The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural systems and aquaculture

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The relationship between body weight and natural mortality in juvenile and adult fish was analysed for different aquatic ecosystems: lakes, rivers, the ocean, and pond, cage and tank aquaculture systems. Mortality was modelled as a power function of weight, and the parameters b (exponent) and M_u (mortality at the unit weight of 1 g) estimated for fish in the six ecosystems, as well as within selected populations, species and families. At the ecosystem level, no significant differences in parameters were found between lakes, rivers and the ocean and a joint mortality–weight relationship for all natural ecosystems was estimated with parameters $b=-0{\cdot}288$ (90% CL[$-0{\cdot}315$, $-0{\cdot}261$]) and $M_u=3{\cdot}00$ (90% CL[2·70, 3·30]) year^{-1}. Among the culture systems, mortality–weight relationships in ponds and cages were not significantly different and a joint relationship was estimated. The weight exponents of mortality in ponds/cages and tanks were very similar at about $b=-0{\cdot}43$, and significantly more negative than in natural ecosystems. Mortalities at unit weight were significantly lower in tanks (0·91 year^{-1}) than in ponds/cages (2·24 year^{-1}), and both were significantly lower than in natural ecosystems. No systematic differences were found between the mortality–weight relationships determined for individual populations, species or families, and fish in the respective ecosystems. It is hypothesized that aquaculture mortality–weight relationships indicate the allometric scaling of non-predation mortality, which is therefore more strongly size dependent than predation mortality. If non-predation mortality in natural ecosystems shows a similar scaling with body weight, then the allometric exponent of predation mortality must be less negative than that observed for total natural mortality. Implications of the established mortality–weight relationships for aquaculture and culture-based fisheries are discussed.

Key words: mortality; body weight; allometry; aquaculture; ecosystem; predation.

INTRODUCTION

The natural mortality rates of fish are closely related to their body weight. This has been demonstrated empirically within populations (Zijlstra *et al.*, 1982; van der Veer, 1986; Post & Evans, 1989), as well as in comparisons between populations and between species (McGurk, 1986, 1987). In a theoretical analysis based on considerations of energy flow and particle size distribution, Peterson & Wroblewski (1984) predicted predation mortality in the marine pelagic ecosystem to be a power function of body weight with an exponent of $-0{\cdot}25$.

The natural mortality rate in an unexploited population at equilibrium equals its intrinsic rate of natural increase r_m, and its production–biomass (P/B) ratio. The mortality–weight relationship between populations thus reflects the well-known relationships of r_m (Fenchel, 1974) and the P/B ratio (Banse & Mosher, 1980) to body weight.

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In an empirical study of natural mortality rates in marine organisms from invertebrates to whales, McGurk (1986, 1987) showed that the overall mortality–weight relationship for all organisms was well described by an exponent of $-0{\cdot}25$, as predicted by Peterson & Wroblewski (1984). However, the analysis of ecologically more homogeneous subsets of the data yielded more negative exponents of $-0{\cdot}37$ for fish of all life stages, $-0{\cdot}34$ for juvenile and adult fish, and $-0{\cdot}49$ for fish eggs and larvae (estimated by predictive linear regression on log-transformed data). Similar observations have been reported for the P/B ratio and other production parameters (Banse & Mosher, 1980; Dickie *et al.*, 1987). Dickie *et al.* (1987) generalized these observations by proposing the existence of two distinct weight relationships for production parameters: a physiological relationship that reflects the weight dependence of the metabolic rate (Hemmingsen, 1960), and an ecological relationship that reflects ecological factors such as spatial dynamics of predator–prey relationships. The physiological relationship is expected to be borne out in broad groups of organisms such as whole communities, while the ecological relationship is evident in ecologically more homogeneous groups such as fish or invertebrates. Empirical studies (Banse & Mosher, 1980; McGurk, 1986, 1987) suggest that ecological weight exponents of P/B and M are generally more negative than the physiological exponent.

The mortality–weight relationship has important implications for the dynamics of wild fish populations as well as the management of aquaculture stocks, and an empirical model of this relationship has a number of potential management applications. The interaction of size-dependent mortality with growth, as determined by environmental and population factors, is seen as a mechanism generating recruitment variability (Shepherd & Cushing, 1980; Anderson, 1988; Post & Evans, 1989). Gulland (1987) has pointed out that the use of a size-dependent (as opposed to constant) mortality model in stock assessments could make these more realistic, in particular when small fish are concerned. In aquaculture, weight-related mortality rates have a bearing on the culture systems used for early life stages and juveniles, and on the size at which fish are transferred between nursing and out-growing systems. A mortality–size model is also an important tool to assess the optimal size and stocking density of seed fish in culture-based and enhanced fisheries (Lorenzen, 1995).

The present study examines the mortality–weight relationships in fish in different natural ecosystems (lakes, rivers and the ocean), and in aquaculture systems (ponds, cages and tanks). The analysis extends to broad groups of fish in particular ecosystems, as well as individual populations, species and families. Results are discussed with respect to sources of mortality and their relationship to body weight, and practical implications for the management of fisheries and aquaculture are discussed.

MATERIALS AND METHODS

DATA

Sources of data

Mortality and weight data for juvenile and adult fish were gleaned from published sources, and classified by ecosystem as follows. Lakes are any standing water bodies not primarily managed for fish production. Rivers are running waters of various extent, from large rivers down to small streams. The ocean comprises all marine habitats. Aquaculture ponds are man-made water bodies lined by soil, which are managed primarily for fish production. Cages enclose fish in nets or screens, suspended in natural water bodies or ponds. Tanks are highly controlled habitats managed exclusively for fish production, and lined by man-made materials such as concrete or fibreglass.

Data for lakes and rivers were obtained primarily from ecological fish production studies. Such studies provide separate estimates of mortality for each age-group present in the population, making it possible to analyse mortality–weight relationships within, as well as between, populations. Data for marine fish were taken from McGurk (1986, 1987), and supplemented with additional data for juvenile and small fish from other sources. Most natural mortality estimates for marine fish originate from assessments of exploited stocks. Data on pond, cage and tank aquaculture systems were obtained from published experiments, and from aquaculture textbooks.

The analysis was restricted to juvenile and adult fish, and any data explicitly concerned with fish eggs or larvae were excluded. However, studies conducted in freshwater habitats or in aquaculture do not always separate larval from juvenile fish, and consequently some mortality estimates for juveniles include late larval stages.

The sources of mortality data used are listed in Appendix B. The full data are available from the author upon request.

Estimation of mortality rates

In ecological production studies, total mortality rates were calculated from the relative abundance of year classes. Natural mortality was assumed to equal total mortality, and when the exploitation status of a population was unclear (mainly in rivers), the potentially exploited size-groups were excluded from the analysis. Age- or length-based catch curves were used to calculate mortality rates in population studies of freshwater fish. The calculation of mortality rates for marine fish is described in McGurk (1986). In aquaculture, mortality rates were calculated from the reported numbers of fish stocked and harvested in experiments. In a few cases, expected loss figures based on experience in commercial farms have been gleaned from textbooks and converted to mortality rates.

Weight

All weights are given as wet weight, in order to facilitate the practical use of the derived relationships. Wherever possible, weight was calculated as weight at mean length during the period for which mortality was measured, assuming an isometric weight–length relationship:

$$W_{\bar{L}}=\left(\frac{W_1^{1/3}+W_2^{1/3}}{2}\right)^3 \tag{1}$$

where $W_{\bar{L}}$ is weight at mean length, and W_1 and W_2 are the weights at the beginning and end of the time period respectively. In cases where only average mortality rates for a population were available, mean weight in the population or weight at maturity were used. Weight data for marine fish from McGurk (1986) were reconverted to wet weight using the relationship given in the original paper.

MORTALITY–WEIGHT MODEL AND PARAMETER ESTIMATION

In accordance with the conventional description of allometric relationships and earlier theoretical and empirical studies (Peterson & Wroblewski, 1984; McGurk, 1986), natural mortality was modelled as a power function of weight:

$$M_W=M_u W^b \tag{2}$$

where M_W is the natural mortality rate at weight W, M_u is the natural mortality rate at unit weight, and b is the allometric scaling factor. All mortality rates are annual, and the unit of weight is 1 g.

Parameter estimates were obtained using the complete Theil estimator, a robust non-parametric regression method (Sprent, 1989). The Theil estimate of a parameter is the median of the parameter values obtained from all possible pairs of data points. Confidence limits for the Theil estimate were constructed on the basis of Kendall's tau (Sen, 1968; Sprent, 1989). All confidence limits are given at the 90% level.

Mortality–weight relationships were estimated for whole ecosystems and culture systems, as well as latitudinal zones and individual populations, species and families. For the analysis of latitudinal effects, data for natural ecosystems and ponds/cages were classified into three zones: tropical/subtropical (0–30°), temperate (30–60°), and polar (60–90°). Mortality–weight relationships were estimated separately for each zone. A cross-validation procedure was used to test whether mortality–weight relationships within populations, species and families differed systematically from the respective ecosystem relationship. Data for selected populations, species and families were analysed separately and the results compared to the ecosystem relationship estimated from the remaining data. Selection criteria were the weight range (two orders of magnitude or more), and the number of mortality estimates per group (at least five for populations, and 10 for species and families). These criteria were applied in order to select populations, species and families that could be expected to show well-defined mortality–weight relationships, while leaving all other data in the remaining ecosystem set.

RESULTS

ECOSYSTEMS

The mortality–weight relationships in the three natural ecosystems were very similar (Fig. 1), with none of the parameter estimates (Table I) being significantly different between lakes, rivers, and the ocean. A joint relationship for fish in natural ecosystems was estimated by pooling data from lakes, rivers, and the ocean (Table I). Parameters for pond and cage aquaculture systems also did not differ significantly, and a joint mortality–weight relationship was estimated (Table I). The weight exponents in pond/cage and tank aquaculture were very similar to each other, and both were significantly more negative than the exponent in natural ecosystems (Fig. 2). The mortality rate M_u at unit weight (1 g) in pond/cage culture was significantly lower than in natural ecosystems, and M_u in tanks was significantly lower than in both natural ecosystems and ponds/cages.

LATITUDINAL EFFECTS

The latitudinal distribution of data for natural ecosystems was very uneven, with most of the data originating from the temperate zone. By contrast, pond/cage culture data were evenly distributed between the temperate and tropical zone. No significant latitudinal differences were found in the mortality–weight relationships in either natural ecosystems or pond/cage culture (Table II). The weight exponents in pond/cage culture were very similar for the two latitudinal zones, and consistently more negative than the natural ecosystem exponents. Mortality at unit weight in pond/cage culture was lower in the tropical than in the temperate zone, but the difference was not statistically significant.

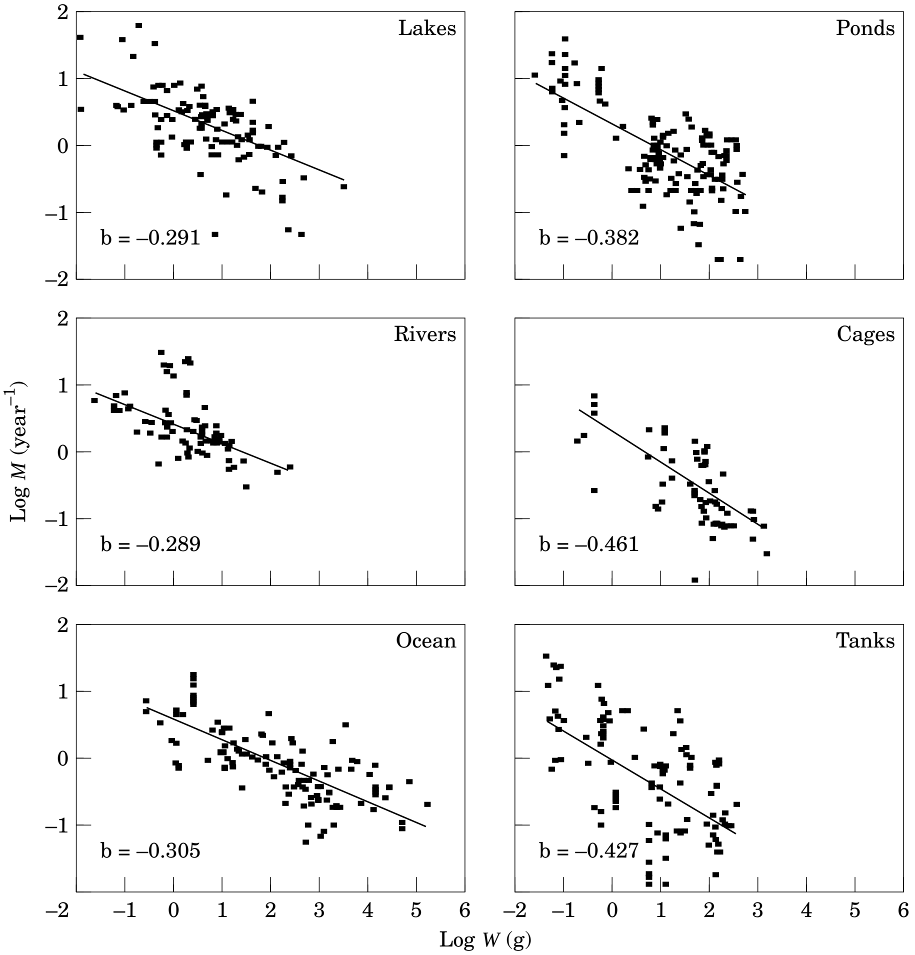

FIG. 1. Mortality–weight relationships of fish in natural ecosystems (lakes, rivers, and the ocean), and in aquaculture (ponds, cages and tanks). The estimated nonparametric (Theil) regression lines, and the values of the exponent *b* are indicated.

INDIVIDUAL POPULATIONS, SPECIES AND FAMILIES

Within-population mortality–weight relationships were determined for seven populations of freshwater fish. Ecosystem parameters differed only slightly from the estimates obtained from the complete data (Fig. 3).

Only one individual population exponent was significantly different from the ecosystem exponent, and none of the population exponents were significantly different from each other. One individual population M_u was different from the ecosystem M_u, and several were different from each other. For species in natural ecosystems (Fig. 4), none of the weight exponent (*b*) estimates were significantly different from the ecosystem exponent or from each other, while mortality at unit weight (M_u) estimates were often different from the ecosystem M_u and from each other. Of the two pond/cage species, no parameter estimates were significantly different from the culture system parameters, but the species exponents were different from each other.

TABLE I. Mortality–weight model parameter estimates for juvenile and adult fish in different natural ecosystems and aquaculture systems

System	n	Weight exponent b	Mortality at unit weight M_u [year^{-1}]
Lakes	121	− 0·291 [− 0·356, − 0·224]	3·37 [2·94, 3·85]
Rivers	74	− 0·289 [− 0·360, − 0·230]	2·53 [2·29, 2·96]
Ocean	113	− 0·305 [− 0·351, − 0·257]	3·69 [2·84, 4·49]
Ponds	154	− 0·382 [− 0·442, − 0·342]	2·23 [1·75, 2·77]
Cages	59	− 0·461 [− 0·583, − 0·339]	2·04 [1·06, 2·94]
Tanks	113	− 0·427 [− 0·526, − 0·329]	0·91 [0·68, 1·35]
Natural	308	− 0·288 [− 0·315, − 0·261]	3·00 [2·70, 3·30]
Ponds/cages	213	− 0·423 [− 0·475, − 0·370]	2·24 [1·82, 2·71]

Theil estimates with 90% confidence intervals.

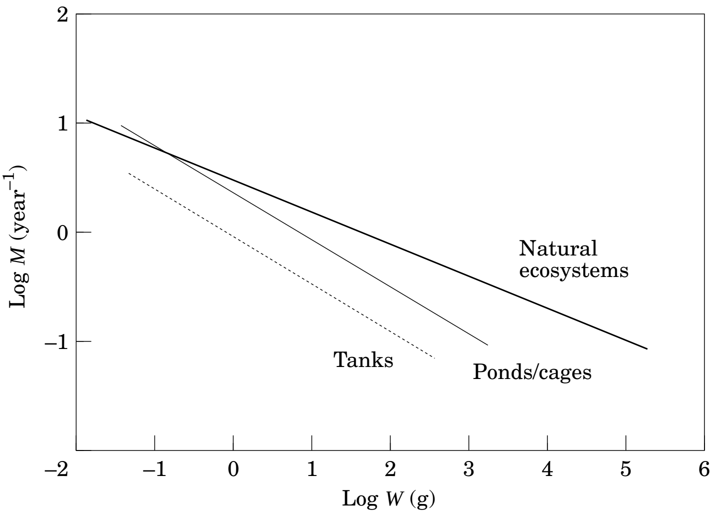

FIG. 2. Comparison of the identified, significantly different mortality–weight relationships for fish in natural ecosystems, ponds/cages and tanks.

Of the seven selected families in natural ecosystems, two b and three M_u estimates were significantly different from the ecosystem estimates, and some were different from each other. In ponds and cages, none of the three family b estimates were different from the system b, but one family b was different from the other two. One pond/cage family M_u was very much lower than the other two family estimates, and the system M_u.

Two families, cyprinids and salmonids, were represented in both natural ecosystems and pond/cage culture. The mortality weight exponents of both families did not differ significantly between natural and culture systems. However, the mortality at unit weight for salmonids was strikingly lower in pond/cage culture than in natural ecosystems.

TABLE II. Latitudinal effects on the mortality–weight relationship in fish in natural ecosystems and pond/cage aquaculture

Latitude zone	n	Weight exponent b	Mortality at unit weight M_u [year^{-1}]
Natural ecosystems			
Tropical	29	$-0{\cdot}210$ [$-0{\cdot}356$, $-0{\cdot}111$]	3·08 [1·87, 4·48]
Temperate	269	$-0{\cdot}309$ [$-0{\cdot}342$, $-0{\cdot}278$]	3·13 [2·79, 3·46]
Polar	10	$-0{\cdot}292$ [$-0{\cdot}450$, $-0{\cdot}151$]	1·69 [0·87, 3·12]
Pond/cage aquaculture			
Tropical	110	$-0{\cdot}416$ [$-0{\cdot}507$, $-0{\cdot}315$]	1·96 [1·45, 2·61]
Temperate	103	$-0{\cdot}427$ [$-0{\cdot}493$, $-0{\cdot}364$]	2·85 [2·03, 3·73]

Mortality–weight model parameter estimates with 90% confidence intervals for the latitudinal zone: tropical (0–30°), temperate (30–60°) and polar (60–90°). None of the estimates are significantly different from each other.

DISCUSSION

PARAMETER ESTIMATION

Previous studies of the relationships between body weight and M, r_m, or P/B have used predictive linear regression (Fenchel, 1974; Banse & Mosher, 1980), or both predictive and functional regression (McGurk, 1986, 1987) on log transformed data.

The Theil estimator used in the current work has a number of advantages over least squares linear regression: it is robust with respect to outliers and non-normality of the data; it does not require errors in x-values (i.e. weight) to be negligible; and it does not require linearization of the data. Houssain & Sprent (1983) have shown that in linear regression, the Theil estimator is nearly as efficient as least squares if the assumption of normality is met, and that it performs significantly better on long-tail distributions, i.e. in the presence of outliers. These properties make the Theil estimator particularly suitable for the analysis of mortality–weight data that are subject to a high degree of variation.

Confidence limits and results of statistical tests are given at a relatively low confidence level of 90%, reflecting the high level of variability in the mortality and weight data used. A higher level of confidence is difficult to attain given the scarcity of suitable data.

MORTALITY–WEIGHT RELATIONSHIPS

Ecosystems

The relationship between body weight and natural mortality in juvenile and adult fish was the same in all natural aquatic ecosystems, i.e. lakes, rivers, and the ocean. The observed weight exponent of fish mortality in natural ecosystems was slightly more negative than the expected physiological exponent of predation mortality, indicating the influence of an ecological scaling factor in the sense of Dickie *et al.* (1987).

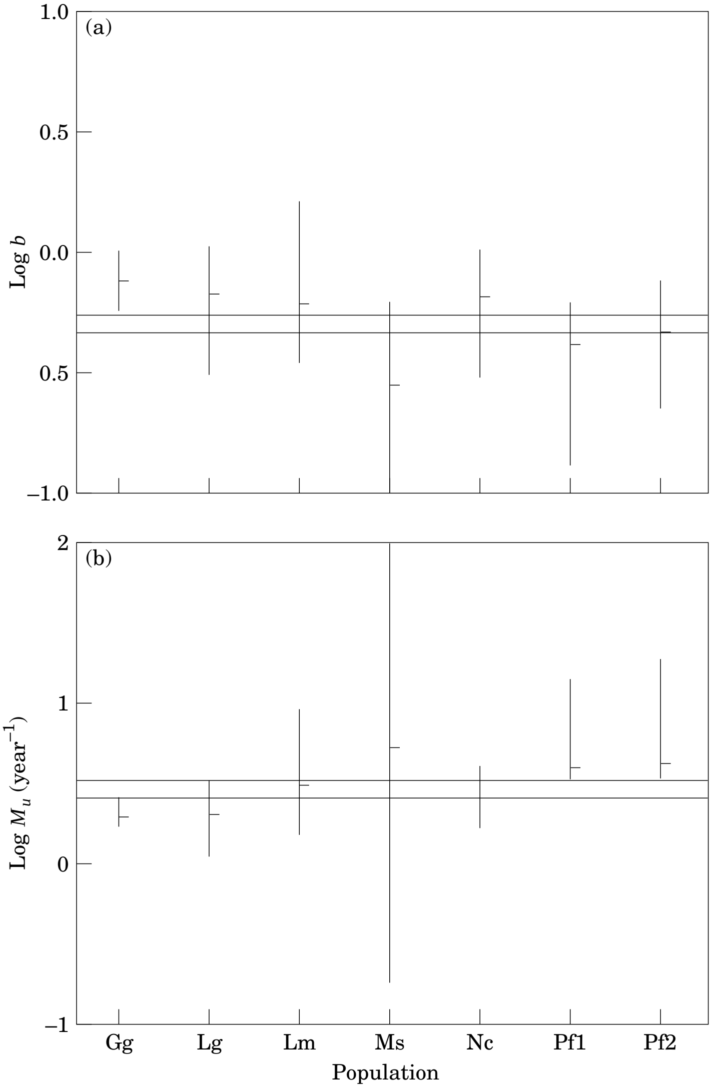

FIG. 3. Parameter estimates for within-population mortality–weight relationships in populations of freshwater fish. (a) Weight exponent b; (b) mortality at unit weight M_u. The populations are (Gg) *Gobio gobio* L. in River Warta, Poland (Penczak, 1992); (Lg) *Lepomis gibbosus* L., (Lm) *Lepomis macrochirus* Rafinesque, (Ms) *Micropterus salmoides* Lacepede, (Nc) *Notemigonus crysoleucas* Mitchill, and (Pf1) *Perca flavescens* Mitchill in Long Pond, Canada (Mahon & Balon, 1977); and (Pf2) *Perca flavescens* in a small lake, Canada (Chadwick, 1976). Theil estimates with 90% confidence limits. The horizontal lines indicate 90% confidence limits for the parameters estimated from the pooled data for natural ecosystems, excluding the populations analysed individually.

The weight exponents of mortality in pond, cage and tank aquaculture systems were similar, and significantly more negative than the exponent estimated for natural ecosystems. Aquaculture weight exponents of mortality were also much more negative than the expected physiological exponent of predation mortality (Peterson & Wroblewski, 1984; Dickie *et al.*, 1987). Mortality rates at unit weight in aquaculture were significantly lower than in natural ecosystems.

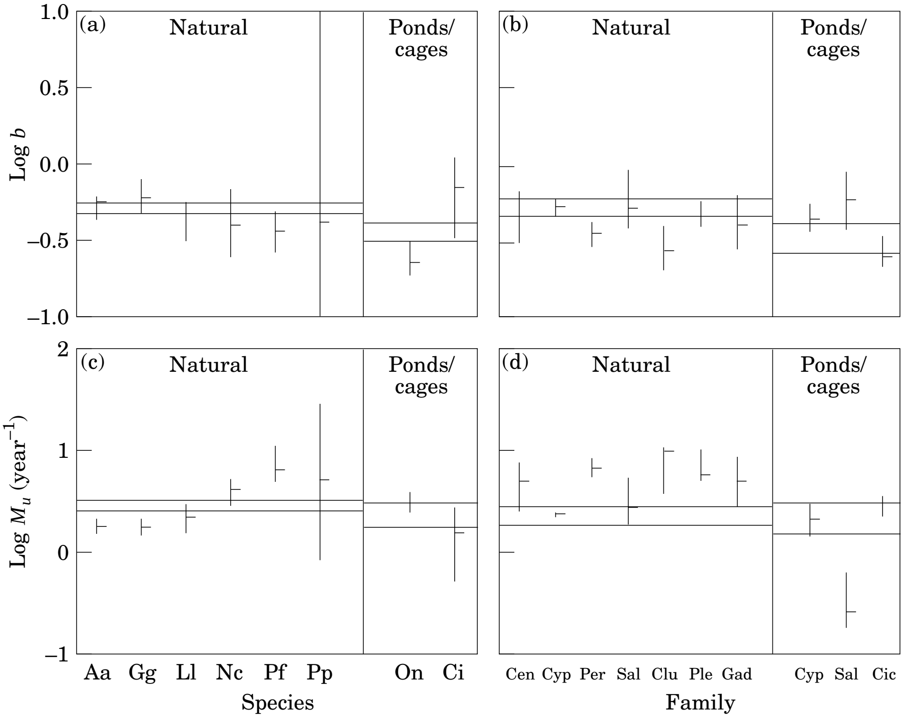

FIG. 4. Parameter estimates for within-species and within-family mortality–weight relationships. Exponent b (a) within species and (b) within families; mortality at unit weight M_u within species (c) and families (d). The species are (Aa) *Alburnus alburnus* L., (Gg) *Gobio gobio* L., (Ll) *Leuciscus leuciscus* L., (Nc) *Notemigonus crysoleucas* Mitchill, (Pf) *Perca flavescens* Mitchill, (Pp) *Pleuronectes platessa* L., (On) *Oreochromis niloticus* L., and (Ci) *Ctenopharyngodon idella* Cuvier & Valenciennes. Families are (Cen) Centrarchidae, (Cyp) Cyprinidae, (Per) Percidae, (Sal) Salmonidae, (Clu) Clupeidae, (Ple) Pleuronectidae, (Gad) Gadidae, and (Cic) Cichlidae. Theil estimates with 90% confidence limits. The horizontal lines indicate 90% confidence limits for the parameters estimated from the pooled data for natural ecosystems or pond/cage culture, excluding the populations analysed individually.

Latitudinal effects

No significant latitudinal effects were detected in natural ecosystems, possibly because the data were drawn largely from temperate populations with only a few mortality estimates in the tropical/sub-tropical and polar zones.

The data for pond/cage aquaculture were evenly distributed between the temperate and tropical/sub-tropical zones. No significant latitudinal differences were detected, and the estimated weight exponents were very similar. Mortality at unit weight in pond/cage culture appeared to be higher in the temperate than in the tropical/sub-tropical zone, but the difference was not statistically significant (Table II).

Individual populations, species and families

Mortality–weight relationships determined for the ecologically more homogeneous sub-groups of populations, species and families were occasionally, but not consistently different from the respective ecosystem relationships. This

TABLE III. Previous estimates of the allometric weight exponent of natural mortality M or equivalent parameters (intrinsic rate of natural increase r_m, and production-biomass ratio P/B) in natural ecosystems

Organisms	Parameter	Weight exponent b	Reference
Poikilotherms	r_m	− 0·275	Fenchel (1974)
Fish	P/B	− 0·26 [− 0·42, − 0·10]	Banse & Mosher (1980)
Marine fish (all life stages)	M	− 0·374 [− 0·390, − 0·358]	McGurk (1986, 1987)
Marine fish (juvenile and adult)	M	− 0·344 [− 0·400, − 0·288]	McGurk (1986, 1987)
Fish (juvenile and adult)	M	− 0·288 [− 0·315, − 0·261]	This study

All estimates were obtained from predictive linear regression on log transformed data, except for the present study which used the nonparametric Theil estimator. 90% confidence intervals are given where available. The exponent for juvenile and adult marine fish in McGurk (1986, 1987) has been estimated from the original data.

indicates that specific ecological processes only occasionally give rise to group-specific weight exponents that are significantly different from the overall fish community exponent.

Mortality at unit weight within population, species or family groups differed more often from the respective ecosystem value or from each other than the weight exponent, indicating that the overall level of mortality is more variable between groups than its allometric scaling.

Comparison to previous estimates

No previous study has been reported comparing mortality–weight relationships in fish between different natural ecosystems and culture systems. However, McGurk (1986, 1987) studied the mortality–weight relationship in marine fish. Also, the intrinsic rate of natural increase r_m and the production–biomass ratio P/B are expected to show the same allometric scaling as the mortality rate. The weight exponent b estimated in the present study for fish in natural ecosystems is consistent with the results of the previous studies, with the exception of McGurk's (1987) estimate for marine fish of all life stages (Table III). McGurk's study includes egg and larval mortality data, and hence its weight range extends to several orders of magnitude below that of the present study. If only juvenile and adult fish are considered, the predictive linear regression estimate of b obtained from McGurk's data is not significantly different from that obtained in the present study.

ECOLOGICAL IMPLICATIONS

Sources of mortality in natural ecosystems and in aquaculture

The principal sources of natural mortality in fish populations are predation, parasitism and infectious diseases, non-infectious diseases, starvation, and hostile environmental conditions. In natural ecosystems, predation is undoubtedly the dominant source of fish mortality (Forney, 1977; Pope & Knight, 1982; Peterson & Wroblewski, 1984; Sissenwine, 1984), but non-predation mortality due to diseases, lethal abiotic conditions, or winter starvation is also present and well documented (Morgan, 1972; Fryer & Iles, 1972; Flath & Diana, 1985;

Sindermann, 1987; Post & Evans, 1989). In aquaculture, mortality is dominated by non-predation sources such as diseases, water quality problems, or winter starvation (Spangenberg & Schreckenbach, 1984; Roberts, 1989; Pillay, 1990). Predation is much reduced in aquaculture as compared to natural ecosystems, but is not entirely absent (Degani & Levanon, 1983; Huet, 1986; Pillay, 1990; Carss, 1993).

If predation is a minor source of mortality in aquaculture, then the observed mortality–weight relationships in ponds/cages and tanks indicate the allometric scaling of the susceptibility of fish to non-predation mortality. The very consistent estimates of the weight exponent in different aquaculture systems support this conclusion. The weight exponent of mortality is more negative in aquaculture than in natural ecosystems, suggesting that non-predation mortality is more strongly weight-dependent than predation mortality. The overall higher mortality rates in ponds and cages are likely to be attributable to sources of mortality that are enhanced at high population densities in semi-natural ecosystems, such as infectious diseases or water quality problems. In tank systems, a high degree of control over pathogens and environmental factors appears to mitigate the detrimental effects of high density.

The susceptibility of wild and farmed fish to non-predation mortality is likely to be determined by the same factors, such as the ontogenic development of the immune system, the ability to survive hostile environmental conditions, or available energy reserves (Ellis, 1988; Post & Evans, 1989; Kalinin *et al.*, 1993). Therefore, non-predation mortality in fish in natural ecosystems can be expected to show a similar scaling with body weight as observed in farm fish. The absolute level of non-predation mortality in natural ecosystems is more difficult to assess, and may also be more variable.

Predation mortality–weight relationship in natural ecosystems

If mortality in natural ecosystems comprises a predation and a non-predation component, and the weight exponents of total natural mortality as well as its non-predation component are known, then this provides a clue to the scaling of predation mortality with body weight. Assuming that the predation and non-predation components of natural mortality are additive, predation mortality $M_{W,P}$ at weight W can be written as the difference between the total natural mortality rate M_W and the non-predation mortality rate $M_{W,\ NP}$:

$$M_{W,P}=M_W-M_{W,NP}=M_uW^b-M_{u,NP}W^{b_{NP}} \quad (3)$$

Here, b and M_u are the parameters of the total natural mortality–weight relationship, and b_{NP} and $M_{u,NP}$ are the parameters of non-predation mortality. Obviously equation (3) applies only when $M_{W,NP}$ is smaller than or equal to M_W, so that the predation mortality $M_{W,P}$ is greater than or equal to zero. The present empirical study provides parameter estimates of $b=-0{\cdot}29$, $M_u=3{\cdot}0$ year^{-1}, and $b_{NP}=-0{\cdot}43$. The non-predation mortality rate at unit weight $M_{u,NP}$ in natural ecosystems can only be estimated on the basis of external information. The predation mortality–weight relationship defined by equation (3) is not a power function, and therefore does not provide a direct estimate of the allometric exponent. However, if non-predation mortality is relatively low

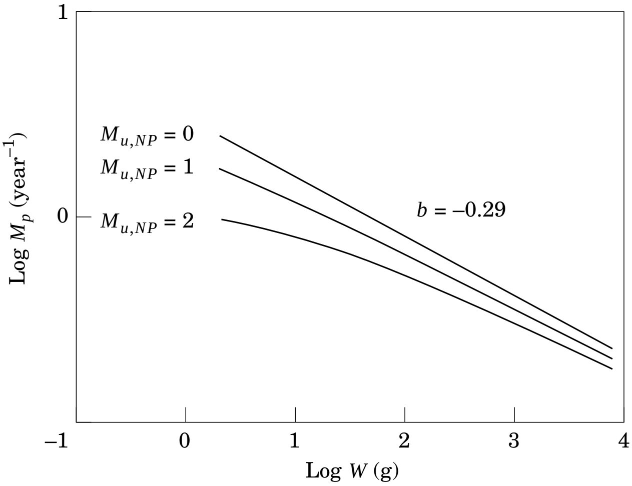

FIG. 5. Predation mortality $M_{W,P}$ in natural ecosystems, estimated as the difference between total natural mortality M_W ($b = -0{\cdot}29$, $M_u = 2{\cdot}85$ year^{-1}) and non-predation mortality $M_{W,NP}$ ($b_{NP} = -0{\cdot}43$). Values of the non-predation mortality rate at unit weight $M_{u,NP}$ are 0, 1, and 2 year^{-1}, so that non-predation mortality accounts for 0, 33, and 67% of total mortality in small fish of 1 g.

and its weight exponent is more negative than that of total mortality, then the contribution of non-predation mortality to the total is greatest in small fish, and decreases with increasing weight. Consequently, predation mortality declines less steeply with weight than total mortality, and the weight exponent of any allometric (power function) approximation to predation mortality must be less negative than that of total mortality. This is shown algebraically in Appendix A to hold for any weight W^* at which M_{W^*NP} is less than M_{W^*}.

Predation mortality–weight relationships calculated from equation (3) are illustrated in Fig. 5, for the estimated parameters $b = -0{\cdot}29$, $M_u = 3{\cdot}0$ year^{-1} and $b_{NP} = -0{\cdot}43$. Non-predation mortality at unit weight $M_{u,NP}$ was assigned values of 0, 1, and 2 year^{-1}, corresponding to 0, 33, and 67% of total natural mortality at unit weight. For $M_{u,NP} = 0$ year^{-1}, non-predation mortality is absent and consequently predation mortality equals total natural mortality and has the same weight exponent. For $M_{u,NP} = 1$ and 2 year^{-1}, the predicted predation mortality–weight relationships depart visibly from power functions, but could well be approximated over any particular weight range by power functions with exponents less negative than $b = -0{\cdot}29$.

The difference found in juvenile and adult fish between the observed (ecological) weight exponent of total natural mortality and the expected (physiological) weight exponent of predation mortality can be explained by the presence of a moderate level of non-predation mortality, with a weight exponent more negative than that of total mortality. This suggests more generally that non-predation mortality is a factor to consider in the interpretation of ecological mortality–weight relationships, in addition or alternative to factors that have been proposed to alter the weight exponent of the predation component of natural mortality from its expected physiological value (McGurk, 1986, 1987; Dickie *et al.*, 1987).

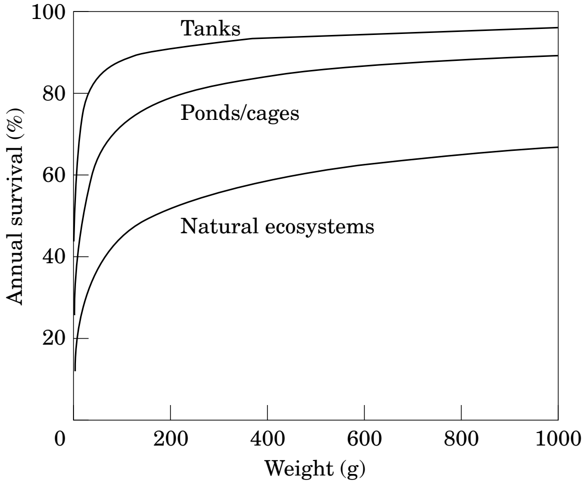

FIG. 6. Average annual survival in fish in natural ecosystems, pond/cage and tank aquaculture in relation to body weight.

PRACTICAL IMPLICATIONS FOR AQUACULTURE AND CULTURE-BASED FISHERIES

The following sections discuss briefly implications of the established mortality–weight relationships for aquaculture and culture-based fisheries. The implications of size-dependent mortality for the assessment and management of capture fisheries have been discussed elsewhere (Anderson, 1988; Gulland, 1987).

Survival and size in different aquaculture systems

In aquaculture, the survival of fish over a culture period is of more direct interest than the instantaneous rate of mortality. It is therefore useful to convert mortality rates into annual survival. Survival increases rapidly with weight in small fish, but changes little once fish have reached a weight of about 200 g (Fig. 6). The greatest differences in survival between unexploited natural ecosystems and pond/cage and tank aquaculture systems occur in small fish. At a body weight of 1 g for example, the average annual survival is 5% in natural ecosystems, 10% in ponds or cages, and 40% in tanks. At a weight of 1000 g, the average annual survival in unexploited natural ecosystems is 66%, compared to 87% in ponds or cages, and 95% in tanks.

Expected survival is one of the criteria that must be considered in the design of aquaculture systems. The analysis of mortality–weight relationships suggests that on average, pond and cage systems can be expected to yield similar survival over the full weight range of farmed fish. Survival in tanks is higher on average than in ponds or cages. The improvement in survival achieved in tanks over ponds or cages is substantial in small fish (300% at 1 g), but only moderate in large fish (< 10% at 1000 g). Given that the investment and operating costs of tank systems are likely to be higher than those of pond or cage farms, and other things being equal, this suggests that small fish are best nursed in tanks, and transferred to ponds or cages for grow-out. Such a pattern of transfer from tanks into ponds or cages as fish grow is borne out in many established aquaculture systems, and the analysis of mortality–size relationships thus corroborates the conventional wisdom of aquaculturalists. The quantitative relationships established here can aid the design of and production planning in aquaculture systems if more specific data are not available.

The estimated mortality–weight relationships describe average mortality. There is considerable variation around these relationships (Fig. 1) and the ranges of observed mortality at weight in the different aquaculture systems overlap completely. Part of the observed variation is likely to be explicable in terms of the species cultivated, and details in the design and management of particular facilities. In practice, management capability, for example, may have a greater bearing on survival rates than the fundamental choice of facility (i.e. tank, pond or cage).

Stocking size in culture-based fisheries

Culture-based fisheries are capture fisheries based on the regular stocking of farm-produced juvenile fish into natural or semi-natural water bodies. A key management problem in culture-based fisheries is the development of optimal stocking strategies, including size and density of seed fish. The effect of seed fish size on survival to harvest is largely determined by the mortality–weight relationship, and a population model incorporating this relationship can be used to assess the optimal stocking size and corresponding density (Lorenzen, 1995). The use of a population model based on the mortality–weight relationship demands that a constant relationship adequately describes the dynamics of the population. Certain populations exhibit regulatory mechanisms such as territoriality and/or cannibalism, which in effect make the mortality–weight relationship (b and/or M_u) a function of density, and therefore require a different model formulation.

The effects of stocking size and density on production in populations subject to a constant, known mortality–weight relationship are demonstrated in Lorenzen (1995). The present empirical study provides *a priori* estimates of the weight exponent of natural mortality that can be used to assess stocking size and density when population-specific data are not available. Similar mortality–weight relationships can be expected in fish in all natural aquatic ecosystems. Within-population weight exponents of mortality are unlikely to differ strongly from the overall fish community exponent of about $-0{\cdot}3$. The estimates of the weight exponent obtained for individual populations, species and families suggest that for any particular group, the exponent is likely to be within the range of $-0{\cdot}5$ to $-0{\cdot}2$. More precise and population-specific estimates can be obtained from stocking experiments. The information derived from the present analysis allows an assessment of the likely benefits and costs of conducting stocking experiments.

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APPENDIX A

WEIGHT EXPONENT OF PREDATION MORTALITY

In equation (3), predation mortality $M_{W,P}$ is defined as the difference between total natural M_W and non-predation mortality $M_{W,NP}$, assuming that $M_{W,NP}$ is smaller than or equal to M_W:

$$M_{W,P}=M_W-M_{W,NP}=M_uW^b-M_{u,NP}W_{b_{NP}} \tag{A1}$$

The difference between two power functions is not itself a power function, and therefore equation (A1) does not provide a general estimate of the weight exponent of predation mortality. However, an exponent of predation mortality can be derived for any arbitrary weight W^* under the assumption that at this particular weight, $M_{W^*,P}$ as defined by equation (A1) is also equal to a power function of weight:

$$M_{u,P}W^{*b_P}=M_uW^{*b}-M_{u,NP}W^{*b_{NP}} \tag{A2}$$

The derivative of predation mortality at W^* must equal the difference between the derivatives of total natural and non-predation mortality, and consequently:

$$b_pM_{W^*,P}=bM_{W^*}-b_{NP}M_{W^*,NP} \tag{A3}$$

This can be rewritten in the following form to allow an assessment of the possible values of b_P:

$$b_P = b + \frac{M_{W*,NP}}{\mathrm{M}_{W*,P}}(b - b_{NP}) \qquad \text{(A4)}$$

The factor $M_{W*,NP}/M_{W*,P}$ is always positive, and it follows that

(1) if $b_{NP}=b$ then $b_P=b$,

(2) if $b_{NP}>b$ then $b_P<b$, and

(3) if $b_{NP}<b$ then $b_P>b$.

APPENDIX B

SOURCES OF MORTALITY DATA

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