

Size, growth, temperature and the natural mortality of marine fish

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Abstract

The natural mortality of exploited fish populations is often assumed to be a species-specific constant independent of body size. This assumption has important implications for size-based fish population models and for predicting the outcome of size-dependent fisheries management measures such as mesh-size regulations. To test the assumption, we critically review the empirical estimates of the natural mortality, M (year⁻¹), of marine and brackish water fish stocks and model them as a function of von Bertalanffy growth parameters, L_{∞} (cm) and K (year⁻¹), temperature (Kelvin) and length, L (cm). Using the Arrhenius equation to describe the relationship between M and temperature, we find M to be significantly related to length, L_{∞} and K , but not to temperature ($R^2 = 0.62$, $P < 0.0001$, $n = 168$). Temperature and K are significantly correlated and when K is removed from the model the temperature term becomes significant, but the resulting model explains less of the total variance ($R^2 = 0.42$, $P < 0.0001$, $n = 168$). The relationships between M , L , L_{∞} , K and temperature are shown to be in general accordance with previous theoretical and empirical investigations. We conclude that natural mortality is significantly related to length and growth characteristics and recommend to use the empirical formula: $\ln(M) = 0.55 - 1.61\ln(L) + 1.44\ln(L_{\infty}) + \ln(K)$, for estimating the natural mortality of marine and brackish water fish.

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Introduction

Natural mortality (M) is one of the essential life-history parameters in the Beverton and Holt (1957) theory of fishing. Without an estimate of M , fishing mortality cannot be estimated from the age or size composition of commercial or research-survey catches, and the yield expected at any future level of fishing cannot be predicted. However, it is often difficult to estimate the M of exploited fish populations (Vetter 1988; Quinn and Deriso 1999). Where an empirical estimate is required, the necessary data are time-consuming and costly to collect and their proper use depends on a number of assumptions that are difficult or impossible to validate. If no information about the age composition of the stock has been collected prior to or during the initial stages of exploitation, M may be estimated from tagging data (e.g. Hampton 2000; Pollock *et al.* 2004), extrapolated from regressions of total mortality vs. total fishing effort (e.g. Jones and Shanks 1990), derived from diet information using models to estimate the part of the total natural mortality caused by predation (e.g. Sparholt 1990), or estimated in statistical stock-assessment models that are simple enough to provide a sufficient number of degrees of freedom to estimate M (e.g. Wang 1999; Wang and Liu 2006). Generally, the less costly methods such as regressions and statistical assessment models make the most tenuous assumptions.

Given the need for estimates of M and the difficulties and costs involved in obtaining these estimates empirically, it is not surprising that fisheries scientists have been inclined to use published relationships between M and life-history parameters to infer its value. Publications providing such empirical relationships, e.g. Beverton and Holt (1959), Pauly (1980) and Gunderson and Dygert (1988), are frequently cited in the fisheries scientific and technical literature. Owing to a scarcity of age- or size-specific estimates of M , the empirical relationships typically assume that M is a species- or stock-specific constant, such that the estimate can be applied to all exploited ages and sizes of the species or stock in question. This assumption has large implications for size-based population models and for predicting the consequences of size-dependent management measures such as mesh-size regulations. In contrast to this practice, some analyses of empirically derived estimates (McGurk 1986, 1987; Lorenzen 1996; Brown *et al.* 2004),

general size-spectrum theory (Peterson and Wroblewski 1984; Andersen and Beyer 2006), multispecies models (Pope *et al.* 2006) and recent developments in the theory to explain the coexistence of species in marine fish communities (Gislason *et al.* 2008) suggest that M should scale with individual body size. McGurk (1987) found M for fish to scale with body weight raised to a power of -0.37 , Lorenzen (1996) found M of juvenile and adult fish to scale with body weight raised to an exponent of -0.29 , Brown *et al.* (2004), analysing the data set of Pauly (1980), found an exponent of -0.24 , while McCoy and Gillooly (2008) found an exponent of -0.27 . Peterson and Wroblewski (1984) used a theoretical size-spectrum model to predict an exponent of -0.25 , Andersen and Beyer (2006) showed analytically that M should scale with body weight raised to an exponent by constructing an elaborate theoretical size-spectrum model accounting for predation and food-dependent growth, while Gislason *et al.* (2008) used a fish community model to show that M would scale with length and asymptotic length. There is clearly a need to reconcile the apparent difference between the findings of the empirical and modelling studies summarized above, and the commonly used sources for estimates of a species- or stock-specific constant M . Fortunately, a number of recent studies contain size- or age-specific estimates of M (e.g. Hampton 2000; Tanasichuk 2000) providing a possibility for improving our understanding of the parameters important for predicting M .

To test the evidence for generally applicable scaling factors, and to improve the general understanding of natural mortality in marine fish communities, we set out to build up a comprehensive data set based on published empirical estimates of M as well as associated information on growth parameters, temperature and length. To this end, we performed an extensive literature search and scrutinized the validity of the M estimates provided in terms of their empirical derivation.

Materials and methods

A list of original publications on M for marine and brackish water fish species and populations was derived from reviews and literature searches. These publications were critically reviewed and estimates of M provided were accepted or rejected according to the following criteria.

1. Estimates were rejected if they had been derived from previously published empirical relationships (e.g. Beverton and Holt 1959; Pauly 1980; Gunderson and Dygert 1988), or 'borrowed' from studies of species considered to be similar.
2. Estimates by size or age were rejected if they had been derived from multispecies modelling (for instance, estimates from Multispecies VPA (e.g. Sparholt 1990) were excluded, even though they had derived from a large body of stomach content data).
3. Estimates were rejected if they were based on an insufficient amount of data, if the authors themselves expressed concern that they could be biased and therefore not be considered trustworthy, or if the sampling gears and/or procedures for working up the samples were likely to have biased the estimates considerably.
4. Estimates of total mortality based on catch-at-length or catch-at-age data were accepted as estimates of M only if the data had been collected from an unexploited or lightly exploited stock over a sufficiently long time period to make it credible that they reflected mortality and not simply differences in year-class strength, and if growth parameters or ageing methods were considered appropriate.
5. Estimates derived from tagging data were included only if due consideration had been given to mortality associated with the tagging operation, tag loss, differences in mortality experienced by tagged and untagged fish, migration out of the study area and uncertainty regarding tag recovery.
6. Estimates derived from regressions of total mortality vs. effort were included only if it was credible that total fishing mortality would be proportional to the measure of fishing effort considered, and if the extrapolation did not result in excessively large confidence limits.

Applying these criteria resulted in only a modest fraction of the total number of published M estimates to be acceptable for further analysis. We screened 367 publications containing estimates for marine and brackish water fish and accepted 168 more or less independent estimates provided in 70 publications as being empirically derived and valid (see Supporting Information).

For each species or stock, the estimates of M were combined with relevant estimates of von Bertalanffy growth parameters, body lengths and the average

annual sea temperatures for the areas from where the individuals had been sampled.

Estimates of growth parameters were only accepted as valid if they had been based on appropriate methods of identifying cohorts or determining age, if their confidence limits were not excessively wide and if they were considered representative of the population for which M had been estimated. Preference was given to growth parameters provided in the same publication as providing the estimates of M , but for 30% of the estimates growth parameters were lacking or could not be readily derived. In these cases, growth parameters representative of the same stock, sex and area were taken from other sources, if possible based on data collected during the same period for which M had been estimated. However, in a few cases it was necessary to utilize growth parameters available for a period that did not closely match the M estimate.

Body length was calculated as the midpoint of the length range of fish included in the samples used for estimating mortality. If only the age range of the fish was provided, the maximum and minimum length of the range were calculated from the von Bertalanffy growth parameters L_{∞} , K and t_0 . Unfortunately, the estimate of t_0 required to translate age to size was not always available. In these cases, we assumed that t_0 was equal to zero. If the original publications differentiated between M estimates by sexes or by length or age interval, these estimates were maintained with the associated body lengths. Obviously, such estimates are not totally independent, but given the aim of investigating the significance of the effect of body length (irrespective of asymptotic length), maintaining estimates by size class was important.

Temperature data were as far as possible taken from the original publications, but sometimes oceanographic summaries of the associated region had to be consulted. The effect of temperature on resting metabolism is generally well represented by the Arrhenius relationship, $\exp(-e/T)$, where e is a constant and T is absolute temperature (Clarke and Johnston 1999; Gillooly *et al.* 2001). Assuming that temperature affects the food intake of predators and hence predation mortality in a similar way, this relationship was used in the model.

Based on our work on size and life-history dynamics of fish communities (Gislason *et al.* 2008), our hypothesis is that M would scale with body length, L , with the von Bertalanffy growth parameters L_{∞} and K , and show an exponential relationship to the

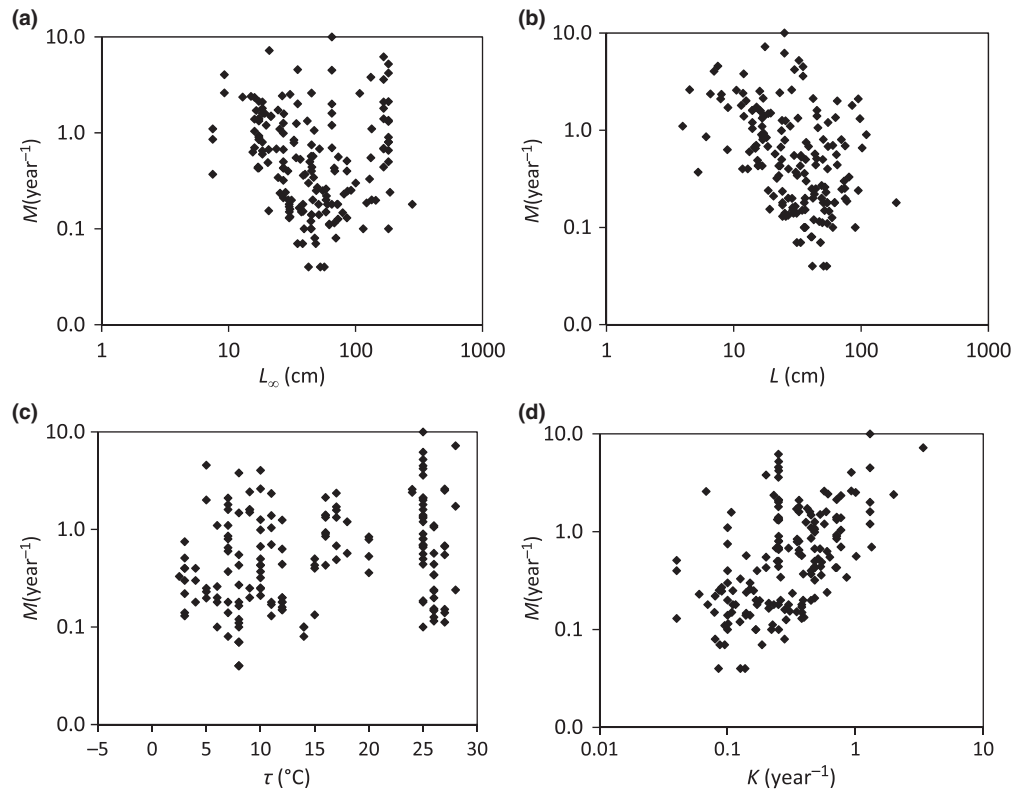


Figure 1 Estimates of natural mortality (M , year⁻¹), vs.: (a) asymptotic length (L_{∞} , cm); (b) length (L , cm); (c) temperature (τ , °C); (d) von Bertalanffy growth parameter (K , year⁻¹).

inverse of temperature. To test this hypothesis the following model was fitted to the data:

$$\ln(M) = a + b \ln L + c \ln L_{\infty} + d \ln K - \frac{e}{T} \quad (1)$$

where M is an annual instantaneous rate (year⁻¹), L_{∞} is the asymptotic length attainable (cm), K is the annual rate (year⁻¹) at which the rate of growth in length declines as length approaches L_{∞} , L is the body length (cm) of the fish for which the M estimate would apply, T is absolute temperature (Kelvin) and a to e are constants.

Results

Plots of M vs. L , L_{∞} , K and temperature (°C) are shown in Fig. 1a–d. M is seen to increase with K and to decline with L , while a possible relationship with L_{∞} and temperature is less apparent. A closer look at the figure reveals additional patterns. In the plot of M vs. L_{∞} , Fig. 1a, there is a collection of high M values around an L_{∞} of 170 cm generated by three species of tuna (*Katsuwonus pelamis*, *Thunnus albacares* and *T. obesus*). Most of these M values had

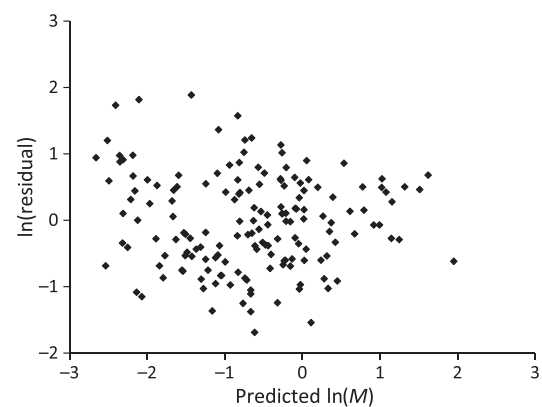


Figure 2 Log residuals vs. the predicted value of $\ln(M)$ from model 1 (see Table 1).

been derived from tagging data for individuals smaller than 50 cm. The vertical lines of points in Fig. 1c are generated by estimates of M obtained at identical temperatures and those in Fig. 1a and d by species for which separate estimates were available for different length groups.

Table 1 Results of fitting different models of natural mortality (M , year⁻¹) to von Bertalanffy growth parameters (L_{∞} , cm; K , year⁻¹), temperature (T , K) and length (L , cm). All data were log-transformed before analysis and non-significant parameters (NS) were removed.

	Model 1	Model 2	Model 3
Parameter	$\ln M = a + b \ln L + c \ln L_{\infty} + d \ln K - e/T$	$\ln(M) = a + b \ln L + c \ln L_{\infty} + \ln K - e/T$	$\ln M = a + b \ln L + c \ln L_{\infty} - e/T$
a	0.61 (0.04, 1.18)	0.55 (-0.02, 1.12)	15.11 (9.99, 20.23)
b	-1.61 (-1.88, -1.34)	-1.61 (-1.88, -1.34)	-1.59 (-1.92, -1.26)
c	1.39 (1.15, 1.64)	1.44 (1.21, 1.67)	0.82 (0.53, 1.11)
d	0.91 (0.75, 1.07)		
e	NS	NS	3891 (2473, 5309)

Values in parentheses are lower and upper 95% confidence intervals ($n = 168$).

Fitting the model given by Equation (1) to the data explained more than half of the variance and the model was highly significant ($R^2 = 0.62$, $P < 0.0001$, $n = 168$, RMSE = 0.73). However, the effect of ambient temperature and the intercept were not significantly different from zero. Removing temperature from the model did not change the overall fit ($R^2 = 0.62$, $P < 0.0001$, $n = 168$, RMSE = 0.72) and only changed the remaining parameters slightly. We found M to scale with L_{∞} raised to a power of 1.39, with L raised to -1.61, and with K raised to 0.91 (Table 1, model 1). The residuals showed no signs of heteroscedacity (Fig. 2). Notwithstanding a significant correlation between the independent variables, inspection of tolerance statistics and condition indices showed the impact of collinearity to be either small or negligible. The estimate of d , the scaling parameter of M with K , was not significantly different from 1.0 and restricting d to 1.0 did not reduce the fit to the data ($R^2 = 0.62$, $P < 0.0001$, $n = 168$, RMSE = 0.73). The temperature term was still insignificant, and the other parameters changed only slightly. M now scaled to L_{∞} raised to 1.44 and to L raised to -1.61 (Table 1, model 2). To study the impact of the high M values around an L_{∞} of 170 cm in Fig. 1a we tentatively removed species with an L_{∞} larger than 150 cm from the regression. This changed the scaling of M with L_{∞} to 1.34 and the scaling with body length to -1.59, but the model was still highly significant ($R^2 = 0.61$, $P < 0.0001$, $n = 147$).

The von Bertalanffy parameter K depends on the activity and metabolism of the fish and may be influenced by temperature. In the data set, $1/T$ is significantly and negatively correlated with $\ln K$

($r = -0.48$; $P < 0.001$; $n = 114$). The correlation between temperature and K may explain the lack of a significant effect of temperature on M in the full model. To investigate this further we removed the $\ln K$ term from the model (Table 1, model 3). This reduced the variance explained ($R^2 = 0.42$, $P < 0.0001$, $n = 168$, RMSE = 0.90), but the fit was still highly significant and so were all remaining parameters, including the temperature term. M scaled to L_{∞} raised to 0.82 and to body length raised to -1.59. The intercept was significantly different from zero and the estimated temperature constant (e) was 3.9×10^3 K.

Discussion

Our results show that M is significantly related to body length raised to an exponent of around -1.6, an estimate that is remarkably robust to alternative model formulations. M is also significantly related to asymptotic length and to K . The significance of a temperature effect depends on whether K is included in the model or not. If K is included, temperature is not significant whereas if K is removed, temperature becomes significant and the exponent of L_{∞} decreases. Both formulations capture one of the likely underlying causes: changes in physiological growth processes as influenced by temperature. However, the fit improves considerably when K is included, and for this reason we recommend to use the formula:

$$\ln(M) = 0.55 - 1.61 \ln L + 1.44 \ln L_{\infty} + \ln K \quad (2)$$

for estimating M .

The significant positive relationship between M and L_{∞} is somewhat surprising, but may be caused

by a trade-off between growth and mortality. Gislason *et al.* (2008) found K to be proportional to L_{∞} raised to a power around -0.6 for demersal species of teleosts. At a given length a large species will therefore grow faster than a small species. For the larger species securing sufficient food to maintain a fast growth rate may entail exposure to a higher M (Fraser and Gillian 1992; Sogard 1997; Biro *et al.* 2004, 2006). In addition, many small demersal species seem to be partly protected against predation by hiding, cryptic behaviour, being flat or by possessing spines. In their analyses of empirical estimates of natural mortality of fish, Griffiths and Harrod (2007) found species that were cryptic, hid in burrows, or had morphological defences against predators to have the lowest rates of natural mortality. Hence, at a given length individuals belonging to species with a high L_{∞} may generally be exposed to a higher M than individuals belonging to species with a low L_{∞} .

When reviewing the existing literature, our selection criteria resulted in the exclusion of the majority of the published M estimates. Each criterion serves as a reasonable scientific standard for application in selecting valid information for analysis. Therefore, the large number of exclusions indicates that there is far less valid empirical information on M than might be inferred from earlier reviews. Consequently, before relationships such as provided by Pauly (1980) are used for

estimating M for specific populations, their validity should be re-evaluated using only data sources screened rigorously using criteria such as applied here.

The effect of applying rigorous quality criteria to the data set used for parameterization of the relationship of M to size and temperature can be observed by comparing our predictions of M to those from the model of Pauly (1980). Despite differences in model structure (different expressions to account for temperature effects; including or excluding the 'cold-adaptation' hypothesis; including length among the independent variables), the two models can be asked to predict M for similar lengths of fish and temperature regimes. Fig. 3 compares the predicted M s for various values of K from Equation (2) (model 2 in Table 1) with predicted M s from Pauly's model for three values of L_{∞} . We assumed as an approximation that the size-independent M estimates used by Pauly were derived from observations on fish with an average length corresponding to 65% of their L_{∞} and used this estimate of body length in our model, while in Pauly's model we used a temperature of 16 °C corresponding to the average ambient temperature of brackish and marine fish in his data set. The two sets of predicted values are not very different, although for all three values of L_{∞} our model predicts natural mortality to increase more strongly with K than does Pauly's model. We cannot establish whether this apparent difference is due to our more rigorous selection of parameterization data, or because the relationship between temperature and M is modelled differently by Pauly (1980). Nonetheless, both models assume a relationship between mortality and growth rate, whereas our model does not invoke any of the hypotheses suggested by Pauly (1980) to explain an additional direct or indirect relationship between mortality and temperature than expressed through K .

Several other studies of the relationship of natural mortality to size and/or growth rate have been published. However, to compare our results to many of these requires adjustments because (i) our analysis is length-based whereas earlier ones were weight-based and (ii) we incorporated asymptotic length as a factor, whereas earlier models rarely considered asymptotic weight.

Beverton and Holt (1959) and others observed a directly proportional relationship between M and K , and Andersen *et al.* (2009) derived this relationship theoretically for M at the size at first maturity. If we

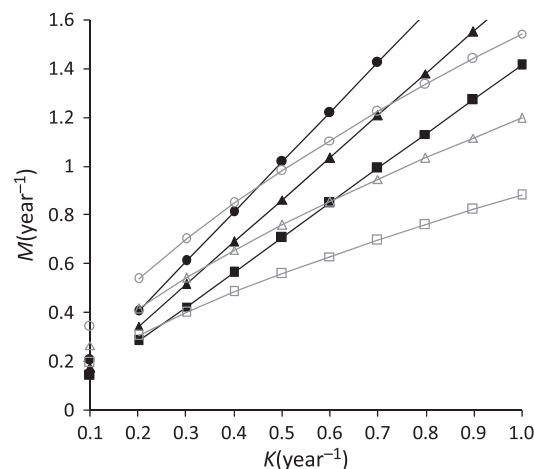


Figure 3 Natural mortality (M , year⁻¹), predicted by model 2 (see Table 1) (filled symbols, black) and by the model of Pauly (1980) (open symbols, grey) for different values of L_{∞} (circles: 20 cm; triangles: 50 cm; squares: 150 cm) and K , an ambient temperature of 16 °C, and for fish of a length, L , corresponding to 65% of their L_{∞} .

assume that the size-independent M estimates used by Beverton and Holt (1959) were derived from observations on fish whose average length to a first approximation can be considered to be a constant fraction, μ , of their asymptotic length then replacing L by μL_∞ in Equation (2) we obtain:

$$M \propto L^{-1.61} L_\infty^{1.44} K \propto (\mu L_\infty)^{-1.61} L_\infty^{1.44} K \propto L_\infty^{-0.17} K \quad (3)$$

Beverton (1992) and Charnov (1993) found M/K to be reasonably constant across species with values in the range from approximately 0.5 to 2.1. Using Equation (2) we obtain ratios between 0.9 and 2.9 for combinations of μ -values between 0.50 and 0.90 and L_∞ -values between 30 and 250 cm. Empirical studies of the relationship between M and body weight report a scaling exponent between -0.24 and -0.37 (McGurk 1986, 1987; Lorenzen 1996; Brown *et al.* 2004; McCoy and Gillooly 2008). If we assume body weight to be proportional to length cubed in the model without the $\ln K$ term (model 3, Table 1), thus scaling M with average body weight, our results produce a similar scaling:

$$M \propto L^{-1.59} L_\infty^{0.82} \propto L^{-1.59} \left(\frac{L}{\mu}\right)^{0.82} \propto L^{-0.77} \propto W^{-0.26} \quad (4)$$

The scaling parameters in model 3 are furthermore very similar to those estimated from a theoretical life-history model of the North Sea demersal fish community, which found M to scale with length (-1.66) and asymptotic length (0.80), and to estimates derived from Multispecies VPA (Gislason *et al.* 2008).

Considering temperature, the constant in model 3 ($e = 3.9 \times 10^3$ K; 95% CL: $2.5\text{--}5.3 \times 10^3$ K) is somewhat lower than expected from previous investigations. Brown *et al.* (2004), fitting the Arrhenius equation to the data from Pauly (1980), estimated an activation energy corresponding to a temperature constant $e = 5.2 \times 10^3$ K (95% CL: $4.3\text{--}6.3 \times 10^3$ K), while McCoy and Gillooly (2008) using a slightly expanded data set including fish and aquatic invertebrates found $e = 6.6 \times 10^3$ K (95% CL: $5.9\text{--}7.3 \times 10^3$ K). However, Pauly (1980) adjusted the temperatures for Arctic and Antarctic fish species to account for cold adaptation of their metabolism, while more recent investigations have not found convincing evidence for such cold adaptation (Clarke and Johnston 1999; Steffensen 2002). McCoy and Gillooly (2008) did not re-adjust Pauly's temperature data for Arctic and Antarctic species prior to their

analysis (e.g. using 16°C for the Antarctic *Notothenia neglecta*, while the samples had been collected in an area with an average annual sea temperature of approximately -1°C ; Everson 1970). It is therefore likely that the temperature constant is overestimated by McCoy and Gillooly (2008). Clarke and Johnston (1999) and Gillooly *et al.* (2001) both used the Arrhenius equation to describe the relationship between the resting metabolism of fish and temperature and independently obtained an estimate of $e = 5.02 \times 10^3$ K. This estimate is higher than our estimate, but not significantly so. Based on a simple dynamic size-based fish community model, Pope *et al.* (2009) found that M should be less sensitive to a change in temperature than the rates of metabolism and predator food intake.

Despite our emphasis on the value of applying high standards to the selection of data for parameterizing these relationships, the available data, and consequently the analyses, have their limitations. In many cases, the publications failed to report size information even though size data were almost certainly used in the calculations of the reported ages and growth rates, which we had to re-convert to sizes using the growth equation given. In other cases they failed to report whether size had been measured as fork, standard or total length. Sometimes we had to assume that a single estimate of M was representative over a fairly large size interval. Importantly, future studies should report data on average size and size interval together with M estimates. Where information has been provided for adjacent length or age groups, estimates are not independent, but we have been unable to take such correlations into account. Finally, when multiple estimates were available for a species or population or size group, these estimates should have been weighted by some quality measure (such as the number of fish involved in the estimation) to produce a single overall estimate for each category distinguished. However, because the methods used varied widely, and reporting of data that might be used as possible weighting factors was inconsistent, it was not straightforward to take their relative quality into account in our analysis. Although the estimates of natural mortality are likely to be the main source of uncertainty, also the temperature data may not accurately reflect the ambient water temperature at the depths at which the various species and life stages occur. In addition, estimates of L_∞ and K are often correlated owing to a lack of large old fish in the samples available, which allows

to estimate only the product of the two with reasonable precision.

Our model assumptions that M is an allometric function of size but constant with time are oversimplifications, ignoring both the effect of temporal changes in species interactions and effects of senescence. Both multispecies modelling and patterns of change in exploited marine ecosystems (e.g. Daan *et al.* 2005; Frank *et al.* 2005; Benoît and Swain 2008), indicate that M is not constant over time, nor independent of changes in prey and predator abundance, but at present insufficient estimates of M are available to take this into account. Fish generally seem to experience delayed senescence relative to other vertebrates (Reznick *et al.* 2002), but senescence mortality can be observed in captivity (e.g. Gerhard 2007) and has also been found in the wild (e.g. Beverton and Holt 1959; Caputo *et al.* 2002; Beverton *et al.* 2004). However, as for studying temporal changes in M , comparisons of senescence mortality across populations will require much more data on numbers of large and old fish to provide less uncertain estimates of their mortality rates. Modelling M as an allometric function of length and using the model to predict an average M for fish in a given length interval is also problematic because the curvilinear relationship between M and length makes the average M for fish in the interval differ from the M predicted at the midpoint of the interval. Finally, within a length interval young rapidly growing fish may have another M than older slow growing fish. All of these issues deserve further study.

One of our objectives was to increase the general understanding of the role of natural mortality in the structuring of marine fish communities. Our results demonstrate that body length itself significantly affects the natural mortality of juvenile and adult fish: body length is highly significant with or without the $\ln K$ term included, the estimate of the exponent in the scaling of M with body length is remarkably robust to alternative model formulations, and the model including the $\ln K$ term accounts for 62% of the total variance in the available estimates of M . Moreover, our model results are in line with the theoretical predictions of Gislason *et al.* (2008) and many previous investigations.

Nonetheless, the spread of the individual estimates of M is large (Figs 1 and 2) and the RMSE of the model is 0.72, signifying that the 95% confidence interval of a predicted M will range from approximately 25% to 410% of its predicted median

value. Thus, predictions of M for individual species or populations will always be highly uncertain. The role of factors such as variation in predator and prey interactions or ocean conditions, or of additional life-history parameters in accounting for parts of the residual variation in M can be investigated, but they are unlikely to contradict the general dependence of mortality rate on size.

The residual variance in M limits the practical use of our models in analytical assessments of individual fish populations, but that is true of any model intended to make precise predictions of M from life-history attributes. This is not a serious failing, though, for two reasons. First, to the extent that annual stock assessments are carried out primarily to support advice on adjustments to annual harvest levels, such single-year adjustments are not particularly sensitive to values of M . Second, the more important consequence of our findings is that M should not be viewed as a constant for a population, or even just the mature ages of a population. Rather, M varies lawfully with size, and factors that change the size composition of a population will change the expected average M for that population as well. Many of these factors are likely to vary without consistent longer-term trends, and contribute background noise to M for a population. However, factors that are expected to result in a consistent change in the size composition of a population will change the average M for that population as well; if M -at-size is consistent and the size frequency distribution of a population changes, the rate of loss of individuals from the population through natural causes will change correspondingly. Altering the target exploitation rate is one important mechanism that affects the size composition of a population or community. Consequently, applying our models in management strategy evaluations (Sainsbury *et al.* 2000) may provide a way to include the effects of changing size composition on M when evaluating the consequences of alternative management strategies. Whether the change in population M is large or small will depend on how alternative strategies increase, decrease or redistribute F on individuals of different sizes in a population, but our models provide a means to investigate the effect systematically. Moreover, the alternative formulations with and without temperature as an independent variable could be used to explore some aspects of the impact of climate change on the sustainability of harvesting strategies. Thus, in addition to increasing our under-

standing of marine fish communities, we hope to have contributed to the scientific basis for improving fisheries management advice.

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References

- Andersen, K.H. and Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist* **168**, 54–61.
- Andersen, K. H., Farnsworth, K. D., Pedersen, M., Gislason, H. and Beyer, J. E. (2009) How community ecology links natural mortality, growth, and production of fish populations. *ICES Journal of Marine Science* **66**, 1978–1984.
- Benoit, H. and Swain, D.P. (2008) Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2088–2104.
- Beverton, R.J.H. (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* **41**(Suppl. B), 137–160.
- Beverton, R.J.H. and Holt, S.J. (1957) On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food. *Fishery Investigations, London*, **2**, 19–533.
- Beverton, R.J.H. and Holt, S.J. (1959) A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *CIBA Foundation Colloquia on Ageing* **5**, 142–180.
- Beverton, R.J.H., Hylan, A., Østvedt, O.-J., Alvsvaag, J. and Iles, T.C. (2004) Growth, maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring. *ICES Journal of Marine Science* **61**, 165–175.
- Biro, P.A., Abrahams, M.V., Post, J.R. and Parkinson, E.A. (2004) Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London B* **271**, 2233–2237.
- Biro, P.A., Abrahams, M.V., Post, J.R. and Parkinson, E.A. (2006) Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology* **75**, 1165–1171.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.
- Caputo, V., Candi, G., Arneri, E. *et al.* (2002) Short lifespan and apoptosis in *Aphia minuta*. *Journal of Fish Biology* **60**, 775–779.
- Charnov, E.L. (1993) *Life History Invariants*. Oxford University Press, Oxford.
- Clarke, A. and Johnston, N.M. (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* **68**, 893–905.
- Daan, N., Gislason, H., Pope, J.G. and Rice, J.C. (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science* **62**, 177–188.
- Everson, I. (1970) The population dynamics and energy budget of *Notothenia neglecta* Nybellin at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* **23**, 25–50.
- Fraser, D. F. and Gilliam, J. F. (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* **73**, 959–970.
- Frank, K.T., Petrie, B., Choi, J.S. and Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623.
- Gerhard, G.S. (2007) Small laboratory fish as models for ageing research. *Ageing Research Reviews* **6**, 64–72.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.
- Gislason, H., Pope, J.G., Rice, J.C. and Daan, N. (2008) Coexistence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science* **65**, 514–530.
- Griffiths, D. and Harrod, C. (2007) Natural mortality, growth parameters, and environmental temperature in fishes revisited. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 249–255.
- Gunderson, D.R. and Dygert, P.H. (1988) Reproductive effort as a predictor of natural mortality rate. *Journal du Conseil International pour l'Exploration de la Mer* **44**, 200–209.
- Hampton, J. (2000) Natural mortality rates in tropical tunas: size really does matter. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1002–1010.
- Jones, R. and Shanks, A.M. (1990) An estimate of natural mortality for North Sea haddock. *Journal du Conseil International pour l'Exploration de la Mer* **47**, 99–103.
- Lorenzen, K. (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* **49**, 627–647.
- McCoy, M.W. and Gillooly, J.F. (2008) Predicting the natural mortality rates of plants and animals. *Ecology Letters* **11**, 710–716.

- McGurk, M.D. (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Marine Ecology Progress Series* **34**, 227–242.
- McGurk, M.D. (1987) Natural mortality and spatial patchiness: reply to Gulland. *Marine Ecology Progress Series* **39**, 201–206.
- Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* **39**, 175–192.
- Peterson, I. and Wroblewski, J.S. (1984) Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1117–1120.
- Pollock, K.H., Jiang, H.H. and Hightower, J.E. (2004) Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society* **133**, 639–648.
- Pope, J.G., Rice, J.C., Daan, N., Jennings, S. and Gislason, H. (2006) Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. *ICES Journal of Marine Science* **63**, 129–1044.
- Pope, J.G., Falk-Petersen, J., Jennings, S., Rice, J.C., Gislason, H. and Daan, N. (2009) Honey, I cooled the cods: modelling the effect of temperature on the structure of Boreal/Arctic fish ecosystems. *Deep-Sea Research II*, **56**, 2097–2107.
- Quinn, T.J. and Deriso, R.B. (1999) *Quantitative Fish Dynamics*. Oxford University Press, Oxford.
- Reznick, D., Ghalambor, C. and Nunney, L. (2002) The evolution of senescence in fish. *Mechanisms of Ageing and Development* **123**, 773–789.
- Sainsbury, K.J., Punt, A.E. and Smith, A.D.M. (2000) Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* **57**, 731–741.
- Sogard, S. M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science* **60**, 1129–1157.
- Sparholt, H. (1990) Improved estimates of the natural mortality rates of nine commercially important fish species included in the North Sea Multispecies VPA model. *Journal du Conseil International pour l'Exploration de la Mer* **46**, 211–223.
- Steffensen, J.F. (2002) Metabolic cold adaptation of polar fish based on measurements of aerobic oxygen consumption: fact or artefact? Artefact! *Comparative Biochemistry and Physiology Part A* **132**, 789–795.
- Tanasichuk, R. W. (2000) Age-specific natural mortality rates of adult Pacific herring (*Clupea pallasii*) from southern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2258–2272.
- Vetter, E.F. (1988) Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin* **86**, 25–43.
- Wang, Y.-G. (1999) A maximum-likelihood method for estimating natural mortality and catchability coefficient from catch-and-effort data. *Marine and Freshwater Research* **50**, 307–311.
- Wang, Y. and Liu, Q. (2006) Estimation of natural mortality using statistical analysis of fisheries catch-at-age data. *Fisheries Research* **78**, 342–351.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Natural mortality, length, growth parameters and temperature. List of references used for Table S1.

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