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# Does natural mortality depend on individual size?

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Abstract

The natural mortality of exploited fish populations is notoriously difficult to estimate. It is therefore often inferred from Pauly's equation using estimates of growth parameters and ambient temperature. However, contrary to the results derived from multispecies and size-spectra models, Pauly's equation assumes that natural mortality is independent of individual size. This assumption has large implications for size-based fish population models and for the success of size-dependent management measures such as mesh-size regulations. Here we reanalyze the existing empirical estimates of natural mortality using a model where individual size, growth characteristics and ambient temperatures are all accounted for. We find natural mortality to scale significantly with individual body size, asymptotic size, and the von Bertalanffy growth parameter K, and our parameter estimates are not significantly different from those derived from a size-based fish-community model.

Keywords: Natural mortality, growth, temperature, size-based, asymptotic size

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## Introduction

Unfortunately, one may say, natural mortality is one of the essential parameters of the Beverton and Holt (1957) theory of fishing. Without an estimate of natural mortality, it is impossible to estimate fishing mortality from the age or size composition of the catch or from surveys, and without information about its relative value the yield expected at any target level of fishing cannot be computed. Where an independent estimate of natural mortality is required to assess the status of an exploited fish population, the necessary data are time consuming and costly to collect and their proper use often depends on a number of assumptions that will be difficult or impossible to check. If information about the age composition of the stock has not been collected prior to or during the initial stages of exploitation, natural mortality must be estimated from tagging data, extrapolated from regressions of total mortality versus total fishing effort, derived from diet information with models providing estimates of the part of the total natural mortality caused by predation, or estimated in statistical fish stock assessment models where survey and fisheries data are combined to yield a sufficient number of degrees of freedom. Given the importance of natural mortality and the difficulties and costs involved in estimating its value, it is not surprising that fisheries scientists have been inclined to use published relationships between natural mortality and life-history parameters to predict its value. Papers providing relationships between M and life-history parameters, e.g. Beverton and Holt (1959), Pauly (1980), range among the most frequently cited publications in the scientific fisheries literature.

The relationships from which M is predicted usually assume that natural mortality is constant for all exploited ages and sizes of the stock or species in question. However, general size-spectrum theory and multispecies models suggest that natural mortality should scale with body size (Peterson and Wroblewsky 1984, Andersen and Beyer 2006), as do recent developments in the theory to explain the coexistence of species in marine fish communities (Pope *et al*. 2006, Gislason *et al*. 2008). Assuming that coexisting fish species must on average be able to replace themselves, Gislason *et al*. (2008) used a theoretical fish-community model to predict that the natural mortality of North Sea fish species should scale with body length raised to a power of -1.66 at current levels of exploitation. Additionally, the natural mortality of the demersal species should scale with asymptotic length raised to a power of 0.80, thus generating a higher natural mortality at a given length for large species than for small ones. The predicted natural mortalities were in agreement with estimates of M from multi-species virtual population analysis (MSVPA) for different species and produced a scaling of the maximum number of recruits per unit of spawning-stock biomass with maximum body length in accordance with independent observations.

We use published estimates of natural mortality, growth parameters and body size to further test the evidence for a general scaling of natural mortality with body size. We do so by expanding the popular model of Pauly (1980) with a body-size term. Because many of the existing estimates of natural mortality used by Pauly (1980) have since been improved and new estimates have become available, we found it necessary to search the literature for additional estimates. We soon discovered that it was also necessary to perform a critical and thorough scrutiny of the validity of the estimates provided in the original literature and elsewhere.

## Materials and methods

Size, growth and mortality data for marine and brackish water species of fish were taken from the literature using published reviews and searches of available databases to generate a list of original publications. These publications were then critically reviewed and estimates of natural mortality (M) accepted or rejected according to the following criteria:

1. Estimates of M were not considered informative if they were not based on actual observations, but derived from previously published relationships between life-history parameters and natural mortality (e.g. Beverton and Holt 1959, Pauly 1980, Gunderson and Dygert 1988). Such estimates were therefore excluded.
2. Estimates of (partial) M by size or age based on multispecies modeling rather than directly on observations were not accepted. Therefore, the estimates based on for instance MSVPA were excluded, even though they have been derived from a large body of stomach content data.
3. Estimates were rejected if they were based on an insufficient amount of data or if the sampling gears and/or procedures for working up the samples were likely to have biased the estimates considerably.
4. Estimates were rejected if the authors of the original publications expressed concern that they could be biased and therefore not trustworthy.
5. Estimates of total mortality based on catch-at-length data were included as estimates of M 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 were considered appropriate.
6. Estimates of total mortality based on catch-at-age data were included as estimates of M 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 the ageing methods used were currently still considered appropriate.
7. Estimates of M 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 area, and uncertainty regarding tag recovery.
8. Estimates of M derived from regressions of total mortality versus effort were only included 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 estimates of natural mortality to be acceptable for our analysis.  We screened more than 300 publications and found 163 original and valid estimates of M for marine and brackish water fish (Table 1) in the 67 publications listed in appendix 1.

These estimates were combined with estimates of von Bertalanffy growth parameters, average body lengths, and the average annual ambient sea temperature for the area from where the individuals had been sampled. Relevant growth parameter estimates from Pauly (1980) or FishBase were used in cases where growth parameters were not provided or could not be readily derived from the data presented in the original publications. Average total length was calculated as midpoints of the length range of fish included in the samples used for estimating mortality. In the cases where only the age range of the fish was provided the average of the maximum and minimum length calculated from the relevant growth parameters was used. If the original publications differentiated between natural mortality estimates by sexes or by length or age interval, these estimates were maintained with the associated mean lengths. Obviously, such estimates are not totally independent, but given the aim of investigating the significance of the effects of size (irrespective of maximum size), maintaining these different estimates was important.

Temperature data were as far as possible taken from Pauly (1980) or from the original publications, but sometimes FishBase or oceanographic summaries of the associated region had to be consulted. Because no evidence appears to exist for the existence of cold adaptation in fish metabolism (Clarke and Johnston 1999), the temperatures for boreal and polar species given in brackets in Pauly (1980), which had been corrected for such an assumed adaptation, were converted back to actual temperatures in the environment. The effect of temperature on metabolism seems generally to be well represented by the Arrhenius relationship (Gillooly *et al.* 2001), and this relationship was therefore used in the model.

Our hypothesis is that M would scale with size and the von Bertalanffy growth parameters $L_\infty$ and *K*, show an exponential relationship to the inverse of temperature. To test this hypothesis the following model was fitted to the data:

$$\ln M = a + b \ln L_\infty + c \ln \bar{L} + d \ln K - e/T$$

where $M$ is an annual instantaneous rate ($y^{-1}$), $L_\infty$ is the asymptotic length attainable (cm), $K$ is the rate at which the rate of growth in length declines as length approaches $L_\infty$ ($y^{-1}$), $\bar{L}$ (cm) is the average length of the fish for which the M estimate would apply, *T* is absolute temperature ($^{o}$Kelvin), and *a* to *e* are constants. To compare the outcome of the scaling relationships obtained with the theoretical one derived by Gislason *et al*. (2008), we also fitted a version of the model without the ln *K* term.

## Results

Plots of M versus $L_\infty$, *K,* temperature ($^{o}$C) and $\bar{L}$ are shown in Figure 1a to 1d. M is seen to increase with *K* and to decline with $\bar{L}$, while a possible relationship with $L_\infty$ and 1/*T* seems less apparent.

Fitting the full model explained around 63% of the variance in the data and the model was highly significant (Table 2). M scaled to $L_\infty$ raised to a power of 1.51 (95% confidence interval: [1.23, 1.79]), and to body length raised to -1.70 [-1.98, -1.42]. The effect of ambient temperature was insignificant and the intercept was not significantly different from zero. Removing temperature from the model (Table 3) hardly reduced the overall fit, but made the intercept significant and changed the others parameters slightly. To compare the parameter estimates to the theoretically derived parameters from the North Sea, we also made a run where 1/*T* replaced the ln(*K*) term, Table 4. The run explained around 45% of the total variance and all parameters, including the temperature term, were highly significant. The intercept was highly significant and M scaled to $L_\infty$ raised to a power of 0.93 (95% confidence interval: [0.61, 1.23], and to body length raised to -1.68 [-2.02, -1.34]. Restricting the analysis to demersal species only provided a scaling of M to $L_\infty$

raised to a power of 0.55 [0.13, 0.97], and to body length raised to -1.72 [-2.15, -1.29].

## Discussion

It came as a surprise to find that applying our selection criteria meant that most of the available estimates of M examined in the existing literature had to be excluded from the analysis. One may agree or disagree with our criteria, but it was quite disturbing to discover how little valid information we could find, and how much of what we considered to be invalid or highly uncertain information had been incorporated in previously published relationships between M and life-history parameters. We call attention to the need to use the original literature on M for investigating such relationships and would like to warn against relying on second-hand sources and estimates from databases without clearly stated quality criteria and quality-assurance procedures.

Our data and analyses have scope for further improvement. We used the information in the original literature to estimate the average size of the individuals for which M had been estimated. In many cases this involved converting age to size using the von Bertalanffy growth equation. Unfortunately, we were sometimes unable to find the estimate of $t_0$ in the available literature required to translate age to size. We have also been unable to take the correlation between estimates of M for adjacent length or age groups into account, so some of the data are not wholly independent. Finally, it was not obvious to us how the estimates of M could be weighted by some quality measure (such as the number of fish involved in the estimation), when very different methods had been used to estimate mortality and when it was not straightforward to calibrate the relative quality of the different methods used. We believe, however, that such considerations are unlikely to affect our overall conclusions substantially.

Some publications suggest that M increased above a certain size or age, suggesting that senescence mortality may be operating at least in unexploited populations. Senescence mortality can be observed in captivity, but has been neglected in most field studies, just as the higher M often found among the smaller sizes within an exploited population has been neglected. The amount of valid information available for M in old fish in the wild does, however, not yet appear sufficient for general comparisons of senescence mortality across populations. The number of large and old fish collected is often low, and their estimated mortality is therefore uncertain. Furthermore, a generally accepted theory of the ecological and evolutionary significance of senescence in fish is lacking.

Our results show that M is significantly related to body size raised to an exponent of around -1.7 and to asymptotic length raised to a power between 0.9 and 1.5. In addition, M scales with *K* raised to a power between 0.9 and 1.0. Removing ln*K* from the equation, but retaining temperature, reduces the fit of the model, but provides estimates that are comparable to the theoretically derived scaling of M with asymptotic length and individual body length estimated by a fish community model (Gislason *et al*. 2008). The estimates of the scaling of natural mortality with length (-1.68 vs. -1.66) and asymptotic length (0.93 vs. 0.8) are almost identical, and when demersal species are analyzed separately, not significantly different. This analysis thus provides an independent confirmation of the model results and confirms a relationship between natural mortality and growth. Our results furthermore show that the model of Pauly (1980) should be improved by taking the actual size of the fish into account. Unfortunately, obtaining the information to derive these results has revealed that much of the data used in previous models does not live up to what we consider to be reasonable minimum quality criteria. We hope to be able to collate additional valid data to test our model further and welcome researchers to forward references to additional relevant information in the fisheries literature.

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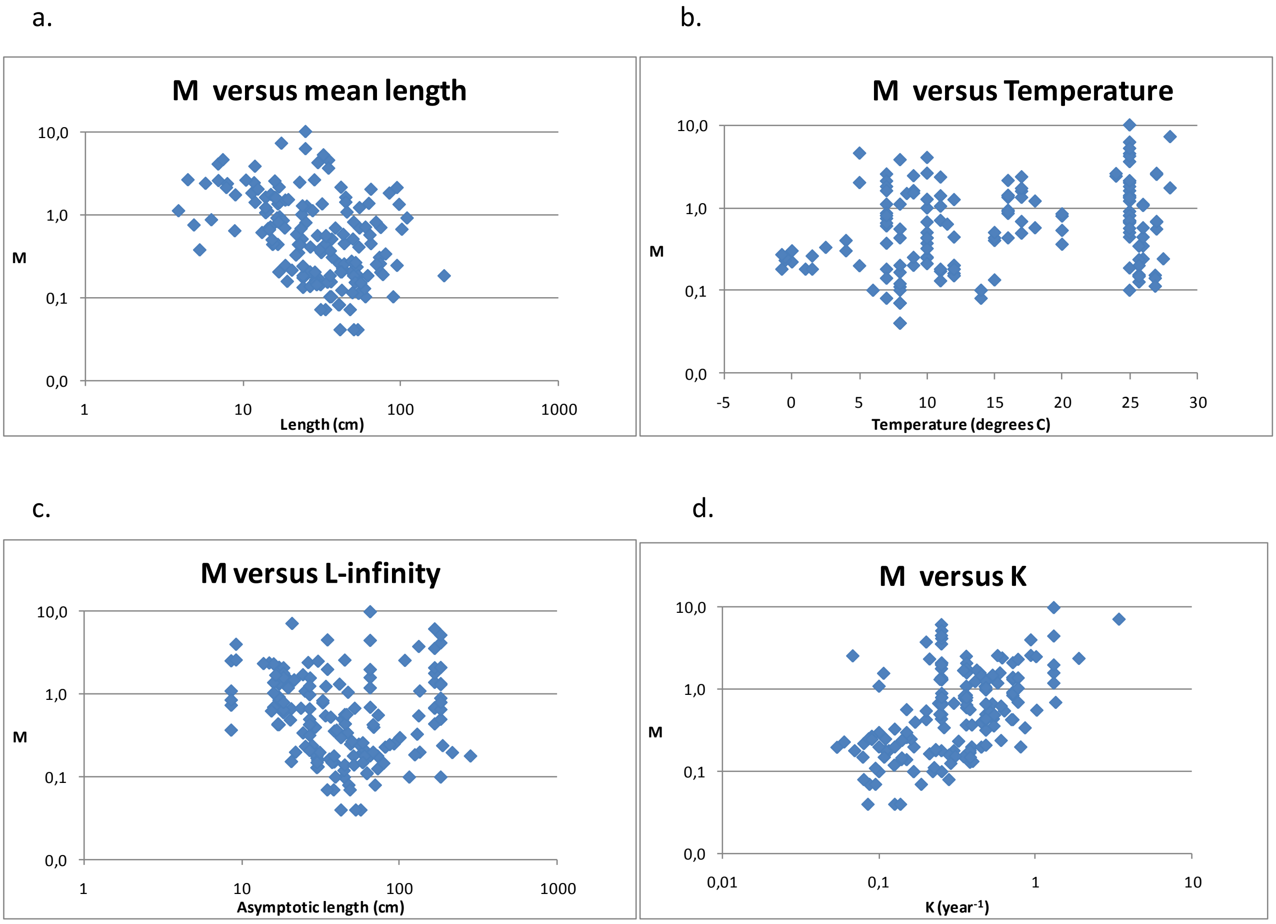


Figure 1. Natural mortality versus a) mean length, $\bar{L}$; b) temperature; c) asymptotic length, $L_\infty$; and d) *K*

Table 1. Species, habitat, natural mortality, sex, average annual ambient temperature, average length of fish for which natural mortality was estimated, von Bertalanffy growth parameters, and reference for natural mortality estimate.

| Species | Habitat | $M$ | Sex | $T$ (ºC) | $\bar{L}$ | $L_\infty$ | $K$ | Reference |
|---|---|---|---|---|---|---|---|---|
| Ammodytes marinus | Demersal | 2,10 | C | 7,0 | 7,9 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes marinus | Demersal | 1,80 | C | 7,0 | 11,5 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes marinus | Demersal | 0,60 | C | 7,0 | 13,3 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes marinus | Demersal | 0,65 | C | 7,0 | 14,8 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes marinus | Demersal | 1,60 | C | 7,0 | 15,9 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes marinus | Demersal | 0,80 | C | 7,0 | 16,9 | 18,5 | 0,36 | Cook(2004) |
| Ammodytes tobianus | Demersal | 2,34 | C | 11,0 | 8,0 | 16,0 | 0,77 | Reay(1973) |
| Ammodytes tobianus | Demersal | 1,39 | C | 11,0 | 12,0 | 16,0 | 0,77 | Reay(1973) |
| Ammodytes tobianus | Demersal | 1,04 | C | 11,0 | 14,0 | 16,0 | 0,77 | Reay(1973) |
| Ammodytes tobianus | Demersal | 0,70 | C | 11,0 | 15,0 | 16,0 | 0,77 | Reay(1973) |
| Anchoa mitchilli | Pelagic | 2,36 | C | 17,0 | 5,8 | 13,8 | 0,21 | Newberger & Houde(1995) |
| Balistes vetula | Demersal | 2,60 | C | 27,0 | 28,5 | 45,0 | 0,57 | Aiken(1983) |
| Benthosema glaciale | Pelagic | 0,74 | C | 7,0 | 4,9 | 8,6 | 0,36 | Gjøsæter(1973) |
| Benthosema glaciale | Pelagic | 1,10 | C | 7,0 | 3,9 | 8,6 | 0,36 | Gjøsæter(1973) |
| Benthosema glaciale | Pelagic | 0,37 | C | 7,0 | 5,3 | 8,6 | 0,36 | Gjøsæter(1973) |
| Benthosema glaciale | Pelagic | 0,86 | C | 7,0 | 6,3 | 8,6 | 0,36 | Gjøsæter(1973) |
| Benthosema glaciale | Pelagic | 2,55 | C | 7,0 | 7,0 | 8,6 | 0,36 | Gjøsæter(1973) |
| Beryx splendes | Demersal | 0,57 | C | 18,0 | 22,0 | 45,0 | 0,15 | Adachi et al.(2006) |
| Brevoortia patronus | Pelagic | 1,09 | C | 26,0 | 14,4 | 25,3 | 0,48 | Ahrenholz(1981) |
| Brevoortia tyrrannus | Pelagic | 0,37 | C | 10,0 | 30,7 | 40,0 | 0,39 | Schaaf & Huntsman(1972) |
| Cephalopholis fulva | Demersal | 0,55 | C | 27,0 | 29,8 | 34,0 | 0,63 | Thompson & Munro(1977) |
| Cetengraulis mysticetus | Pelagic | 2,40 | C | 24,0 | 11,8 | 15,0 | 1,88 | Bayliff(1967) |
| Cheilodactylus macropterus | Demersal | 0,08 | C | 14,0 | 41,0 | 47,7 | 0,28 | Vooren(1977) |
| Cheilodactylus macropterus | Demersal | 0,10 | F | 14,0 | 35,8 | 44,6 | 0,22 | Annala et al.(1989) |
| Cheilodactylus macropterus | Demersal | 0,10 | M | 14,0 | 35,8 | 44,7 | 0,17 | Annala et al.(1989) |
| Clupea harengus | Pelagic | 0,17 | C | 8,0 | 30,4 | 36,0 | 0,21 | Beverton & Holt(1959) |
| Clupea harengus | Pelagic | 0,20 | C | 12,0 | 26,8 | 29,5 | 0,39 | Beverton(1963) |
| Clupea harengus | Pelagic | 0,17 | C | 11,0 | 24,2 | 30,0 | 0,38 | Cushing(1959) |
| Clupea harengus | Pelagic | 0,13 | C | 11,0 | 24,2 | 30,0 | 0,38 | Cushing(1959) |
| Clupea harengus | Pelagic | 0,18 | C | 11,0 | 24,2 | 30,0 | 0,38 | Cushing(1959) |
| Clupea harengus | Pelagic | 0,16 | C | 12,0 | 29,0 | 30,4 | 0,28 | Burd(74) |
| Clupea pallasii | Pelagic | 4,56 | C | 5,0 | 7,5 | 35,0 | 0,25 | Stokesbury et al.(2002) |
| Clupea pallasii | Pelagic | 2,01 | C | 5,0 | 12,5 | 35,0 | 0,25 | Stokesbury et al.(2002) |
| Clupea pallasii | Pelagic | 0,21 | C | 10,0 | 20,5 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 0,32 | C | 10,0 | 21,8 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 0,43 | C | 10,0 | 22,6 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 0,43 | C | 10,0 | 23,1 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 0,67 | C | 10,0 | 23,4 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 0,99 | C | 10,0 | 23,7 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallasii | Pelagic | 1,26 | C | 10,0 | 23,9 | 27,0 | 0,48 | Tanasichuk(2000) |
| Clupea pallassii | Pelagic | 0,20 | C | 12,0 | 17,0 | 22,0 | 0,80 | Beverton(1963) |
| Clupea pallassii | Pelagic | 0,50 | C | 10,0 | 23,8 | 27,0 | 0,48 | Beverton(1963) |
| Cololabis saira | Pelagic | 1,25 | C | 12,0 | 25,5 | 34,2 | 0,41 | Hughes(1974) |
| Coris julis | Demersal | 1,58 | C | 17,0 | 16,2 | 27,2 | 0,11 | Macpherson et al.(2000) |
| Diplodus annularis | Demersal | 0,49 | C | 17,0 | 15,4 | 20,4 | 0,54 | Macpherson et al.(2000) |
| Diplodus sargus | Demersal | 1,33 | C | 17,0 | 31,9 | 41,7 | 0,25 | Macpherson et al.(2000) |
| Engraulis anchoita | Pelagic | 0,43 | C | 16,0 | 16,7 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 0,85 | C | 16,0 | 17,0 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 0,93 | C | 16,0 | 17,2 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 1,41 | C | 16,0 | 17,2 | 17,3 | 0,71 | Brandhorst et al.(1974) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Engraulis anchoita | Pelagic | 1,33 | C | 16,0 | 16,7 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 2,13 | C | 16,0 | 17,0 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 1,39 | C | 16,0 | 17,2 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis anchoita | Pelagic | 0,90 | C | 16,0 | 16,5 | 17,3 | 0,71 | Brandhorst et al.(1974) |
| Engraulis japonicus | Pelagic | 0,63 | C | 11,5 | 8,9 | 15,5 | 0,60 | Iversen et al.(1993) |
| Eopsetta jordani (female) | Demersal | 0,20 | F | 9,0 | 49,0 | 58,6 | 0,17 | Ketchen & Forrester(1966) |
| Eopsetta jordani (male) | Demersal | 0,25 | M | 9,0 | 41,0 | 49,0 | 0,16 | Ketchen & Forrester(1966) |
| Epinephelus guttatus | Demersal | 0,68 | C | 27,0 | 38,7 | 52,0 | 0,24 | Thompson & Munro(1977) |
| Gadus morhua | Demersal | 0,10 | C | 6,0 | 60,0 | 115,0 | 0,10 | Dickie(1963) |
| Gadus morhua | Demersal | 0,18 | C | 1,0 | 62,0 | 65,0 | 0,30 | Pinhorn(1975) |
| Gadus morhua | Demersal | 0,40 | C | 4,0 | 54,5 | 68,6 | 0,17 | Sinclair(2001) |
| Gadus morhua | Demersal | 0,30 | C | 4,0 | 73,6 | 100,3 | 0,15 | Sinclair(2001) |
| Gadus morhua | Demersal | 0,33 | C | 2,5 | 80,4 | 129,0 | 0,13 | Garrod(1967 |
| Gadus morhua | Demersal | 3,80 | C | 8,0 | 12,0 | 132,0 | 0,20 | Juilliard et al.(2001) |
| Gadus morhua | Demersal | 0,55 | C | 8,0 | 33,7 | 132,0 | 0,20 | Juilliard et al.(2001) |
| Gadus morhua | Demersal | 1,10 | C | 8,0 | 27,8 | 134,0 | 0,10 | Larsen & Pedersen(2002) |
| Gadus morhua | Demersal | 0,20 | C | 8,0 | 41,9 | 134,0 | 0,10 | Larsen & Pedersen(2002) |
| Glaucosoma buergeri | Demersal | 0,14 | C | 26,9 | 29,5 | 51,5 | 0,14 | Newman(2002a) |
| Hippocampus guttulatus | Demersal | 1,20 | C | 18,0 | 14,0 | 19,8 | 0,57 | Curtis et al.(2006) |
| Hippoglossoides platessoides | Demersal | 0,22 | F | 0,0 | 43,0 | 59,0 | 0,08 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,23 | F | -0,5 | 53,0 | 81,1 | 0,06 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,18 | F | -0,8 | 54,0 | 60,0 | 0,07 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,18 | F | 1,5 | 62,0 | 72,5 | 0,11 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,30 | M | 0,0 | 37,0 | 42,6 | 0,10 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,25 | M | -0,5 | 44,0 | 55,2 | 0,11 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,27 | M | -0,8 | 49,0 | 50,0 | 0,09 | Pitt(1973) |
| Hippoglossoides platessoides | Demersal | 0,26 | M | 1,5 | 52,0 | 58,5 | 0,15 | Pitt(1973) |
| Hippoglossus stenolepis | Demersal | 0,20 | C | 5,0 | 75,0 | 215,0 | 0,05 | Chen & Xiao(2006) |
| Hyporhamphus melanochir | Pelagic | 0,53 | M | 20,0 | 34,0 | 36,7 | 0,51 | Jones(1990) |
| Hyporhamphus melanochir | Pelagic | 0,36 | F | 20,0 | 35,9 | 38,7 | 0,54 | Jones(1990) |
| Katsuwonus pelamis | Pelagic | 10,00 | C | 25,0 | 25,0 | 65,1 | 1,30 | Hampton(2000) |
| Katsuwonus pelamis | Pelagic | 4,50 | C | 25,0 | 35,0 | 65,1 | 1,30 | Hampton(2000) |
| Katsuwonus pelamis | Pelagic | 1,60 | C | 25,0 | 45,0 | 65,1 | 1,30 | Hampton(2000) |
| Katsuwonus pelamis | Pelagic | 1,20 | C | 25,0 | 55,0 | 65,1 | 1,30 | Hampton(2000) |
| Katsuwonus pelamis | Pelagic | 2,00 | C | 25,0 | 65,0 | 65,1 | 1,30 | Hampton(2000) |
| Lamna nasus | Pelagic | 0,18 | C | 7,0 | 189,0 | 280,0 | 0,12 | Aasen(1963) |
| Lethrinus miniatus | Demersal | 0,44 | C | 26,0 | 44,0 | 45,3 | 0,48 | Williams et al.(2007) |
| Lethrinus miniatus | Demersal | 1,06 | C | 26,0 | 45,8 | 47,2 | 0,48 | Williams et al.(2007) |
| Lethrinus miniatus | Demersal | 0,57 | C | 26,0 | 43,4 | 46,3 | 0,38 | Williams et al.(2007) |
| Lopholatilus chamaeleontoceps | Demersal | 0,25 | M | 10,0 | 74,5 | 92,2 | 0,09 | Harris & Grossman(1985) |
| Lopholatilus chamaeleontoceps | Demersal | 0,25 | F | 10,0 | 70,5 | 86,5 | 0,09 | Harris & Grossman(1985) |
| Lutjanus adetii | Demersal | 0,24 | C | 25,7 | 24,1 | 25,4 | 0,32 | Newman et al.(1996) |
| Lutjanus carponotatus | Demersal | 0,20 | C | 25,7 | 28,7 | 31,3 | 0,45 | Newman et al.(2000a) |
| Lutjanus erythropterus | Demersal | 0,15 | C | 25,7 | 51,7 | 58,5 | 0,38 | Newman et al.(2000b) |
| Lutjanus malabaricus | Demersal | 0,11 | C | 26,9 | 49,6 | 62,2 | 0,23 | Newman(2002b) |
| Lutjanus malabaricus | Demersal | 0,13 | C | 25,7 | 59,1 | 72,8 | 0,29 | Newman et al.(2000b) |
| Lutjanus quinquilineatus | Demersal | 0,15 | C | 25,7 | 19,2 | 20,7 | 0,31 | Newman et al.(1996) |
| Lutjanus ruselli | Demersal | 0,15 | C | 26,9 | 36,4 | 38,6 | 0,35 | Newman(2002) |
| Lutjanus sebae | Demersal | 0,15 | C | 25,7 | 56,1 | 79,2 | 0,14 | Newman et al.(2000b) |
| Lutjanus vitta | Demersal | 0,34 | C | 25,7 | 22,6 | 24,5 | 0,85 | Newman et al.(2000a) |
| Melanogrammus aeglefinus | Demersal | 0,43 | C | 8,0 | 33,3 | 68,0 | 0,20 | Jones & Shanks(1990) |
| Merluccius angustimanus | Demersal | 0,79 | C | 20,0 | 25,2 | 32,7 | 0,35 | Mathews(1975) |
| Merluccius angustimanus | Demersal | 0,84 | C | 20,0 | 18,1 | 32,7 | 0,35 | Mathews(1975) |
| Nemipterus japonicus | Demersal | 2,52 | C | 27,0 | 16,0 | 30,5 | 1,00 | Vivekanandan & James(1986) |
| Nemipterus marginatus | Demersal | 1,73 | C | 28,0 | 15,1 | 24,5 | 0,42 | Pauly & Martosubroto(1980) |
| Pagrus auratus | Demersal | 2,58 | C | 24,0 | 10,5 | 107,9 | 0,07 | Wakefield et al.(2007) |
| Pleuronectes platessa | Demersal | 0,20 | C | 12,0 | 42,5 | 68,0 | 0,13 | Siddeek(1989) |
| Pleuronectes platessa | Demersal | 0,14 | M | 7,0 | 31,2 | 45,0 | 0,15 | Beverton(1964) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Pleuronectes platessa | Demersal | 0,08 | F | 7,0 | 40,5 | 70,0 | 0,08 | Beverton(1964) |
| Pneumatophorus japonicus | Pelagic | 0,50 | C | 15,0 | 36,7 | 43,6 | 0,24 | Parrish & MacCall(1978) |
| Pomatoschistus minutus | Demersal | 2,61 | C | 10,0 | 4,5 | 9,3 | 0,93 | Fonds(1973) |
| Pomatoschistus minutus | Demersal | 4,04 | C | 10,0 | 7,0 | 9,3 | 0,93 | Fonds(1973) |
| Pseudotolithus elongatus | Demersal | 0,34 | C | 26,0 | 31,5 | 46,7 | 0,26 | Le Guen(1971) |
| Rastrelliger neglectus | Pelagic | 7,22 | C | 28,0 | 17,6 | 20,9 | 3,38 | Hongskul(1974) |
| Rhizoprionodon taylori | Demersal | 0,70 | M | 25,0 | 60,0 | 65,2 | 1,34 | Simpendorfer(1999) |
| Rhizoprionodon taylori | Demersal | 0,56 | F | 25,0 | 64,0 | 73,2 | 1,01 | Simpendorfer(1999) |
| Sardinella longiceps | Pelagic | 0,67 | C | 27,0 | 14,5 | 20,7 | 0,53 | Banerji(1973) |
| Sardinops caerulea | Pelagic | 0,40 | C | 15,0 | 26,9 | 29,3 | 0,45 | Beverton(1963) |
| Sardinops sagax | Pelagic | 0,13 | C | 15,0 | 26,7 | 30,5 | 0,40 | Silliman(1943) |
| Sardinops sagax | Pelagic | 0,43 | C | 15,0 | 15,5 | 17,0 | 0,70 | Fletcher(1995) |
| Sebastes alutus | Demersal | 0,04 | C | 8,0 | 41,5 | 42,6 | 0,13 | Archibald et al.(1981) |
| Sebastes brevispinis | Demersal | 0,04 | C | 8,0 | 53,7 | 56,8 | 0,09 | Archibald et al.(1981) |
| Sebastes crameri | Demersal | 0,07 | C | 8,0 | 33,5 | 38,3 | 0,09 | Archibald et al.(1981) |
| Sebastes elongatus | Demersal | 0,15 | M | 12,0 | 29,0 | 30,1 | 0,11 | Shaw & Gunderson(2006) |
| Sebastes elongatus | Demersal | 0,15 | F | 12,0 | 34,5 | 37,5 | 0,08 | Shaw & Gunderson(2006) |
| Sebastes emphaeus | Demersal | 0,44 | F | 12,0 | 15,7 | 17,1 | 0,54 | Beckmann et al.(1998) |
| Sebastes flavidus | Demersal | 0,07 | C | 8,0 | 48,0 | 48,6 | 0,19 | Archibald et al.(1981) |
| Sebastes pinniger | Demersal | 0,04 | M | 8,0 | 50,7 | 52,8 | 0,14 | Archibald et al.(1981) |
| Sebastes pinniger | Demersal | 0,11 | F | 8,0 | 54,2 | 62,1 | 0,10 | Archibald et al.(1981) |
| Sebastes prioriger | Demersal | 0,10 | C | 8,0 | 36,5 | 39,3 | 0,17 | Archibald et al.(1981) |
| Sebastes reedi | Demersal | 0,12 | C | 8,0 | 42,5 | 44,5 | 0,13 | Archibald et al.(1981) |
| Sebastes zacentrus | Demersal | 0,07 | C | 8,0 | 31,3 | 34,9 | 0,10 | Archibald et al.(1981) |
| Serranus cabrilla | Demersal | 0,68 | C | 17,0 | 18,5 | 23,8 | 0,30 | Macpherson et al.(2000) |
| Sparisoma viride | Demersal | 0,24 | C | 27,5 | 18,7 | 28,1 | 0,60 | Choat et al.(2003) |
| Symphodus roissali | Demersal | 1,71 | C | 17,0 | 9,0 | 16,5 | 0,35 | Macpherson et al.(2000) |
| Thunnus alalunga | Pelagic | 0,19 | C | 25,0 | 77,4 | 124,7 | 0,23 | Wang & Liu(2006) |
| Thunnus albacares | Pelagic | 6,20 | C | 25,0 | 25,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 3,60 | C | 25,0 | 35,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 1,40 | C | 25,0 | 45,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 0,68 | C | 25,0 | 55,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 0,44 | C | 25,0 | 65,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 0,69 | C | 25,0 | 75,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 1,80 | C | 25,0 | 85,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 2,10 | C | 25,0 | 95,0 | 166,4 | 0,25 | Hampton(2000) |
| Thunnus albacares | Pelagic | 5,22 | C | 25,0 | 32,5 | 181,7 | 0,25 | Adam et al.(2003) |
| Thunnus albacares | Pelagic | 0,80 | C | 25,0 | 50,5 | 181,7 | 0,25 | Adam et al.(2003) |
| Thunnus albacares | Pelagic | 1,31 | C | 25,0 | 98,0 | 181,7 | 0,25 | Adam et al.(2003) |
| Thunnus maccoyii | Pelagic | 0,24 | C | 26,0 | 95,1 | 186,9 | 0,14 | Hampton(1991) |
| Thunnus obesus | Pelagic | 4,20 | C | 25,0 | 30,0 | 181,7 | 0,25 | Hampton(2000) |
| Thunnus obesus | Pelagic | 0,50 | C | 25,0 | 50,0 | 181,7 | 0,25 | Hampton(2000) |
| Thunnus obesus | Pelagic | 0,80 | C | 25,0 | 70,0 | 181,7 | 0,25 | Hampton(2000) |
| Thunnus obesus | Pelagic | 0,10 | C | 25,0 | 90,0 | 181,7 | 0,25 | Hampton(2000) |
| Thunnus obesus | Pelagic | 0,90 | C | 25,0 | 110,0 | 181,7 | 0,25 | Hampton(2000) |
| Thunnus obesus | Pelagic | 2,12 | C | 25,0 | 42,0 | 181,7 | 0,25 | Adam et al.(2003) |
| Thunnus obesus | Pelagic | 1,35 | C | 25,0 | 63,0 | 181,7 | 0,25 | Adam et al.(2003) |
| Thunnus obesus | Pelagic | 0,66 | C | 25,0 | 102,0 | 181,7 | 0,25 | Adam et al.(2003) |
| Trachurus declivis | Pelagic | 0,18 | C | 12,0 | 50,4 | 51,1 | 0,25 | Horn(1993) |
| Trachurus novaezelandiae | Pelagic | 0,18 | C | 12,0 | 35,8 | 38,5 | 0,23 | Horn(1993) |
| Trisopterus esmarkii | Demersal | 1,60 | C | 9,0 | 14,0 | 19,3 | 0,59 | Raitt(1968) |
| Trisopterus esmarkii | Demersal | 1,60 | C | 9,0 | 14,0 | 19,0 | 0,44 | Raitt(1968) |
| Trisopterus esmarkii | Demersal | 1,48 | C | 8,5 | 18,6 | 21,5 | 0,45 | Bailey & Kunzlik(1984) |
| Trisopterus esmarkii | Demersal | 1,50 | C | 9,0 | 19,5 | 21,6 | 0,53 | Bailey & Kunzlik(1984) |
| Trisopterus esmarkii | Demersal | 2,43 | C | 9,0 | 23,0 | 26,4 | 0,61 | Bailey & Kunzlik(1984) |

# Table 2. Output from full GLM model

Dependent Variable: lnM

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 4 | 141.6908793 | 35.4227198 | 68.12 | <.0001 |
| Error | 158 | 82.1560337 | 0.5199749 | | |
| Corrected Total | 162 | 223.8469130 | | | |

| R-Square | Coeff Var | Root MSE | lnM Mean |
|---|---|---|---|
| 0.632981 | -113.8942 | 0.721093 | -0.633125 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 42.12584965 | 42.12584965 | 81.02 | <.0001 |
| LnLinf | 1 | 40.33016462 | 40.33016462 | 77.56 | <.0001 |
| LnK | 1 | 58.68683224 | 58.68683224 | 112.86 | <.0001 |
| 1/T | 1 | 0.54803276 | 0.54803276 | 1.05 | 0.3062 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 74.06892924 | 74.06892924 | 142.45 | <.0001 |
| LnLinf | 1 | 59.20266892 | 59.20266892 | 113.86 | <.0001 |
| LnK | 1 | 41.73691321 | 41.73691321 | 80.27 | <.0001 |
| 1/T | 1 | 0.54803276 | 0.54803276 | 1.05 | 0.3062 |

| Parameter | Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|
| Intercept | -2.1104327 | 2.7124553 | -0.78 | 0.4377 |
| lnL | -1.7023068 | 0.1426300 | -11.94 | <.0001 |
| LnLinf | 1.5067827 | 0.1412119 | 10.67 | <.0001 |
| LnK | 0.9664798 | 0.1078757 | 8.96 | <.0001 |
| 1/T | 763.5074169 | 743.7058357 | 1.03 | 0.3062 |

## Table 3. Output from GLM model without temperature

Dependent Variable: lnM

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 3 | 141.1428465 | 47.0476155 | 90.45 | <.0001 |
| Error | 159 | 82.7040665 | 0.5201514 | | |
| Corrected Total | 162 | 223.8469130 | | | |

| R-Square | Coeff Var | Root MSE | lnM Mean |
|---|---|---|---|
| 0.630533 | -113.9136 | 0.721215 | -0.633125 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 42.12584965 | 42.12584965 | 80.99 | <.0001 |
| LnLinf | 1 | 40.33016462 | 40.33016462 | 77.54 | <.0001 |
| LnK | 1 | 58.68683224 | 58.68683224 | 112.83 | <.0001 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 73.52822554 | 73.52822554 | 141.36 | <.0001 |
| LnLinf | 1 | 66.90637851 | 66.90637851 | 128.63 | <.0001 |
| LnK | 1 | 58.68683224 | 58.68683224 | 112.83 | <.0001 |

| Parameter | Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|
| Intercept | 0.659044546 | 0.28305697 | 2.33 | 0.0212 |
| lnL | -1.691163861 | 0.14224058 | -11.89 | <.0001 |
| LnLinf | 1.444042278 | 0.12732422 | 11.34 | <.0001 |
| LnK | 0.897624850 | 0.08450636 | 10.62 | <.0001 |

Table 4 Output from GLM model without the lnK term.

Dependent Variable: lnM

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 3 | 99.9539661 | 33.3179887 | 42.76 | <.0001 |
| Error | 159 | 123.8929469 | 0.7792009 | | |
| Corrected Total | 162 | 223.8469130 | | | |

| R-Square | Coeff Var | Root MSE | lnM Mean |
|---|---|---|---|
| 0.446528 | -139.4233 | 0.882724 | -0.633125 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 42.12584965 | 42.12584965 | 54.06 | <.0001 |
| LnLinf | 1 | 40.33016462 | 40.33016462 | 51.76 | <.0001 |
| 1/T | 1 | 17.49795179 | 17.49795179 | 22.46 | <.0001 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| lnL | 1 | 72.33324872 | 72.33324872 | 92.83 | <.0001 |
| LnLinf | 1 | 28.31962098 | 28.31962098 | 36.34 | <.0001 |
| 1/T | 1 | 17.49795179 | 17.49795179 | 22.46 | <.0001 |

| Parameter | Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|
| Intercept | 13.251643 | 2.5728399 | 5.15 | <.0001 |
| lnL | -1.682031 | 0.1745781 | -9.63 | <.0001 |
| LnLinf | 0.925713 | 0.1535527 | 6.03 | <.0001 |
| 1/T | -3379.057142 | 713.0609570 | -4.74 | <.000 |