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Original Article

Effects of density dependence in growth and natural mortality on F_{MSY} and maximum sustainable yield

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Abstract

In fisheries management, it is generally assumed that density-dependent processes are confined to the pre-recruit stage of a fish. Consequently, current calculations of fishing mortality reference points include density dependence (DD) solely in recruitment dynamics. However, several studies have reported the importance of DD in growth and natural mortality (M). In this study, we tested the effect of DD on estimates of fishing mortality producing maximum sustainable yields (F_{MSY}), comparing these estimates to those resulting from constant growth and M. We simulated fish populations with a wide range of life-history traits (LHTs), applying either constant or density-dependent growth and M and derived F_{MSY} for each stock. Results showed that including DD in growth and M led to higher F_{MSY} and often also higher yield estimates (MSY). The effect of DD was found to be greater in growth than in M. Additionally, F_{MSY} estimates derived from surplus production models fitted to generated stocks with density-dependent growth and/or M were generally closer to true F_{MSY}, compared to those from age-based long-term predictions assuming constant growth and M. However, due to the inherent uncertainties in estimates of stock dynamics and biological reference points (BRPs), caution is suggested before implementing DD in F_{MSY} calculations. Equilibrium yield curves relating production to stock size were right-skewed, shape parameters from production models were slightly below 1 for scenarios assuming constant growth and M, but declined to 0.5 with increasing DD.

Keywords: MSY; reference points; density-dependence; growth; natural mortality

Introduction

The concept of Maximum Sustainable Yield (MSY) originated in the 1930s (Russell 1931) and its application considerably expanded with the development of stock-production models (Schaefer 1954, Pella and Tomlinson 1969, Mace 2001). Following several international agreements and laws [e.g. the Ecosystem Approach to Fisheries (FAO 2003), the Marine Strategy Framework Directive (MSFD) (EC 2008), and the Common Fisheries Policy of the European Union (EU 2013)], maintaining catches at levels that do not exceed MSY has been the main goal of fishery management for two decades.

The International Council for the Exploration of the Sea (ICES), the main advisory body of the EU and ICES Member Countries, introduced in 2009 the MSY approach to provide recommendations on catch opportunities (Lassen et al. 2014). The fishing mortality expected to produce maximum long-term yield (F_{MSY}) is often the chosen management target, acting as an upper limit of fishing mortality rate. Similarly, MSY-based objectives or approaches were introduced in the USA, Canada, and by the Northwest Atlantic Fisheries Organization (NAFO) (Shelton and Morgan 2014).

Current F_{MSY} estimations for data-rich fisheries are predominantly based on age-structured assessments of stock size and long-term stochastic simulations of biomass and catches across various fishing mortality scenarios. These simulations typically assume that recruitment follows a density-dependent pattern based on the stock-recruitment relationship. This approach overlooks the variability of other important factors of stock dynamics (i.e. growth, M, and maturity), which are generally assumed constant (Sparholt et al. 2021). As a result, density-dependent processes are often assumed to only occur in the early life stage of fish. However, substantial evidence shows that growth in many fish stocks is density-dependent (Horbowy et al. 2018, Zimmermann et al. 2018, Grossman and Simon 2020, Matte et al. 2020, Rindorf et al. 2022).

The variability in fish growth over time has been shown to be a plastic response to environmental conditions and food availability (Lorenzen 2016). Recently, Croll et al. (2023) demonstrated that density-dependent growth in four flatfish stocks in the North Sea was driven by resource availability and shows how this influences optimal fishing efforts. Similarly, Rose et al. (2001) showed the importance of compensatory DD in fisheries management, but also pointed out challenges in quantifying the strength of DD in specific populations. The lack of DD observations in growth may result from fishing-induced selection, where fast-growing fish are removed, favoring slower-growing fish. This observational challenge probably acts as a barrier to the inclusion of DD in all parameters of fish population dynamics, especially because it implies that recovered fish populations could be fished more intensively to avoid large population sizes (Sparholt et al. 2021). Nonetheless, the effects of density-dependent growth and M on reference points remain largely unexplored in age-based models. To our knowledge, only two fish stocks include these dynamics, the Icelandic cod (Danielsson et al. 1997) and Northeast Arctic cod (Kovalev and Bogstad 2005). In many cases, DD in growth and occasionally in M are implicitly accounted for in the historical stock assessment using yearly weight-at-age and M-at-age data. These data are based on intensive annual sampling of fisheries and surveys, as well as multispecies mod-

els. However, there is rarely any attempt to relate it to stock size, and when models are used in predictions to estimate reference points, weight-at-age and M-at-age data are reduced to moving averages (e.g. average of recent years). Current calculations of reference points generally exclude changes in multispecies interactions, ecosystems effects, climate, and fisheries-induced evolutionary changes. Instead, these factors are rather assumed to be stable over the time series of the assessment data or, in some cases, a shorter period if an ecosystem regime shift is identified.

Here, we tested the hypothesis that including DD in growth and *M* impacts fishing mortality reference points estimations. Because including such DD directly into long-term simulations for deriving F_{MSY} is not always feasible (e.g. due to a lack of data or of DD sub-model), we also used surplus production models (SPMs) as an alternative approach (Sparholt et al. 2021). SPMs represent the rate of change in biomass as proportional to the ratio of biomass and carrying capacity and thus have, theoretically, the potential to reflect some degree of DD in F_{MSY} estimates. The SPM used was the state-space model SPiCT (Pedersen and Berg 2017), which has been extensively tested and has been applied for several stocks within ICES and GFCM (General Fisheries Council for the Mediterranean) (ICES 2021, 2023a, Cousido-Rocha et al. 2022). The advantage of SPiCT is the consideration of process error and the possibility to reflect observation errors both in the index of stock size and in the catches.

Specifically, this study had three objectives:

(1) Assess the effects of DD in growth and natural mortality on F_{MSY} using age-structured models.
(2) Estimate F_{MSY} using surplus-production models.
(3) Compare these two F_{MSY} estimates, considering both constant and density-dependent growth and *M*.

We generated a wide range of stocks with varying life history parameters under scenarios with or without DD in growth and/or *M*. Long-term simulations and SPMs were then applied to these generated stocks to derive F_{MSY} estimates.

Methods

Stock simulation

Stocks were generated based on a variety of factors: steepness (h) of stock–recruitment (S–R) relationship, growth parameter (K) from the von Bertalanffy equation, and *M* levels (see Supplementary material for details and the equations used). The following values for h, K (year^{-1}), and M (year^{-1}) were used: $h = 0.5, 0.7, 0.9$; $K = 0.2, 0.4, 0.7, 1.2$; and $M = 0.2, 0.3, 0.4$. For each combination of above values (36 in total), one stock was simulated (Table 1). The asymptotic weight (W_{inf}) and the theoretical age (year) at 0 size (a_0) in the von Bertalanffy equation were set at 1 and 0, respectively. The maximal age for simulated stocks (*aMax*) was set consistent with *M*, following recommendation of Hamel and Cope (2022), where $M = 5.4/aMax$.

Logistic maturities (*mat*) were assumed

$$mat\,(a) = \frac{1}{1 + e^{\frac{-\ln(19)(a - aMat50)}{aMat95 - aMat50}}}, \tag{1}$$

where *aMat50* and *aMat95* is age of 50% maturity and age of 95% maturity, respectively. The level of *aMat50* was assumed based on Beverton and Holt invariants (Beverton 1992, Charnov 1993), where the ratio of length at 50% maturity to asymptotic length of von Bertalanffy equations equals 0.66. Consequently, $aMat50 = -\ln(0.34)/K$, and the value was rounded to the nearest integer. The *aMat95* was assumed to be $aMat50 * 1.8$ following Horbowy and Hommik (2022). Selectivity to the fishery were used as equal to maturities.

Table 1. The parameters of the generated stocks (steepness, *h*; growth, *K*; natural mortality, *M*; age at 50% maturity, aMat50; maximal age, aMax) and its F_{MSY} ('true' F_{MSY}) derived assuming constant growth and natural mortality

	h	*K*	*M*	*aMat50*	*aMax*	F_{MSY}
1	0.5	0.2	0.2	5	27	0.128
2	0.7	0.2	0.2	5	27	0.22
3	0.9	0.2	0.2	5	27	0.34
4	0.5	0.4	0.2	3	27	0.15
5	0.7	0.4	0.2	3	27	0.25
6	0.9	0.4	0.2	3	27	0.40
7	0.5	0.7	0.2	2	27	0.17
8	0.7	0.7	0.2	2	27	0.30
9	0.9	0.7	0.2	2	27	0.50
10	0.5	1.2	0.2	1	27	0.18
11	0.7	1.2	0.2	1	27	0.33
12	0.9	1.2	0.2	1	27	0.54
13	0.5	0.2	0.3	5	18	0.21
14	0.7	0.2	0.3	5	18	0.35
15	0.9	0.2	0.3	5	18	0.55
16	0.5	0.4	0.3	3	18	0.22
17	0.7	0.4	0.3	3	18	0.38
18	0.9	0.4	0.3	3	18	0.61
19	0.5	0.7	0.3	2	18	0.26
20	0.7	0.7	0.3	2	18	0.45
21	0.9	0.7	0.3	2	18	0.74
22	0.5	1.2	0.3	1	18	0.27
23	0.7	1.2	0.3	1	18	0.48
24	0.9	1.2	0.3	1	18	0.77
25	0.5	0.2	0.4	5	14	0.30
26	0.7	0.2	0.4	5	14	0.52
27	0.9	0.2	0.4	5	14	0.84
28	0.5	0.4	0.4	3	14	0.31
29	0.7	0.4	0.4	3	14	0.54
30	0.9	0.4	0.4	3	14	0.86
31	0.5	0.7	0.4	2	14	0.35
32	0.7	0.7	0.4	2	14	0.62
33	0.9	0.7	0.4	2	14	1.02
34	0.5	1.2	0.4	1	14	0.36
35	0.7	1.2	0.4	1	14	0.64
36	0.9	1.2	0.4	1	14	1.03

Recruitment (R) dynamics followed Beverton and Holt (1957) S–R relationship (B&H), expressed as $R = B/(\alpha + \beta B)$, where B is spawning-stock biomass and parameters α and β are generated from the steepness of stock-recruitment relationship (Francis 1992).

$$\alpha = \frac{B_0\,(1 - h)}{4hR_0} \tag{2.a}$$

$$\beta = \frac{5h - 1}{4hR_0}. \tag{2.b}$$

Recruitment to the virgin stock (R_0) was assumed to be 1, so $B_0 = SPR\,(0)$, where B_0 represents unexploited equilibrium spawning biomass, and *SPR* is stock-per-recruit.

The parameters steepness h, growth K, and natural mortality M, along with assumed values for selectivity, maturity, and derived parameters of the B&H S–R relationship, enable the estimation of F_{MSY} by maximising equations for equilibrium yields (Y) (Horbowy and Luzeńczyk 2012, Horbowy and

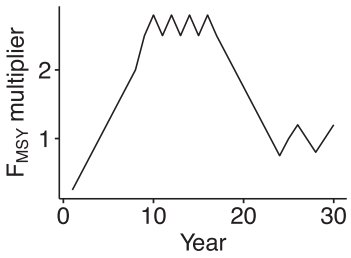

Figure 1. Multipliers of F_{MSY} in consecutive years, used to simulate fishing mortality in generated stocks.

Hommik 2022):

$$Y_{eq}(F) = YPR(F)\frac{SPR(F) - \alpha}{\beta * SPR(F)}, \quad (3)$$

where YPR is the yield-per-recruitment, and the subscript *eq* stands for equilibrium. So, for each combination of *h*, *K*, *M*, and assumed maturities and selectivities, the F_{MSY} was estimated assuming constant growth (Table 1).

Then, fishing mortality was generated for each stock for a period of 30 years as a product of estimated F_{MSY} and assumed year dependent multipliers, which aimed to reflect possible development of the fishery (Fig. 1). Fishing mortality generated was:

- increasing in the first 10 years to a high level, from $0.25*F_{MSY}$ to $2*F_{MSY}$,
- fluctuating in the next 8 years at high levels of $2.5*F_{MSY}$ to $2.8*F_{MSY}$,
- declining in the following years with *F* close to F_{MSY},
- fluctuating at F_{MSY} in final years of the 30 years period.

Density dependency inclusion

In addition to constant growth and *M*, DD in growth (DDG), DD in natural mortality (DDM), and DD in both growth and natural mortality (DDG&*M*) were incorporated in the generated stocks. The inclusion of DD in growth followed the approach of Horbowy and Luzeńczyk (2017):

$$w(a, y) = wconst(a)\, corrW(y), \quad (4.a)$$

where *w*(*a*, *y*) is weight-at-age *a* in year *y*, *wconst(a)* is constant weight-at-age *a*, and the term *corrW* is a 'correction' to constant weight, when DD is included in the analysis and is expressed as:

$$corrW(y) = \frac{aW}{bW + stock(y)}, \quad (4.b)$$

where *aW* and *bW* are parameters related to density dependence in growth, and *stock* is a measure of stock size used to model density dependence, e.g. total stock biomass, spawning-stock biomass, or total numbers.

DD in *M* was modelled following Lorenzen (1996, 2000)'s equation, in which *M* is proportional to the power function of body weight. As body weight is proportional to *corrW*, DDM is:

$$M(y) = M * corrM(y), \quad (5.a)$$

where

$$corrM(y) = corrW(y)^p = \left(\frac{aW}{bW + stock(y)}\right)^p. \quad (5.b)$$

The exponent *p* usually ranges between −0.3 and −0.37 and was assumed to be equal to −0.37 in this analysis to reflect the highest DD effects on *M*.

Two options for strength of DD were considered:

(a) medium DD in which *corrW* ranged approximately between 0.75 and 1.25,
(b) strong DD in which *corrW* ranged approximately between 0.57 and 1.43.

In option (a), the minimum weight is 60% of the maximal weight, whereas in option (b), the minimum weight is 40% of the maximal weight. This was based on the weight variations in Baltic sprat and herring (Horbowy 1997, Cardinale and Arrhenius 2000, ICES 2023a, 2024) and similar findings reported by Lorenzen (2016) based on his own analyses and a literature review.

Parameters *aW* and *bW* were derived by fitting *corrW* to 1, 0.75, and 1.25 at average, maximum, and minimum stock levels, respectively, in option (a). Similarly, for option (b), *corrW* was fitted to 1, 0.57, and 1.43. For *stock* total biomass generated under constant growth and *M* was used. High weight (equal to 20) was imposed on fits to 1 at average biomass, so that *corrW* at average biomass is very close to 1.

An example of a generated stock dynamic (stock 19 from Table 1) is illustrated in Fig. 2 for both constant and density-dependent growth and *M*. For each of the 36 stocks characterized by constant growth and/or *M*, three additional stocks were generated, where the growth and/or *M* were density-dependent. Thus, 144 stocks were generated in total. This section of the study which simulates 30 years of fish stock dynamics will be referred to as the 'generated part'.

The 144 generated stocks were the basis for further analyses:

(1) Long-term predictions: long-term predictions were performed to derive F_{MSY} and MSY. Those will be referred to as a 'true' F_{MSY} and 'true' MSY. long-term predictions extended to 500 years, starting from year 30 (terminal year) of the generated part.
(2) Production models: Surplus Production in Continuous Time models [SPiCT, Pedersen and Berg (2017)] were fitted to the generated stocks (i.e. to biomass and catches from the 'generated part') and F_{MSY} and MSY were estimated within these models.

Considering DD, the following options were simulated:

(1) Scenario 1 (noDD): constant growth and *M* were assumed in the generated and long-term predictions parts.
(2) Scenario 2 (DDG, DDM or DDG&M): DD in growth, *M* and in both were assumed in the generated and long-term predictions parts.
(3) Scenario 3: DD was assumed in the generated part (DDG, DDM, or DDG&M), but for long-term predictions, constant growth and *M* were assumed, as per scenario 1. This involved implementing constant growth using the average of weights from the generated part over selected years. The average weights were calculated in several ways, for example:
    (a) over the first three years of the generated part,
    (b) over last three years of the generated part,
    (c) over three middle years of the generated part.

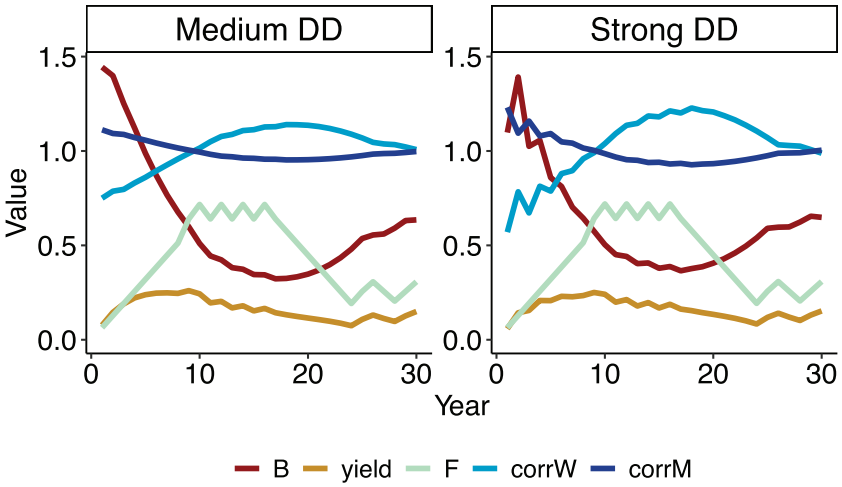

Figure 2. An example of a generated stock dynamics (biomass, yield, *F* for stock 19 from Table 1) with medium and strong density dependence in growth and *M*. The *corrW* and *corrM* are 'correction' factors for constant weight and *M* to get density-dependent growth and natural mortality.

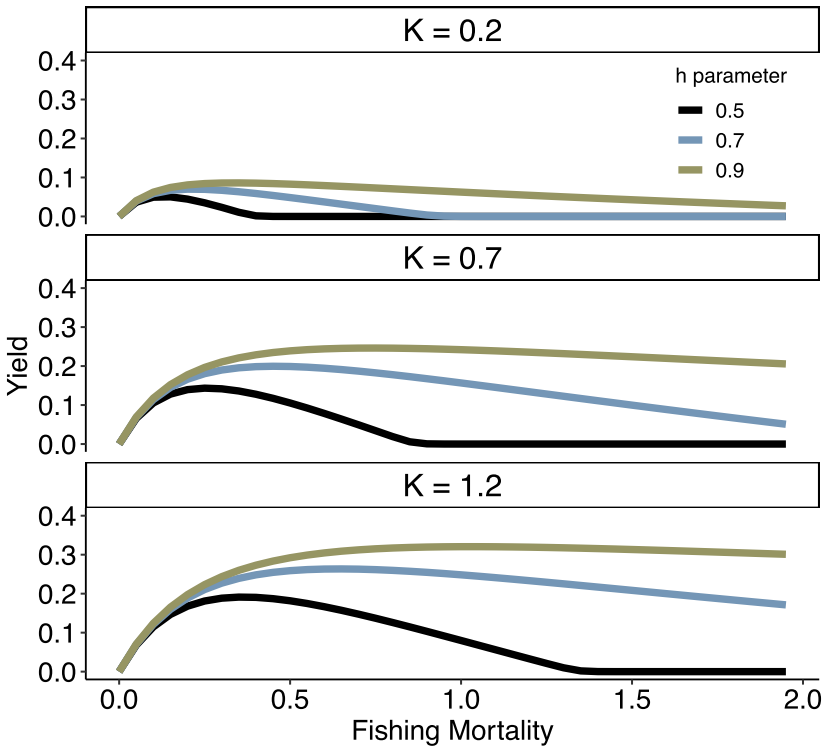

Figure 3. Plots of the equilibrium yield against fishing mortality for constant growth and *M* option and stocks 1–3 ($K = 0.2$), 19–21 ($K = 0.7$) and 34–36 ($K = 1.2$). Within each growth panel stock differ by steepness.

Options 3a and 3b represent rather extreme weights-at-age, i.e. lowest and highest (see examples of stock biomass and *corrW* in Fig. 2) and option 3c represents moderate weight-at-age. In total for each stock, 13 long-term predictions were performed, one for scenario 1, three for scenario 2 (DDG, DDM, and DDG&M), and nine for scenario 3. Results from the terminal year of the generated part were the starting point for long-term predictions.

In the SPiCT models fitted to the generated stocks, the shape parameter (n) was estimated. Following the skewed shaped of equilibrium yield curve (Fig. 3), the prior on n was set assuming that $\log(n)$ is normally distributed with mean of $\log(1)$ and standard deviation (σ) of 1. In addition, a prior was set on the ratio of initial biomass to carrying capacity (mean of log(ratio) assumed $\log(0.8)$, $\sigma = 0.5$) and default priors were set on the ratios of measurement to process errors following SPiCT manual (Mildenberger et al. 2021). All simulations were performed deterministic and were run in R (R Core Team 2020).

F_{MSY} estimated in SPMs is not directly comparable to F_{MSY} estimated within age-structured models (Sparholt et al. 2021). Fishing mortality in SPMs reflects the ratio of total yield in weight to mean exploitable biomass, while in age-structured

models, F reflects usually average ratio of catch-at-age in numbers to mean stock numbers-at-age. Thus, simple linear regressions of F generated for each of the 36 stocks vs F estimated from SPMs (30 years series) were fitted and were used to scale SPMs-based F_{MSY} to comparable F_{MSY} derived from age-structured model.

Sensitivity tests

According to Horbowy and Hommik (2022), effects of maturity on F_{MSY} can be expected to be low. Thus, DD in maturity was not considered in the analyses. However, we tested the sensitivity of F_{MSY} estimates to possible changes in maturity. Vatnehol et al. (2024) analysed maturity of Norwegian spring-spawning herring (NSSH) as dependent on year-class strength. They considered logistic maturity and found that age of 50% maturation was significantly dependent on year-class density, while steepness of the fitted maturity was insignificant. The lowest and the highest age of 50% maturity for NSSH were estimated at 3.7 and 4.4 years, respectively. Therefore, in our sensitivity analyses, F_{MSY} values were estimated assuming that *aMat50* was 10% lower and 10% higher than the values provided in Table 1. These F_{MSY} estimates were compared with F_{MSY} derived using *aMat50*. For *aMat50* values of 3 and 5 years, a 10% change results in a difference of 0.6 and 1.0 years between the lowest and highest *aMat50*. This variation is similar to the range of 50% maturity changes for NSSH.

The estimates of F_{MSY} for generated stocks were derived deterministic. However, in reality the recruitment to the stocks may undergo large variability. Thus, additional simulations with stochastic recruitment were performed to assess whether the density-dependent effects on F_{MSY} under stochasticity were consistent with those obtained deterministically. At a given SSB, recruitment was assumed to undergo log-normal distribution and a bias correction factor was considered: $R = B/(\alpha+\beta B)\exp(\varepsilon)$, where ε is normally distributed random variable with standard deviation σ and average $-\sigma^2/2$. Simulations were performed for a range of F values covering 500 years with 1000 repetitions. Stock 2 and stock 11 were selected for such stochastic analyses; they represent stocks with steepness 0.7 and 0.5, respectively, and M/K ratios of 1 and much lower than 1, as classified by Prince et al. (2015). Analysis for stock 2 was conducted assuming strong DD, while the analysis for stock 11 was performed with medium DD. In both cases, the σ was set to 0.6.

Results

For all stocks, F_{MSY} values derived from long-term predictions with constant growth and M (scenario 1) were very similar to F_{MSY} values estimated by maximising equilibrium yields expressed by Equation (3) (Table 1). The maximum relative difference between values from both series was 0.04%. Equilibrium yields plotted against fishing mortality showed a right-skewness (see Fig. 3 for selected stocks and Figure S1 for all stocks). B_{MSY} estimates were linearly related to B_0 (r^2 of 0.94). The slopes of these regressions ranged from 0.31 under constant growth and M to 0.33 when DDG&M was simulated. These relationships were similar for medium (Fig. 4) and strong DD. However, under strong DD, B_0 and B_{MSY} estimates were, on average, 10%–20% lower than those under medium DD. The average ratio of B_{MSY} to B_0 ranged from 0.31 to 0.34 for both medium and strong DD. The lowest ratio was observed in the 'noDD' scenario, while the highest ratio occurred when DD in M was simulated. The ratio under DDG&M was slightly lower than that for DDM.

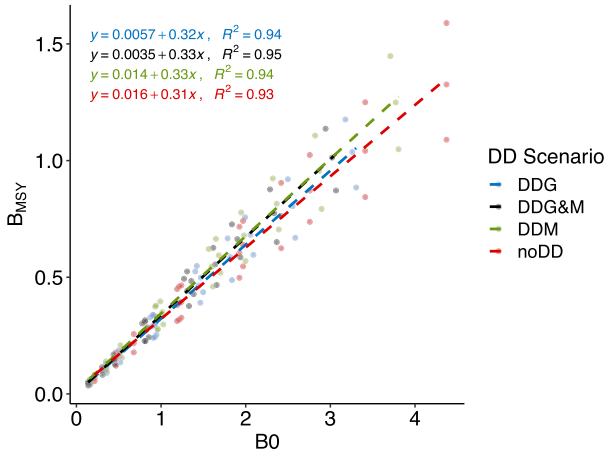

Figure 4. B_{MSY} plotted against B_0 for generated stocks and medium density dependence. Estimates for constant growth and M as well as for medium density dependence are shown (noDD = constant growth and M, DDG = DD in growth, DDM = DD in M, DDG&M = DD in growth and M). Trend lines, equations and r^2 are also presented.

F_{MSY} and MSY with and without DD effects in long-term predictions

For stocks where DD in growth and/or M was considered (scenario 2), F_{MSY} values were higher than those calculated under the assumption of constant growth and M (scenario 1) (Fig. 5a). Specifically, when only DDM was considered, F_{MSY} exceeded the 'noDD' scenario by an average of 17% for medium DD and by 33% for strong DD. The impact of DDG on F_{MSY} was found to be more pronounced, with F_{MSY} surpassing the 'noDD' scenario by an average of 43% for medium DD and by 99% for strong DD. When both DDG and DDM are accounted for, the difference in F_{MSY} compared to the 'noDD' increased to 58% for medium DD and 130% for strong DD.

The impact of DD on yields (i.e. MSY) was less pronounced than its effects on F_{MSY} (Fig. 5b). This could be expected, as higher F_{MSY} leads to lower stock numbers but higher weights, so both effects can offset each other to some extent. Similar to the observations for F_{MSY}, the least effects were observed with DDM, while the combined effects of DDG and DDM were more substantial. Under medium DD conditions, yields were on average 0%, 3%, and 5% higher, for DDM, DDG, and DDG&M, respectively, compared to the 'noDD' scenario. In the case of strong DD, these averaged relative differences in yield increase to 2%, 9%, and 15% for DDM, DDG, and DDG&M, respectively.

The parameters h, K, M, and *aMat50* had minimal impact on the ratios of MSY estimated for DDG&M compared to MSY derived for constant growth and M. MSY values were slightly more similar with increasing steepness and decreasing *aMat50*, whiles changes in K and M had very little effect on differences between MSY's.

Comparison of F_{MSY} and MSY from SPiCT and long-term predictions

SPiCT diagnostic runs were somewhat better when the first two data years (with relatively sharp changes in biomass, Fig.

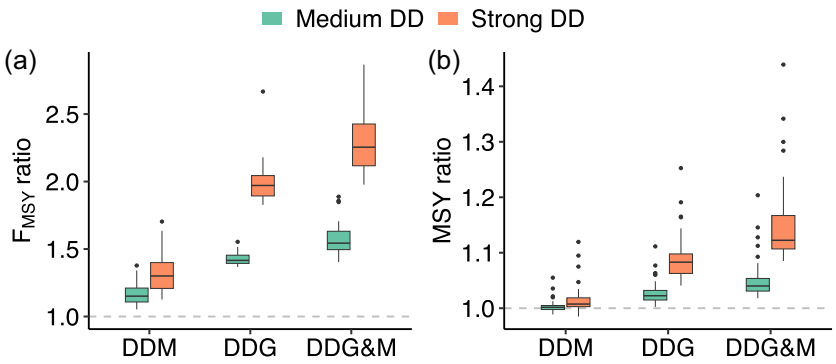

Figure 5. Ratios of F_{MSY} when density dependence in growth and/or M is considered to F_{MSY} when growth and M is constant (noDD) (a) and ratios of yield at F_{MSY} estimated assuming density-dependent growth and/or M to yield at F_{MSY} estimated for constant growth and M (b) for medium and strong DD. DDG = DD in growth, DDM = DD in M, DDG&M = DD in growth and M.

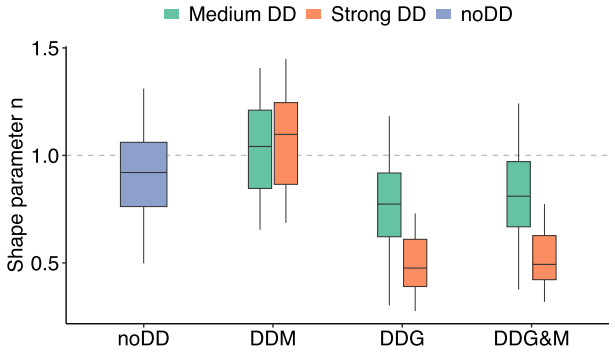

Figure 6. Production model estimates of shape parameter (n) for stocks with constant growth and M (noDD) and for stocks with density dependence in growth and/or M for medium and strong DD. DDG = DD in growth, DDM = DD in M, DDG&M = DD in growth and M.

2) were excluded from the analyses. Thus, the final fits omitted data from years 1–2. As an example, model fits for stock 19 with constant growth and M and with medium DDG&M are shown in Fig. S2. Estimates of the shape parameter (n) were mostly below 1 for constant growth and M with an average of 0.92 (Fig. 6). When DDM was considered, the average n increased to 1.03 and 1.08 for medium and strong DD, respectively. Estimates of n were markedly lower in DDG and DDG&M scenarios; the average n equalled 0.78 and 0.83, respectively, for medium DD and around 0.5 for strong DD. The discrepancy between SPiCT estimates of F_{MSY} (scaled to levels comparable with estimates from age-structured simulations) and the 'true' F_{MSY} varied based on the stock and type of DD considered (Fig. 7a). For stocks with constant growth and M, SPiCT estimates of F_{MSY} were on average 22% higher than 'true' F_{MSY} (ratios ranging mostly between 1.0 and 1.4). When DD was considered in both growth and M, SPiCT estimates of F_{MSY} were on average 3% and 19% lower than 'true' values for medium and strong DD, respectively. For scenarios including DDG, discrepancies were similar to the scenario including DDG&M (with exception of a few higher differences for stocks with strong DD). When DD was only considered in M, the ratio of SPiCT-based F_{MSY} to 'true' F_{MSY} was on average 1.17 and 1.14 for medium and strong DD, respectively, and the ratios ranged mostly between 1.0 and 1.2 (Fig. 7a).

Relative discrepancies between SPiCT estimates of MSY and 'true' MSY were lower than the differences between SPiCT-based F_{MSY} and 'true' F_{MSY} (Fig. 7b). For stocks generated with constant growth and M, the MSY derived with SPiCT were on average 5% lower than 'true' MSY and the ratios of SPiCT-based MSY to 'true' MSY ranged mostly from 0.9 to 1.0. With the inclusion of DD, the average differences between SPiCT-based MSY and 'true' MSY were similar for DDM, DDG, and DDG&M scenarios (−2% to 3% differences) and they ranged mostly from −5% to 10% for both medium and strong DD.

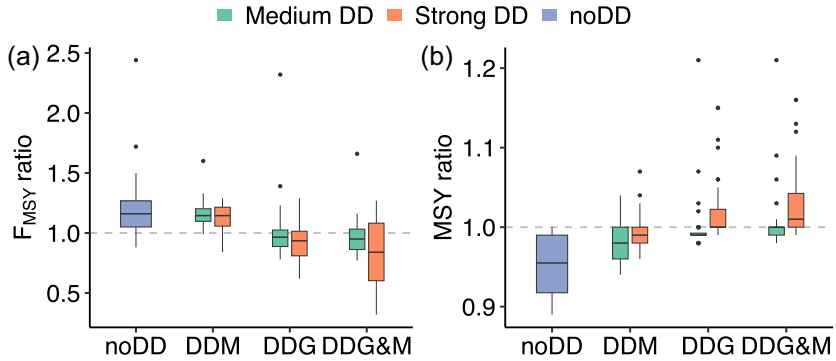

Figure 7. Ratio of SPiCT estimates of F_{MSY} (scaled to comparable units, see text) to 'true' F_{MSY} (a) and the ratio of SPiCT based MSY to 'true' MSY (b) for constant growth and M (noDD) and for medium and strong density dependence. DDG = DD in growth, DDM = DD in M, DDG&M = DD in growth and M.

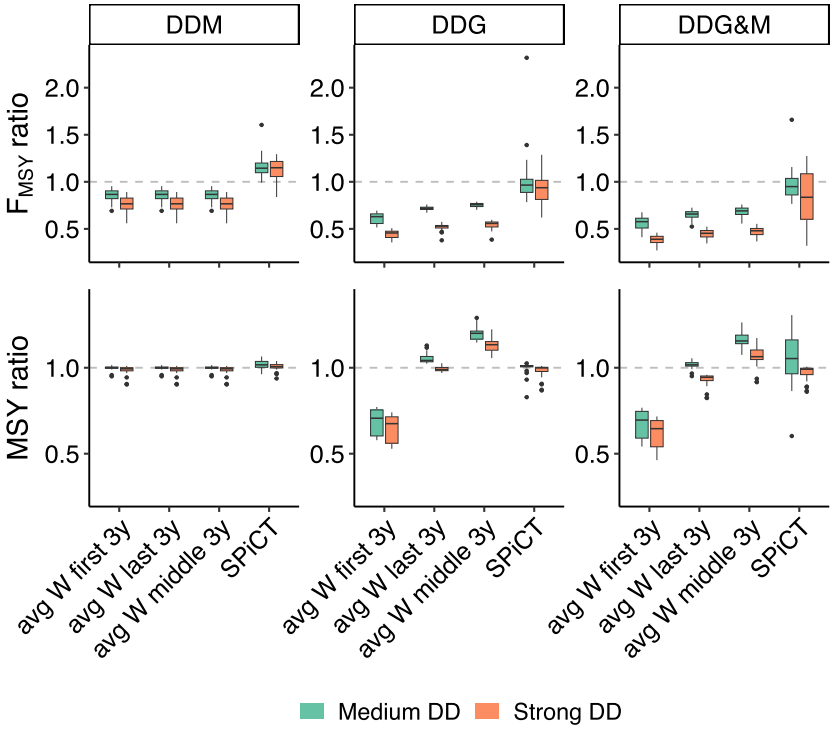

Figure 8. Ratio of F_{MSY} and MSY estimates from long-term projections assuming constant growth and *M*, to 'true' F_{MSY} for stocks with density dependence in growth, DD in *M*, and DD in growth and *M*. Medium and strong DD is considered. F_{MSY} and MSY estimates for constant growth and *M* were based on average weights from the first, last, and the middle 3 years (avg W first 3y, avg W last 3y, avg W middle 3y). For comparison, ratios of SPiCT estimated F_{MSY} and MSY to 'true' F_{MSY} and MSY are shown.

Misspecification of F_{MSY} by assuming constant growth and *M* in case of DD

Fig. 8 shows the ratio of F_{MSY} estimated using constant growth and *M* in long-term predictions to 'true' F_{MSY} following scenarios 3a-c in methods. The differences in F_{MSY} estimates greatly depended on the difference between the average weight assumed in long-term predictions with constant growth and the mean weight in long-term predictions using DDG. When DDG was considered (to derive 'true' F_{MSY}), F_{MSY} estimated with constant growth was on average between 25%–40% and 45%–55% lower than the 'true' F_{MSY} for medium and strong DD, respectively. Effects of DDM on F_{MSY} estimates were lower and F_{MSY} estimated assuming constant *M* was on average 14% and 24% lower than the 'true' F_{MSY} for medium and strong DD, respectively. When both DDG and DDM were simulated, the differences between F_{MSY} estimated assuming constant growth and *M* were on average a few % higher than in case of DDG (Fig. 8).

In Fig. 8 also, the ratio of SPiCT estimated F_{MSY} to 'true' F_{MSY} is presented for comparison. In most cases, SPiCT estimates of F_{MSY} were much closer to 'true' F_{MSY} than in case of F_{MSY} derived from long-term predictions with constant growth and/or *M*.

Similarly to F_{MSY}, the ratio of MSY estimates assuming constant growth and *M* to 'true' MSY (Fig. 8) depended on the difference between the average weight assumed in long-term predictions with constant growth and the mean weight in long-term predictions using DDG. Changes in *M* had very little effect on these ratios. When the mean weight in long-term predictions was based on the lowest average weights in the series, estimated MSY were on average 32% lower than MSY estimated in DDG and DDG&M scenarios under medium DD. In the case of strong DD, respective yields were on average about 40% lower than MSY estimated in DDG and DDG&M scenarios. However, when the mean weight in long-term predictions was based on the highest average weights in the series, the estimated MSY could be 13%–20% higher than MSY derived assuming DD in growth or in both growth and *M*.

Sensitivity tests

A ± 10% change in *aMat50* had a minimal effect on estimated F_{MSY} values. When *aMat50* was increased by 10% F_{MSY} under the 'noDD' scenario decreased on average by 3%, while a 10% decrease in *aMat50* resulted in an average F_{MSY} increase of 4%. Scenarios including DDG and DDG&M showed slightly larger effects, with F_{MSY} changes being about 1% greater than those observed under the noDD and DDM scenarios. The maximum decrease in F_{MSY} was 5% (stock 28) and maximum increase was 7% (stock 25). Given that DDG and/or DDM can affect F_{MSY} by 20%–130% (Fig. 5), the effects of potential DD in maturity would only have a minor impact on the overall influence of DD on F_{MSY}.

Estimates of F_{MSY} assuming stochasticity in recruitment are somewhat lower than deterministic estimates (Table 2). The difference between deterministic and stochastic estimates was greater when both DDG and DDM were considered. However, the general trends observed in deterministic estimates of F_{MSY} were confirmed by stochastic simulations. DD had strong effects on F_{MSY} estimates, with the strongest influence observed for DD in growth.

Discussion

In this study, we provide modelling evidence that including DD in growth and *M* increases estimates of F_{MSY} and to a

Table 2. Comparison of F_{MSY} estimates between deterministic and stochastic analyses for stock 2 and stock 11.

Stock	Analysis	noDD	DDG	DDM	DDG&M	Remark
Stock 2	Deterministic	0.22	0.41	0.31	0.49	Strong DD
	Stochastic	0.21	0.40	0.29	0.46	
Stock 11	Deterministic	0.33	0.45	0.35	0.47	Medium DD
	Stochastic	0.32	0.42	0.32	0.45	

smaller extent MSY, relative to estimates resulting from constant growth and *M*. In addition, F_{MSY} estimates derived from production models fitted to generated stocks with density-dependent growth and/or natural mortality were generally closer to the 'true' F_{MSY} than estimates from long-term predictions assuming constant growth and *M*. In case of DD in growth, estimation of F_{MSY} assuming constant growth also has led to F_{MSY} lower than the 'true' one, but MSY could be both lower **or** higher than the 'true' MSY depending on mean weights used in long-term-predictions. Thus, ignoring DD in stock management may lead either to loses of long-term yield or setting too large catch limits and possible overexploitation.

Effects of density dependence on other BRPs

Because DD affects biomass, which may be a basis for derivation of some precautionary approach reference points, we argue that DD would influence those as well. For example, B_{lim} represents the minimum biomass at which the fish population have full reproductive capacity (ICES 2023b) and B_0 represents the unexploited stock biomass under current biological conditions (ICES 2022). In several management systems and for some stocks, a selected fraction of B_0 is used to define B_{lim} (~10%–25% of B_0) or B_{MSY} (mostly ~30%–50% of B_0) (Ministry of Fisheries 2011, ICES 2022). With DDG and/or DDM, B_0 would be lower than estimated under constant growth and/or *M* (Fig. 4), and thus biomass reference points dependent of B_0 will be different than in case of B_0 estimated under constant growth and *M*. We therefore suggest that the fishing mortality leading to B_{lim} in the long-term (in ICES terminology referred to as F_{lim}), could also be impacted when DD in growth is observed and included in the analysis.

Uncertainty in estimation of density dependence and estimation of BRPs

Density-dependent processes are key in fish populations dynamics and imply that an exploited population is more productive (i.e. in terms of growth rate, *M*, maturity timings, and juvenile survival) because the removal of adults by fishing increases the availability of resource for the remaining individuals (e.g. Lorenzen 2016, Rindorf et al. 2022, Croll et al. 2023). While most scientists agree that intra- and interspecific competition for resource eventually limits a population growth, there are important uncertainties associated with DD strength, consistency across life stages and species, making it complex to extrapolate in long-term management. Over- or under-estimating DD in fisheries management has important consequences and it is critical to understand the biological processes behind DD (Rose et al. 2001). Without such understanding, estimation of DD may be analogous to 'correlation without supporting information on cause and effect' (Rose et al. 2001).

Stock assessment, catch predictions, estimation of reference points, and management are inherently uncertain due to variability in observed data, estimated parameters and process errors within the assessment or management model applied. We propose periodic revisions of reference point calculations for a given fish stock (e.g. every 5 to 10 years), when new data and knowledge have been obtained. This will implicitly take **into** account of some of the changes in multispecies interactions, ecosystems effects, climate, or fisheries induced evolution, that might have happened recently. Regarding fisheries induced evolutionary changes, Liu et al. (2024) noted that 'Clearly pinpointing exact evidence of genetic alterations in wild-capture fisheries has, however, remained challenging'. Nevertheless, life-history theory suggests that sustained high fishing pressure tends to favour traits such **as** slower growth, earlier maturation at a smaller size, and increased energy allocation to reproduction (Jørgensen et al. 2007). This implies that analyses of DD in growth for a given stock based on historic data covering a time of overfishing, might in fact underestimate the effect of DD, because **evolutionary** changes will counteract the DD effect. Thus, care needs to be taken to avoid such counteraction when analysing DD in growth. Evolutionary changes generally work on a longer time horizon than DD do.

The considered DD in *M* was based on Lorentzen (1996, 2000)'s equation, which relates *M* to weight. As such, it may be primarily considered in combination with DD in growth. However, the effects of DD in *M* could still be tested directly from eq. 5b, using its form and parameters, even in the absence of observed DD in growth. We acknowledge that such analyses would serve only as sensitivity tests as we lack empirical observations to validate the right-hand side of eq. 5b when DD in growth in not observed.

Van Gemert and Andersen (2018) showed that with the recent recovery of some previously overexploited stocks, we may observe increased DD in growth, leading to a reduced asymptotic size of fish. They argued that merely updating the mean size of fish is insufficient for accounting for DD and accurately estimating biological reference points. Instead, there is a need for dynamic integration of density-dependent growth into stock assessment and reference point estimations. For example, Croll et al. (2023) assessed the impact of DD in growth on stock management and F_{MSY} estimates using a physiologically structured population model. This model includes DD in growth resulting from competition for shared food resources. They applied the model to four North Sea flatfish stocks, finding that F_{MSY} estimates were higher when growth exhibited strong DD compared to scenarios with low or no DD in growth.

Density-dependent F_{MSY} derived from age-structured model vs surplus-production models based F_{MSY}

When DD was considered, the production model implemented through SPiCT estimated F_{MSY} that when scaled to similar units, were closer to 'true' estimates of F_{MSY} compared to long-

term predictions using constant growth and *M*. This comparison would not need scaling if selectivity and maturity for all ages in the simulated stocks were set to 1. In reality, selectivity and maturity rates at younger ages are usually lower than 1, so fishing mortalities estimated in production and age-structured models are not directly comparable. Similarly, biomass estimated in production models is the exploitable biomass and is usually different from spawning or total stock biomass derived in age-structured assessments. If a production model is used for F_{MSY} estimation but management is based on age-structured models, F_{MSY} estimates from production models would need to be scaled to units used in age-structured models (Sparholt et al. 2021). This conversion was done by regressing fishing mortality rates from age-structured models on *F* estimates from production models. However, this method introduces a degree of uncertainty in the converted F_{MSY} estimates.

In their comprehensive study, Sparholt et al. (2021) assessed F_{MSY} for 53 data-rich fish stocks in the North-east Atlantic, employing a variety of methods and accounting for DD within these populations. Among their methodologies, the authors applied several stock-production models, tailored to fit catch data and analytical estimates of exploitable biomass. Their findings revealed that F_{MSY} estimates derived from production models—which were adjusted to align with age-structured estimates provided by ICES—significantly exceeded the F_{MSY} values reported by ICES. Specifically, for groups of fish such as Pleuronectiformes, Perciformes, Clupeiformes, and others, the shape parameters derived from production models generally fell within the range of 0.8 to 1.4, matching the trends observed in the present study. However, for Gadiformes, the shape parameter approached 2. Notably, Sparholt et al. (2021) found that incorporating DD into F_{MSY} estimates resulted in values nearly 50% higher on average than those provided by ICES, which did not account for DD.

Implications of density dependence for management

If DD were to be included in the management model, our analyses shows that F_{MSY} would be higher than F_{MSY} estimated assuming constant growth and/or *M*. This result therefore suggests caution before implementing DD in F_{MSY} calculations. When providing estimates of limit reference points under DD conditions, it is crucial to ensure that those F_{MSY} estimates are lower than the fishing mortality limit (F_{lim}) with a high probability. It is prudent to also define stock biomass reference points and harvest control rules, that reduces the applied *F* when a stock gets lower than its biomass reference point. This should safeguard against depleting a stock by too heavy fishing.

The current ICES methodology of assessment and estimation of F_{MSY} is mainly based on density independent growth and *M*, where DD is included only through the stock-recruitment relationships.

Because considering DD in fish stock management directly impacts biological reference points, including compensatory mechanisms in fish population processes other than recruitment have been a source of debates (Rose et al. 2001).

Hordyk et al. (2019) showed that risk to yields and biomass due to biases in parameters or misspecification of the biological process in assessment and management may be highly asymmetric. The authors recommended using management strategy evaluations (MSEs) (closed-loop simulations, where operating model simulates plausible scenarios for stock dynamics and collection of assessment data and management procedures are simulated) to investigate these possible asymmetries and its effects on management based on any harvest control rule (HCR). Following that recommendation, the implementation of DD in estimation of F_{MSY} and management based on density-dependent F_{MSY} should also be preceded by extended MSE to investigate the risks to the stock.

Horbowy and Luzeńczyk's (2017) study demonstrated that for sprat, the F_{MSY} estimated under DDG conditions could be nearly double that derived from models assuming constant growth. The influence of DDM on F_{MSY} was minimal, matching the findings of our present study. The equilibrium yield of sprat at F_{MSY} under DD, was approximately 30% higher compared to yields under the assumption of constant growth. This observation aligns with the current analysis, which also demonstrated an increase in yield under simulated DD conditions.

Other aspects

This analysis also revealed that equilibrium yields were predominantly right-skewed, with the ratio of B_{MSY} to B_0 being 0.35 for no DD. This finding aligns with results from Horbowy and Hommik (2022), who reported an average ratio of B_{MSY} to B_0 of 0.34 across a broader spectrum of LHTs than those considered in our study. Thorson et al. (2012) identified an average of B_{MSY} to B_0 of 0.4, with variations ranging from 0.26 to 0.46 depending on taxonomic group of fish species examined.

In our analysis, we modelled DDG as a hyperbolic function of the stock size, drawing on the Andersen and Ursin (1977) model. Their model links the anabolic parameter of von Bertalanffy growth equation to feeding level and the search rate Q to biomass concentration, suggesting that DD primarily affects the asymptotic size, similarly to how *corrW* influences weight in our study. Similar approaches where DD is included in the asymptotic size of fish have been used by Lorenzen and Enberg (2002), Lorenzen (2016), van Gemert et al. (2018), Stenevik et al. (2022), Croll et al. (2023). Matte et al. (2020) found that DD in salmonids growth had mostly logarithmic patterns; in our work, the hyperbolic shape used to model DD growth can be also approximated with logarithmic function with high accuracy (generally $r^2 > 0.9$).

Conclusion

Density dependence, particularly in growth, has a significant impact on estimates of F_{MSY}, which may be up to twice as large as estimates derived under the assumption of no density dependence. However, the effects of density dependence on yield at F_{MSY} were much smaller. Surplus production model estimates of F_{MSY} were closer to the 'true' values (derived under density dependence) than estimates obtained from age-structured models that assume no density dependence.

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Author contributions

All authors actively contributed to the conception, analysis, and revision of the study.

Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: The authors declare no conflicts of interest.

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Data availability

The data underlying this article will be shared on reasonable requests to the corresponding author.

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