



Original Article

Age-specific natural mortality rates in stock assessments: size-based vs. density-dependent

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Natural mortality (M) rates are difficult to measure empirically and are often specified in stock assessments based on life history characteristics. More recently, these specifications have included M as a function of the size or age of a fish. However, natural mortality is a dynamic parameter that will change with the suite of predators and, thus, indirectly with cohort size and age. As an alternative, a density-dependent M rate function is derived and compared with the commonly used Lorenzen model, where M at age forms an allometric relationship with weight-at-age. The density-dependent model expresses M as a function of two parameters: one density dependent and one density independent. Properties of the two models (size-based vs. density-dependent) were explored to indicate conditions where the results are and are not similar. Associated catch equations, equilibrium analyses, and non-linear replacement lines in stock–recruitment theory are examined. Just as with density-independent values of M , most assessment data are not sufficient to provide precise estimates of density-dependent M parameters. However, the density-dependent model provides a basis for incorporating ecological variability into single-species assessments, noting the differing dynamics between short- and long-lived species. The incorporation of dynamic natural mortality has implications when estimating abundance trends and stock status, and ultimately setting management reference points.

Keywords: age-structured model, density-dependence, ecological variability of natural mortality, Lorenzen relationship, mathematical model, stock assessment analyses.

Introduction

Implementation of ecosystem-based marine fishery management implies that ecological effects are acknowledged and addressed when evaluating fish stock status and developing management strategies (Link, 2002, 2005; Livingston *et al.*, 2005). However, incorporation of ecologically related data and model structures into single-species assessment models has traditionally been limited (Trites *et al.*, 1999; Mace, 2001). Despite this, single-species assessment methods have been the primary scientific tool for understanding current status and guiding management (NMFS, 1999), and these methods supply estimates of stock dynamics and status that are useful both scientifically and for management (Hall and Mainprize, 2004; Quinn and Collie, 2005). One reason for this is that assessment model fitting is a statistical interpolation process within the confines of existing dataserries, and thus simple model structures still provide stock status estimates of useful precision. However, concerns about ecological interactions and the

extrapolation of assessment results beyond current data time-series suggest that improvements are needed in estimating those ecological impacts within single-species assessments. One important step in integrating ecological concepts into assessments would be through more complex modelling of natural mortality (M) rates.

The specification or estimation of the M rate in fishery stock assessments remains an important aspect in evaluating a stock's status (Vetter, 1988; Mertz and Myers, 1997; Williams and Shertzer, 2003). Direct estimates of the instantaneous M rate can be made in some circumstances from controlled studies (Lorenzen, 1996). Additionally, M can sometimes be estimated within an assessment model when data from tagging or closed area studies provide information on M independent of fishing mortality rates (Haist, 1998; Fu and Quinn, 2000; Maunder, 2001; Pine *et al.*, 2003). However, in most instances, the M rates used are based on life history characteristics (e.g. Gunderson, 1980; Pauly, 1980; Hoenig, 1983; Gunderson and Dygert, 1988; Hewitt and Hoenig, 2005).

Assessments have attempted to incorporate the consequences of age-specific M into the analysis (Methot, 1990; Hampton, 2000). This has become especially important since the need to evaluate ecosystem effects on stocks has been emphasized (Fu and Quinn, 2000; Murawski, 2000; Yodzis, 2001; Gaichas, 2008). In many stocks, an important ecosystem effect on a fish stock is likely to be predator signals, which, in turn, are translated into M . However, it is unlikely that this mortality would be constant over the lifespan of a cohort (Clark, 1999; Hollowed *et al.*, 2000). To address this, meta-analyses have been used to derive empirical relationships between size and M (Myers and Doyle, 1983; Peterson and Wroblewski, 1984; McGurk, 1986; Chen and Watanabe, 1989). In particular, relationships developed by Lorenzen (1996, 2000) are now being commonly used in stock assessments.

It has long been noted that M rates are inversely related to the size of animals at the species level (e.g. Pauly, 1980). However, natural mortality-at-age does not arise from a fish's age itself but rather from factors such as predation. As fish get older, the suite of predators shifts both in terms of abundance and the species involved, and the impact declines with age. One assumption that addresses this is that the mortality rate decline is fixed over age.

The Lorenzen relationship (Lorenzen, 1996) extends this to relate mortality to the size of individuals within a species. An alternative assumption is that the mortality rate is a function of the abundance of a cohort. One such model is the density-dependent mortality model used to derive the Beverton–Holt stock–recruitment model (Beverton and Holt, 1957; Brooks and Powers, 2007). Other density-dependent models, such as Ricker (1958), might also be applied, but these are not examined here.

There are several implications of density-dependent mortality. One implication is that the suite of predators changes with the abundance of the cohort. Over the lifespan of the cohort, this is generally true. There are fewer older fish, and if the mortality rate is lower for older fish, then one explanation is that the abundance of the fish in the cohort is related. Another implication is that there is some form of prey switching as the fish gets older and larger. This is the basis for assuming density-dependent mortality during recruitment. Thus, it may well continue into post-recruitment stages. Other sources of mortality, such as competition for resources, may also be important density-dependent factors. However, the nature of this kind of density dependence is that just like recruitment processes, stronger cohorts experience higher M . Therefore, the debate becomes not about whether there is density dependence, but about when in the post-recruitment stage it stops. Of course, neither density-dependent models nor fixed-mortality-at-age models are correct; neither the size nor the number of individuals is the causative agent of mortality. Both models are pragmatic relationships resulting in declining mortality-at-age, which may be useful in the assessment process, although neither model addresses senescence that might occur in some stocks, and those effects are not addressed in this analysis. Effects of senescence can be examined separately with alternative models for ages where it is expected to occur.

The objective of this paper is to compare the properties of the two modelling approaches—size-based relationships vs. a cohort-based, density-dependent relationship—by examining parameter sets of the two models and the resulting population responses. The paper does not address estimation of M rate parameters using assessment data, as that is outside the scope of this investigation. The first section of the report presents the Lorenzen relationship and the density-dependent differential equation, its solution, and the associated density-dependent catch equation and compares this for the

models. The second section presents the properties of parameter alternatives on abundance, yield and production. Finally, the choice and implementation of the models into stock assessments is discussed.

Mortality models

Lorenzen

Lorenzen (2000) noted that theoretical and empirical studies point to the existence of an allometric relationship between M and body weight in fish of the form:

$$M_W = M_u W^d, \quad (1)$$

where M_W is M at weight W , M_u is M at unit weight, and d is an allometric exponent from empirical relationships shown to range from -0.3 to -0.37 . He also noted that since weight is approximately proportional to the third power of length, d values of approximately $-1/3$ imply that M is inversely proportional to body length. Following Lorenzen (1996, 2000), current applications of equation (1) in stock assessments often use the relationship

$$M_t \propto W_t^{-0.305} = M_\infty (W_t/W_\infty)^{-0.305}, \quad (2)$$

where M_t is the instantaneous M rate per year at age t and M_∞ is the asymptotic M rate at the asymptotic weight W_∞ . By a von Bertalanffy growth curve, ($L_t = L_\infty \{1 - \exp[-K(t-t_0)]\}$), then

$$M_t = M_\infty (1 - e^{-K(t-t_0)})^{-b(0.305)}, \quad (3)$$

where K is the growth rate, t_0 is the age at which length is zero for the von Bertalanffy model, and the allometric relationship is $W = aL^b$. Given that the von Bertalanffy and length–weight parameters are known, then the mortality rate schedule is defined by the Lorenzen parameters M_∞ and $d = -0.305$. Note that the scale of the mortality rate schedule in equation (3) is provided by the parameter M_∞ , where M_∞ is based on maximum age (Hoenig, 1983; Hewitt and Hoenig, 2005) or other life history characteristics (Pauly, 1980).

Density-dependent

The density-dependent (DD) mortality model for a cohort that was examined here is:

$$dN_t/dt = -M_\infty N_t - F_t N_t - AN_t^2 \quad (4)$$

where abundance (N_t) declines with age (t). The rates of mortality include a density-independent component (M_∞), a DD component (A), and age-specific fishing mortality rates (F_t). As t (age) increases, the M rate asymptotically decreases towards M_∞ , as before. The integral solution to equation (4) over one time-step is

$$N_{t+1} = \frac{N_t \exp[-M_\infty - F_t]}{1 + N_t \frac{A}{M_\infty + F_t} \{1 - \exp[-M_\infty - F_t]\}}$$

$$N_t = \frac{N_{t+1} \exp[M_\infty + F_t]}{1 - N_{t+\Delta t} \frac{A}{M_\infty + F_t} \{\exp[M_\infty + F_t] - 1\}} \quad (5)$$

(Forrest *et al.*, 2013). As t approaches infinity with no fishing, the exponential term approaches zero, the denominators of equation (5)

approach 1, and the model simplifies to the exponential decay model $N_{t+1} = N_t \exp(-M_\infty)$. Also, when $A = 0$, the model reduces to exponential decay.

$$C_t = \frac{F_t}{A} \ln \left[1 + N_t \frac{A}{M_\infty + F_t} [1 - \exp(-M_\infty - F_t)] \right] \\ = -\frac{F_t}{A} \ln \left[1 - N_{t+1} \frac{A}{M_\infty + F_t} [\exp(M_\infty + F_t) - 1] \right] \quad (6)$$

Equations (5–6) can be computed either backwards or forwards (Powers and Brooks, 2005), as one would do with the standard density-independent catch equation noting that M_t and M_∞ are not the same.

Fishing mortality rates for individual ages within an age-structured assessment model are usually estimated using numerical methods. These methods require that there is an observed catch and abundance at the beginning or end of an interval, and that M parameters are known. Fishing mortality rates by age can be estimated numerically using equations (5–6), the observed catch, an abundance estimate at the beginning or end of an age interval, and parameters M_∞ and A for that age interval.

All such methods select an F that results in a model catch-at-age that is numerically equal to the observed catch-at-age. Therefore, implementation of DD within existing F -estimation schemes requires that function evaluations ($C_{\text{model}} - C_{\text{observed}} = 0$) use equation (6) rather than the density-independent form. Also, some estimation methods, such as Newton-Raphson, require evaluations of

derivatives. In that case, the derivative dC_{model}/dF also uses equation (6). Thus, implementation of the DD model within an F -estimation module usually requires the simple modifications mentioned.

Properties

Equilibrium properties of a cohort described by Lorenzen and the DD models were examined by evaluating a suite of Lorenzen mortality rates at age vectors based on an exponent of the weight-length relationship being 3.0 and alternative values of the von Bertalanffy parameters K and t_0 and the asymptotic mortality at age M_∞ [equation (3)]. Then, a per-recruit analysis was conducted. These parameter sets were chosen to provide a range of behaviours. Noting the importance of M/K ratios (Lorenzen, 1996 and others), that ratio was used to categorize model outcomes. This allowed the analysis to explore a range of behaviour and life history characteristics with a single value of K . In order to compare the survival consequences with and without the DD model, a “realized” M -at-age was computed based on the survival rate. This is denoted by $M'_t \equiv \ln(N_t/N_{t+1}) - F_t$ from both mortality models.

In the first example, Lorenzen vectors were compared with the DD model with the same M_∞ and with no fishing. In both models, recruitment was specified to occur at age 1, and recruitment strength was set at unity ($N_1 = 1$). In the case of the DD model, the density-dependence is manifested through scaling of the parameter A with cohort strength N_1 . Therefore, by setting recruitment equal to unity, the DD parameter is expressed in units of AN_1 .

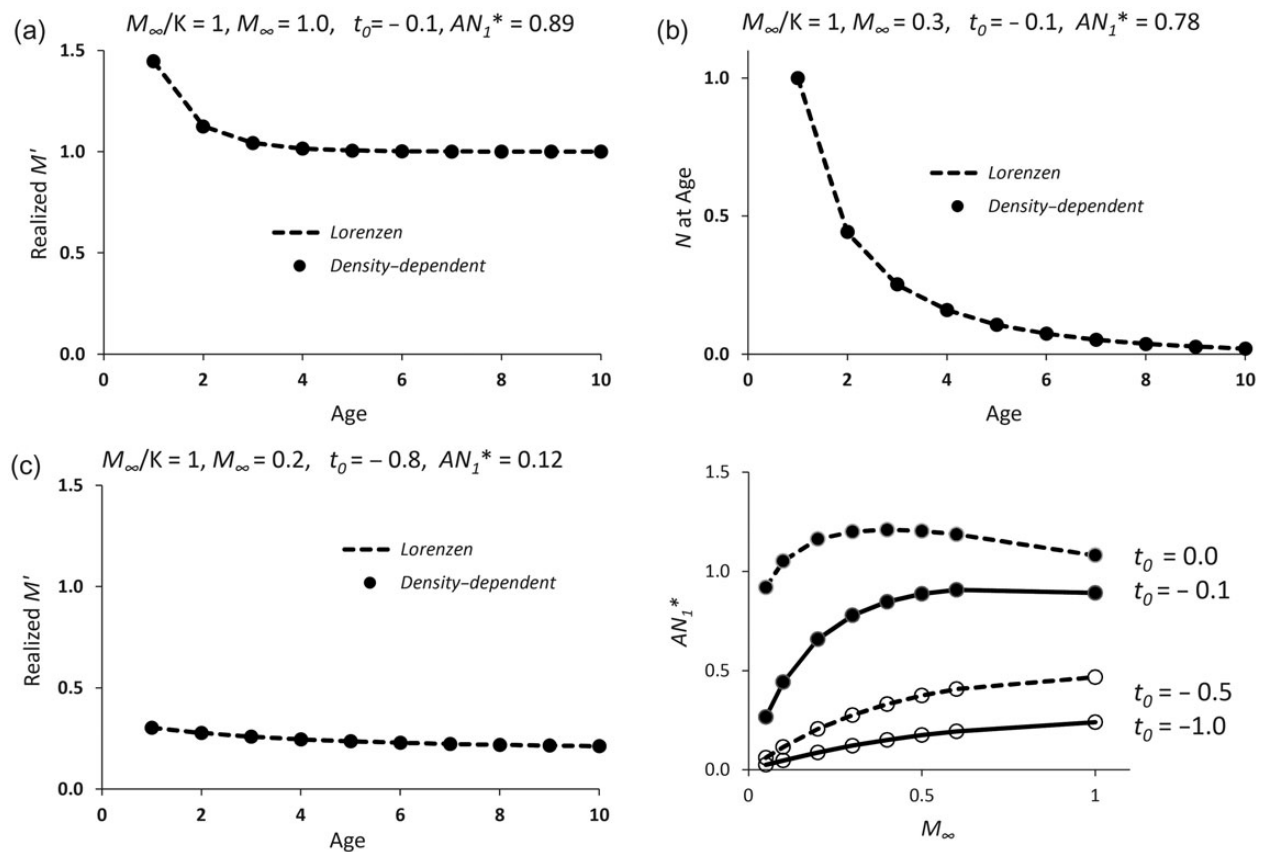


Figure 1. Upper and lower left quadrants: demonstration of equivalence of Lorenzen and density-dependent equilibrium models when $M_\infty/K = 1$ for three examples with no fishing. Lower right quadrant: relationship between AN_1^* and M_∞ for specified values of t_0 when $M_\infty/K = 1$.

Numbers at age were computed using the appropriate equation and parameters. Additionally, the value of AN_1 that provided the best fit between the numbers at age for the two models was found using simple minimum squared deviances as the criterion. This value is denoted as AN_1^* .

Interestingly, for $M_\infty/K = 1$ and specific values of t_0 and M_∞ , the equilibrium DD model with parameter AN_1^* provides a virtually exact match with the equilibrium Lorenzen model (Figure 1). The parameter AN_1^* that produces the same equilibrium mortality schedule as the Lorenzen model for $M_\infty/K = 1$ can be predicted from M_∞ and t_0 (Figure 1). But when $M_\infty/K > 1$, the two equilibrium models deviate from one another to some degree, with the DD schedule exhibiting somewhat lower survival rates (Figure 2).

The DD catch model [equation (6)] results in the same catch-at-age for different years (C_t) for a given fishing mortality rate (F_t) as the density-independent model, provided that the realized M_t' are the same in both models. However, cohorts of the same age with the same catch or fishing mortality rate will have different realized values of M_t' based on their prior abundance history.

The properties of the DD M rate model were explored using an artificial cohort, whose parameters are given in Table 1. The cohort recruits at age 1 with an initial cohort abundance of $N_1 = R = 1$. The fish of this cohort live until age 50, an age sufficient to encompass the dynamics of most fish life histories. Spawning production at age (P_t) was computed by $P_t = Mat_t(L_\infty\{1 - \exp[-K(t - t_0)]\})^3$, which uses the common assumption that spawning production (*per capita* egg production) is proportional to biomass. Since maturity simply scales the reproductive output, it was chosen to

mimic common groundfish and tuna maturity schedules. Likewise selectivity at age (Sel_a) from a single fishery was specified (Table 1). The fishing mortality for an age is $F_{t,a} = F_t Sel_a$ for the F -multiplier F_t . As with maturity, the selectivity schedule simply scales the outcomes to a schedule typical in many fisheries, where fish initially recruit starting at age 1 and have full recruitment at age 5.

In order to demonstrate the properties of a DD M rate, alternative values of A , M_∞ , and N_1 were used with equations (3–5) to compute quantities of cohort abundance N_t , realized M rate (M_t'), and equilibrium replacement lines.

The equilibrium replacement line has a slope of R_{rep}/S and is the number of recruits per spawning individual needed for a population in equilibrium to replace itself under a particular fishing regime. When there is no fishing, $S = S_0$ and $R = R_0$, and the replacement line slope is equal to the inverse of S_0/R_0 . When mortality rates are density-independent, the replacement line is linear, i.e. $R_{rep} = S/(S_0/R_0)$. However, DD mortality rates result in a curvilinear replacement line (Figure 3). Replacement lines are important in determining excess recruitment, which is the “surplus” of recruits that will be produced in order for a population to maintain itself at a fixed stock size. Maximum excess recruitment (MER) occurs at the stock size where the difference between recruits from the stock–recruitment curve and recruits from the replacement line is the largest, and occurs where their derivatives relative to S are equal (Figure 3). MER has important implications in determining biological reference points, such as maximum sustainable yield (Goodyear, 1980; Brooks *et al.*, 2009; Rothschild and Jiao, 2009). In the case where stock–recruitment

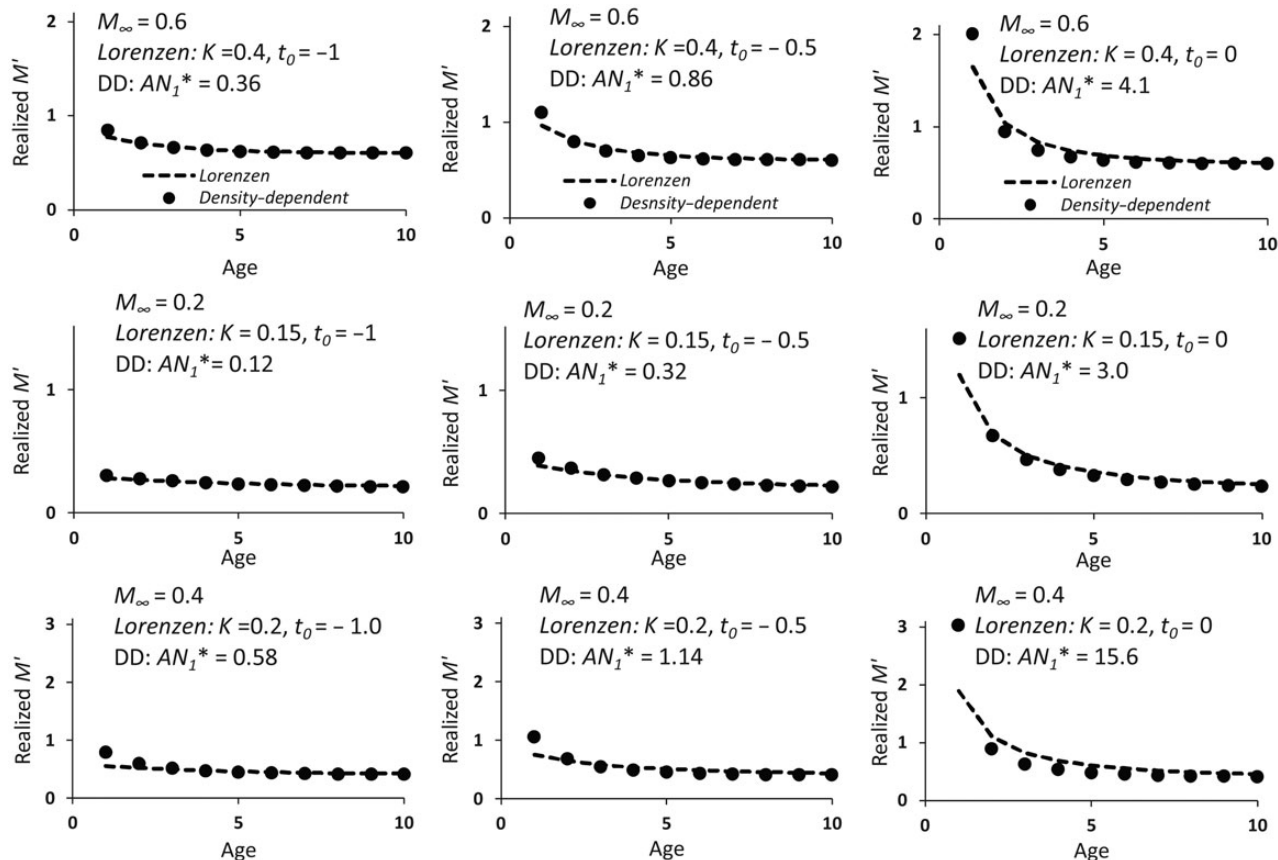


Figure 2. Examples of the realized M' -at-age derived from Lorenzen and DD models when $M_\infty/K > 1$ with no fishing.

Table 1. Population parameters of hypothetical Lorenzen and DD populations.

Stock – recruit		Growth	
R_0	10^6	a	10^{-7}
h	0.9	b	3.00
		L_∞	10
		K	0.2
		t_0	-0.5
Mortality			
	M_∞	0.2	
	A	2.052×10^{-7}	
	d	-0.305	
Age	Maturity-at-age	Selectivity-at-age	
1	0.0	0.1	
2	0.1	0.3	
3	0.3	0.5	
4	0.5	0.8	
5	1.0	1.0	
6	1.0	1.0	
...	
50	1.0	1.0	

Parameter A was chosen such that equilibrium-realized natural mortality rates at age with no fishing are the same between the two models.

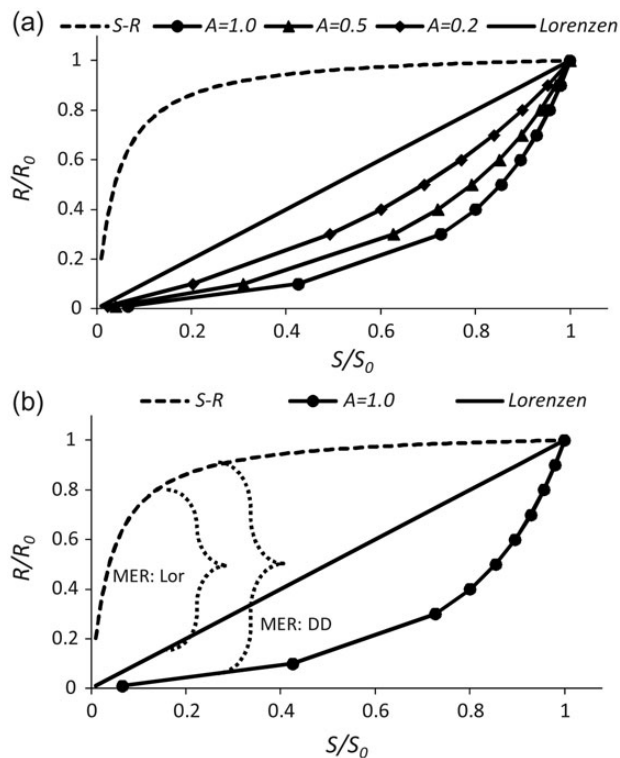


Figure 3. Top panel: replacement lines with no fishing from Lorenzen and selected DD models compared with an arbitrary Beverton–Holt stock–recruitment model (S-R; dashed line). Bottom panel: Maximum Excess Recruitment (MER, dotted brackets) where the slope of the S-R curve equals the slope of the replacement line for Lorenzen (Lor) and a DD model ($AN_1 = 1$).

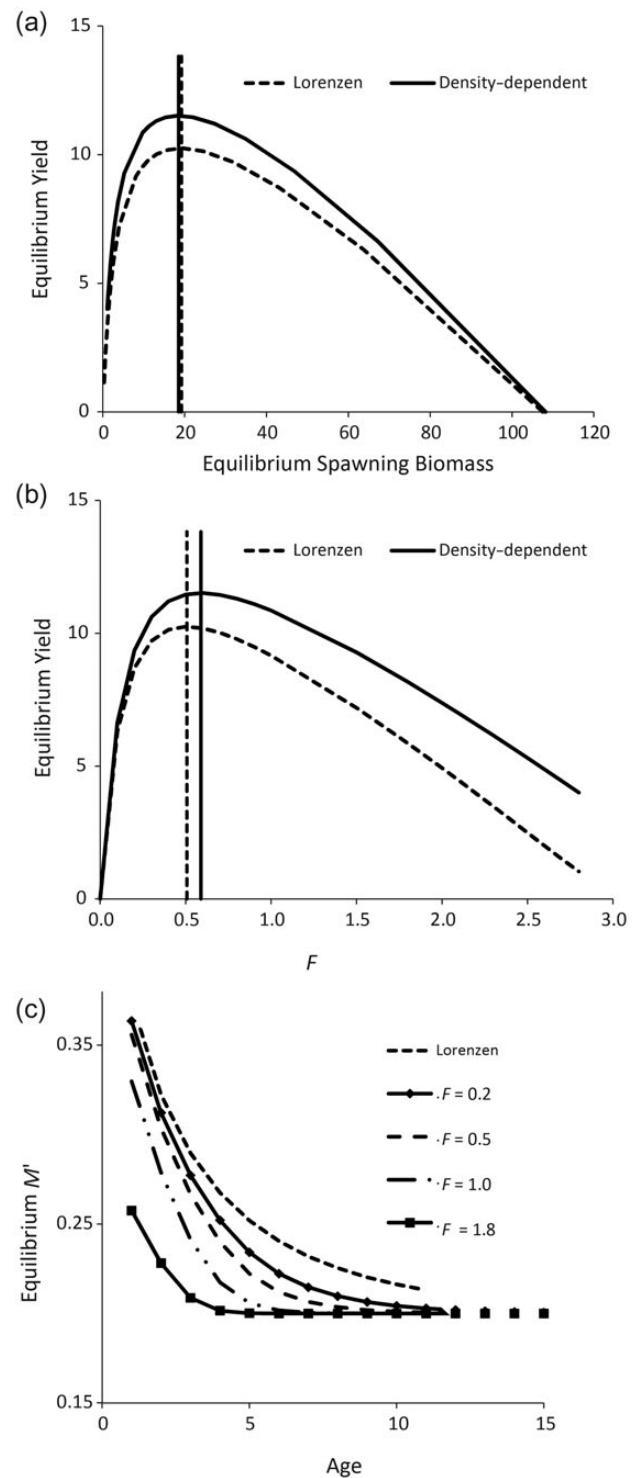


Figure 4. Equilibrium yield of Lorenzen and DD populations defined in Table 1. Vertical lines denote spawning biomass and F at maximum sustainable yield. Lower panel compares M'_t

has a monotonically decreasing derivative (as in Beverton–Holt S–R curves) and post-recruitment density-dependence is governed by an increasing derivative [equation (5)], MER is larger and occurs at higher stock sizes than that coming from the Lorenzen relationship (Figure 3). Additionally, the DD stock size that produces an excess recruitment equal to the Lorenzen MER occurs at a lower stock

size (Figure 3). These relationships hold for both the Beverton–Holt and Ricker stock–recruit models. The implications of the curvilinear replacement lines are that there will be a broader range of stock sizes at which productivity (excess recruitment) is high compared with the density-independent model.

However, the comparisons in Figures 1–3 are for equilibrium conditions, i.e. fixed recruitment. Therefore, the equivalence of the two models relates to “average” recruitment conditions when there is no fishing. But, recruitment in fish stocks is highly variable even for unexploited stocks. Therein is the difference between the two models. The Lorenzen relationship, as it is used in assessments, fixes the mortality rate vector regardless of year-class strength, whereas the DD model results in a modified mortality rate vector that is higher with larger recruitments.

When there is no fishing, a cohort that has twice the original abundance, but half the density-dependence (A), will result in the same DD mortality rate schedule as the original. For example, if A is 20% of the cohort strength N_1 , the additional M rate at the beginning of age 1 is 0.2 with a total M rate of $0.2 + M_\infty$. As the cohort ages, the mortality rate reduces toward the asymptote M_∞ ; hence, the effect of density-dependence diminishes with age. Variation in cohort strength results in variation in mortality-at-age, all else being equal.

Example of age-structured model

Artificial populations were created using the selected growth, maturity, and fishery selectivity parameters as listed in Table 1, with the addition of a stock–recruitment relationship. The populations were specified to have 10^6 recruits when in equilibrium with no fishing (R_0). A Beverton–Holt stock–recruitment relationship was assumed:

$$R = 0.8 R_0 h S / [0.2 S_0 (1 - h) + (h - 0.2) S], \quad (7)$$

where spawning–stock biomass S and S_0 were computed from the weight-at-age and maturity schedules (Table 1). A steepness of $h = 0.9$ was assigned. While steepness is notoriously difficult to estimate, the value of 0.9 is commonly used. The specific value of h did not change the basic relationship of results obtained from the two models, only the degree of difference. Therefore, only one value of h was presented. Given h , S_0 and R_0 , the stock–recruitment relationship was fully specified (Table 1). Note the parameters a and L_∞ were given an arbitrary scale since the choice of these parameters simply defines the units of biomass.

Two populations were defined which were identical under unfished equilibrium conditions. Both assumed mortality and growth parameters $M_\infty = 0.2 = K$, as in Table 1. M -at-age for the

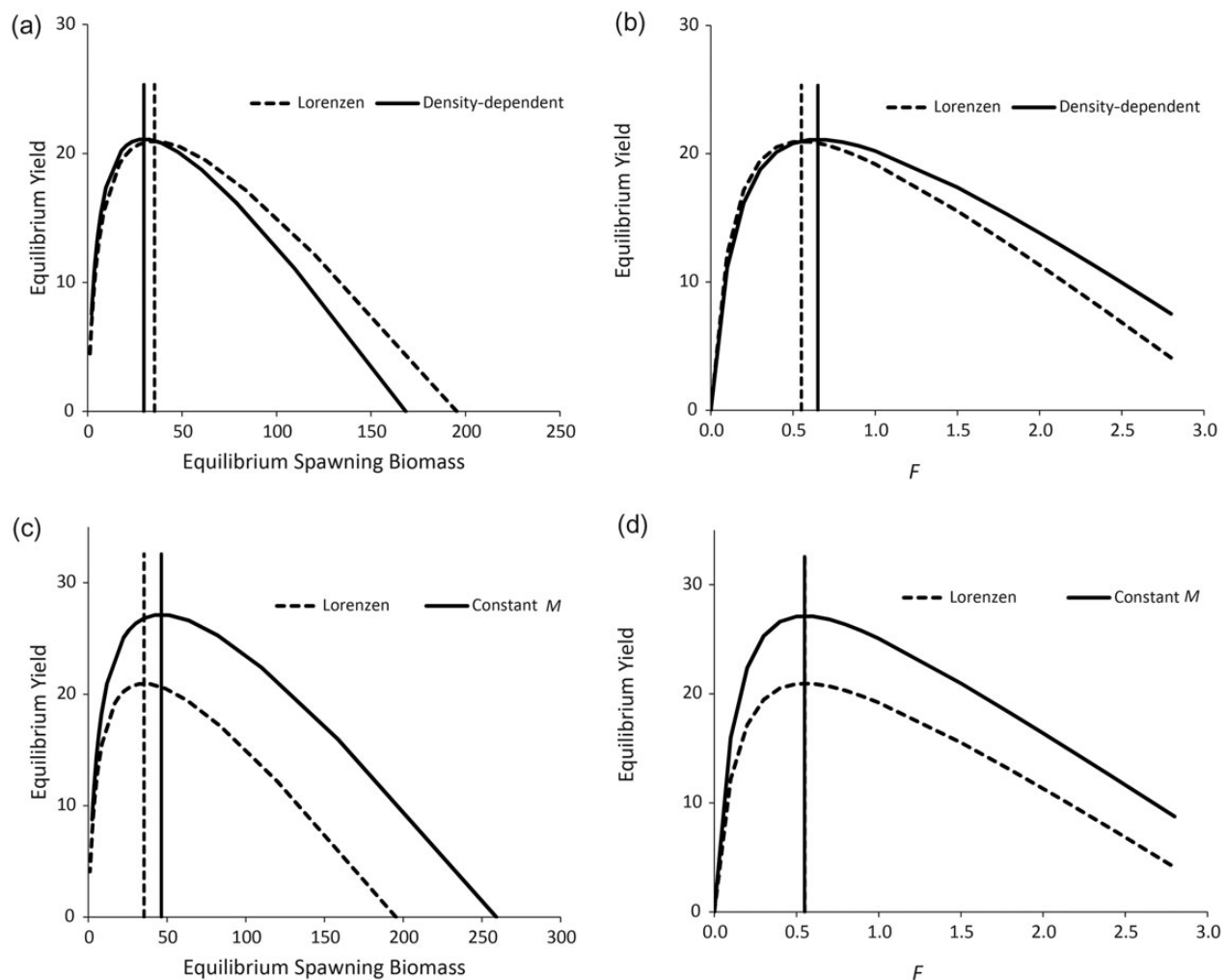


Figure 5. Equilibrium yield of Lorenzen and DD populations where $K = 0.4$, $A = 1.5 \times 10^{-7}$ and all else as defined in Table 1. Vertical lines denote spawning biomass and F at maximum sustainable yield.

Lorenzen population was computed using equation (3). The mortality schedule for the DD population was computed by numerically selecting the parameter A such that the equilibrium M'_t was the same for both populations, then each population's response to fishing was compared. This scenario tested the difference between DD and density-independent mortality rates when other biological characteristics of the two populations in equilibrium were the same (Figure 4).

As an alternative scenario, assume that the two populations had the same equilibrium mortality schedules during a period when the populations were near full exploitation. This scenario might occur if the M schedule was, indeed, imposed by DD factors, but the population was modelled as if the Lorenzen schedule were true. Additionally, perceptions of the M schedule were based on the experience during a period of full exploitation. This scenario was implemented by specifying $K = 0.4$, $A = 1.5 \times 10^{-7}$ when $F = 0.5$ and all else as in Table 1 (Figure 5). A third scenario compares a Lorenzen population with another population with a constant $M_t = 0.2$ for all ages (Figure 5).

Finally, 50-year projections were made for the two populations (Lorenzen and DD) when they experienced the same recruitment and fishing mortality rates (Figure 6). The DD M rates are manifested through scaling of the parameter A with cohort strength N_t , i.e. through the product AN_t . When there is no fishing, a cohort that has twice the original abundance, but half the

density-dependence (A), will result in the same DD M -at-age contribution as the original. For example, if A is 20% of the cohort strength N_t , the additional M rate at the beginning of age 1 is 0.2 with a total M rate of $0.2 + M_\infty$. As the cohort ages, the M approaches a constant M_∞ (Figure 1); hence, the effect of density-dependence diminishes with age. Variation in cohort strength results in variation in M -at-age, all else being equal. The DD catch model [equation (6)] results in the same catch-at-age C_t for a given fishing mortality rate F_t as the density-independent model, provided that the realized M'_t is the same in both models.

Discussion

The DD model [equation (6)] is a simple mechanism to implement age-specific M rates within a stock assessment by incorporating density-dependence throughout a fish's life history. It is an alternative to methods based on life history meta-analyses (Lorenzen, 1996) or to modelling M as a function of age, e.g., by an inverse logistic function. However, density-dependence, as implemented here, is not equivalent to simple age-specific values of M . The DD model maintains variability in M -at-age through year-class variability. In many assessments of stocks with low M , the implications of density-dependence to the estimation are likely to be small relative to equivalent M -at-age from other methods (see example). However, stocks with high recruitment variability would result in high variation in M that would

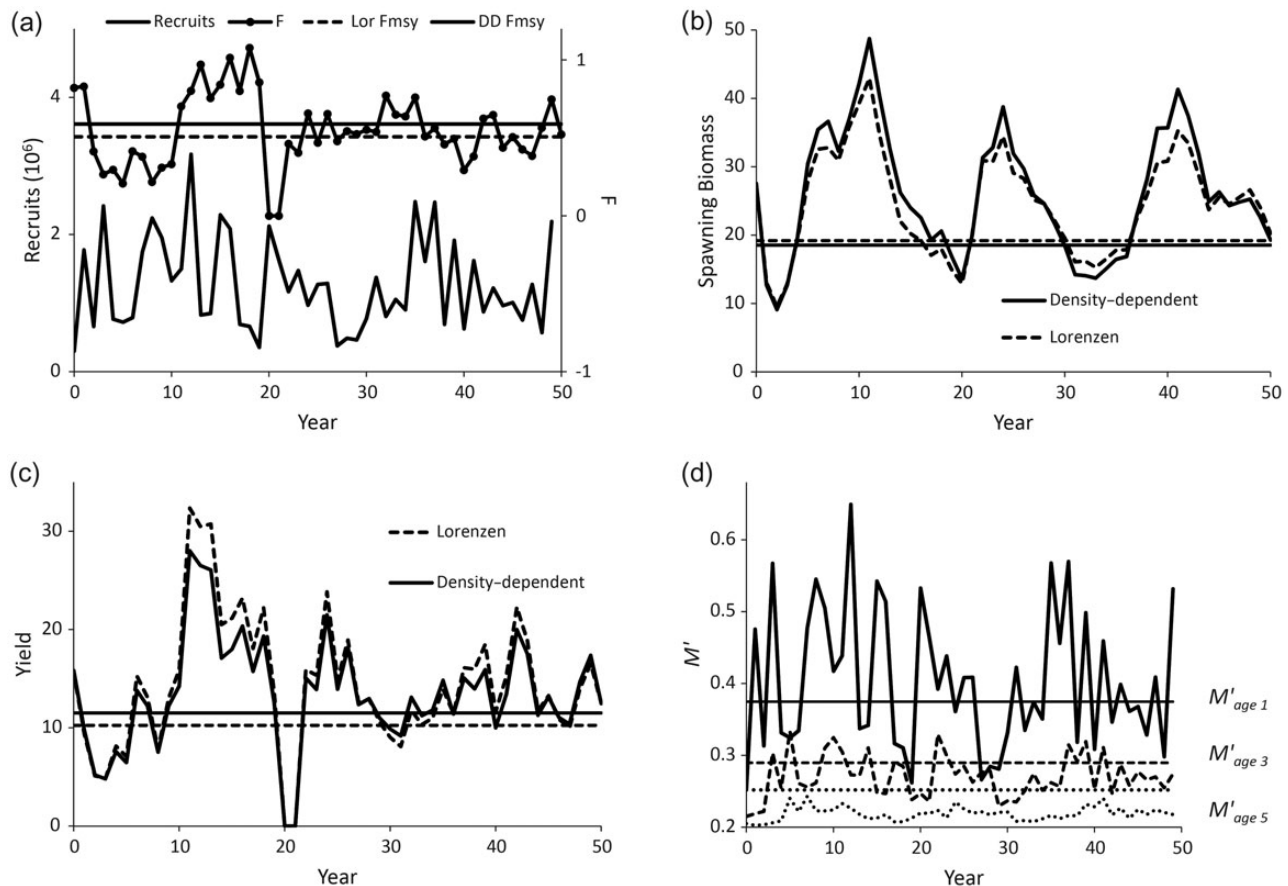


Figure 6. Comparison of Lorenzen and DD population projections using the same initial abundance-at-age, fishing mortality rates and recruitment history. Horizontal lines are the associated maximum sustainable yield reference points for fishing mortality rate F , spawning biomass and yield. The lower right quadrant compares realized M' at ages 1, 3 and 5 between the DD and Lorenzen models (Lorenzen M s are the horizontal lines).

influence both abundance trends and status. Therefore, applying M models should always be preceded by asking the following questions: Is density-dependence likely? What evidence exists for it external to the assessment? Are there diagnostics within the assessment that provide guidance?

While density-dependence through equations (4–6) incorporates notions of both age-specific M and year-class variability, the model is still based on overall life history characteristics and “average” effects of the ecosystem on a cohort. Thus, density-dependence is being evaluated relative to cohort strength, rather than the abundance of all fish in the stock or groups of adjacent cohorts. To address this, implementations of equations (5–6) might include year effects in which density-dependence within the assessment is modelled as $A' = A \exp(I_{\text{year}})$, where a year effect I_{year} is a normal deviate from zero. This could be done for appropriate blocks of years, as indicated by external ecological information. Similarly, A could be modelled for different life stages. For example, A may differ before and after movement from inshore to offshore environments that occur at specific ages.

The estimation of A and M_{∞} will suffer similar difficulties to those encountered in the estimation of M in stock assessments (Fu and Quinn, 2000). Correlations between catchability coefficients and M_{∞} and limited age-specific index or tagging data are expected to be factors limiting the ability to estimate M rates. Therefore, life-history-based estimates of M_{∞} using, e.g., Pauly (1980) or Hoenig (1983), may still be required, as currently done with density-independent assessments. If A is estimated, a likelihood ratio test or model selection criterion might be used to determine if the DD mechanism is plausible. Additionally, meta-analysis approaches, similar to Lorenzen (1996), should be useful in defining Bayesian priors on the A parameter. Nevertheless, further work is needed to explore estimation properties. Of particular interest would be estimates of A and d obtained within the assessment model when M_{∞} is fixed.

Incorporating density-dependence into current assessment models is relatively simple. Equation (2) is a general case of the usual exponential population model in which $A = 0$. Therefore, the same likelihood functions can be constructed for maximum likelihood estimations for any current assessment modelling. For example, catch-at-age can be modelled with error. Separate fisheries and selectivities can be modelled, and a stock–recruitment function may be incorporated. The major difference in coding is in the DD catch [equation (6)]. Estimates of fishing mortality rates, given catches in equation (6), require separate solution code (and derivatives) from that used for equation (4). Also, when an index of abundance monitors abundance throughout the year rather than at a particular time within the year, the appropriate equation for that index is based on equation (6).

An assessment model in which density-dependence extends into post-recruitment ages provides a flexible modelling approach for estimating M -at-age and variability in the rate, particularly in younger ages. As with most assessment approaches, indices of abundance and catch-at-age information will often not be sufficient to fully estimate M . Nevertheless, equations (5–6) are the mechanisms for incorporating dynamic values of M into assessments. As with any assessment approach, model fits and diagnostics should be critically examined to determine whether the inclusion of a parameter into the model is warranted, as is the case for inclusion of the DD parameter A . However, the inclusion of A provides a framework for interpreting ecological effects on single-species dynamics.

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