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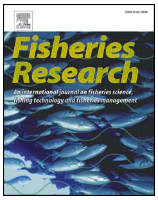

Natural mortality and body size in fish populations

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ABSTRACT

Fisheries stock assessments increasingly account for size-dependence in natural mortality rates, usually by modeling mortality as a power function of body length. Various empirical studies have indicated a scaling of mortality with length in the range of − 0.84 to − 1.11, but substantially different scaling exponents ranging from − 0.75 to − 1.5 have been proposed on theoretical grounds or derived from some empirical models. To resolve these controversies and provide a well-supported default estimate of scaling for stock assessments, we re-analyzed two major data sets used in previous studies that supported different scaling exponents, and a combined data set. Both original data sets and the combined data yielded within-population exponents close to − 1 when analyzed using joint-slope mixed-effects models with population as a random effect. When population effects were disregarded, regression models yielded exponents that did not correctly reflect within-population scaling. The greatest deviations from the correct within-population scaling of approximately − 1 occurred in multiple regression models of mortality, size, and growth parameters. We conclude that within- and among-population scaling of natural mortality should be clearly distinguished, and that within-population scaling of natural mortality with length in fish populations is highly consistent at approximately − 1. We also explored empirical models for predicting the intercept of the mortality-length relationship for a given population from growth parameters.

1. Introduction

Modeling of natural mortality M forms part of all age and size-based fisheries assessment methods, from Beverton and Holt’s (1957) yield-per-recruit model to today’s integrated assessment models (Methot and Wetzel, 2013; Brodziak et al., 2011). Traditionally, natural mortality has been assumed to be constant (independent of size and age, and time invariant) within the recruited stock. Natural mortality is regarded as difficult to estimate within stock assessment models and it is common practice to fix M or estimate a prior for M from empirical models relating M in the recruited stock to growth parameters, environmental temperature, or longevity (Pauly, 1980; Then et al., 2015; Beverton and Holt, 1959; Hoenig, 1983).

More complex and realistic mortality models are increasingly being used in fisheries models and stock assessments. In particular, size-dependent and equivalent age-dependent patterns are often incorporated into assessments. Accounting for such patterns is particularly important for example when juvenile fish are harvested or stocked into the population (Lorenzen, 2005) and has become increasingly common practice in assessments. Lorenzen (1996, 2000, 2005) conducted an extensive meta-analysis of mortality-size relationships in juvenile and adult fishes and pioneered the use of the resulting relationships with a mortality-length scaling of approximately − 1 in fish population modeling and assessment. Such ‘Lorenzen M′ natural mortality models, often converted to age-based mortality relationships using a stock-specific growth function and scaled to constant M estimates for the recruited stock, have found wide application in fisheries stock assessments (e.g. McKechnie et al. (2017); ICCAT International Commission for the Conservation of Atlantic Tunas (2018), SEDAR (Southeast Data, Assessment and Reviews (2018)) and other applications such as mark-recapture studies (Coggins et al., 2006; Lorenzen, 2006).

The scaling of M with body size in fishes has been investigated at the population and community level (Peterson and Wroblewski, 1984; McGurk, 1986; Lorenzen, 1996). From a theoretical perspective, multiple authors have suggested a ‘metabolic’ scaling exponent for mortality with length of − 0.75 (Peterson and Wroblewski, 1984; Andersen, 2019). Major empirical studies have demonstrated a broadly consistent allometric scaling with weight exponents between − 0.28 and − 0.37 and/or corresponding to length exponents between − 0.84 and − 1.11 assuming isometric growth (Table 1; except for two studies based on the

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Table 1
Previous estimates of the scaling of natural mortality with body length in fishes.

Exponent c	Method	Source
-1.02	Functional regression, juvenile/adult marine fish	(McGurk, 1986, 1987)
-0.86	Theil regression, juvenile/adult fish	(Lorenzen, 1996)
-1.11	Functional regression, Pacific salmon	(McGurk, 1996)
-1.12	Survival modeling of fish stocking experiments	Lorenzen (2000)
-1.0	Simplified model	
-0.81	Multiple regression for fishes	(McCoy and Gillooly, 2008)
-1.61	Multiple regression (L)	(Gislason et al., 2010)
-1.46	Multiple regression (L/L_∞)	(Charnov et al., 2013)
-1.5	Simplified model	

same data set, Gislason et al., 2010 and Charnov et al., 2013).

Gislason et al. (2010) and Charnov et al. (2013) aimed to place the size-dependence of M within the wider context of fish life histories, in effect unifying concepts of life history correlates commonly applied to constant M values for mature fish with size-dependent mortality patterns. For this purpose, Gislason et al. (2010) assembled a data set comprising M-at-size estimates together with growth parameters for the respective populations. Some populations are represented by multiple M estimates and some by only one. Using multiple regression of M against growth parameters, Gislason et al. (2010) estimated a steep scaling of natural mortality with length of -1.61 and Charnov et al. (2013) proposed a simplified general model for size-dependent mortality of $M(L) = (L/L_\infty)^{-1.5} K$. This model and the implied -1.5 scaling of M with length, colloquially known as 'Charnov M' has since been used occasionally in stock assessments (e.g. SEDAR (Southeast Data, Assessment and Reviews (2020)) as an alternative to the "Lorenzen M" models with a more moderate length scaling of mortality of around -1.

Assessment results are often sensitive to the scaling and intercept parameters of the mortality-length relationship, which are fixed a priori in most assessments. Considerable discussion has therefore ensued in stock assessment panels about the reasons for and implications of the substantially different scaling relationships implied by the Lorenzen and Charnov M models. Here we revisit evidence for population-level scaling in both data sets from which the different models were derived and a combined data set. We also re-evaluate patterns of population-level and ensemble-level scaling and their relationships with life history traits. We conclude by providing robust estimates for within-population scaling of natural mortality with body length for use in stock assessments and explore empirical models for predicting the intercept of mortality-length relationships from growth parameters.

2. Materials and methods

2.1. Data

We retrieved the data sets used in the studies of Lorenzen (1996) (which includes the data from McGurk, 1986) and Gislason et al. (2010). The data used by Lorenzen (1996) included only mortality and corresponding weight estimates, but no length data or growth parameters. We used length-weight relationships and growth parameters from FishBase (Froese and Pauly, 2021) or from the original or additional data sources to convert weight to length and add growth parameter estimates for each population. For length-weight relationships, we used those directly associated with the original study when possible, but resorted to average relationships provided by FishBase otherwise. For growth parameters, we took a different approach. Since the Lorenzen (1996) data include many studies on freshwater fishes and juveniles of marine fishes conducted on relatively small spatial scales and often with limited representation of large and old individuals, growth parameters corresponding to the study populations were often unavailable or unreliable. For growth parameters we therefore used averages for the species and region, or global averages for the species derived from FishBase unless reliable estimates were provided in the original study, or no estimates were available in FishBase. In the former case, we used the specific estimates. In the latter case, we conducted a literature search for growth estimates that could be transferred. Using these approaches, we obtained growth parameter estimates for all populations represented in Lorenzen (1996).

It should be noted here that the Lorenzen (1996) data were assembled to cover a wide range of fish sizes and ecosystems and include a mixture of relatively short-term ecological studies of localized freshwater fish populations as well as typically longer-term and larger-scale studies in marine populations. The Lorenzen (1996) data cover a substantially wider range of body lengths and natural mortality rates than the Gislason et al. (2010) data (Fig. 1). In particular, the Lorenzen (1996) data include a large number of observations for small fish below 10 cm in length. Moreover, the original mortality and size data were supplemented with life history information that often represents global averages. By contrast, the Gislason et al. (2010) data have been assembled from fisheries surveys and assessments of commercially important marine fish stocks and only studies with very reliable data on all life history parameters were included. This has resulted in a smaller data set covering a more restricted length range. The combined data set therefore represents a compromise of data contrast and quality attributes. The data are provided as supplementary information in Table S1.

Both the Lorenzen (1996) and Gislason et al. (2010) data contain a mixture of populations for which multiple mortality estimates were obtained for fish at different sizes, and populations that are represented by only one estimate. We refer to these data sets as ensembles because they combine selectively sampled data from populations that do not necessarily co-occur in nature. The data sets thus differ (to an unknown extent) from community-level data which would be collected from co-occurring and potentially interacting populations while aiming for

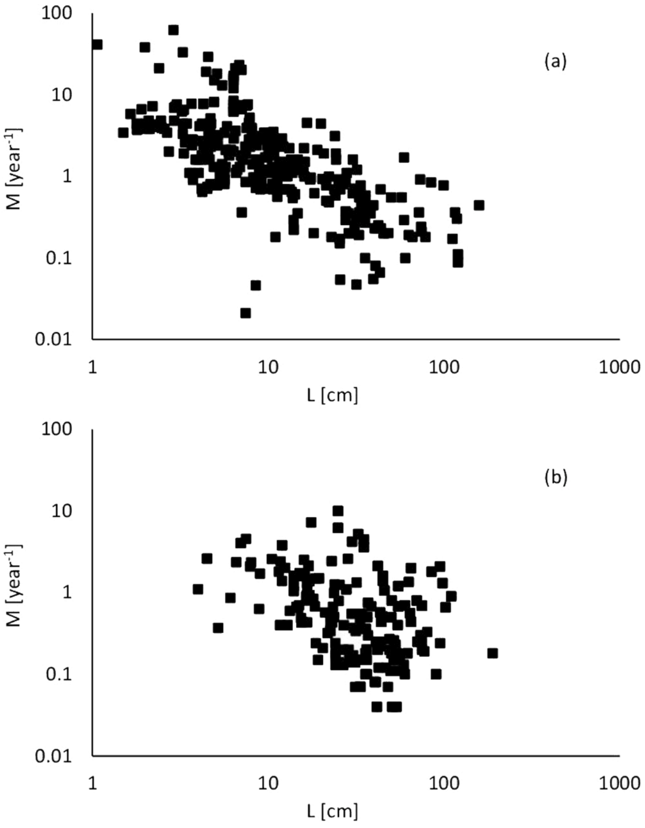

Fig. 1. Natural mortality M and length L in the data sets assembled by (a) Lorenzen (1996) and (b) Gislason et al. (2010).

representative sampling of size and age grups.

We created sub-samples of both data sets with only populations for which multiple mortality estimates were included, and combined data sets while eliminating duplicates of studies that were included in both.

2.2. Analyses

We re-analyzed the data used by Lorenzen (1996) (extended with length data and growth parameters) and by Gislason et al. (2010). We started by examining the spread of length and mortality estimates graphically. We then applied multiple different models to both data sets and a combined data set (Table 2). The models were: (1) a joint-slope mixed-effects model of mortality vs. body length L, with population as a random effect applied to the intercept; (2) a joint-slope mixed-effects model of mortality M vs. body length relative to population asymptotic length (L/L_∞), with population as a random effect; (3) a regression model of mortality vs. body length L; (4) a regression model of mortality M vs. body length relative to population asymptotic length (L/L_∞); (5) a multiple regression model of M vs. L and L_∞; (6) a multiple regression model of M vs. L, L_∞, and growth rate parameter K. (7) a multiple regression model of M vs. (L/L_∞) and growth rate parameter K. Model (1) provides the most direct estimate of within-population scaling of mortality with length, because it accounts for population effects and uses only direct measurements of mortality and size. Model (2) brings in additional life history information (L_∞) to construct the composite variable (L/L_∞) and re-scales the length range for all populations to a relative scale between 0 and 1. Models (3) and (4) are the conventional regression equivalents of models (1) and (2), which means they do not account for population effects and therefore allow the exponent to deviate from the best estimate of the within-population exponent. Models (5), (6) and (7) further open the slope estimate to the influence of covariates, the growth parameters L_∞ and K. We applied this set of models to the full data used by Lorenzen (1996), Gislason et al. (2010), and a combined set. We also applied them to sub-sets of these data containing only populations for which multiple mortality estimates and corresponding body size have been reported. This restricted the analysis to only those populations which provided direct information on within-population scaling of mortality. We also estimated the scaling of M separately for immature and mature fish by dividing the data set into immature and mature fish based on an average fish length at maturity at 2/3 L_∞ (Charnov, 1993; Charnov et al., 2013).

After establishing strong evidence for a universal scaling of M with L in fish populations of approximately − 1, we applied this scaling to all individual mortality estimates and for each value of M(L) calculated the corresponding mortality at unit length $M_1 = M(L) \times L$ and the mortality at L_∞, $M_{L\infty} = M(L) \times (L/L_\infty)$. Mortality at unit length (M_1) allows for easy comparison of the overall level of size-dependent mortality among populations, while mortality at asymptotic length ($M_{L\infty}$) characterizes late adult mortality. Mortality at asymptotic length ($M_{L\infty}$) is closely related to constant adult M traditionally used in fisheries assessments. We then explored empirical models to predict M_1 and $M_{L\infty}$ from growth parameters. We also tested the utility of a previously established empirical predictor of constant adult mortality M from growth parameters (the (Then et al., 2015) growth-based predictor) for predicting $M_{L\infty}$ by estimating the relationship between the Then predictions of $M_{Then\text{-}g}$ and our estimates of $M_{L\infty}$.

Finally, we graphically explored within and among-population relationships between natural mortality and body length to better understand how analyses across multiple populations that do not account for population effects can yield scaling parameters that deviate substantially from those governing the within-population scaling of mortality.

3. Results

The joint slope mixed effects models with random intercepts for populations indicate very consistent slopes close to − 1 for relationships between lnM and lnL or ln(L/L_∞) across all data sets (Table 2, Fig. 2). When random intercept effects for population are eliminated, the resulting linear regression of lnM vs. lnL yields a slope that is less

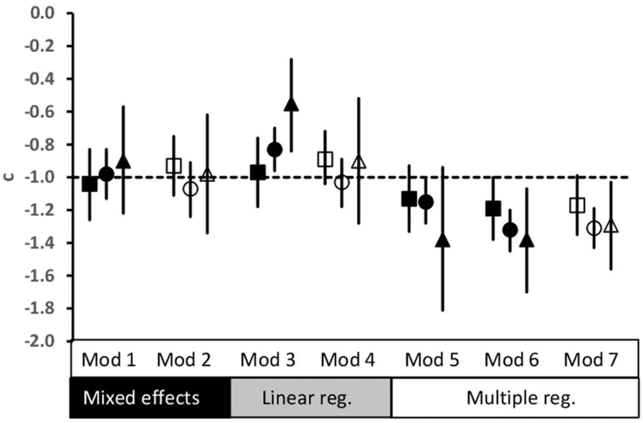

Fig. 2. Estimates of the scaling of natural mortality with body length from different data sets and models, for populations with multiple estimates (Table 2). Data sets: Lorenzen (1996) (■,□), combined (●, ○) and Gislason et al. 2010 (▲,△). Solid symbols denote models that use absolute length L whereas open symbols denote models that use relative length (L/L_∞).

Table 2
Estimates of the scaling of natural mortality with body length from different data sets and models. In the models, subscript j denotes a random effect of population j.

Model	Lorenzen (1996) expanded with length data and life history parameters		Gislason et al. (2010),Charnov et al. (2013)		Combined	
	Populations with multiple estimates (n = 175)	All populations (n = 308)	Populations with multiple estimates (n = 114)	All populations (n = 168)	Populations with multiple estimates (n = 268)	All populations (n = 445)
(1) $lnM=a_j + c\ lnL$	-1.04 [− 1.26, − 0.83]	-0.95 [− 1.06, − 0.84]	-0.90[− 1.22, − 0.57]	-0.95 [− 1.20, − 0.71]	-0.98 [− 1.13, − 0.83]	-0.97 [− 1.08, − 0.87]
(2) $lnM=a_j + c\ ln(L/L_\infty)$	-0.93 [− 1.11, − 0.75]	-1.09 [− 1.23, − 0.96]	-0.98 [− 1.34, − 0.62]	-1.04 [− 1.37, − 0.71]	-1.07 [− 1.24, − 0.91]	-1.15 [− 1.27, − 1.03]
(3) $lnM=a + c\ lnL$	-0.97 [− 1.18, − 0.76]	-0.94 [− 1.04, − 0.83]	-0.55 [− 0.84, − 0.28]	-0.72 [− 0.95, − 0.48]	-0.83 [− 0.96, − 0.70]	-0.91 [− 1.00, − 0.82]
(4) $lnM=a + c\ ln(L/L_\infty)$	-0.89 [− 1.04, − 0.72]	-1.07 [− 1.20, − 0.95]	-0.90 [− 1.28, − 0.52]	-1.00 [− 1.35, − 0.66]	-1.03 [− 1.18, − 0.89]	-1.15 [− 1.26, − 1.03]
(5) $lnM=a_j + c\ ln(L) + d\ ln(L_\infty)$	-1.13 [− 1.33, − 0.93]	-1.21 [− 1.33, − 1.10]	- 1.38 [− 1.81, − 0.94]	-1.58 [− 1.94, − 1.21]	- 1.15 [− 1.28, - 1.01]	-1.25 [− 1.36, − 1.15]
(6) $lnM=a + c\ ln(L) + d\ ln(L_\infty) + f\ lnK$	-1.19 [− 1.38, − 1.00]	- 1.26 [− 1.37, − 1.14]	- 1.38 [− 1.70, − 1.07]	-1.61 [− 1.89, − 1.34]	- 1.32 [− 1.45, - 1.20]	- 1.36 [− 1.45, − 1.26]
(7) $lnM=a + c\ ln(L/L_\infty) + f\ lnK$	-1.17 [− 1.35 − 0.99]	-1.24 [− 1.36, − 1.13]	-1.29 [− 1.56, − 1.03]	-1.46 [− 1.71, − 1.22]	-1.31 [− 1.43, − 1.19]	-1.35 [− 1.44, − 1.25]

negative than the corresponding joint slope estimate for the mixed effects model. This holds across all data sets. The slope of lnM vs. $\ln(L/L_\infty)$ is not as strongly affected by the removal of random effects. However, when that regression model is extended to a multiple regression model with $\ln(L/L_\infty)$ and lnK as independent variables, the slope of lnM vs. lnL is estimated to be much more steeply negative (-1.2 to -1.46).

To test whether the estimated slope of lnM vs. lnL of around − 1 applies throughout the juvenile and adult life stages or only to juveniles, we split the data at $L/L_\infty = 2/3$, the average relative length at maturity (Charnov, 1993; Charnov et al., 2013). The slopes in both life stages were significantly negative at − 0.87 [− 1.05, − 0.69] for juveniles and − 0.72 [− 1.24, − 0.20] for mature fish, and not significantly different between stages (combined data for populations with multiple estimates).

Following the above results where analyses of all data sets indicate a scaling of M with L of approximately − 1, we fixed the scaling parameter at this value. We then explored relationships between the intercept of the mortality-length relationship and life history and parameters (Table 3). The intercept of a population-level mortality-length relationship may be described by either mortality at a fixed length such as unit length (M_1), or by mortality at asymptotic length for the population ($M_{L\infty}$). As mentioned above, mortality at unit length (M_1) allows for easy comparison of the overall level of size-dependent mortality among populations, while mortality at asymptotic length ($M_{L\infty}$) characterizes late adult mortality and is related to the constant M traditionally used in fisheries assessments. Empirical predictors for M_1 and $M_{L\infty}$ from life history and environmental parameters are given in Table 3. Significant predictors for M_1 included L_∞ and K with positive coefficients. The best predictor with the smallest RMSE was a multiple regression model incorporating L_∞ and K (Model 4, Table 3, RMSE=0.78). Significant predictors for $M_{L\infty}$ included K with a positive coefficient and L_∞ with a negative coefficient. Note that L_∞ has a negative coefficient as a predictor for $M_{L\infty}$ but a positive coefficient for M_1. The best predictor of $M_{L\infty}$ with the smallest RMSE was a single regression model using K (Model 6, Table 3, RMSE=0.78). It should be noted that some predictors for M_1 and $M_{L\infty}$ are equivalent both conceptually and in predictive power. For example, models (4, Table 3) and (6, Table 3) use information from the same parameters, L_∞ and K, but L_∞ is implicit in the definition of $M_{L\infty}$ in model (6, Table 3). The models developed here are similar in predictive performance to 'Charnov-type' models that do not account for population effects (and misrepresent population-level scaling of M) but nonetheless predict M at the ensemble-level: a model of this structure fitted to the same data shows slightly higher predictive performance than the best model using population-level scaling (RMSE= 0.74 vs. 0.78) while the original Charnov model shows slightly lower performance (RMSE= 0.82 vs. 0.78)(Table 3).

Table 3

Regression models for mortality M_1 at unit length (1 cm) and $M_{L\infty}$ at L_∞, given a scaling of $M \sim L^{-1}$. Based on the combined data from populations with multiple values of M and L, n = 266 (after exclusion of two extreme outliers). Also provided for comparison of predictive performance are two 'Charnov-type' M predictors, one fitted to the same data set (Model 7 in Table 2) and the original Charnov model derived in Charnov et al. (2013).

Model	Parameters [95% CI]			R^2	P	RMSE
	a	b	c			
Mortality at unit length (M_1)						
(1) $\ln M_1 = a$	2.79 [2.67, 2.91]					
(2) $\ln M_1 = a + b \ln L_\infty$	0.86 [0.37, 1.34]	0.56 [0.42, 0.69]		0.20	< 0.0001	0.89
(3) $\ln M_1 = a + c \ln K$	3.03 [2.77, 3.30]		0.21 [0.01, 0.41]	0.02	0.040	0.99
(4) $\ln M_1 = a + b \ln L_\infty + c \ln K$	0.65 [0.23, 1.07]	0.91 [0.77, 1.05]	0.87 [0.68, 1.05]	0.39	< 0.0001	0.78
Mortality at L_∞ ($M_{L\infty}$)						
(5) $\ln M_{L\infty} = a + b \ln L_\infty$	0.86 [0.38, 1.34]	-0.44 [− 0.58, − 0.31]		0.14	< 0.0001	0.89
(6) $\ln M_{L\infty} = a + c \ln K$	0.42 [0.21, 0.63]		0.93 [0.77, 1.09]	0.34	< 0.0001	0.78
(7) $\ln M_{L\infty} = a + b \ln L_\infty + c \ln K$	0.65 [0.23, 1.07]	NS	0.87 [0.68, 1.05]	0.34	< 0.0001	0.78
Comparison with M predictors						
Best fit (Model 7,Table 2) $\ln M = a + b \ln(L/L_\infty) + c \ln K$	0.28 [0.07, 0.48]	-1.30 [− 1.42, -1.19]	1.08 [0.92, 1.24]	0.67	< 0.0001	0.74
Charnov model $\ln M = a + b \ln(L/L_\infty) + c \ln K$	0	-1.5	1			0.82

The intercept of the mortality-length relationship is positively related to maximum growth in the population. Model 4, Table 3, with coefficients of both $\ln L_\infty$ and lnK not significantly different from 1 implies that M_1 is proportional to K L_∞, the maximum length growth rate in the von Bertalanffy growth model. This relationship is clearly evident in Fig. 3(a). The maximum growth rate K L_∞ is highly variable among populations but on average, increases with L_∞ (Fig. 3b). When combined, these relationships give rise to a pattern where on average, large-growing species and populations are subject to higher mortality-at-length than smaller-growing ones (Fig. 3c). Fig. 4 shows this pattern more clearly, illustrating average mortality-length relationships for four species with four different asymptotic lengths (based on Model (4), Table 3, and the empirical relationship between K L_∞). On average, larger-growing species are subject to higher mortality-at-length than smaller-growing ones throughout their lifetime, but experience lower mortality in adulthood due to their large size.

In addition to the empirical predictors developed in Table 3, previously published predictors of mortality M in the adult phase of the life cycle can be used to estimate $M_{L\infty}$. For example, the growth-based empirical predictor $M_{Then\text{-}g}$ developed by Then et al. (2015) can be used to estimate $M_{L\infty}$ and explain some variability in the data. Based on the combined data from populations with multiple values of M and L (n = 266, after exclusion of two extreme outliers), $\ln(M_{L\infty}) = -0.16$ [− 0.29, 0.03] + 0.87 [0.72, 1.03] $M_{Then\text{-}g}$ (K, L_∞). Given a coefficient not significantly different from 1 and an intercept of − 0.16, the best general estimate is that $M_{L\infty}$ is at 0.85 of the growth-based predictor of M. Since when $M \sim L^{-1}$, $M_{L\infty}/M_L = L/L_\infty$, M_L intersects constant M near the center of the adult length range (0.66 L_∞ to L_∞), at 0.85 L_∞ for the growth-based predictor of M.

To explore why ensemble-level scaling of M with L is more variable and can differ systematically from the very consistent within-population scaling, it is useful to examine population and ensemble-level patterns explicitly (Fig. 5). We illustrate these patterns using the Gislason et al. (2010) data which show the greatest differences between population and ensemble-level scaling patterns, while noting that qualitatively similar patterns of lesser magnitude are also seen in the Lorenzen (1996) and combined data (Table 2, Fig. 2). The composition of the data set in terms of the asymptotic length L_∞ of the stocks and the lengths L for which mortality estimates have been obtained are shown in Fig. 5(a). For any given stock, L_∞ is a life history parameter while the length L to which the mortality M estimate refers is determined by the method of field sampling and/or analysis for mortality estimation. In the data set, some stocks are represented by separate mortality estimates for multiple lengths while others are represented with only one estimate. Since L_∞ is

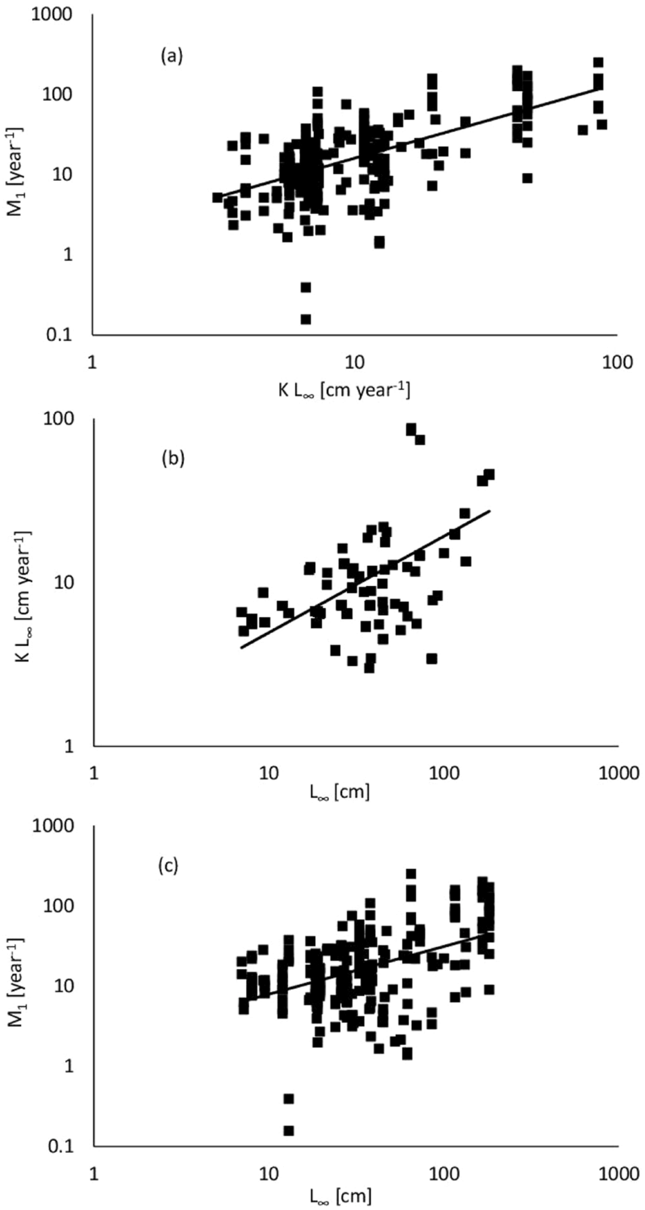

Fig. 3. Relationships between: (a) natural mortality at unit length (M_1) and maximum length growth rate (K L_∞) in the population; (b) (K L_∞) and asymptotic length (L_∞); (c) M_1 and L_∞ (c). Combined data for all populations with multiple values of M and L per population.

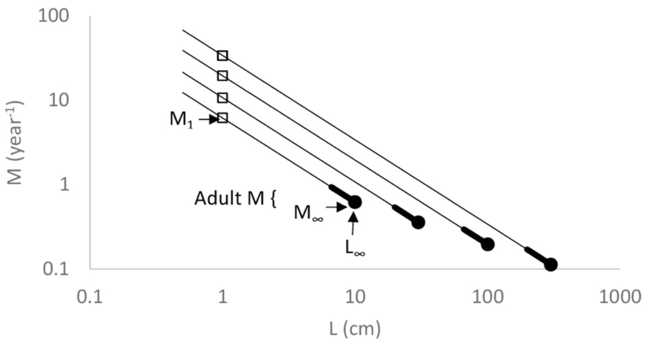

Fig. 4. Length-dependence in natural mortality M for populations with different asymptotic lengths L_∞, based on Model (4) (and equivalent to Model (6)), Table 3.

the asymptotic or mean maximum length of fish in the population, $L \leq L_\infty$, many mortality estimates were obtained for lengths L close to L_∞, but some have been obtained for substantially smaller and younger fish in the same population (low L/L_∞). Importantly, the majority of mortality estimates for fish at low L/L_∞ have been obtained from species that grow to a very large individual size. This may reflect the selection of studies included but also the fact that very small fish are often poorly represented in fisheries surveys, so that only juveniles of larger-growing species are well represented and assessed. Since the main focus of our analysis is the estimation of the scaling of mortality M with length L, it is also useful to examine a plot of L_∞ against L (Fig. 5b). This illustrates that M estimates for the largest size fish represent large-growing fish near their L_∞, but estimates for intermediate sizes represent a mixture of estimates for juveniles of large-growing fish and mostly adults of fish that grow to intermediate maximum sizes. The implication of this pattern for the ensemble-level mortality-length relationship is that the largest-growing fish, which on average suffer high mortality-at-length (Fig. 3 and 4), are strongly represented throughout the intermediate-to-large size range, while smaller-growing fish with lower mortality-at-length predominate in the small-to-intermediate size range. Overall, this distribution of data from different populations results in an ensemble-level mortality-length relationship that is less steep than the underlying population level scaling (-0.72 vs. -1 in this case) (Fig. 5c). The imbalanced distribution of mortality estimates for juvenile fish (low L/L_∞) is strikingly illustrated when data for all populations are scaled relative to L_∞ (Fig. 5d-f). Data for juveniles originate very predominantly from populations of large-growing fish with high L_∞ (Fig, 5 d) and medium-to-low K (Fig, 5 e). The ensemble-level relationship of M to L/L_∞ scales at -1.04 (Table 2, Fig. 5f). The multiple regression model $\ln M = 1.46 \ln(L/L_\infty) + \ln K$ improves the overall fit to the data by modeling the effect of the imbalanced representation of populations between adult and juvenile fish, but it does so by distorting the scaling of M with L/L_∞ in a way that is not representative of its within-population scaling. The performance of the model in this case is very much predicated on the peculiarities of the data set for which it has been developed.

4. Discussion

4.1. Natural mortality and body size in fish populations

By re-analyzing the data sets assembled by Lorenzen (1996), Gislason et al. (2010) and a combined data set using joint slope mixed effects models, we provide strong evidence that within fish populations, natural mortality scales with length to the power of -1. This corroborates a range of earlier empirical studies that have yielded exponents close to -1 (Table 1). Furthermore, we show that natural mortality is size-dependent in both juvenile and adult fish and that the scaling is not significantly different between juvenile and adult life stages. A qualitatively similar result was also derived by Charnow et al. (2013). Therefore, it is appropriate to model natural mortality in fish populations throughout the juvenile and adult stages as a function of length to the power of -1. Constant mortality in the recruited phase, the traditional assumption in fisheries models, is a simplification of the actual mortality pattern.

The intercept of the mortality-length relationship is positively related to maximum body growth in the population: M_1 is proportional to K L_∞, the maximum length growth rate in the von Bertalanffy growth model. Maximum growth rate is variable among populations but on average, increases with asymptotic size. Therefore, large-growing species and populations are subject to higher mortality-at-length than smaller-growing species throughout their lives, but suffer low adult mortality as a result of their large adult size. This generalizes a similar result obtained by Gislason et al. (2008) for North Sea fish communities. Growth-mortality tradeoffs are well documented in ecology. The nature of the growth-length-mortality tradeoffs identified here, however, with large-growing animals “paying” for low adult mortality by suffering

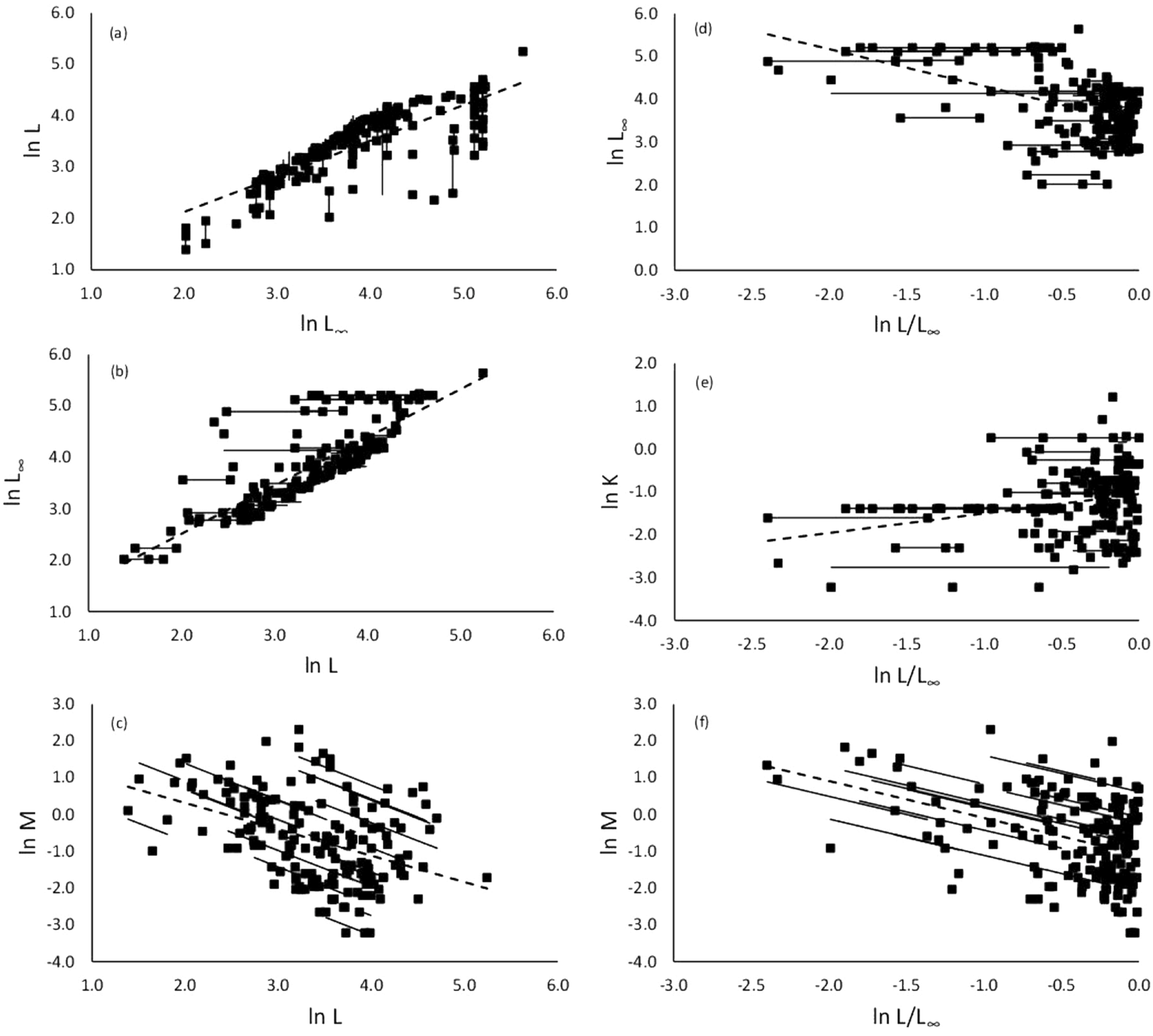

Fig. 5. Population and ensemble-level patterns in the Gislason et al. (2010) data: (a) Body length lnL vs. asymptotic length $\ln L_\infty$; (b) asymptotic length $\ln L_\infty$ vs. length lnL; (c) natural mortality lnM vs. lnL; (d) $\ln L_\infty$ vs. $\ln(L/L_\infty)$; (e) lnK vs. $\ln(L/L_\infty)$; and (f) lnM vs. $\ln(L/L_\infty)$. Solid lines indicate population-level relationships, while dashed lines indicate ensemble-level relationships estimated without accounting for population effects. Short lines denoting populations represented by samples from a very narrow length range have been omitted for clarity.

higher mortality-at-length warrants further analysis from an ecological and evolutionary perspective.

4.2. Modeling size-dependent natural mortality in stock assessment applications

The aim of modeling size-dependent mortality in stock assessments is to account for changes in mortality with size and age of fish within the assessed stock (population). Therefore, in the absence of any stock-specific information on scaling, such models should use the best general estimate of mortality-length scaling, derived from the joint slope mixed-effects models accounting for population effects: − 1. Substantially different scaling exponents such as the theoretical metabolic scaling of − 0.75 (Peterson and Wroblewski, 1984) or the 'Charnov M' scaling of − 1.5 (Charnov et al., 2013) are not representative of the scaling M within fish populations (even though they may describe mortality-size relationships at the assemblage or ecosystem scales under certain conditions, see below). While many general ecological implications of size-dependence in natural mortality rates hold regardless of the precise scaling (Andersen, 2019, 2020), the purpose of modeling such relationships in stock assessment applications is to derive quantitative estimates of stock status and evaluate the effects of alternative management measures and therefore, the quantitative characterization of the scaling relationship matters. Use of scaling exponents substantially different from best estimate of − 1 are likely to lead to systematic biases in assessments.

We explored empirical relationships for predicting the intercepts (M_1 and $M_{L\infty}$) of the mortality-length relationship from growth parameters (L_∞, K). The empirical predictors explored here are structurally similar to established predictors for constant adult M, such as the Then et al. (2015) estimator, but perform less well in terms of their prediction error (RMSE=0.78 for models 4, 6, and 7, Table 3, vs. RMSE=0.6 for the Then growth-based estimator). This is likely to reflect the variability found in the large, combined data set (see materials and methods). We also tested the utility of predicting the intercepts of the mortality-length relationship from the $M_{\text{Then-g}}$ prdictor for (constant) adult M (Then et al., 2015). We found that on average, empirical predictions of constant M were equal to size-dependent M values around the center of the adult size range. This supports the established practice of scaling the 'Lorenzen M' so that its average over the adult size or age groups equals empirical estimates of constant M (SEDAR (Southeast Data, Assessment and Reviews), 2018).

4.3. Deviations from within-population scaling at the ensemble or ecosystem level

Scaling exponents substantially different from the best within-population estimate of − 1 have been derived from the application of single and multiple linear regression models to ensembles of data of multiple populations without accounting for population effects (Gislason et al., 2010; Charnov et al., 2013). These ensemble-level estimates are sensitive to the assembly of populations and length samples in the combined data set. In general, ensemble-level scaling estimates do not represent within-population scaling of mortality correctly and should not be used for this purpose in stock assessments. Nonetheless, to the extent that an ensemble of mortality-size data from multiple populations is reflective of the structure of actual ecosystems, relationships estimated from such data may apply at the ecosystem level (but not within the component populations).

CRediT authorship contribution statement

Kai Lorenzen: Conceptualization, Methodology, Data curation, Writing – original draft preparation. **Edward Camp:** Writing – review & editing. **Taryn Garlock:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106327.

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