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Original Article

Implications of late-in-life density-dependent growth for fishery size-at-entry leading to maximum sustainable yield

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Currently applied fisheries models and stock assessments rely on the assumption that density-dependent regulation only affects processes early in life, as described by stock–recruitment relationships. However, many fish stocks also experience density-dependent processes late in life, such as density-dependent adult growth. Theoretical studies have found that, for stocks which experience strong late-in-life density dependence, maximum sustainable yield (MSY) is obtained with a small fishery size-at-entry that also targets juveniles. This goes against common fisheries advice, which dictates that primarily adults should be fished. This study aims to examine whether the strength of density-dependent growth in actual fish stocks is sufficiently strong to reduce optimal fishery size-at-entry to below size-at-maturity. A size-structured model is fitted to three stocks that have shown indications of late-in-life density-dependent growth: North Sea plaice (*Pleuronectes platessa*), Northeast Atlantic (NEA) mackerel (*Scomber scombrus*), and Baltic sprat (*Sprattus sprattus balticus*). For all stocks, the model predicts exploitation at MSY with a large size-at-entry into the fishery, indicating that late-in-life density dependence in fish stocks is generally not strong enough to warrant the targeting of juveniles. This result lends credibility to the practise of predominantly targeting adults in spite of the presence of late-in-life density-dependent growth.

Keywords: density dependence, maximum sustainable yield, selective fishing, size spectrum

Introduction

Density dependence is a key process in population ecology. Negative (or compensatory) density dependence takes place when an increase in population size results in a decrease in individual growth, reproduction, or survival, usually due to increased intraspecific competition or increased predation mortality. Density dependence due to intraspecific competition can, for instance, stem from competition for food (Hassell, 1975) or spawning sites (Reichard *et al.*, 2004). Likewise, density dependence as a result of predation mortality can stem from cannibalism (Ricker, 1954), or from the predator switching to the most abundant prey (type III functional response; Holling, 1959). Because population density is changed by exploitation, it is essential to understand how density dependence operates within a population when predicting how that population may respond to exploitation.

The strength of density dependence varies with the size of the individual. Here we distinguish between two mechanisms of density dependence: early-in-life density-dependent recruitment and late-in-life density-dependent growth. In many stocks, individuals experience strong density dependence during the larval and early-juvenile stage. In spite of the wide prevalence of this early-in-life density dependence, its causal mechanisms are usually poorly understood. Therefore, it is sometimes referred to as density-dependent recruitment, as it takes place before the individual enters the “recruited” component of the stock. Whereas density-dependent recruitment takes place early in life, density-dependent growth can be assumed to be strongest later in life, after an individual reaches size-at-maturity. This is because density-dependent growth emerges due to resource competition, at the adult size where biomass of a cohort (and therefore its

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consumption) is usually the largest (e.g. Munch *et al.*, 2005; Jennings *et al.*, 2007). However, in spite of its potentially significant role in population regulation, late-in-life density-dependent growth is rarely incorporated in the calculation of fisheries reference points.

Instead, current fisheries advice is generally given under the assumption that all density dependence occurs early in life, in the form of density-dependent recruitment (e.g. Beverton and Holt, 1957; Myers and Cadigan, 1993). This early-in-life density dependence is either described as a constant recruitment (yield-per-recruit models), or through a stock–recruitment relationship. This assumption of only early-in-life density dependence is likely acceptable for fish stocks that experience heavy fishing pressure, where fishing mortality relieves the exploited population component from late-in-life density dependence. However, during the last decade, improved fisheries management has led to many fish stocks in the NEA gradually showing signs of recovery from overfishing (Fernandes and Cook, 2013). For some species, this recovery coincided with reduced individual growth of older juveniles and adults, possibly as a result of late-in-life density-dependent resource competition (e.g. Cormon *et al.*, 2016; Olafsdottir *et al.*, 2016). Therefore, it may be problematic that late-in-life density-dependent growth is rarely taken into account in fisheries management.

Optimal management strategies could differ substantially for stocks that experience late-in-life density-dependent growth. For example, a model study by Andersen *et al.* (2017) showed that if density-dependent regulation mainly happens late in life, maximum sustainable yield (MSY) is obtained by fishing on juvenile fish. This relieves the remaining juveniles from density dependence, thereby increasing the productivity of the entire stock. This prediction challenges reigning fisheries management procedures, which enforce minimum landing size regulations to avoid excessive fishing mortality on juveniles. The study of Andersen *et al.* (2017) only compared scenarios for hypothetical stocks, where density dependence either occurred mainly early in life or mainly late in life. However, density-dependent population regulation need not necessarily occur at only a single bottleneck.

Given the widespread nature of density-dependent processes, it is likely that many fish stocks experience some form of density-dependent regulation at multiple life stages. For instance, Dover sole (*Solea solea*) recruitment appears to follow a classic Beverton-Holt stock–recruitment relationship (Lorenzen, 2005). This is indicative of strong early-in-life density dependence, but the stock also shows significant density-dependent growth in the recruited phase (Lorenzen and Enberg, 2002). Another example is North Sea plaice (*P. platessa*), which shows strong early-in-life density dependence when larvae settle in their nursery grounds (Van der Veer, 1986), but has also shown significant late-in-life density-dependent growth (Rijnsdorp and Van Leeuwen, 1992). Based on the findings of Andersen *et al.* (2017), fishery size-at-entry at which MSY is obtained should gradually decrease when the strength of late-in-life density-dependent growth increases (relative to that of early-in-life density dependence). However, it is unknown whether the late-in-life density-dependent growth that is experienced by marine fish stocks is actually strong enough to trigger a reduction in optimal fishery size-at-entry.

We aim to explore whether marine fish stocks can actually experience late-in-life density-dependent growth that is strong enough to reduce optimal fishery size-at-entry (i.e. size-at-entry at which MSY is obtained). To this end we estimated the relative strengths of early- and late-in-life density dependence in three fish stocks, by fitting a dynamic single-stock size-structured model to empirical stock data. The three examined fish stocks, North Sea plaice (*P. platessa*) (Rijnsdorp and Van Leeuwen, 1992), NEA mackerel (*S. scombrus*) (Olafsdottir *et al.*, 2016), and Baltic sprat (*S. s. balticus*) (Eero, 2012), have shown indications of experiencing some late-in-life density-dependent resource competition and only show little cannibalism.

We focus on density-dependent resource competition as the primary mechanism behind late-in-life density-dependent regulation, to avoid any confounding effects of cannibalism. In our model, early-in-life density dependence is described by a stock–recruitment relationship. Late-in-life density dependence is not described with a single equation, but emerges through feeding on a dynamic resource spectrum. Varying the relative strengths of early- and late-in-life density dependence was possible by varying the stock–recruitment relationship's maximum recruitment relative to the resource spectrum's carrying capacity. This allowed us to examine whether the strength of density-dependent growth experienced by the stock is high enough so that optimal fishery size-at-entry is below size-at-maturity.

Methods

We apply a standard size-spectrum model (Andersen *et al.*, 2015), adapted to represent only a single stock (Andersen *et al.*, 2017). The model describes the population dynamics of a single fish stock feeding on a dynamic resource spectrum and incorporates early-in-life density dependence through a Beverton-Holt stock–recruitment relationship, and late-in-life density dependence emerges through size-based resource competition. Here we describe the main assumptions and principles of the model. Detailed descriptions of the assumptions and equations used in size-spectrum models such as this one can also be found e.g. in Hartvig *et al.* (2011), Andersen and Beyer (2015), and Andersen *et al.* (2015). All model equations and parameters are listed in Tables 1 and 2, and the numerical implementation of our model is given in Supplementary Appendix A. Throughout, size refers to body weight, w.

Growth, mortality, and demography

We assume that individuals feed on a resource $N_{\mathrm{R}}(w_{\mathrm{R}})$ that represents food of all sizes in the ecosystem. Individuals prefer food a factor $\beta = 100$ smaller than themselves (Jennings *et al.*, 2002). Multiplying an individual's size-preference with the biomass of that resource size, and integrating over all resource sizes, gives the total amount of food available to the individual. When multiplied with clearance rate γw^q, this then gives the food actually encountered by the individual $E_e(w)$ (M2). Consumption is described by a functional response type II (M3), with maximum consumption hw^n and $n = 3/4$, giving the feeding level $f(w)$ as consumed food relative to maximum consumption. From consumption we calculate the energy available for somatic growth and reproduction from an energy budget (M4). Energy is assimilated from consumed food with efficiency α and costs of standard metabolism ($k_{\mathrm{r}} w^n$) and activity ($k_{\mathrm{a}} w$) are paid. The remaining available

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Table 1. Governing model equations.

Consumption		
Size preference for prey	$\varphi\left(\frac{w}{w_R}\right) = \exp\left[-\left(\ln\left(\frac{w}{w_R\beta}\right)\right)^2/(2\sigma^2)\right]$	M1
Encountered food	$E_e(w) = \gamma w^q \int_0^\infty \varphi\left(\frac{w}{w_R}\right) w_R N_R(w_R) dw_R$	M2
Feeding level	$f(w) = \frac{E_e(w)}{E_e(w)+hw^n}$	M3
Growth		
Available energy	$E_a(w) = \alpha f(w)hw^n - k_r w^n - k_a w$	M4
Switching function	$H(x) = (1+x^{-10})^{-1}$	M5
Maturation	$\psi(w) = H\left(\frac{w}{\eta_m W_\infty}\right)\frac{1-\varepsilon_a}{(w/W_\infty)^{n-1}-\varepsilon_a}$	M6
Growth rate	$g(w) = (1-\psi(w))E_a(w)$	M7
Mortality		
Background predation	$\mu_0(w) = a_p w^{n-1}$	M8
Fishing, trawl selectivity	$\mu_F(w) = FH\left(\frac{w}{w_F}\right)$	M9
Reproduction		
Egg production	$R_p = \int_{w_{egg}}^{W_\infty} \frac{\psi(w)E_a(w)}{2w_{egg}} N(w) dw$	M10
Recruitment	$R = R_{max}\frac{\varepsilon_r R_p}{R_{max}+\varepsilon_r R_p}$	M11
Mortality		
Background predation	$\mu_0(w) = a_p w^{n-1}$	M12
Fishing, trawl selectivity	$\mu_F(w) = FH\left(\frac{w}{w_F}\right)$	M13
Population structure		
Abundance spectrum	$\frac{\partial N(w)}{\partial t} + \frac{\partial g(w)N(w)}{\partial w} = -[\mu_0(w)+\mu_F(w)]N(w)$	M14
Boundary condition	$g(w_{egg})N(w_{egg}) = R$	M15
SSB	$B_{SSB} = \int_{w_{egg}}^{W_\infty} H\left(\frac{w}{\eta_m W_\infty}\right) wN(w) dw$	M16
Fishery performance		
Yield	$Y = \int_{w_{egg}}^{W_\infty} \mu_F(w)wN(w) dw$	M17
Resource		
Predation on resource	$\mu_p(w_R) = \int_{w_{egg}}^{W_\infty} \varphi\left(\frac{w}{w_R}\right)(1-f(w))\gamma w^q N(w) dw$	M18
Resource spectrum	$\frac{\partial N_R(w_R)}{\partial t} = r_0 w_R^{n-1}[\kappa w_R^\lambda - N_R(w_R)] - \mu_p(w_R)N_R(w_R)$	M19

energy $E_a(w)$ is divided between somatic growth and reproduction, with individual growth rate $g(w)$:

$$g(w) = [1-\psi(w)][\alpha f(w)hw^n - k_r w^n - k_a w] \qquad (1)$$

Here $\psi(w)$ represents the fraction of available energy invested into reproduction. The remaining available energy, $(1-\psi(w))$, is invested into growth. $\psi(w)$ approaches 0 so long as individual size w remains well below size at 50% maturation $\eta_m W_\infty$. The switch to maturity is described by a sigmoid function that smoothly varies between 0 and 1 around size at 50% maturation (M5). Mature individuals still invest energy in growth, but this investment decreases as their size approaches W_∞, until at size W_∞ all energy is invested into egg production (M6). This procedure results in a von Bertalanffy-like weight-at-age curve if food is plentiful, $f(w) = f_0$, but reduces growth if the resource has become depleted, $f(w) < f_0$.

The energy not used for growth is invested into egg production: $\psi(w)E_a(w)$. Total egg production of the stock R_p emerges by integrating egg production over all individual sizes, taking into account that only females produce eggs (M10).

We assume that natural mortality rate $\mu_0(w)$ is mainly due to predation by other species, and decreases with individual size according to $\mu_0(w) = a_p w^{n-1}$ (M8). We assume that mortality due to cannibalism is negligible.

The fishing mortality rate $\mu_F(w)$ is the product of a level F and a size-specific gear selectivity (M9). We use a sigmoid function that smoothly switches from 0 to 1 around size-at-entry into the fishery w_F to resemble a trawl selectivity curve.

The density of individuals across all sizes within the population makes up the abundance size-spectrum $N(w)$ as calculated by the McKendrick-von Foerster conservation equation:

$$\frac{\partial N(w)}{\partial t} + \frac{\partial g(w)N(w)}{\partial w} = -[\mu_0(w)+\mu_F(w)]N(w) \qquad (2)$$

Spawning stock biomass B_{SSB} can be calculated from the abundance size-spectrum by integrating mature biomass over all sizes (M16). Yield from fishing can be calculated by multiplying stock biomass targeted by the fishing gear with fishing mortality, and integrating over all sizes (M17).

Density dependence

Density dependence emerges from two sources: a stock–recruitment relationship determines the strength of density dependence early in life, and competition for food from the resource spectrum determines the strength of density dependence late in life. The relative importance of the two processes is described by the ratio between the parameters that describe the carrying capacity of the early life environment and the late-life environment. Below we first describe both of these processes individually, and then explain how they interact.

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Table 2. Model parameters.

Symbol	Description	Value	Unit	Footnote(s)
Body size				
W_∞	Asymptotic size (weight)*	stock specific	g	
w_{egg}	Egg weight	0.001	g	a
Consumption				
n	Metabolic exponent	3/4	–	b
β	Preferred predator–prey mass ratio	100	–	c
σ	Range of preferred prey size	1.3	–	d
q	Clearance rate exponent	0.8	–	e
γ	Clearance rate coefficient	$6.57/\kappa$	$\text{g}^{-q}\ \text{year}^{-1}$	f
f_0	Standard feeding level	0.6	–	f
f_c	Critical feeding level	0.2	–	f
h	Maximum consumption*	$\approx 3KW_\infty^{1/3}/[\alpha(f_0-f_c)]$	$\text{g}^{1-n}\ \text{year}^{-1}$	g
Growth				
α	Assimilation efficiency	0.6	–	f
η_m	Size at maturation rel. to W_∞	0.25	–	h
ϵ_a	Fraction of energy for activity	0.8	–	i
k_r	Standard metabolism coefficient	$f_c\alpha h$	$\text{g}^{1-n}\ \text{year}^{-1}$	f
k_a	Activity coefficient	$\varepsilon_\text{a}\alpha h(f_0-f_c)W_\infty n-1$	year^{-1}	i
Mortality				
α_p	Mortality level*	$\approx M(\eta_\text{m}W_\infty)^{1-n}$	$\text{g}^{1-n}\ \text{year}^{-1}$	j
Reproduction				
$R_{\max}$	Maximum recruitment*	stock specific	year^{-1}	
ϵ_r	Recruitment efficiency*	stock specific	–	
Fishery performance				
w_F	Mean size-at-entry into the fishery	variable	g	
F	Fishing mortality	variable	year^{-1}	
Resource				
κ	Carrying capacity magnitude*	stock specific	$\text{g}^{-1-\lambda}$	
λ	Carrying capacity exponent	$-2-q+n$	–	e
r_0	Resource growth rate coefficient	4	$\text{g}^{1-n}\ \text{year}^{-1}$	f, k

Parameters marked with an asterisk are specific for each stock, and the relation to standard parameters (K, W_∞, and M) are provided.

[a] Neuheimer *et al.* (2015).

[b] West *et al.* (1997).

[c] Jennings *et al.* (2002).

[d] Andersen *et al.* (2017).

[e] Andersen and Beyer (2006).

[f] Hartvig *et al.* (2011).

[g] Juvenile growth rate (g/year) for $w \ll W_\infty$ from (M7) is $\approx \alpha h(f_0-f_c)w^n$. A von Bertalanffy growth equation gives the growth rate for $w \ll W_\infty$ as $3KW_\infty^{-1/3}w^{2/3}$. Ignoring the small difference in exponents gives the approximation in the table.

[h] Jensen (1996), Froese and Binohlan (2000), and He and Stewart (2001).

[i] Andersen and Beyer (2015).

[j] The adult mortality from (M8) is $M = a_\text{p}(\eta_\text{m}W_\infty)^{n-1}$, from which α_p follows as $a_\text{p} = M(\eta_\text{m}W_\infty)^{1-n}$.

[k] Savage *et al.* (2004).

A standard Beverton-Holt stock–recruitment relationship (Beverton and Holt, 1957) is used to describe recruitment R:

$$R = R_{\max}\frac{\varepsilon_\text{r}R_\text{p}}{R_{\max}+\varepsilon_\text{r}R_\text{p}} \tag{3}$$

where $R_{\max}$ is the maximum recruitment, R_p is the number of eggs produced by the spawning stock, and ϵ_r is the stock–specific recruitment efficiency which accounts for costs of reproduction and egg survival.

The recruitment R is used as a boundary condition for the conservation Equation (2): $g(w_{\text{egg}})N(w_{\text{egg}}) = R$. Which specific type of stock–recruitment relationship we use here is of lesser importance; the most important thing is that it describes the density dependence that takes place early in life. We have used a Beverton-Holt stock–recruitment relationship because it is both simple and well-known. We consider the recruitment efficiency ϵ_r as constant for each stock. The maximum recruitment $R_{\max}$ represents the carrying capacity of the early life environment and we therefore use this parameter to determine the strength of early-in-life density dependence relative to the strength of late-in-life density dependence.

The resource spectrum $N_\text{R}(w_\text{R})$ represents all individuals, of all sizes, that do not belong to the focal stock. The change in resource abundance is described with a semi-chemostat:

$$\frac{\text{d}N_\text{R}(w_\text{R})}{\text{d}t} = r_0 w_\text{R}^{n-1}\left[\kappa w_\text{R}^{\lambda} - N_\text{R}(w_\text{R})\right] - \mu_\text{p}(w_\text{R})N_\text{R}(w_\text{R}) \tag{4}$$

where $r_0 w_\text{R}^{n-1}$ is the size-specific resource regeneration rate and $\mu_\text{p}(w_\text{R})$ (M18) is the size-specific resource mortality due to predation by the focal stock. Food abundance is determined by the

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carrying capacity of the resource κw_R^λ. The value of the slope λ has been determined as $-2 - q + n$ (Andersen and Beyer, 2006), meaning that the resource carrying capacity follows a Sheldon spectrum (Sheldon *et al.*, 1977), where biomass is approximately constant in logarithmically-spaced size groups. Food availability is therefore largely independent of size, with the overall level determined by κ. The value of κ then determines the resource availability, and thereby the level of density-dependent competition and growth.

Intraspecific competition for resources emerges when the consumption of any given resource size exceeds the regeneration of that resource size, thereby reducing its abundance (Figure 1a, grey lines). In fish, cohort biomass usually increases until maturity (and fishing) sets in. As the biomass of the fish stock increases with size (Figure 1a, black lines), the highest competition will be for the resource sizes that are targeted by mature fish. Density-dependent competition for resources therefore mainly takes place late in life, amongst the mature and late juvenile portion of the stock.

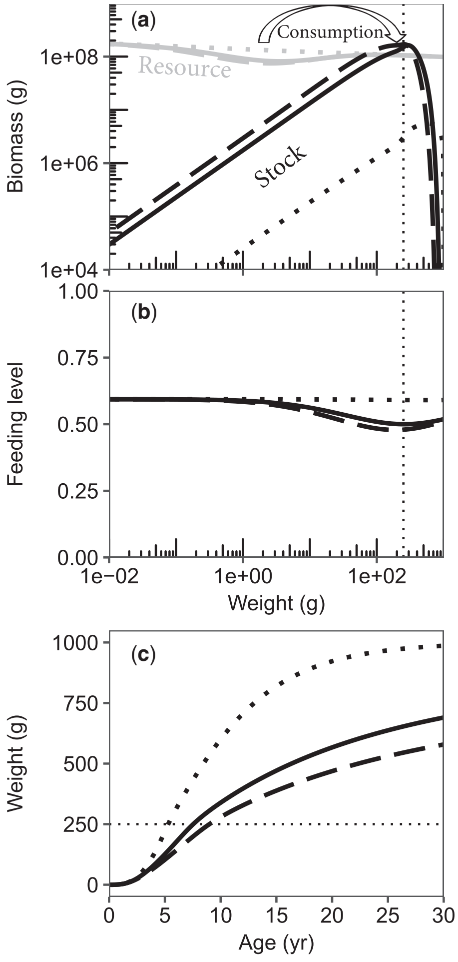

Figure 1. Mechanisms of density dependence in the model, illustrated with three different R_{max} to κ ratios: 0.01 (dotted), 1 (solid), and 100 (dashed) $g^{1+\lambda}$/year. These describe scenarios of only early-in-life, a mix of early- and late-in-life, and only late-in-life density dependence, respectively. The thin dotted lines indicate size-at-maturity. Shown for a W_∞ of 1000 g, and no fishing mortality. (a) Stock (black) and resource (grey) biomass as a function of size. Note that the dotted stock line intersects the y-axis outside of the plotted range. (b) Feeding levels (ratio between consumption and maximum consumption) associated with the different R_{max} to κ ratios, indicating that resource competition peaks around maturation size. (c) Weights-at-age associated with the different R_{max} to κ ratios, showing how different strengths of early- and late-in-life density dependence affect growth.

In the model, density-dependent population regulation emerges from two sources: early-in-life stock–recruitment, as determined by $R_{max,}$ and density-dependent growth as determined by the resource carrying capacity κ. Their ratio, R_{max}/κ, controls the relative importance of the two processes of density dependence: a low value of R_{max}/κ leads to a dominance of early-in-life density-dependent recruitment, whereas a high value leads to a dominance of late-in-life density-dependent growth (Figure 1).

Fitting the model to fish stocks

To find realistic R_{max} to κ ratios for the examined stocks, we fitted the model to empirical data of three fish stocks: North Sea plaice, NEA mackerel, and Baltic sprat. These stocks vary in asymptotic size, show little-to-no cannibalism, and all have shown indications of density-dependent growth beyond the juvenile stage. The dynamics of each stock depend on stock-specific physiological parameters describing: growth (h), asymptotic size (W_∞), recruitment (ϵ_r), and mortality (α_p), and on parameters that influence density dependence: maximum recruitment (R_{max}) and resource abundance (κ).

The physiological parameters are determined from classical parameters, the von Bertalanffy growth coefficient K, and adult mortality M, with the procedure described in Andersen *et al.* (2009); see Table 2 for relations, and Table 3 for parameters for each stock. For plaice and sprat, W_∞ was calculated from the stock's observed length-at-maturity (L_m) (Supplementary Appendix B). For mackerel, W_∞ was calculated from the L_∞ that was associated with the used value for K. Values for K are taken from empirical studies, and values for M from ICES assessments. Recruitment efficiency (ϵ_r) was set so that the model's F_{MSY} matched the advised F_{MSY} of the stock, having set the size at 50% fisheries selectivity, w_F, according to fisheries data. A more detailed explanation of the parameterization process for each stock can be found in Supplementary Appendix B.

After having parameterized the model with stock-specific parameters, realistic R_{max} to κ ratios were determined for each stock. For this, the aim was to match simulated density-dependent changes in individual growth and SSB with observed changes in individual growth and SSB, while also matching modelled fishery yield with historical yield data. To observe density-dependent changes in growth, the model was fitted to two historical scenarios between which there were significant differences in both SSB and individual growth (one scenario with low SSB and fast individual growth, and a second scenario with high SSB and slow individual growth).

For North Sea plaice, the two scenarios were before and at the end of the Second World War. No fishing during the war resulted in roughly a tripling of plaice SSB at the end of the war (Margetts and Holt, 1948), and coincided with a reduction in late-juvenile and adult growth (Rijnsdorp and Van Leeuwen, 1992). No actual SSB data is known from this time, with SSB changes instead having been inferred from changes in catch-per-unit-effort. To be able to fit our model to plaice data, we therefore assumed that plaice SSB and yield figures from the 1990s would have been

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Table 3. Stock-specific parameters that were used as input for the model, and the resulting SSB and yield predicted by the model.

		Baltic sprat	NEA mackerel	North Sea plaice
Parameters				
Asymptotic size	W_∞ (g)	21	890	1600
Von Bertalanffy growth constant	K (year^{-1})	0.68	0.18	0.16
Recruitment efficiency	ϵ_r (−)	0.0055	0.00060	0.10
Size-at-entry into fishery	w_F (g)	3.6	240	120
Maximum recruitment	R_{max} (year^{-1})	$2.5 \cdot 10^{13}$	$4.5 \cdot 10^{10}$	$5.0 \cdot 10^{9}$
Resource carrying capacity coeff.	κ (g$^{-1-\lambda}$)	$2.5 \cdot 10^{12}$	$1.5 \cdot 10^{13}$	$3.3 \cdot 10^{12}$
Low-SSB scenario				
Natural mortality	M (year^{-1})	0.50	0.15	0.10
Fishing mortality	F (year^{-1})	0.23	0.46	0.60
High-SSB scenario				
Natural mortality	M (year^{-1})	0.20	0.15	0.10
Fishing mortality	F (year^{-1})	0.39	0.29	0.050
Results				
Low-SSB scenario				
SSB	B_{SSB} (Mt)	0.36	1.7	0.15
Annual yield	Y (Mt/year)	0.094	0.77	0.28
High-SSB scenario				
SSB	B_{SSB} (Mt)	2.1	3.0	2.7
Annual yield	Y (Mt/year)	1.0	0.86	0.18

The input parameters include the R_{max} and κ values that resulted in the best model fit for each stock. Sources for the parameter values are listed in Supplementary Appendix B.

similar to those of pre-WWII, as for both these times F was around 0.6 year^{-1} (Beverton and Holt, 1957; ICES, 2015b).

The model was fitted to NEA mackerel using scenarios from 2003 and 2013. In 2003 NEA mackerel was heavily fished (F: 0.46 year^{-1}, Y: 680 kt; ICES, 2015a), SSB was relatively low (1900 kt; ICES, 2015a) and individual growth was fast (Olafsdottir *et al.*, 2016). In 2013 fishing mortality had been decreased to 0.29 year^{-1} (ICES, 2015a), though yield had increased to 930 kt/year (ICES, 2015a). At the same time, SSB almost doubled to around 3600 kt (ICES, 2015a), and individual growth had decreased (Olafsdottir *et al.*, 2016).

Last, the model was fitted to Baltic sprat using scenarios from 1988 and 1998. The main predator of Baltic sprat, Eastern Baltic cod (*Gadus morhua*), suffered a large decrease in abundance during the mid-1980s (Köster *et al.*, 2003). The reduction in predators reduced Baltic sprat mortality, and after 1988 sprat SSB started to increase. Whereas Baltic sprat SSB was around 415 kt in 1988, SSB had more than tripled to around 1400 kt in 1998 (ICES, 2015c) with a concurrent decrease in late-juvenile and adult growth (Eero, 2012). Furthermore, whereas in 1988 Baltic sprat yield was around 80 kt/year with a fishing mortality of 0.23 year^{-1}, in 1998 yield had increased to 417 kt/year with a fishing mortality of 0.39 year^{-1} (ICES, 2015c).

Using the empirical data from the above scenarios, the model was fitted to each of the three stocks. A detailed description of this fitting procedure is given in Supplementary Appendix B. After fitting, the size-at-entry into the fishery w_F which yielded MSY was determined by running the fitted model with a range of w_F and F combinations. For each value of w_F, this resulted in a different highest sustainable yield and a different value of F leading to that highest sustainable yield. The w_F with the largest value for highest sustainable yield is the w_F that yields MSY. Furthermore, a sensitivity analysis was performed of the fitted variables ϵ_r and R_{max}/κ, by varying their values with a factor 2. Those values were subsequently used to recalculate F_{MSY} and optimal fishery size-at-entry respectively. The sensitivity analysis and its results are presented in more detail in Supplementary Appendix C.

Results

Fitted parameters, including the R_{max} and κ values, are shown in Table 3. The resulting weight-at-age curves for both the high- and low-SSB scenarios are shown in Figure 2.

Baltic sprat

The modelled growth for Baltic sprat approaches the empirical weight-at-age data points of the high- and low-SSB scenarios (Figure 2a). In the low-SSB scenario modelled growth is high, and closely follows the reference line for only early-in-life density dependence. In the high-SSB scenario modelled growth is reduced by strong late-in-life density-dependent growth, and closely follows the reference line for only late-in-life density dependence.

Fishery size-at-entry for which MSY is obtained is close to asymptotic size in the low-SSB scenario (Figure 2d), and closely follows the reference line for only early-in-life density dependence. In the high-SSB scenario, fishery size-at-entry for which MSY is obtained is smaller, but still greater than size-at-maturity. Again, the fitted curve closely follows the reference line for only late-in-life density dependence.

The sensitivity analysis shows that both weight-at-age and optimal fishery size-at-entry are relatively unaffected by changes in the R_{max} to κ ratio (Supplementary Appendix C). This indicates that, for Baltic sprat, a change in natural mortality M has a far stronger impact on strength of density-dependent growth than a change in the R_{max} to κ ratio.

NEA mackerel

The historical change in weight-at-age of NEA mackerel could not be replicated (Figure 2b). Changing F from 0.46 to 0.29 year^{-1} resulted in only a minor reduction in growth. However,

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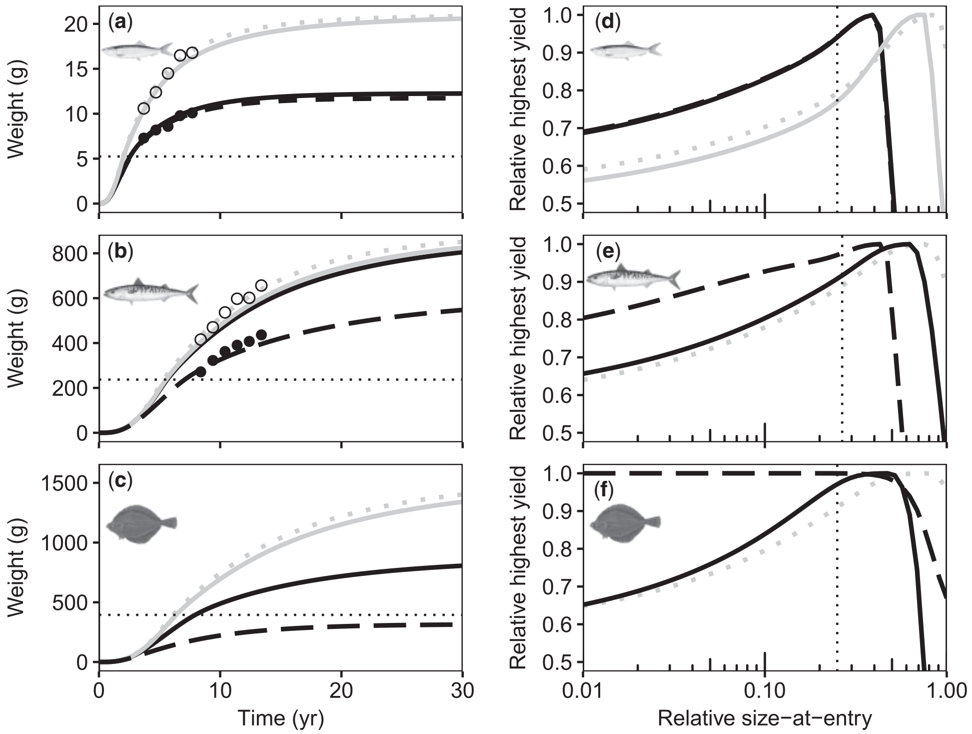

Figure 2. Weight-at-age (a–c) and highest sustainable yield as a function of size-at-entry into the fishery (d–f), modelled for Baltic sprat (a, d), NEA mackerel (b, e), and North Sea plaice (c, f). Highest sustainable yield is calculated separately for each size-at-entry value and, for each scenario, is shown relative to its maximum value among all size-at-entry values (MSY). Size-at-entry into the fishery is shown relative to W_∞. Grey lines represent the stock's low-SSB scenario, and black lines represent the stock's high-SSB scenario (Table 3). These lines overlap in (e) and (f), because only fishing mortality changes between scenarios there. The solid lines show the model fit of each stock. The grey dotted lines show the hypothetical model fit of each stock if all density dependence would occur early in life ($R_{\max}/\kappa = 0.00001\,\mathrm{g}^{1+\lambda}$/year). They are only shown for each stock's low-SSB scenario (Table 3), and act as a reference to that scenario's fitted curve (solid). The black dashed lines show the hypothetical model fit of each stock if all density dependence would occur late in life ($R_{\max}/\kappa = 100\,000\,\mathrm{g}^{1+\lambda}$/year). They are only shown for each stock's high-SSB scenario (Table 3), and act as a reference to that scenario's fitted curve (solid). The thin dotted lines show size-at-maturity. Historical weight-at-age data points are shown for the low-SSB (open points) and high-SSB (filled points) scenarios of sprat and mackerel. They are not shown for plaice, because Rijnsdorp and Van Leeuwen (1992) do not show changes in weight-at-age but in growth-increments of length groups. Supplementary Appendix B contains an overview of how the model fit for plaice overlaps with this data type.

the reference line for only late-in-life density dependence is close to the high-SSB scenario data points. According to these results, it is likely that the observed decrease in NEA mackerel weight-at-age is not solely the result of a decrease in fishing mortality.

For the $R_{\max}$ to κ ratio predicted for NEA mackerel, MSY exploitation occurs with a large size-at-entry into the fishery (Figure 2e). Furthermore, the reference line for only late-in-life density dependence also peaks at a large size-at-entry into the fishery. This suggests that even if NEA mackerel would experience strong late-in-life density-dependent growth, optimal fishery size-at-entry would still be large.

North Sea plaice

For North Sea plaice, the fitted model was able to replicate historical growth data (Figure 2c, Supplementary Appendix B). For a high fishing mortality, growth is fast and almost all density dependence takes place early in life. When fishing mortality drops to nearly zero, late-in-life density dependence becomes stronger due to increased SSB, and growth is decreased. The reference line for only late-in-life density dependence predicts a scenario of severely reduced growth: density-dependent growth would be so strong that an average individual would not be able to grow to 50% size-at-maturity.

For the $R_{\max}$ to κ ratio predicted for North Sea plaice, MSY exploitation occurs with a large size-at-entry into the fishery (Figure 2f). The sensitivity analysis (Supplementary Appendix C) shows that this would still be the case if the $R_{\max}$ to κ ratio would be a factor 2 higher (stronger density-dependent growth). The dashed reference line shows that, when late-in-life density dependence is very strong, there is a wide range of fishery size-at-entries for which MSY is obtained: from very small to larger than size-at-maturity. This is because throughout this size-at-entry range, the stock remained in a state of severe growth reduction. In this state, the stock had almost no tolerance for fishing mortality, so the yield was very small and almost independent of fishery size-at-entry.

Discussion

For all three analysed stocks the model predicts that fishing at MSY occurs with a large fishery size-at-entry. The optimal fishery size-at-entry can decrease somewhat when the strength of late-in-life density-dependent growth is high, but for the fitted stocks it

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always remained above size-at-maturity. Therefore, for the examined stocks this study indicates that the current practice of setting size-at-entry such that predominantly adults are targeted is sound, in spite of the presence of strong late-in-life density-dependent growth. However, this does not mean that late-in-life density-dependent growth should be completely disregarded when calculating fisheries reference points. For other stocks, if late-in-life density dependence is very strong, the optimal size-at-entry could be smaller than size-at-maturity. Further, strong late-in-life density-dependent growth will influence a stock's F_{MSY} reference point. Fishing on a stock that experiences strong late-in-life density-dependent growth will increase individual growth rate by relieving the stock of density dependence, and will thereby increase stock productivity. If this is ignored when calculating fisheries reference points, it is likely that the calculated F_{MSY} will be lower than the actual F_{MSY}. This would cause the fishery to lose out on potential yield. Therefore, it is important to consider density-dependent growth when calculating fisheries reference points.

Previous theoretical work has indicated that stocks with a larger asymptotic size should have a larger density-dependent buffer against population decline, or in other words, they should experience stronger density-dependent regulation (Andersen and Beyer, 2015). Consequently, the issue of density-dependent growth might be most important for stocks of large-bodied species. Our results for North Sea plaice (which in this study is the stock with the greatest asymptotic size) give some confirmation of this. The model predicts that North Sea plaice is at risk of "stunted growth" (Alm, 1946; Ylikarjula *et al.*, 1999) when late-in-life density-dependent growth is very strong, with growth stopping before size-at-maturity. Cases of stunted growth are, however, rarely observed in marine fish populations, possibly due to the large spatial extent of the habitat for adults in marine systems (Andersen *et al.*, 2017). Whether our model is correct in predicting that North Sea plaice could become subject to stunted growth is therefore not completely certain.

Model limitations

We were unable to replicate NEA mackerel's observed reduction in growth by only changing fishing mortality. We therefore assume that the observed reduction in NEA mackerel individual growth (Olafsdottir *et al.*, 2016) is not, or not solely, the result of a reduction in fishing mortality and a subsequent SSB increase. If the observed growth reduction did occur via intraspecific density dependence, some environmental change should then be the cause. A possibility would be increased sea surface temperatures in NEA waters, which have been thought to have extended NEA mackerel's feeding range northwards to Svalbard (Berge *et al.*, 2015), and to have shifted the egg production centre-of-gravity of NEA mackerel's western spawning component northward (Hughes *et al.*, 2014). However, it is also possible that the observed growth reduction of NEA mackerel individuals is rather due to interspecific competition instead of intraspecific competition, as suggested by Olafsdottir *et al.* (2016). They show that the increase in NEA mackerel SSB occurred simultaneously with an increase in SSB of its competitor: Norwegian spring-spawning herring. Thus, increased interspecific competition for resources could also have caused or contributed to the observed growth decrease in NEA mackerel.

Our model assumes a homogeneously distributed resource spectrum with a carrying capacity that follows a Sheldon spectrum (Sheldon *et al.*, 1977). As a result of this, late-in-life resource competition is automatically highest for individuals with a size that is near the size-spectrum's biomass peak (Figure 1). In reality however, marine fish often move through different habitats and resources as they grow. These may differ in a multitude of aspects from each other, with each habitat or resource type being able to contribute to density-dependent effects. It is especially important to consider habitat size, as this can be a major factor in shaping density dependence (Casini *et al.*, 2016), in particular if habitat size changes during ontogeny (Andersen *et al.*, 2017). To truly consider density dependence taking place throughout life requires incorporating this heterogeneity into the resource spectrum. Since this heterogeneity will be highly stock-specific, that can only be properly done when sufficient knowledge is available about it. This is only rarely the case. In the absence of this knowledge, our model offers a simplified method for incorporating density dependence both early and late in life.

We have assumed that decreased resource availability reduces the feeding level of the individual, and thereby its growth rate, without affecting size-specific mortality. A reduced growth rate does cause individuals to spend a longer time at a smaller size, where mortality rate is higher (Peterson and Wroblewski, 1984), which decreases their chances of survival. Nevertheless, this does not change the size-specific mortality rate. In an experiment on reef fish, Forrester (1990) shows that density-dependent growth can take place without an associated mortality increase. However, other studies show that decreased resource availability can increase mortality rate, resulting in density-dependent mortality as well as density-dependent growth. For instance, individuals can attempt to prevent their feeding level from decreasing too much by increasing their time spent searching for food (Wyatt, 1972; Walters and Juanes, 1993) or by taking greater risks during foraging (Damsgird and Dill, 1998). An increase in search rate or risk-taking puts the individual at a greater risk of predation (Walters and Juanes, 1993; Biro *et al.*, 2003, 2004), leading to an increased mortality rate. Furthermore, many fish stocks experience a reduction in body condition due to an increased stock density (e.g. Winters and Wheeler, 1994; Schindler *et al.*, 1997; Olafsdottir *et al.*, 2016). A decline in body condition can increase mortality rate. It may for instance decrease an individual's ability to avoid predation (Hoey and McCormick, 2004), or increase mortality risk after spawning (Lambert and Dutil, 2000). We have not incorporated such density-dependent mortality mechanisms in this study. If these above processes have influenced the data to which we have fitted our model, this could therefore influence the interpretation of our results. An additional presence of density-dependent mortality alongside the observed density-dependent growth would indicate that late-in-life density dependence was stronger than what we have found. Optimal size-at-entry for MSY exploitation would then likely be smaller than what we have found.

Interspecific density dependence

We have mainly focussed on intraspecific density dependence, providing a method for analysing density dependence in fish stocks from a single-stock management perspective. For a while now however, an increasing amount of fisheries research has been devoted to ecosystem-based management. When modelling

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density dependence from an ecosystem perspective it is important to incorporate that fish stocks do not only experience intraspecific density dependence, but also react to density changes of interspecific prey, competitors, and predators. The model type that we have used can be a useful tool for describing density dependence throughout life from an ecosystem perspective. We have already partly done so in this study, by linking Baltic sprat predation mortality to Eastern Baltic cod stock size. However, we did this in a simplified way, and not for NEA mackerel or North Sea plaice. Fully incorporating interspecific density dependence into the model will require the addition of dynamic prey, competitor, and predator stocks. Unfortunately, the interplay between interspecific and intraspecific density dependence is hard to extract from field observations, and therefore difficult to accurately model. Nevertheless, understanding both of these processes is important for making long-term stock predictions, especially from an ecosystem point-of-view.

Conclusion

It is unlikely that the stocks examined in this study experience late-in-life density-dependent growth strong enough to decrease optimal fishery size-at-entry to below size-at-maturity. However, this could still change on a case-by-case basis, especially now that increased sustainable exploitation is increasingly leading to stock recovery in the NEA. This will likely lead to more available data on late-in-life density-dependent growth, which may change this conclusion. Nevertheless, right now the practice of advising a large fishery size-at-entry seems to be valid for the examined stocks, even in the presence of strong late-in-life density-dependent growth.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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