fishing mortality \( (Y_{eq}) \) and natural mortality \( (M_{eq}) \) represents the biomass of total deaths \( (D_{eq}) \), hence

\[ M_{eq} = R_{eq} \times MpR, \]

(8)

\[ D_{eq} = Y_{eq} + M_{eq}. \]

(9)

We also define \( D_{MSY} \), which represents the biomass of all fish dying through both \( M \) and \( F \) at \( MSY \).

For a given exploitation pattern and range of fishing mortalities, we estimate an alternative biomass reference point; \( MSDB \), which is defined by the maximum of the curve of \( D_{eq} \) and corresponds to the maximum productivity of the stock (Mertz and Myers, 1998). Associated with \( MSDB \) are the corresponding reference points for fishing mortality \( (F_{MSDB}) \), yield \( (Y_{MSDB}) \), and spawning-stock biomass \( (SSB_{MSDB}) \).

**Virtual stock and fishery data**

The stock-specific parameters defining the spawning stock–recruitment \( (S–R) \) relationship of the virtual stock are \( a = 5.0 \) and \( b = 500 \, 000 \, t \). Substituting them in Equation (1), results in a maximum value of 900 million recruits (age 1) at \( ~500 \, 000 \, t \) of spawning-stock biomass (Figure 1).

Table 1 lists age-specific input data for the virtual stock. Mean weights-at-age in the stock and the catch are identical and the proportion mature \( (\text{maturity ogive}) \) indicates that most fish in age group 3 (80%) and all fish at age groups 4 and older are mature. The variable \( M \) is highest on age 1 and significantly reduced for ages 2 and 3 to account for decreasing predation with increasing age/size (Gulland, 1987; Abella et al., 1998; Gislason et al., 2008; Andersen et al., 2009). The variable \( M \) is kept constant at the arbitrary value of \( M = 0.1 \) for older fish. The arithmetic mean value over the ages 1–4 is \( M_{1–4} = 0.4 \), which is used as the reference level for natural mortality. The oldest age \( (age 7) \) is defined as a plus-group and represents all fish at age 7 and older.

Six different vectors of \( F \)-at-age over ages 1–7 (scenarios F1–F6; Table 1) describe the different selection patterns used for the estimations. Scenario F1 defines that \( F = M \) for each age group. Scenarios F2–F6 represent a progressively reduced selectivity for young fish through a stepwise reduction of \( F \) by 0.2 at age 1.

Using the dynamic pool model, we also assess the effects of a compensatory variation in \( M \) and \( F \)-at-age on \( MSY \) and \( MSDB \). The compensatory relationship between \( M \) and \( F \) is assumed linear and inverse (Hansen et al., 2011):

\[ M' = M - b \times F, \]

(10)

where \( M' \) is \( M \) after compensation.

Such a relationship implies that under equilibrium conditions, an increase in \( F \) results in a proportional reduction in \( M \). We tested six progressively increasing compensation scenarios C1–C6 from no compensation of \( M \) with \( F \) (\( F = M = \text{constant} \)) to the maximum compensation possible, i.e. where \( M \) is reduced to 0 and \( F \) remains the only contributor to total mortality \( (Z) \). While

<table>
<thead>
<tr>
<th>Age group (years)</th>
<th>Stock and catch weight (kg)</th>
<th>Proportion mature</th>
<th>M</th>
<th>F1</th>
<th>F2</th>
<th>F3</th>
<th>F4</th>
<th>F5</th>
<th>F6</th>
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<td>1</td>
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<td>0.6</td>
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<td>0.25</td>
<td>0.20</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Listed are the age-specific parameters of mean weight in the stock and the catch, proportion mature (relative), coefficients of annual natural mortality \( (M) \), and fishing mortality \( (F) \).

Six distinct selection patterns are defined as F1–F6. Note that the selection pattern F1 is identical with \( M \), while the selectivity of age group 1 is progressively reduced in F2–F6. Selection coefficients \( M \) and \( F \) are averaged over ages 1–4, respectively. The resulting estimates for catch and total deaths are illustrated in Figure 3.
recognizing that for a natural population, a value for \( M = 0 \) is not realistic, we use it simply to illustrate the entire range of hypothetical scenarios. Panels C1–C6 (Figure 2) illustrate the resulting relationships between \( F \) and \( M \) and \( Z \). Scenarios C1–C6 were applied to

exploitation patterns F1–F6 to compute 36 separate sets of results from the dynamic pool model.

**Figure 2.** Compensation effects of natural mortality \( M \) with fishing mortality \( F \) (dashed line) as total mortality \( Z \) (solid line) varies, as applied in the dynamic pool production model. The difference between the lines gives the value of \( M \). Panels illustrate increasing compensation of \( M \) with \( F \) from C1 (no compensation) to C6 (0–100% compensation) over a \( Z \) range from 0.4 to 1.0.
Results
Results of scenarios F1–F6 (changes in exploitation pattern through progressively reduced $F$ on age group 1, at constant $M$ at age) are given in Figure 3. Figure 3a shows that $SSB_{eq}$ ranges from $\sim 1.28$ million t when $F = 0$ (i.e. $Z = M$), to stock collapse ($SSB_{eq} = 0$ t) at $Z$ between $Z = 0.94$ and $Z = 1.07$. In the absence of fishing ($F = 0$), the total-stock biomass is $\sim 1.4$ million t and collapses to $0$ t at fishing mortality rates between $F = 0.54$ and $F = 0.67$ (Figure 3b). For scenarios F1–F6, the curves for $Y_{eq}$ and $D_{eq}$ (Figure 3c) indicate that MSY increases from $\sim 85,000$ t (scenario F1) to $150,000$ t (scenario F6). The corresponding $F_{MSY}$ reference points for the same scenarios range from $F_{MSY} = 0.29$ to $F_{MSY} = 0.32$.

Figure 3. Stock parameters and reference values related to MSY and MSDB, mortality coefficients and yield as obtained when applying the six fishing patterns F1–F6 (Table 1) under the assumption of constant $M$ (average $M$ over age groups $1–4 = 0.4$). Bold lines indicate the exploitation pattern for $F$ at age $= M$ at age (exploitation pattern F1, Table 1). Thinner lines illustrate progressive reduction in $F$ on age group 1 (scenarios F2–F6, Table 1). (a) Spawning stock size $SSB_{eq}$ over increasing mortality profiles (mean over age groups 1–4). Trend in total mortality ($Z$), natural mortality ($M$), and the resulting fishing mortality ($F$) is represented by the distance between the solid and the dashed lines. Note: The variation in $F$ on age group 1 has little influence on spawning-stock biomass except when $F$ on age 1 is zero. (b) Total-stock biomass as a function of increasing fishing mortality. Note: The variation in $F$ on age group 1 has little influence on total-stock biomass except when $F$ on age 1 is zero. (c) Yield $Y_{eq}$ (solid black lines) and estimated biomass of total deaths $D_{eq}$ (solid grey lines) as function of increased fishing mortality $F$. Maximum sustainable yield-related reference points are shown for yield and $F$ as horizontal and vertical dashed black lines, respectively. (d) Yield $Y_{eq}$ (solid black lines) and estimated biomass of total deaths $D_{eq}$ (solid grey lines) as function of increased fishing mortality. Maximum sustainable deaths-related reference points are shown for yield and $F$ as horizontal and vertical dashed grey lines, respectively.
Figure 3d shows that for the different scenarios, MSDB ranges from 210,000 t (scenario F1) to 280,000 t (scenario F6). The corresponding reference values for fishing mortality range from $F_{MSDB} = 0.19$ to $F_{MSDB} = 0.24$.

The results given in Figure 3c and d clearly indicate that for the different exploitation pattern scenarios examined, the absolute values for $F_{MSY}$ all exceed the values for $F_{MSDB}$. Hence, in all scenarios, the fishing mortality reference points associated with MSY ($F_{MSY}$) all exceed those that are associated with maximum stock productivity ($F_{MSDA}$).

Results from scenarios C1 to C6 are given in Figure 4. Figure 4a simply illustrates for the fixed exploitation pattern (F1), with progressive compensation of $M$ with $F$, the values of $M$, $F$, and $Z$ (averages over age groups 1–4) relative to $SSB_{eq}$ over a range of $Z$ from $Z = 0.4$ to the $Z$ required to crash the stock. Figure 4b shows total biomass of the unfished stock is $\approx 1.4$ million t. However, the stock collapses to 0 t at

![Graphs showing spawning stock size, total stock biomass, yield, and estimated biomass of total deaths as functions of fishing mortality.](https://academic.oup.com/icesjms/article-abstract/72/8/2257/2458743)

**Figure 4.** Stock parameters and reference values related to MSY and MSDB, mortality coefficients and yield as obtained from scenarios C1–C6 (Figure 2). Scenarios are based on the exploitation pattern F1 (Table 1). Bold lines indicate scenario C1 under the classic assumption of constant $M = 0.4$. Thinner lines demonstrate a progressive compensation of $M$ with $F$ (scenarios C2–C6, Figure 2). (a) Spawning stock size $SSB_{eq}$ over increasing mortality profiles (mean over age groups 1–4). Trend in total mortality ($Z$), natural mortality ($M$), and the resulting fishing mortality ($F$) is represented by the distance between the solid and the dashed lines. (b) Total-stock biomass as a function of increasing fishing mortality. (c) Yield $Y_{eq}$ (solid black lines) and estimated biomass of total deaths $D_{eq}$ (solid grey lines) as function of increased fishing mortality. (d) Yield $Y_{eq}$ (solid black lines) and estimated biomass of total deaths $D_{eq}$ (solid grey lines) as function of increased fishing mortality. Maximum sustainable yield-related reference points are shown for yield and $F$ as horizontal and vertical dashed black lines, respectively. (d) Yield $Y_{eq}$ (solid black lines) and estimated biomass of total deaths $D_{eq}$ (solid grey lines) as function of increased fishing mortality. Maximum sustainable deaths-related reference points are shown for yield and $F$ as horizontal and vertical dashed grey lines, respectively.
fishing mortality rates between $F = 0.53$ (scenario C1) and $F = 0.93$ (scenario C6). Figure 4c shows the curves for $Y_{eq}$ and $D_{eq}$ against increasing $F$ for scenarios C1–C6 and the associated reference points $MSY$ and $F_{MSY}$. With increasing compensation of $M$ with $F$, $F_{MSY}$ increases by $\sim 70\%$ from 84 000 t (scenario C1) to 145 000 t (scenario C6). Similarly, $F_{MSY}$ increases from $F_{MSY} = 0.32$ (scenario C1) to $F_{MSY} = 0.55$ (scenario C6). In contrast, $D_{eq}$ is stable and peaks at 210 000 t in all scenarios. Figure 4d depicts the range of fishing mortality reference points associated with $MSDB$ ($F_{MSDB}$) for each scenario. The estimated yields at $MSDB$ ($Y_{MSDB}$) range from 67 000 t (scenario C1) to $\sim 116 000$ t (scenario C6) and the associated estimates for $F_{MSDB}$ vary from $F_{MSDB} = 0.19$ to $F_{MSDB} = 0.33$. In addition, comparing Figure 4c and d, it is evident that the range of values for $F_{MSDB}$ is lower than the range for $F_{MSY}$ with minimal overlap.

Furthermore, it is clear from Figures 3c, d and 4c, d, that for all scenarios, fishing at $F_{MSY}$ exceeds the $F_{MSDB}$ exploitation rate.

Figure 5. Isopleths of yield ($MSY$ and $Y_{MSDB}$) reference values (t) as derived from scenarios F1 to F6 (y-axis, decreasing selection of age group 1, Table 1) over scenarios C1 to C6 (x-axis, increasing compensation of $M$ with $F$, Figure 2). Gridding method is linear kriging. (a) Variation in $MSY$, data range 84 000 – 216 000 t. (b) Variation in $Y_{MSDB}$, data range 67 000 – 201 000 t.

Figure 6. Isopleths of fishing mortality ($F_{MSY}$ and $F_{MSDB}$) reference values (average of ages 1 – 4) as derived from scenarios F1 – F6 (y-axis, decreasing selection of age group 1, Table 1) over scenarios C1 – C6 (x-axis, increasing compensation of $M$ with $F$, Figure 2). Gridding method is linear kriging. (a) Variation in $F_{MSY}$, data range 0.29 – 0.55. (b) Variation in $F_{MSDB}$, data range 0.19 – 0.39.
that will deliver maximum stock productivity. We demonstrate (Appendix) that this result holds true for all exploitation patterns and values of $M$ greater than zero.

$MSY$ and $MSDB$ reference points for yield, fishing mortality, spawning stock, and total deaths are compared in the form of iso-pleth diagrams (Figures 5–8) over the range of exploitation patterns (Table 1, scenarios F1–F6) and compensation effects (Figure 2, scenarios C1–C6) considered. Figure 5a and b shows the isopleths for $MSY$ and $YMSDB$, respectively, resulting from changes in exploitation pattern (scenarios F1–F6) and variations in $M$ in response to changes in $F$ (scenarios C1–C6). While both $MSY$ and $YMSDB$ both increase in response to improvements in exploitation pattern (reduced $F$ on age group 1) and with increased compensation of $M$ with $F$, the absolute values of $YMSDB$ are less than for $MSY$ in all scenarios and the range of $YMSDB$ is less than the range of $MSY$ across scenarios.

Figure 7. Isopleths of spawning-stock biomass ($SSB_{MSY}$ and $SSB_{MSDB}$) reference values (t) as derived from scenarios F1–F6 (y-axis, decreasing selection of age group 1, Table 1) over scenarios C1–C6 (x-axis, increasing compensation of $M$ with $F$, Figure 2). Gridding method is linear kriging. (a) Variation in $SSB_{MSY}$, data range 395 000 – 481 000 t. (b) Variation in $SSB_{MSDB}$, data range 530 000 – 794 000 t.

Figure 8. Isopleths of $MSDB$ ($DMSY$ and $DMSDB$) reference values (t) as derived from scenarios F1–F6 (y-axis, decreasing selection of age group 1, Table 1) over scenarios C1–C6 (x-axis, increasing compensation of $M$ with $F$, Figure 2). Gridding method is linear kriging. (a) Variation in $DMSY$, data range 190 000 – 296 000 t. (b) Variation in $DMSDB$, data range 210 000 – 306 000 t.
The isopleths shown in Figure 6 indicate that both $F_{\text{MSY}}$ and $F_{\text{MSDB}}$ increase with increasing compensation of $M$ with $F$. The variable $F_{\text{MSY}}$ is rather insensitive to the changes in selection on age group 1, while $F_{\text{MSDB}}$ increases with lower selection of age group 1 (from scenario F1 to F6). Furthermore, the lighter shading in Figure 6b indicates that the values for $F_{\text{MSDB}}$ are lower than those for $F_{\text{MSY}}$. The variable $F_{\text{MSDB}}$ values are $\sim 29–34\%$ lower than the corresponding $F_{\text{MSY}}$ estimates and the range of $F_{\text{MSDB}}$ is less than that for $F_{\text{MSY}}$.

The isopleths of $SSB_{\text{MSY}}$ and $SSB_{\text{MSDB}}$ (Figure 7) indicate that $SSB_{\text{MSY}}$ appears relatively constant for the different scenarios investigated when $F$ on age group 1 is high, but declines when $F$ on age group 1 is low and compensation of $M$ with $F$ is high (Figure 7a). The range of $SSB_{\text{MSDB}}$ is greater than that for $SSB_{\text{MSY}}$, the dynamic mainly driven by the change in selectivity for age group 1; $SSB_{\text{MSDB}}$ increases in response to increased $F$ on age group 1. The $SSB_{\text{MSDB}}$ estimates exceed those for $SSB_{\text{MSY}}$ by $34–65\%$ as indicated by the dark shading in Figure 7b.

The variation in biomass of sustainable total deaths ($D_{\text{eq}}$) in relation to $MSY$ and $MSDB$ for the different scenarios is shown in Figure 8a and b, respectively. Both $D_{\text{MSY}}$ and $MSDB$ show high variation mainly in response to changes in selection on age group 1. The ranges for $D_{\text{MSY}}$ and $MSDB$ are quite similar.

### Discussion

There is substantial interest in how mortality rates affect animal populations, but mechanisms to explain when and under what circumstances particular causes of death incur demographic responses are far from clear (Ruan et al., 2007; Murray et al., 2010; Schoenebeck and Brown, 2011), e.g. Périon (2013) found that short-lived species compensate more under cause-specific mortalities than long-lived species. For a single fish stock, the present analyses investigate a compensatory mechanism whereby fishing mortality replaces the natural mortality that would otherwise have occurred. The compensatory mechanism used is applied linearly (max $M$ at $F = 0$ to min $M$ at max $F$) and while recognizing that such a mechanism could also be extended to cover complex multispecies relations, for reasons of simplicity and clarity, we have deliberately restricted our analyses to an individual stock under equilibrium conditions. The compensation of $M$ with $F$ implies a density-dependent effect such as varying predation- or competition-induced mortality and is considered over a range of values from constant $M$ at 0.4, implying density independence, to the maximum possible compensation where $M = 0$ and all mortality is due to fishing. While recognizing that for a natural population, a value for $M = 0$ is not realistic, we use it simply to illustrate the entire range of hypothetical scenarios. The incorporation of dynamic $M$ has implications when estimating abundance trends and stock status, and ultimately setting management reference points (Powers, 2014).

As might be expected, the results from our analyses indicate that increasing compensation of $M$ with $F$ increases potential yields and related management reference points for exploitation (Figures 5 and 6). In an ecological context, fisheries management reference points are moving limits (Collie and Gislason, 2001) and depend on the variable productivity of the stocks and a priori management choices. The Advisory Committee of the International Council for the Exploration of the Sea and the Scientific, Technical and Economic Committee for Fisheries, the main providers of scientific advice on fisheries management to the EU have only recently begun to initiate multispecies advice for selected ecosystems in European waters. Consistent with the present findings, both of these scientific advisory bodies have advised that fishing mortalities leading to maximum average yield across species in a multispecies context are in general higher than the single-species values for $F_{\text{MSY}}$ (STECF, ICES, 2012; ICES, 2014).

$MSDB$ relates to maximum stock-specific productivity, and accounts for all sources of mortality in the ecosystem, rather than just an optimum yield of fisheries from added anthropogenic mortality as is true for $MSY$ (Mace, 2001). Our results (Figure 6) indicate that $F_{\text{MSY}}$ and $F_{\text{MSDB}}$ are sensitive to compensation of $M$ with $F$ (increasing ratio $F/Z$). The variable $F_{\text{MSDB}}$ appears more sensitive than $F_{\text{MSY}}$ to changes in exploitation pattern. The variable $SSB_{\text{MSDB}}$ is more sensitive to changes in selectivity than $SSB_{\text{MSY}}$ and less sensitive to compensation of $M$ with $F$ (Figure 7). These findings were robust to different stock–recruitment relationships (e.g. Beverton and Holt, 1957) and different selection patterns (e.g. flat topped); results not shown. Given that selection pattern can be influenced through fishery input measures (e.g. technical gear measures, decisions on areas, and/or times of fishing), whereas variations of $M$ in response to $F$ are not controllable (indeed poorly understood), $MSDB$ may represent an appropriate alternative management reference to $MSY$ under an ecosystem approach to fisheries management, particularly when fisheries can potentially select for young age groups.

A major observation is that the concept of $MSY$ and its associated reference points $F_{\text{MSY}}$ and $SSB_{\text{MSY}}$ are not consistent with maximum stock productivity, estimated as $MSDB$. The appendix demonstrates the general applicability of this conclusion. In our examples, yields to the fishery that correspond to $MSDB$ are estimated to be slightly lower ($7–20\%$) than the equivalent $MSY$ estimates. This is because the fishing mortality rates that correspond to $MSDB$ are lower, and hence more precautionary than those that can deliver $MSY$. Hence, using $MSDB$-based reference points reduce the risk of stock decline especially if uncertainty in pertinent stock production parameters remains high (Mace, 2001). $MSDB$-based reference points are also consistent with the current perception of $F_{\text{MSY}}$ as a limit to be avoided rather than a target that can routinely be exceeded (Mace, 2001).

Feedback effects on mortality have been considered in various multispecies models of marine ecosystems (Gislason and Helgason, 1985; Lewy and Vinther, 2004; A’mar et al., 2010; Garrison et al., 2010; Kempf et al., 2010) and continued research in this area is important as provision for life-history and ecosystem effects remain major challenges to improve the assessments of productivity in marine ecosystems under given fishing strategies and address major concerns in EBFM (Hixon and Carr, 1997; Hollowed et al., 2000). Full multispecies models, however, are demanding in terms of data, computing and expertise, especially as the number of species in a system and the links between them increase. Consequently, for the future, such models are unlikely to be routinely used to provide ecosystem-based advice for fisheries management under the CFP. We therefore conclude that adoption of the concept of $MSDB$ as an alternative to $MSY$ for the provision of fisheries management advice would be a relatively simple way to contribute to the objectives of the EBFM not only in European waters, but also in other areas around the world where ecosystem-level concepts are to be implemented.

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References


Appendix

This document shows (using the equations in Mertz and Myers (1998)) how for any given exploitation pattern

(i) \( F_{\text{MSY}} \geq F_{\text{MSDB}} \)

(ii) \( B_{\text{MSDB}} \geq B_{\text{MSY}} \)

(iii) If \( F_{\text{MSY}} = F_{\text{MSDB}} \) then \( Y_{\text{MSY}} = Y_{\text{MSDB}}, \ P_{\text{MSY}} = P_{\text{MSDB}} \) and \( B_{\text{MSY}} = B_{\text{MSDB}} \)

(iv) \( F_{\text{MSY}} = F_{\text{MSDB}} \) only when \( M = 0 \)

The notation stays as close to Mertz and Myers (1998) as possible, so it varies from that in the article. Most important is \( D_{eq} \) is equivalent to \( P \) at equilibrium here.

The starting point is Equation (15) of Mertz and Myers (1998), i.e.

\[
\frac{Y}{P} = \frac{\tilde{F}}{\tilde{F} + \tilde{M}}
\]

where \( \tilde{F} \) and \( \tilde{M} \) are the "biomass-averaged" fishing and natural mortalities and \( Y \) and \( P \) are yield and production at equilibrium, respectively.

Yield is maximized at \( MSY \) so \( Y_{\text{MSY}} \geq Y_{\text{MSDB}} \) and production is maximized at \( MSDB \) so \( P_{\text{MSY}} \geq P_{\text{MSDB}} \) given \( M \) at age, \( M(a) \), stays the same then

\[
\frac{Y_{\text{MSY}}}{P_{\text{MSY}}} = \frac{Y_{\text{MSDB}}}{P_{\text{MSDB}}}
\]

which implies

\[
\frac{\tilde{F}_{\text{MSY}}}{\tilde{F}_{\text{MSY}} + \tilde{M}} \geq \frac{\tilde{F}_{\text{MSDB}}}{\tilde{F}_{\text{MSDB}} + \tilde{M}}. \quad (A1)
\]

which implies

\[
(\tilde{F}_{\text{MSDB}} + \tilde{M})\tilde{F}_{\text{MSY}} \geq (\tilde{F}_{\text{MSY}} + \tilde{M})\tilde{F}_{\text{MSDB}}.
\]

or

\[
\tilde{F}_{\text{MSY}} \geq \tilde{F}_{\text{MSDB}}. \quad (A2)
\]

From eqn (11) of Mertz and Myers,

\[
P = B(\tilde{F} + \tilde{M}),
\]

where \( B \) is the total biomass of fish. Given \( P_{\text{MSDB}} \geq P_{\text{MSY}} \) then

\[
B_{\text{MSDB}}(\tilde{F}_{\text{MSDB}} + \tilde{M}) \geq B_{\text{MSY}}(\tilde{F}_{\text{MSY}} + \tilde{M}),
\]

and given \( F_{\text{MSY}} \geq F_{\text{MSDB}} \) from (A1) this implies

\[
B_{\text{MSDB}} \geq B_{\text{MSY}}. \quad (A3)
\]
If \( F_{\text{MSY}} = F_{\text{MSDB}} \) then the terms in (A1) become equivalent meaning

\[
\frac{Y_{\text{MSY}}}{P_{\text{MSY}}} = \frac{Y_{\text{MSDB}}}{P_{\text{MSDB}}},
\]

and if \( Y_{\text{MSY}} \) and \( P_{\text{MSDB}} \) are unique (maximums) then

\[
Y_{\text{MSY}} = Y_{\text{MSDB}}, P_{\text{MSY}} = P_{\text{MSDB}}, \text{and from eqn (11) of Mertz and Myers}
\]

\[
B_{\text{MSDB}} = B_{\text{MSY}}. \tag{A4}
\]

The variable \( MSDB \) equates to maximum production. For given selection patterns for \( M \) and \( F \) and a given absolute level of \( M \), maximum production occurs when \( \frac{dP}{dF} = 0 \). Starting from eqn (11) of Mertz and Myers

\[
\frac{dP}{dF} = \frac{dB}{dF} \hat{M} + B \frac{d\hat{M}}{dF} + \hat{P} \frac{dB}{dF} + B \frac{d\hat{P}}{dF} = \frac{dB}{dF} \hat{M} + \frac{dB}{dF} \hat{P} + B = 0,
\]

The variable \( MSY \) is given when \( \frac{dY}{dF} = 0 \). Starting from eqn (14) of Mertz and Myers (1998) (i.e. \( Y = FB \))

\[
\frac{dB}{dF} \hat{F} + B \frac{d\hat{F}}{dF} = \frac{dB}{dF} \hat{F} + B = 0.
\]

If \( F_{\text{MSY}} = F_{\text{MSDB}} \), then \( \frac{dY}{d\hat{F}} = 0 \) when \( \frac{dP}{d\hat{F}} = 0 \) so that from the above two equations

\[
\frac{dB}{dF} \hat{M} + \frac{dB}{dF} \hat{P} + B = \frac{dB}{dF} \hat{F} + B.
\]

which implies

\[
\frac{dB}{dF} \hat{M} = 0.
\]

which implies either \( \frac{dB}{dF} = 0 \) or that \( \hat{M} = 0 \).

But from eqn (9) of Mertz and Myers (1998) and using the relationships \( Wc(a) = n_0 s(a) w(a) \), where \( Wc(a) da \) is the mass per unit of a cohort at age \( a \), \( n_0 \) is the number (per unit area) of age 0 fish, and \( s(a) \) is the ratio of number of fish at age \( a \) to \( n_0 \) and

\[
s(a) = \exp \int_0^a [-M(a') - F(a')] da',
\]

The \( B = \int_0^{\hat{m}} Wc(a) da = \int_0^{\hat{m}} n_0 s(a) w(a) da \)

\[
= n_0 \int_0^{\hat{m}} \exp \int_0^{aw(a)} [-M(a') - F(a')] da' w(a) da.
\]

For given \( M(a), w(a), \) and \( n_0 \), \( B \) clearly is a function of \( \hat{F} \) so \( \frac{dB}{d\hat{F}} \neq 0 \).

Therefore, \( \frac{dB}{d\hat{F}} \times \hat{M} = 0 \) implies \( \hat{M} = 0 \).

Therefore, \( F_{\text{MSY}} = F_{\text{MSDB}} \) only when \( \hat{M} = 0 \), i.e. \( M(a) = 0 \) for all ages.

This means that for any non-zero \( M \), \( F_{\text{MSDB}} \) is less than \( F_{\text{MSY}} \) and \( B_{\text{MSDB}} \) is greater than \( B_{\text{MSY}} \).