

# A life-history evaluation of the impact of maternal effects on recruitment and fisheries reference points

Núria Calduch-Verdiell, Brian R. MacKenzie, James W. Vaupel, and Ken H. Andersen

**Abstract:** Fishing causes dramatic changes in the age and size structure of fish stocks. In particular, the targeting of the largest and oldest individuals in a stock changes the age and size distribution of that stock. A large female produces a higher quantity of eggs than a young female because of its larger size, but recent laboratory evidence further indicates that large females also produce eggs of higher quality, a phenomenon known as maternal effects. However, most traditional management models assume that all female fish contribute equally per unit biomass to future recruitment. Here we investigate whether this assumption is valid by calculating the impact of maternal effects both before and after accounting for density-dependent effects. We find that the contribution of large individuals to reproduction is much more pronounced for unfished than for fished stocks. Fisheries reference points are largely unaffected by maternal effects. Our results indicate that the incorporation of maternal effects into impact assessments of fisheries is not expected to change advice substantially. Important exceptions are stocks whose demography is very vulnerable to fishing (and which therefore have low fishing reference points) for which maternal effects are relevant and necessary to consider.

**Résumé :** La pêche entraîne des modifications drastiques de la structure par âge et par taille des stocks de poissons. Le ciblage des individus les plus grands et les plus âgés au sein d'un stock, en particulier, modifie les distributions d'âges et de tailles dans ce stock. Si une grosse femelle produit une plus grande quantité d'œufs qu'une jeune femelle en raison de sa plus grande taille, de récentes observations en laboratoire indiquent aussi que les grosses femelles produisent des œufs de meilleure qualité, soit le phénomène des effets maternels. Cependant, la plupart des modèles de gestion traditionnels partent du principe que la contribution au recrutement futur par unité de biomasse est la même pour tous les poissons femelles. Nous examinons la validité de cette hypothèse en calculant l'incidence des effets maternels avant et après l'intégration d'effets dépendant de la densité. Nous constatons que la contribution de gros individus à la reproduction est beaucoup plus prononcée dans les stocks non exploités que dans les stocks exploités. Les effets maternels n'ont pas une grande incidence sur les points de référence pour les pêches. Nos résultats indiquent que l'intégration des effets maternels aux évaluations des impacts des pêches ne devrait pas avoir une incidence significative sur les avis concernant les pêches. Les stocks dont la démographie est très vulnérable à la pêche (et qui sont donc caractérisés par des points de référence très faibles) constituent d'importantes exceptions pour lesquelles il est donc pertinent et nécessaire de tenir compte des effets maternels. [Traduit par la Rédaction]

## Introduction

Many marine fish stocks are reported as heavily fished on a global scale (Hilborn 2003; Pauly 2008; Worm et al. 2009). Fishing not only removes fish biomass but also truncates the age and size structure of fish stocks (Jackson et al. 2001; Longhurst 2002; Berkeley et al. 2004).

Several studies on specific fish stocks and species indicate that not only do largest females spawn more eggs in each spawning event than smaller females, but their eggs are larger and of higher quality in terms of survival probability than the eggs from smaller females (Hixon et al. 2013). Moreover, the spawning times and durations of individuals having different ages and sizes can differ within populations, which could expose eggs and larvae to more or less favorable ocean conditions for survival and growth (Wright and Trippel 2009). Such effects have been demonstrated for Atlantic

cod (*Gadus morhua*) (Kjesbu et al. 1996; Trippel 1998; Marteinsdóttir and Steinarsson 1998), haddock (*Melanogrammus aeglefinus*) (Hislop 1988), black rockfish (*Sebastes melanops*) (Berkeley et al. 2004), and winter flounder (*Pseudopleuronectes americanus*) (Buckley et al. 1991). All these studies suggest that age and size of spawners are very important in determining the number and the quality of eggs produced by a stock. This has prompted the moniker “big old fecund females” (BOFF) to the largest individuals in a stock. However, these studies do not address whether the increased reproductive output and quality of large females translate into major impacts on population dynamics. To do so, one must consider the number of those individuals in exploited stocks. In most exploited stocks, the number of large females is very low relative to the number of younger, smaller females because of natural and fishing mortality. It is therefore unclear whether the relatively small

Received 21 January 2014. Accepted 8 April 2014.

Paper handled by Associate Editor Yong Chen.

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number of large females can contribute substantially to production of new recruits even given the documented beneficial effects of such individuals on production and quality of eggs and larvae.

The field evidence for an impact of the large females on recruitment is ambiguous. Given the observations of maternal effects on females, one might hypothesize that recruitment per spawning stock biomass would decrease when the age structure of a stock is skewed towards younger individuals. For example, [Marteinsdóttir and Steinarsson \(1998\)](#), [Jarre-Teichmann et al. \(2000\)](#), and [Cardinale and Arrhenius \(2000\)](#) observed that diversity of age structure of spawner biomass explained significant variation in recruitment in Icelandic and Baltic cod populations. More recently [Venturelli et al. \(2009\)](#) found that maximum reproductive rates in 25 wild fish stocks representing 25 species were higher when stocks were characterized by older and larger individuals than by younger and smaller individuals. However, [Morgan et al. \(2007\)](#), studying American plaice (*Hippoglossoides platessoides*) and Atlantic cod stocks, were unable to find a consistent influence of spawner age and size structure on recruitment. In addition, an analysis of the relationship between age and size structure of spawners and recruitment for a large number of species revealed a relationship for some stocks, but not for the majority of them, and opposite relationships were also found ([Brunel 2010](#)). These contradictory findings suggest that the importance of the age and size structure of spawners on recruitment is not fully understood and the effects might differ between species.

One of the main goals in fisheries science and management is maintenance of the stock reproductive potential (i.e., the ability of the stock to produce new recruits at long-term sustainable levels; [Hilborn and Walters 1992](#)). Thus, given the importance of reproductive potential to scientific advice for fisheries, it is important to understand the role of maternal effects on population dynamics and how such effects may be influenced by differences in species life-history traits. It has therefore been suggested that maternal effects must be incorporated into considerations of reference points used in fisheries management advice ([Birkeland and Dayton 2005](#); [Morgan 2008](#); [Field et al. 2008](#); [Mangel et al. 2010](#)).

This article considers the influence of maternal effects on recruitment and on commonly used reference points, such as the fishing mortality rate corresponding to the maximum sustainable yield ( $F_{msy}$ ) and the fishing mortality where the population collapses ( $F_{crash}$ ). The questions addressed here are as follows: Which parts of the size structure are most important for the population egg production and recruitment? How are egg production, recruitment, and fisheries reference points influenced by maternal effects?

To do so we apply a recent size-based model of fish stock demography and recruitment ([Andersen and Beyer 2014](#)). The model uses life-history invariants to constrain the parameter values in the model. In this way the diversity of fish life histories is projected onto a single axis of variation: asymptotic size. The model therefore makes it possible to go beyond considering the impact of maternal effects on specific species (e.g., [Murawski et al. 2001](#); [Spencer et al. 2014](#); [Arlinghaus et al. 2010](#)) to make general statements about the impact of fishing on fish stocks only by considering the variation in asymptotic size. The model is augmented with a new model component representing maternal effects. The importance of maternal effects are considered initially on the demography (size structure) of the stock, secondly on recruitment, and finally on fisheries reference points.

## Methods

The size-based demographic model calculates population-level properties like total egg production and recruitment from a description of individual physiology. The model is essentially a reformulation of the classic Beverton–Holt framework ([Beverton and Holt 1959](#)) in terms of individual size (body mass,  $w$ ) instead of

age. Size is used instead of age, firstly because body size is more important for physiology, mortality, and fisheries selection than age and secondly because the size-based formulation makes it possible to parameterize the model using life-history invariants ([Charnov 1993](#)), such that only one free parameter describes the life history: the asymptotic size,  $W_\infty$ . The basic model (without maternal effects) is described and analysed in detail elsewhere ([Andersen and Beyer 2014](#)). Here we represent maternal effects via a modification of the calculation of the spawning-stock biomass entering into the stock–recruitment relationship. We provide a general overview of the model with a focus on the mass-balance equation of an individual and the novel representation of maternal effects. Equations and parameters are summarized in [Tables 1 and 2](#).

Individual growth (mass per time) is described by a mass-balance equation similar to the von Bertalanffy equation ([von Bertalanffy 1957](#)) but with an explicit representation of maturation and allocation of energy to reproduction ([West et al. 2001](#); [Lester et al. 2004](#)) (eq. M1). The equation consists of three terms: available energy (in terms of mass)  $Aw^n$  (anabolic term), expenditure on activity and maintenance  $k_a w$  (catabolism), and investment in reproduction  $k_{gsi} w \psi(w, \eta_m)$ . The term  $\psi(w, \eta_m)$  is the maturity ogive represented as a function switching smoothly from 0 to 1 around the size of maturation ([Hartvig et al. 2011](#)) (eq. M2). Size at maturation is assumed proportional to asymptotic size  $\eta_m W_\infty$  ([Beverton 1992](#)). Despite the addition of explicit representation of reproduction to the von Bertalanffy growth equation, a growth trajectory calculated from eq. M1 is almost indistinguishable from a von Bertalanffy growth curve ([Andersen and Beyer 2014](#), their fig. A1). The parameter  $A$  is related to the von Bertalanffy growth parameter as  $K \approx AW_\infty^{1-n}/3$  ([Andersen et al. 2009](#)). When size reaches the asymptotic size, growth is zero. This makes it possible to express the total mass-specific catabolic energy available (activity, metabolism, and reproduction) in terms of asymptotic size as  $k_a + k_{gsi} = AW_\infty^{n-1}$ . We assume that the total catabolic energy is split between activity and maintenance ( $k_a$ ) and reproduction ( $k_{gsi}$ ) with a factor  $\varepsilon_a$ , such that  $k_a = \varepsilon_a AW_\infty^{n-1}$  (eq. M3) and  $k_{gsi} = (1 - \varepsilon_a) AW_\infty^{n-1}$  (eq. M4). The factor  $k_{gsi}$  can be thought of as an annual gonado-somatic index ([Gunderson 1997](#)), and by multiplying it with an efficiency  $\varepsilon_r$  accounting for losses during the conversion of catabolic energy to eggs and prerecruit mortality, and dividing by the size of a recruit  $w_r$ , it becomes an expression for the total density-independent recruit production of an individual fish per body mass:  $\alpha = \varepsilon_r k_{gsi} / w_r$  (numbers per mass per time) (eq. M5). Thus, through the account of the mass-balance (eq. M1), we have now been able to relate density-independent recruit production of an individual  $\alpha w$  to asymptotic size.

Density-dependent effects are assumed to happen at a size  $w_r$  larger than the size where maternal effects occur but before fishing and maturation and also assumed to affect offspring equally regardless of the size and age of the mother. A Beverton–Holt relationship is used to describe density-dependent recruitment  $R$  (numbers per time), with maximum recruitment  $R_{max}$  and spawning stock biomass  $B$  (eq. M6).  $R_{max}$  represents the carrying capacity of the stock. All presented results are normalized by  $R_{max}$ , and it is therefore not a relevant parameter here. The spawning stock biomass is found by integrating over the abundance distribution  $N(w)$  multiplied by the mass. To account for maternal effects, whereby the quality of recruit production depends on size, the integral is augmented by a size-dependent weighing factor  $\varepsilon_{boff}(w)$  (eq. M7). The weighing factor represents maternal effects as any effect resulting in an increase in egg production, egg viability, and larval survival until the size of recruitment  $w_r$ . Maternal effects therefore influence the density-independent recruit production (hereafter referred to as just “recruit production”). We do not know the shape of the function  $\varepsilon_{boff}(w)$  in general. Here we are inspired by the laboratory experiments of [Berkeley et al. \(2004\)](#) on rockfish

**Table 1.** Equations in the model.

Description	Dimensions	Equation	No.
Individual growth	Mass·time <sup>-1</sup>	$g(w) = Aw^n - k_a w - k_{gsi} w \psi(w, \eta_m)$	M1
Switching function	—	$\psi(w, \eta) = \left[ 1 + \left( \frac{w}{\eta W_\infty} \right)^{-10} \right]^{-1}$	M2
Specific investment in reproduction	Time <sup>-1</sup>	$k_r = A(1 - \varepsilon_a) W_\infty^{n-1}$	M3
Specific investment in activity	Time <sup>-1</sup>	$k_a = A \varepsilon_a W_\infty^{n-1}$	M4
Specific recruit production	Numbers·biomass <sup>-1</sup> ·time <sup>-1</sup>	$\alpha = \varepsilon_r (1 - \varepsilon_a) A W_\infty^{n-1} / w_r$	M5
Recruitment	Numbers·time <sup>-1</sup>	$R = R_{\max} \frac{\alpha B}{R_{\max} + \alpha B}$	M6
Spawning stock biomass	Biomass	$B = \int_{w_r}^{W_\infty} N(w) \psi(w, \eta_m) w \varepsilon_{\text{boff}} dw$	M7
Maternal effects	—	$\varepsilon_{\text{boff}}(w) = 1 + 2 \frac{\phi - 1}{1 - \eta_m} \left( \frac{w}{W_\infty} - \eta_m \right)$	M8
Mortality	Time <sup>-1</sup>	$\mu = a A w^{n-1} + \mu_F(w)$	M9
Fishing mortality	Time <sup>-1</sup>	$\mu_F(w) = F \psi(w, \eta_F)$	M10
Abundance distribution	Numbers·mass <sup>-1</sup>	$N(w) = \frac{R}{g(w)} P_{w_r \rightarrow w}$	M11
Survivorship	—	$P_{w_1 \rightarrow w_2} = \exp \left[ - \int_{w_1}^{w_2} \frac{\mu(w)}{g(w)} dw \right]$	M12
Yield from the fishery	Biomass·time <sup>-1</sup>	$Y = \int_{w_r}^{W_\infty} N(w) w \mu_F(w) dw$	M13

**Note:** Individual size is represented by  $w$  and asymptotic size by  $W_\infty$ .

**Table 2.** Parameters in the model.

Parameter	Value or unit
$w$	Individual mass g
$W_\infty$	Asymptotic mass g
$n$	Metabolic exponent 3/4
$A$	Factor for consumption rate* 4.5 g <sup>1-n</sup> ·year <sup>-1</sup>
$a$	Physiological level of mortality† 0.35
$\varepsilon_a$	Fraction of energy for activity 0.8
$\eta_m$	Size at maturation relative to $W_\infty$ 0.25
$\eta_F$	Start of fishing relative to $W_\infty$ 0.05
$\varepsilon_r$	Recruitment efficiency 0.45
$w_r$	Size of recruits 0.01 g
$\phi$	Strength of maternal effects Free
$F$	Fishing mortality at full selection Free
$R_{\max}$	Maximum recruitment Not relevant

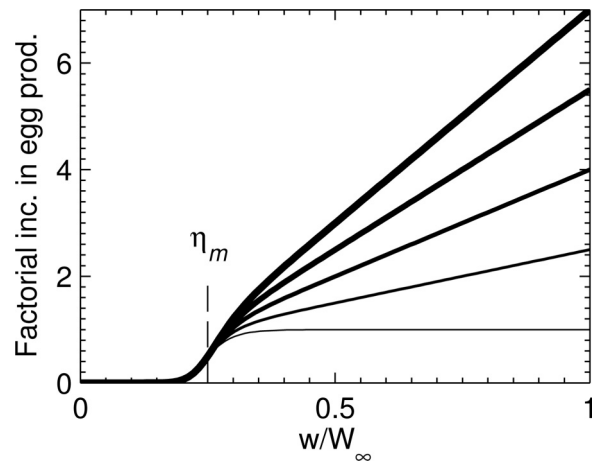
**Note:** All values are from Andersen and Beyer (2014) except  $\phi$ , which is specific to this work.

\* $A$  is related to the classic von Bertalanffy growth parameter as  $K \approx A W_\infty^{n-1} / 3$  (Andersen et al. 2009).

† $a$  is related to the classic  $M/K$  ratio as  $M/K \approx 3a \eta_m^{n-1} \approx 1.48$  (Andersen et al. 2009) and to adult mortality  $M$  as  $M \approx a A (\eta_m W_\infty)^{n-1}$ .

that found larval growth rates to be an increasing but saturating function of mother age. A function that saturates with age becomes an increasing function of size. Therefore, we construct a function where maternal effects are an increasing function of size (eq. M8). The strength of maternal effects is characterized by the free parameter  $\phi$ , which represents the mean fractional increase in recruits: when  $\phi = 1$  there are no maternal effects, when  $\phi = 4$  recruit production is on average increased by a factor 4 (Fig. 1). We use a strength of maternal effects of  $\phi = 4$  frequently, noting that this represents very strong maternal effects where the density-independent recruit production per mass of a mother of asymptotic size is about seven times higher than that from a first-time spawner. Empirical studies have found a one- to twofold higher egg survival of eggs produced by an age-10 cod relative to those produced by an age-3 cod (Shelton et al. 2012). A factor seven increase is therefore expected to be an absolute upper limit on the strength of maternal effects. The effect of maternal effects in the recruitment function is similar to an increase in  $\alpha$ , which again

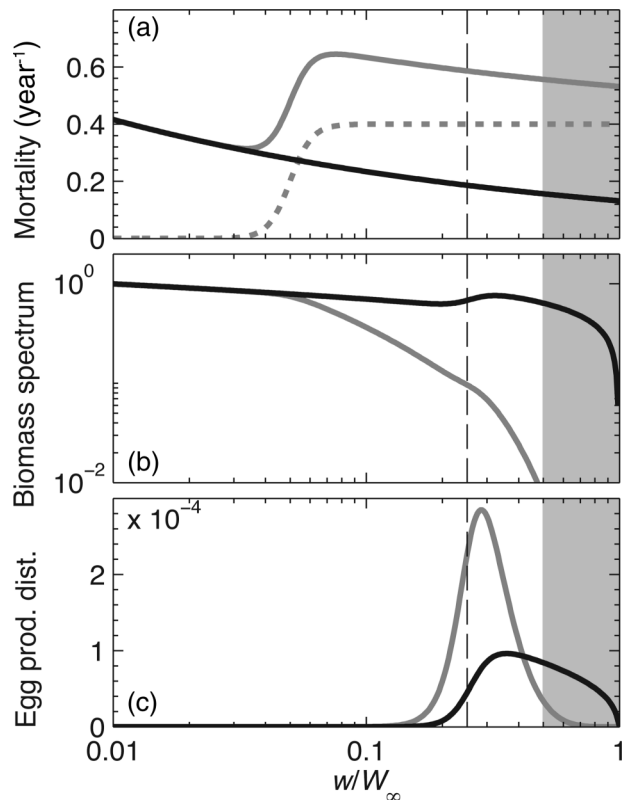
**Fig. 1.** Factorial increase in egg production due to maternal effects multiplied by the maturity ogive ( $\varepsilon_{\text{boff}} \psi(w, \eta_m)$ ) for the maternal effect parameter taking five values from  $\phi = 1$  (no maternal effects; thinnest line) to  $\phi = 4$  (thickest line). The value of  $\phi$  reflects the factorial increase of the mean egg production.



corresponds to an increase in steepness of the stock–recruitment relationship.

Instantaneous rate of mortality is size-dependent and consists of a natural and a fishing mortality:  $\mu(w) = \mu_p + \mu_F$ . The natural mortality declines with size as a power-law with exponent  $-1/4$  (Peterson and Wroblewski 1984), and the level is characterized by the dimensionless parameter  $a$  (Andersen and Beyer 2006) (eq. M9). With this formulation, adult natural mortality  $M$  is approximately constant:  $M \approx \mu_p (\eta_m W_\infty)$ , while juvenile mortality is substantially higher (Fig. 2a). The ratio between adult natural mortality and the von Bertalanffy growth constant  $K$  is  $M/K \approx a \eta_m^{n-1} / 3$  (Andersen et al. 2009) (i.e., a constant in accordance with observations; Beverton and Holt 1959; Gislason et al. 2010). Fishing mortality is specified via a trawl selectivity curve  $\mu_F = F \psi(w, \eta_F)$  with the same type of switching curve used for the maturity ogive (eq. M2) but with inflection point at  $\eta_F W_\infty$  (eq. M10).

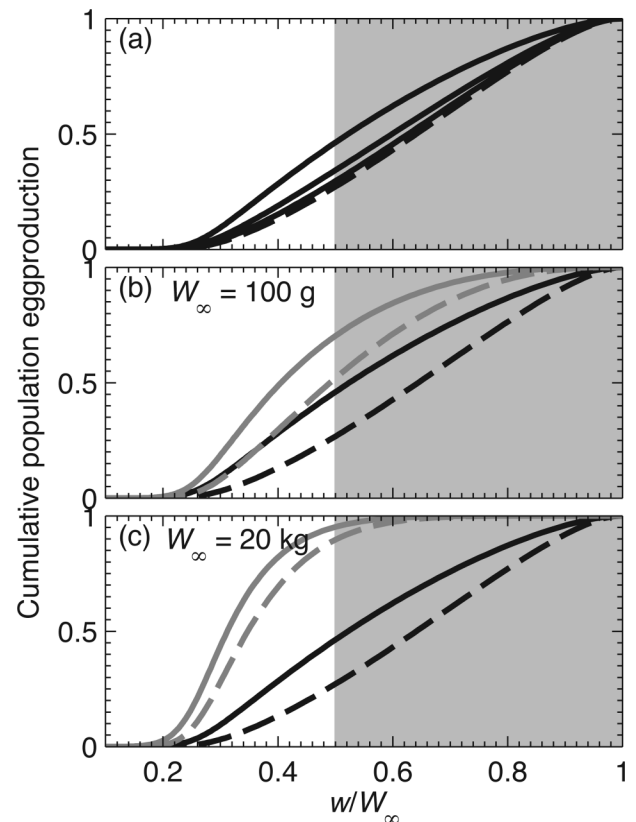
**Fig. 2.** Mortality, size spectrum, and distribution of density-independent recruit production as a function of mass divided by asymptotic mass for a species with  $W_\infty = 20$  kg. (a) Natural mortality (black line), fishing mortality (dashed grey line) with  $F = 0.4$  year<sup>-1</sup>, and total mortality (solid grey line). (b) Biomass size spectrum  $N(w)w$  in the unfished (black line) and fished (grey line) situation. The size spectrum has a bump around the size at maturation (vertical dashed line) where growth slows down owing to the investment in reproduction. (c) Distribution of egg production (i.e., the egg production normalized by the total recruit production such that the area beneath the two curves are the same). The grey area represents the “big old fecund females” (BOFF) individuals larger than  $0.5W_\infty$ .



The size distribution is calculated by multiplying recruitment with survivorship (eqs. M11–M12). Division by growth rate is a requirement when the formulation is made in terms of size instead of age (Jones 1974; Beyer 1989; Andersen and Beyer 2014). Yield from the fishery is calculated by accounting for recruitment (i.e., going beyond a yield-per-recruit analysis; eq. M13). Two representative reference points are calculated: the fishing mortality that gives the maximum yield  $F_{msy}$  and the fishing mortality that leads to zero recruitment  $F_{crash}$ . Two other reference points are commonly used:  $F_{lim}$  and  $F_{max}$  (fishing mortality leading to maximum yield per recruit); however,  $F_{lim}$  is qualitatively characterized by  $F_{crash}$ , and  $F_{max}$  is an inappropriate reference point in most situations (Andersen and Beyer 2014).

The impact of maternal effects on recruit production and fisheries reference points is illustrated by two contrasting life histories: a small species with  $W_\infty = 100$  g, typical of pelagic forage fish with a short life-span, large von Bertalanffy growth constant  $K \approx 0.5$  year<sup>-1</sup>, and high natural adult mortality  $M \approx 0.35$  year<sup>-1</sup>; and a large species with  $W_\infty = 20$  kg, typical of a large demersal species with small  $K \approx 0.13$ , low mortality  $M \approx 0.1$  year<sup>-1</sup>, and a long life-span. The effect of other life histories beyond these “average” life histories are examined by a sensitivity analysis of the central parameters regulating recruitment  $\varepsilon_r$ , the fisheries selectivity  $\eta_F$ , and the natural mortality  $a$ . Changes in  $\varepsilon_a$  would result in changes

**Fig. 3.** The cumulative distribution of density-independent recruit production of an entire population as a function of individual size. (a) Recruit production for values of the maternal effect parameter varying from  $\phi = 1$  (no maternal effects; solid line) to  $\phi = 4$  (dashed line). This graph is independent of asymptotic size. (b and c) Recruit production with fishing mortality  $F = 0.4$  year<sup>-1</sup> (grey lines) and without fishing mortality (black lines). Dashed lines are with  $\phi = 4$ . The grey area represents the BOFF individuals.



in density-independent recruit production with similar effects to changes in  $\varepsilon_r$ .

## Results

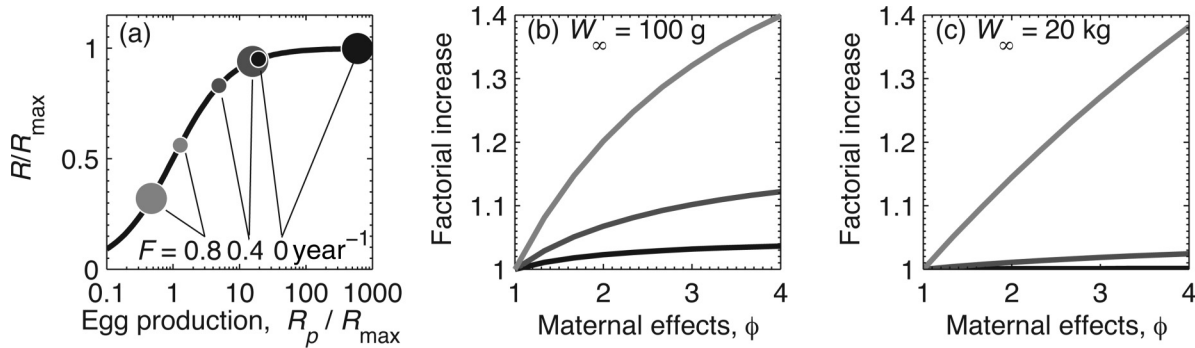
To facilitate presentation of results, we refer to individuals larger than a fixed size as the BOFF individuals. The size where individuals change status to BOFF is set rather arbitrarily at 50% of the asymptotic size. For a fish with an asymptotic size of 20 kg, which matures around 5 kg, the size of the transition to BOFF status is at 10 kg.

Individual growth and mortality (Fig. 2a) are scaled up to generate the biomass distribution (Fig. 2b) and the distribution of recruit production (Fig. 2c). In the unfished situation, the distribution of recruit production extends well into the size range of the BOFF individuals. Fishing has a clear impact on the distribution of the recruit production. Because fishing truncates the biomass distribution, the ratio between small and large adults becomes skewed in favor of the smaller adults, leading to the population-level recruit production being dominated by younger mothers.

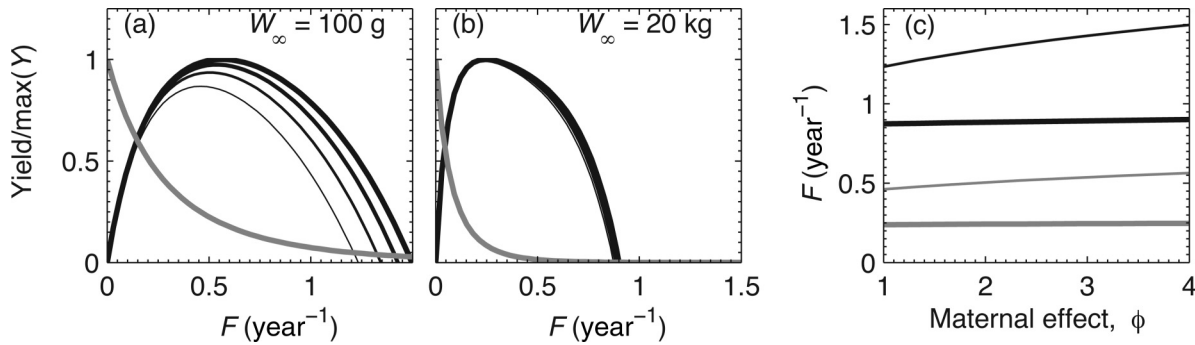
The influence of including maternal effects on the distribution of recruit production is described by the cumulative distribution function of the egg production (Fig. 3). In the unfished situation the impact of maternal effects is independent of asymptotic size. This is because demography (i.e., the size distribution  $N(w)$ ) is the same for all species when scaled with asymptotic size in the absence of density-dependent effects or fishing mortality (Andersen and Beyer 2014). About half of the recruit production in the pop-



**Fig. 4.** Impact of maternal effects on density-dependent recruitment. (a) The scaled stock–recruitment function showing recruitment for large species ( $W_\infty = 20$  kg; large circles) and small species ( $W_\infty = 100$  g; small circles) for fishing mortalities  $F = 0$  year<sup>-1</sup> (black circles),  $F = 0.4$  year<sup>-1</sup> (dark grey circles), and  $F = 0.8$  year<sup>-1</sup> (light grey circles). (b, c) The factorial increase in recruitment  $R(\phi)/R(\phi = 1)$  as a function of the strength of maternal effects for the three fishing mortalities:  $F = 0$  year<sup>-1</sup> (black lines);  $F = 0.4$  year<sup>-1</sup> (dark grey lines); and  $F = 0.8$  year<sup>-1</sup> (light grey lines).



**Fig. 5.** Yield as a function of fishing mortality for various strengths of maternal effects indicated by increasing line width: thinnest line:  $\phi = 1$ ; thickest line:  $\phi = 4$ . Note that all four lines are indistinguishable from one another in panel (b). Grey lines are the mean size of mature individuals:  $\int w\psi(w, \eta_m)N(w) dw$  divided by the mean size at zero fishing. Yield and population size are divided by their maximum values. (c) Fisheries reference points for increasing maternal effects for small species ( $W_\infty = 100$  g; thin lines) and large species ( $W_\infty = 20$  kg; thick lines). Black lines:  $F_{\text{crash}}$ ; grey lines:  $F_{\text{msy}}$ .



ulation originates from BOFF individuals. Maternal effects only increases this proportion slightly; maternal effects of  $\phi = 4$  only increases the percentage to about 75%. Fishing substantially changes these fractions by removing large individuals, in particular for large species. In the case of a fishing mortality of 0.4 year<sup>-1</sup>, only 5% to 15% of the recruit production comes from BOFF for the large species and 35% and 50% for the small species. The importance of BOFF individuals is therefore severely reduced for fishing, particularly so for large species.

Density-dependent recruitment decreases the importance of maternal effects, in particular at high levels of recruit production (Fig. 4). The impact of maternal effects depends upon whether recruitment is saturated (i.e., on the horizontal section of the stock–recruitment curve) or unsaturated (i.e., on the linearly increasing section; Fig. 4a). If recruitment is on the saturated section, changes in recruit production have little effect on recruitment because of density-dependent effects during prerecruit stages, so maternal effects have less of an influence on recruitment than would otherwise be the case. Conversely, if recruitment is unsaturated, density-dependent effects are small; however, egg production is only weakly affected by maternal effects because the number of BOFF individuals in the fished populations is so small (Fig. 2b). Even with quite heavy fishing of 0.8 year<sup>-1</sup>, the increase in recruitment brought about by strong maternal effects (i.e.,  $\phi = 4$ ) is less than 40% (Figs. 4b, 4c).

The influence of accounting for recruitment is reflected in the yield curves (Figs. 5a and 5b). Yield increases as a function of fishing mortality, reaches a maximum at  $F_{\text{msy}}$ , and declines to zero at  $F_{\text{crash}}$ . Maternal effects change this pattern, but only

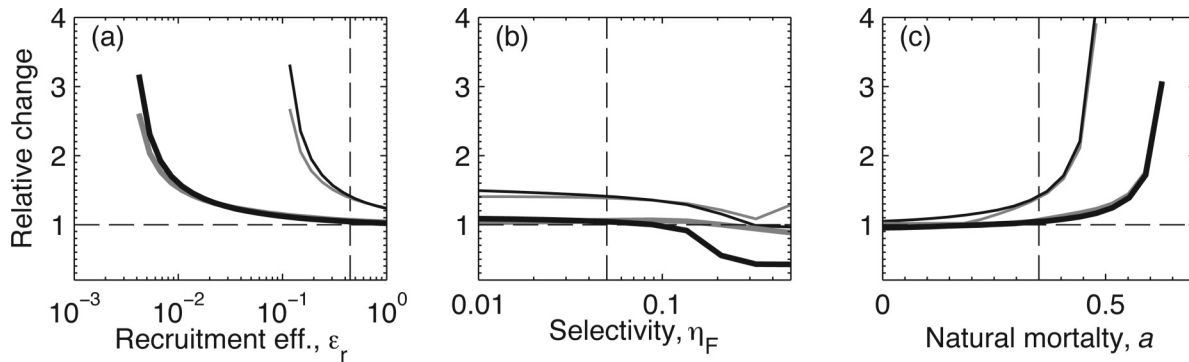
slightly for the small species and negligibly for the large species (Fig. 5c). The difference in the sensitivity to maternal effects is due to the difference in the response of the stock structure to fishing between small and large species. The changes in stock structure are reflected in the mean size of adults, shown with grey lines in Figs. 5a and 5b. For the large species, mean size declines sharply towards zero as fishing increases. Therefore, BOFF individuals play a small role for the reference points. In contrast, the mean adult size in the small species decline less rapidly, which is why the BOFF individuals play a role in determining recruitment and therefore the reference points.

The sensitivity of the results was examined by varying the central parameters around their default values and calculating the ratio between the reference point without maternal effects,  $\phi = 1$ , and with maternal effects,  $\phi = 4$ . This ratio provides a measure of the importance of taking maternal effects into account when assessing reference points (Fig. 6).

Changing the selectivity of fishing has relatively small impact on the importance of maternal effects for the reference points when the selectivity happens well before maturity ( $\eta_F < 0.25$ ). When fishing is only targeting mature individuals ( $\eta_F > 0.25$ ), maternal effects have a major negative impact on the reference points, because in this case BOFF are being selectively targeted for fishing.

Increasing the natural mortality  $a$  or decreasing the recruitment efficiency  $\varepsilon_r$  results in a dramatic increase in the importance of maternal effects. The higher the natural mortality or the lower the recruitment efficiency, the less fishing the population can sustain, and therefore the exploitation reference points become

**Fig. 6.** The effect of changing one parameter on the reference points  $F_{msy}$  (grey lines) and  $F_{crash}$  (black lines) for small species ( $W_{\infty} = 100$  g; thin lines) and large species ( $W_{\infty} = 20$  kg; thick lines). The vertical dashed lines indicate the default value of the parameter. Each panel shows how much the reference point changes when using a maternal effect of  $\phi = 4$  relative to the case without maternal effects: (a) change in recruitment efficiency,  $\varepsilon_r$ ; (b) change in the size where fishing starts,  $\eta_F$ ; (c) change in the level of natural mortality,  $a$ .



smaller. In a situation when the reference points are small, the stock structure more closely resembles that in an unexploited situation than when the reference points are large, simply because of the difference in fishing mortalities. Small fishing mortality, as seen in Fig. 3, means that maternal effects are more important. This result can be extended to include all changes in parameters that make the stock more vulnerable to fishing impacts. It is therefore important to account for maternal effects when assessing reference points for stocks that are very vulnerable to fishing measured as having low values of the exploitation reference points.

## Discussion

Our results lead to four conclusions regarding population-level density-independent recruit production and the importance of maternal effects for recruitment and fisheries reference points:

- (1) The BOFF individuals contribute significantly to population-level recruit production in an unfished situation. Specifically, about half of the recruit production comes from those individuals larger than half the asymptotic mass. This result implies that half of the adult biomass consists of those individuals larger than half the asymptotic mass, since recruit production is proportional to individual mass. The result is independent of the asymptotic size. Maternal effects may therefore promote resilience of unfished stocks to declines due to changes in environmental conditions.
- (2) Fishing reduces the importance of BOFF individuals for recruit production because fishing reduces the relative abundance of BOFF individuals remaining in the population. This is mostly pronounced for species with large asymptotic size; for a cod-like species, the BOFF individuals will contribute less than 5% of the recruit production when the stock is fished with  $F = 0.4 \text{ year}^{-1}$  and less than 0.5% when  $F = 0.8 \text{ year}^{-1}$ . Maternal effects are therefore of limited importance for rebuilding times of such depleted stocks, since they contain insignificant numbers of BOFF. For smaller species, the BOFF individuals still have an important influence even when they are fished.
- (3) For an average life history, fisheries reference points are weakly influenced by maternal effects. However, even small effects (up to 20% reduction for small species) can have important real-world implications for harvest specifications. The relatively small sensitivity comes about partly as a consequence of the conclusion above and partly because density dependence decreases the importance of the density-independent recruit production when fishing mortality is low. This result is in accordance with some other stock-specific analyses. Murawski et al. (2001) pointed out that for Georges Bank cod,

ignoring maternal effects is not expected to have a high impact on long-term fishing mortality rate that would allow for stock replacement. Similarly, a study for Pacific ocean perch (*Sebastes alutus*) found  $F_{msy}$  to be relatively insensitive to the presence of maternal effects (Spencer et al. 2007). O'Farrell and Botsford 2006 found that for black rockfish (*Sebastes melanops*) the addition of maternal age effects had small fisheries implications, and Arlinghaus et al. (2010) found maternal effects irrelevant for northern pike (*Esox lucius*). Finally, an analysis of different reproductive indices for mostly cod stocks found that  $F_{msy}$  was not affected much by which index was used (Morgan et al. 2009). In contrast, Field et al. (2008) used an age-structured model to conclude that older fish contribute more to the recruits than younger fish. They used very large maternal effects (roughly corresponding to  $\phi = 10$ ); furthermore, they did not account for the mortality from recruitment to the age of BOFF and therefore overestimate the importance of BOFF and maternal effects. Spencer et al. (2014) found that fishing mortality reference points decrease when maternal effects are considered. However, in contrast with the approach taken here, they modelled maternal effects as a lower survival of offspring from young mothers. Therefore, their results are qualitatively in accordance with our results. The effect that they find is, however, much larger, which is due to larger maternal effects.

- (4) An important exception is fish stocks whose life histories and dynamics make them particularly vulnerable to fishing. For such stocks, maternal effects may indeed be relevant. This is partly because of the large fraction of the egg production coming from BOFF individuals when fishing mortality is low and partly because these stocks are expected to be on the linear part of the stock–recruitment curve, where the damping effect of density-dependent processes in the prerecruit phase is small. Such a vulnerability would be reflected in low values of fisheries reference points and could stem from slower than average growth combined with higher than average natural mortality, from lower than average reproductive rates, or from lower than average recruitment. Usually slower growth is accompanied by a lower mortality. This is embodied in the fairly constant value of the “ $M / K$ ” ratio (Beverton 1992; Gislason et al. 2010), which is here represented by the physiological rate of fishing,  $a$ . Therefore, slower growth or higher mortality alone does not lead to a more vulnerable stock, only the ratio between growth and mortality influences vulnerability.

Another exception would be for stocks where recruitment occurs in pulses of very high recruitment interspersed by several years of low recruitment. In such stocks the spawners will be

dominated by BOFF individuals during the periods when the last major recruitment occurred substantially longer ago than the age of maturation, and therefore maternal effects could be an important factor. A similar situation would occur for a stock with nonpulsed recruitment following a change in environmental conditions affecting, for example, egg survival or carrying capacity of the stock. Since our analysis assumed a population in steady state, such cases were not covered by the analysis.

Our results are conditioned on the stocks following the general life-history model (Andersen and Beyer 2014). This model covers a lot of the variation between species with different sizes, life-spans, levels of natural mortality, etc. It does not, however, cover specific life histories that shift the balance between the importance of young or small versus old and large fish in a stock. This could occur because of spatial heterogeneity in environmental conditions in a stock area combined with a heterogeneous distribution of fish exploitation. Differential occupation of some habitat types by certain size groups (e.g., owing to competition) that may be less heavily exploited than others (e.g., owing to distance from shore, depth, or bottom type) could allow a local area to develop a size structure with a relatively large share of BOFFs. Such an area could provide offspring to surrounding areas via drift or emigration and, if sufficiently large, impact recruitment. Mechanisms such as these may be associated with the effects of marine protected areas or other low-exploitation areas on population dynamics in surrounding areas. Another specific life history not covered explicitly by the model is the semelparous life history adopted, for example, by salmonoid species.

We have incorporated maternal effects in a fish stock model and in the Beverton–Holt recruitment function to analyze the effect of age and size structure on recruitment and reference points. We have used the Beverton–Holt recruitment function because it ensured stable population structure. Had we used a nonmonotonic recruitment curve (e.g., the Ricker curve; Ricker 1954), we may have had unstable (oscillating or chaotic) population dynamics for low fishing mortalities and large species (Levin and Goodyear 1980). However, qualitatively the results are expected to be similar with the two recruitment functions. The Ricker curve may still be used for statistical estimation of maternal effects, as done by Shelton et al. (2012) for Icelandic cod.

We have generalized previous calculations made on specific stocks such that our calculation covers all species characterized by their asymptotic size, and we have shown the results for two typical life histories (a small, short-lived species and large, long-lived species). To assess the impact of maternal effects, both the impact due to the age and size structure and the recruitment–spawner biomass relationship should be accounted for. The former is easily assessed, but the recruitment curve may be difficult to estimate. We showed that the stock–recruitment function is expected to have a large dampening effect for large species, so it should not be ignored when the effect of maternal effects are assessed. Ignoring the recruitment curve (e.g., O’Farrell and Botsford 2006) will lead to an overestimation of the importance of maternal effects.

The natural mortality that we use (eq. M9) declines with size, which is a departure from the usual assumption of a constant adult mortality. We use this formulation of mortality to comply with evidence that mortality is indeed decreasing with size (Peterson and Wroblewski 1984; Gislason et al. 2010) and to be consistent with community ecology (Dickie 1976; Andersen and Beyer 2006; Andersen et al. 2009). The size-based formulation of mortality has two effects: (i) the adult mortality of small species is larger than that for large species (Beverton and Holt 1959; Gislason et al. 2010); (ii) mortality is declining throughout the life of an individual. The first effect links the variation in adult mortality to asymptotic size and makes it possible to characterize the two life histories that we use just by asymptotic size. The second effect is not essential in the present context, where we are mainly

concerned with adults for whom the mortality is only weakly declining with size (Fig. 2a; it varies a factor of  $\eta_m^{1/4} \approx 0.7$  between a small adult and an individual of asymptotic size). The size-dependent mortality is therefore not crucial for the comparison between small and large adults. What may play a role, though, is senescent mortality, which leads to an increased mortality for the large and old individuals. Senescent mortality therefore decreases the performance of the large and old individuals, thereby reducing the importance of maternal effects. We have ignored senescent mortality, partly because there is no generally accepted way of parameterizing senescent mortality and partly because we wanted to make an upper-limit estimate on the importance of maternal effects. Had we included senescent mortality, the importance of the BOFF individuals would have been smaller.

The damping of maternal effects by the saturation of the stock–recruitment function depends on the fishing mortality. Unfished larger species are on the saturated (horizontal) part of the stock–recruitment function, and therefore changes in density-independent recruit production do not influence recruitment. Small species, on the other hand, have a less saturated recruitment even in the absence of fishing (i.e., on the rising part of the stock–recruitment function), and therefore changes in the density-independent recruit production due to maternal effects have a higher impact on recruitment. Stocks on the rising part of the stock–recruitment curve (small and (or) fished stocks) are more prone to environmental variation influencing density-independent recruit production ( $\alpha$ ). These results are consistent with Brunel (2010), whose meta-analysis provides a positive correlation between three indices of age structure and the variability in recruitment, but not with recruitment in absolute terms. Moreover, Venturelli et al. (2009), using both a population model and a meta-analysis, show that maternal quality can have a strong effect on a population’s maximum reproductive rate. However, that study did not account for changes in the age structure.

In conclusion, our study suggests that the incorporation of maternal effects into the recruitment equation has little importance when interpreting and forecasting population dynamics of fished stocks and will not result in better scientific advice for a stock being managed to achieve maximum sustainable yield. The only exception is stocks that are very vulnerable to fishing.

## Acknowledgements

The work is a contribution to the EU FP7 program MEECE. KHA was supported by the Villum Kann Rasmussen Center of Excellence, Ocean Life. BRM acknowledges the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate.

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