

Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes

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Abstract: This study evaluates the use of general mortality–size relationships for the assessment of release size in stocked fisheries. Seven release experiments (53 stocking events) are analysed, using a survival model based on allometric mortality and linear-length growth, allowing variation between experiments in both the allometric exponent and the level of mortality at reference length or generalising in one or both of the parameters. Results support the existence of a consistent allometry that applies independently of the overall level of mortality. The best-performing model is one in which the length exponent of mortality is set to -1 a priori, while mortality at reference length is allowed to vary between experiments (ranging from 0.7 to 33 per year at 15 cm in the present study). Even though the allometry of mortality is constant, the relative survival advantage of stocking large fish increases with the level of mortality at reference length. Using the identified length exponent of mortality of -1 , survival models are derived for the linear, exponential, and von Bertalanffy growth equations. The models can be used to assess alternative release sizes, given an estimate of mortality at reference length, to facilitate comparative studies and to aid in the design of release experiments.

Résumé : Le but de cette étude est d'évaluer l'utilité des relations générales entre la mortalité et la taille pour établir la taille des poissons à l'ensemencement dans les pêches qui dépendent de l'alevinage. Sept expériences d'ensemencement (53 événements) servent de base à des analyses à l'aide d'un modèle de survie basé sur une mortalité allométrique et une croissance en longueur linéaire, qui permet des variations, d'une expérience à l'autre, tant du coefficient d'allométrie que du taux de mortalité à la longueur de référence, ou alors qui autorise des généralisations de l'un ou de l'autre de ces variables. Les résultats laissent croire à l'existence d'une allométrie uniforme qui s'applique indépendamment du taux global de mortalité. Le modèle le plus performant est celui où l'exposant de la longueur dans l'estimation de la mortalité est fixé a priori à -1 , alors que la mortalité à la longueur de référence peut varier d'une expérience à l'autre (allant de 0,7 à 33 par année à 15 cm dans notre étude). Bien que l'allométrie de la mortalité soit constante, l'avantage relatif pour la survie d'ensemencer avec de plus gros poissons s'accroît avec le taux de mortalité à la longueur de référence. En utilisant un exposant de la longueur de -1 , j'ai pu élaborer des modèles de survie incorporant les équations de croissance linéaire, exponentielle et de von Bertalanffy. Les modèles peuvent servir à évaluer les effets des ensemencements à différentes tailles pour une estimation donnée de la mortalité à la taille de référence; ils peuvent aussi faciliter les études comparatives et contribuer à l'élaboration d'expériences d'ensemencement.

[Traduit par la Rédaction]

Introduction

Stocking is widely used in the management of freshwater and, to a lesser extent, coastal-marine fisheries (e.g., Leber and Blankenship 1995; Welcomme and Bartley 1998; Heindinger 1999). A key problem in the management of stocked fisheries is the optimisation of release size (e.g., Cowx 1994; Leber and Blankenship 1995). The optimal release size depends on the contribution that fish of a particular size will make to the catch or fishable stock and on the resources required to produce seed fish of that size. Of the data required

to assess optimum size, the expected survival of seed fish of different sizes to the fishable stock (and (or) contribution to the catch) are the most difficult to obtain. Systematic assessments have been either entirely empirical (release–recapture of marked seed fish of different sizes) or based on detailed ecological studies (Wahl et al. 1995; Szendrey and Wahl 1996). However, the costs and effort involved in both approaches restrict their use to a small number of fisheries, and the results are not readily generalised. An alternative approach that implies a simple generalisation is the use of allometric mortality–size relationships (Lorenzen 1995; Lorenzen et al. 1997). Provided that natural mortality in stocked fish is subject to a consistent allometry, then an estimate of mortality for a single reference size is sufficient to predict survival for a range of different release sizes.

Theoretical and empirical studies (Peterson and Wroblewski 1984; McGurk 1986; Lorenzen 1996) point to the existence of an allometric relationship between natural mortality and body weight, in fish, of the form:

$$(1) \quad M_w = M_u W^b$$

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where M_w is natural mortality at weight W , M_u is mortality at unit weight, and b is the allometric exponent. Empirical studies combining data from a large number of populations have yielded estimates for the exponent b of -0.37 for marine fish of all life stages (predictive regression; McGurk 1986) and of -0.29 for juvenile and adult freshwater and marine fish (nonparametric regression; Lorenzen 1996). The study by Lorenzen (1996) also indicates that within-population estimates of b rarely differ significantly from the overall average. Given that weight is approximately proportional to the third power of length, b values of approximately $-1/3$ imply that natural mortality is inversely proportional to body length. An inverse relationship between natural mortality and fish length has been assumed in a number of population-dynamics studies (e.g Logan 1985; Beyer et al. 1999) but has not been tested explicitly.

Allometric mortality–size relationships have been used in a theoretical study of the population dynamics of stocked fisheries (Lorenzen 1995) and in a practical assessment of a culture-based fishery (Lorenzen et al. 1997). However, the general applicability of such relationships to the analysis of stocking experiments has not yet been tested. In particular, it is unclear whether the mortality of stocked fish is subject to a consistent allometric relationship and, if so, whether the allometry is the same as that observed in wild fish.

The purpose of the present study is to test the applicability of survival models based on allometric mortality–size relationships to the analysis of stocking experiments, and to provide practical models for the assessment of release size based on such relationships. An equation is derived to predict the survival of stocked fish from length at release, based on linear-length growth and allometric mortality equations. Alternative models based on this survival equation, but assuming different generalisations in the mortality–size relationship, are used to analyse a set of stocking experiments. Results support the hypotheses that survival of stocked fish is governed by a consistent allometry and that the length exponent of the relationship is approximately -1 (i.e., mortality is inversely proportional to length). The dynamics of survival implied by this relationship are explored. Finally, survival models based on this relationship are presented for linear, exponential, and von Bertalanffy growth equations, and their use in practical assessments is discussed.

Materials and methods

Empirical data

Seven published stocking experiments comprising a total of 53 stocking events (cohorts stocked) were identified from the literature. Criteria for selection were the reporting of true-survival estimates (as opposed to recapture in the fishery or other measures of relative survival), the number of stocking events, and the range of release sizes. Key information on the studies selected is given in Table 1. Each study is restricted to a single species and water body, but often comprises experiments carried out over more than 1 year. The time at large between stocking and survival estimate ranged from 0.1 to 1.3 years. Because the time at large was generally short, growth was described by a linear length growth rate (see below). Average linear-growth rates, u , were estimated from data for the populations analysed, except for studies A and B, in which cases data for neighbouring populations reported in the same publication (Margenau 1992) were used. Refer to Seber (1982) for a de-

Table 1. Details of stocking experiments analysed.

Experiment	Species	Location	N	l_0	t	u	Method	Reference
A	<i>Esox masquinongi</i>	Clear Lake, Wis., U.S.A.	6	20–28	0.10–0.16	11	SMR	Margenau 1992
B	<i>Esox masquinongi</i>	Twenty-six Lake, Wis., U.S.A.	6	20–28	0.11–0.17	11	SMR	Margenau 1992
C	<i>Esox masquinongi</i>	Lake George, Ill., U.S.A.	6	11–25	0.16–0.50	20	SEMR	Szendrey and Wahl 1996
D	<i>Oncorhynchus mykiss</i>	Englishman River, B.C., Canada	9	3–8 ^a	0.67–1.08	5 ^a	SLD	Hume and Parkinson 1988
E	<i>Oncorhynchus mykiss</i>	Moriarty Creek, B.C., Canada	10	3–8 ^a	0.67–1.08	5 ^a	SLD	Hume and Parkinson 1988
F	<i>Stizostedion vitreum</i>	East Okerboji Lake, Iowa, U.S.A.	7	1–13	0.04–0.54	17	SEMR	Larscheid 1995
G	<i>Stizostedion vitreum</i>	Ridge Lake, Ill., U.S.A.	9	5–22	0.83–1.33	10	PMR	Santucci and Wahl 1993

Note: N , number of stocking events; l_0 , length at release (cm); t , time at large (years); u , linear length growth rate (cm/year; eq. 4); abbreviations used for method of estimating survival: PMR, Petersen mark-recapture; SEMR, Schumacher–Eschmeyer multiple mark – recapture; SLD, Seber–Le Cren depletion sampling; SMR, Schnabel mark-recapture.

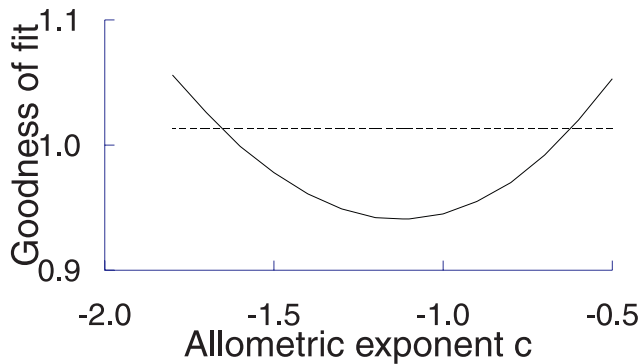
^aLength (L) data converted from weight (W), using $L = 4.68 W^{0.32}$.

Table 2. Parameter estimates and goodness-of-fit criteria.

	Model 1		Model 2		Model 3		Model 4		Model 5	
	M_r	c	M_r	c	M_r	c	M_r	c	M_r	c
Experiment										
A	10.8	-1.18	10.5	-1.12	9.9	-1	4.2	0.68	5.5	0.95
B	23.6	-1.79	17.1	-1.12	16.1	-1	4.2	1.58	5.5	0.95
C	135.8	-5.21	20.7	-1.12	19.8	-1	4.2	4.44	5.5	0.95
D	0.9	-0.80	0.7	-1.12	0.8	-1	4.2	0.95	5.5	0.95
E	0.9	-0.60	0.6	-1.12	0.7	-1	4.2	1.22	5.5	0.95
F	2.2	-24.58	32.3	-1.12	32.7	-1	4.2	-19.11	5.5	0.95
G	3.7	-1.74	3.1	-1.12	3.0	-1	4.2	-2.01	5.5	0.95
SSQ		0.741		0.941		0.945		1.966		6.096
n		53		53		53		53		53
m		14		8		7		7		2
$SSQ(n - 2m)^{-1}$		0.030		0.025		0.024		0.050		0.124

Note: M_r is the mortality at reference length $l_r = 15$ cm, c is the allometric length exponent of mortality, n is the number of observations, m is the number of parameters estimated, and $SSQ(n - 2m)^{-1}$ is the goodness-of-fit criterion.

Fig. 1. Goodness-of-fit profile (sum of squares (SSQ)) of the allometric mortality exponent, c , using model 2. The horizontal line defines the approximate 95% confidence interval for c .



scription of the methods used to estimate post-stocking abundance and survival.

Survival model

The allometric relationship between natural mortality and body length may be described by the equation

$$(2) \quad M_l = M_r \left(\frac{l}{l_r} \right)^c$$

where M_l is the mortality rate at length l , M_r is the instantaneous mortality rate at reference length l_r , and c is the allometric exponent of the mortality-length relationship.

If this relationship governs mortality in the stocked population, then the decline in numbers, N , of a stocked cohort (organisms of the same age and size) is described by the differential equation

$$(3) \quad \frac{dN_t}{dt} = -N_t M_r \left(\frac{l_t}{l_r} \right)^c$$

where l_t is length at time t . This differential equation may be solved explicitly if a growth model is substituted for l_t . A linear length growth model is used in the empirical analysis, because time at large is short and the size of the fish is small relative to the reported maximum sizes in all stocking experiments analysed (Table 1). A model of the form

$$(4) \quad l_t = l_0 + ut$$

is used, where l_0 is the length at stocking, t is the time since stocking, and u is the linear length growth rate. Substitution of eq. 4 into eq. 3, integration, and division by N_0 on both sides gives the following equation to predict survival, S_t (proportion of stocked fish surviving), from the time of stocking to time t :

$$(5) \quad S_t = \frac{N_t}{N_0} = \begin{cases} \left(\frac{l_0}{l_0 + ut} \right)^{\frac{M_r l_r}{u}} & (\text{for } c = -1) \\ e^{-\frac{M_r \left(l_0 \left(\frac{l_0}{l_r} \right)^c + (l_0 + ut) \left(\frac{l_0 + ut}{l_r} \right)^c \right)}{(1+c)u}} & (\text{for } c \neq -1) \end{cases}$$

Analysis

To test whether the observed patterns in survival are consistent with the hypothesis of a single underlying allometry, five different models are fitted to the full data set:

- (6) Model 1: $S = f(l_r, l_{0i}, t_i, u_j \mid M_j, c_j)$
- Model 2: $S = f(l_r, l_{0i}, t_i, u_j \mid M_j, c)$
- Model 3: $S = f(l_r, l_{0i}, t_i, u_j \mid M_j, -1)$
- Model 4: $S = f(l_r, l_{0i}, t_i, u_j \mid M, c_j)$
- Model 5: $S = f(l_r, l_{0i}, t_i, u_j \mid M, c)$

where the index i denotes individual stocking events ($i = 1$ to 53), and j denotes the experiment ($j = A-G$). While in model 1, both M_r and c are estimated separately for each experiment, the other models generalise across experiments by estimating a single value for either or both of the parameters. In model 3, c is not estimated but is fixed at -1 a priori, reflecting the assumption that mortality is inversely proportional to length.

Because the survival estimates have been obtained using a variety of different methods, they do not have a coherent error structure, making the application of maximum-likelihood methods difficult. Hence, the models are fitted by the method of least squares, applying an arcsine square-root transformation to observed and predicted survival, to stabilise the variance. The sum of squares (SSQ) is thus defined as

Fig. 2. Observed (■) and predicted (●) (model 3) survival in the seven stocking experiments analysed. Letters refer to the experiment codes in Table 1. Confidence limits (95%) are indicated when available from the original publication.

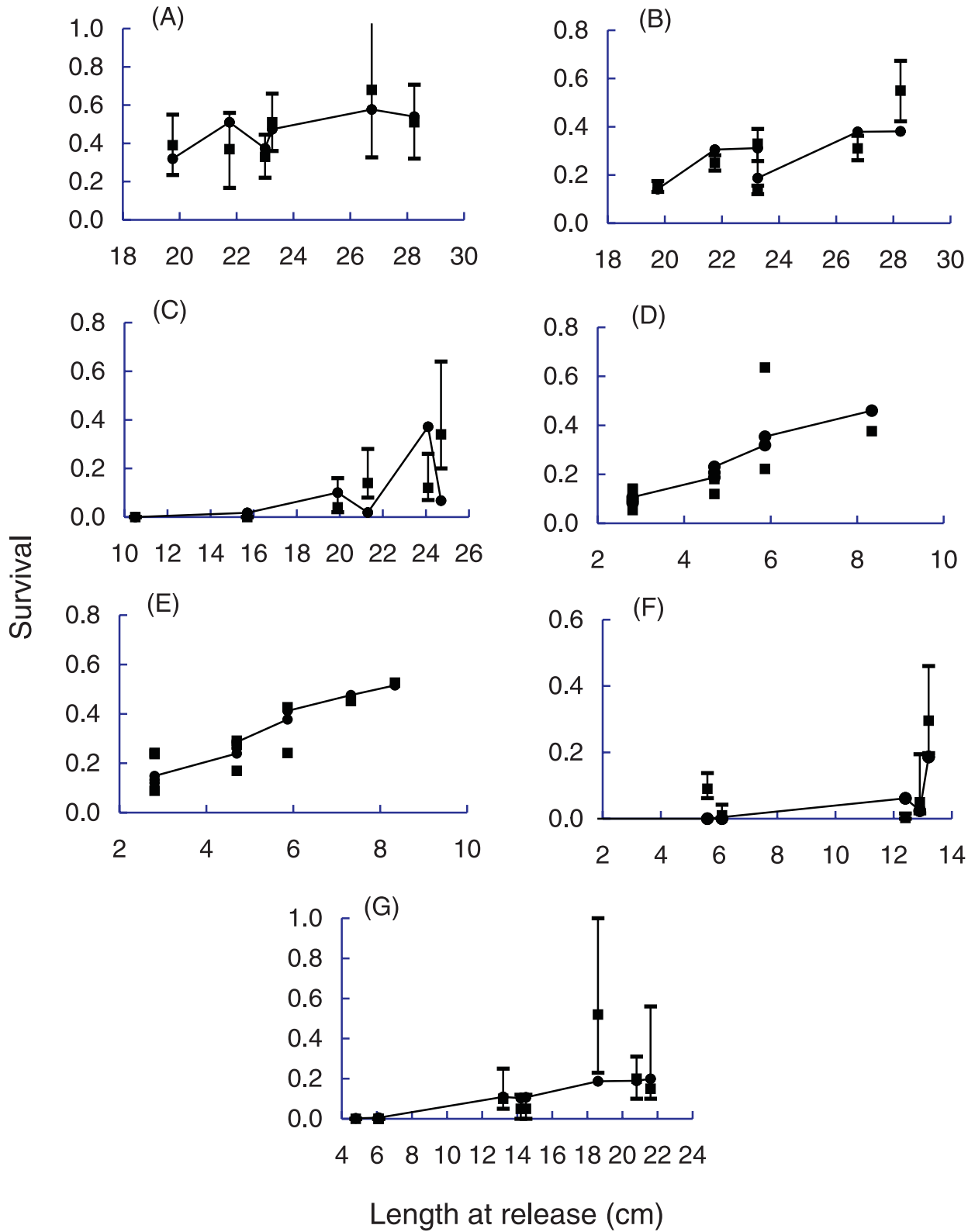
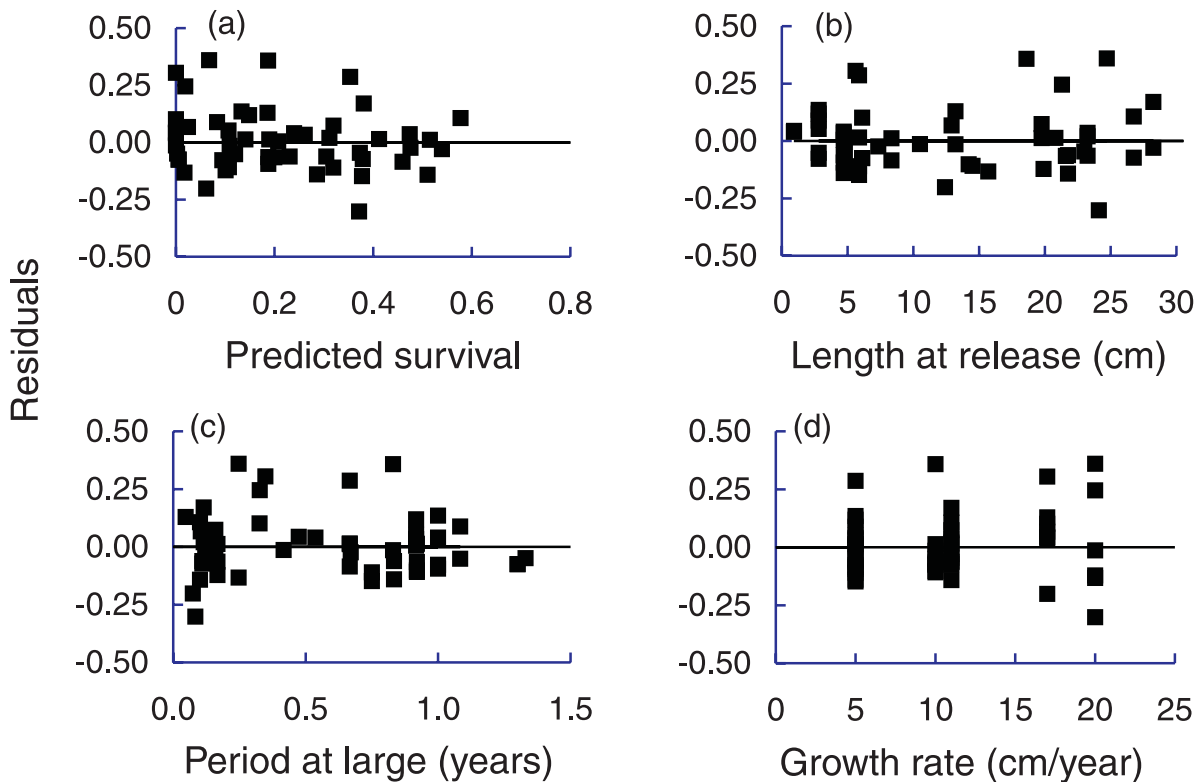


Fig. 3. Diagnostic plots of model 3 ($c = -1$) residuals against predicted survival (a), length at release (b), period at large (c), and growth rate (d).



$$(7) \quad SSQ = \sum_{i=1}^n \left(\arcsin \sqrt{S_{i,o}} - \arcsin \sqrt{S_{i,p}} \right)^2$$

with $S_{i,o}$ the observed survival and $S_{i,p}$ the survival predicted from eq. 5. To compare the alternative models, the criterion

$$(8) \quad \frac{SSQ}{n - 2m}$$

is used, where n is the number of observations and m is the number of parameters estimated (Hilborn and Mangel 1997). The model with the lowest value of the criterion is selected as the best model.

A goodness-of-fit (SSQ) profile was generated for the allometric exponent c (Hilborn and Mangel 1997). Approximate confidence bounds for c were determined from the profile as the values of c that satisfy

$$(9) \quad SSQ(c) = SSQ(\hat{c}) \left(1 + \frac{1}{n-1} F(1, n-1, 1-\alpha) \right)$$

where $SSQ(\hat{c})$ is minimum SSQ, F is the F distribution, and $1-\alpha$ is the confidence level (Draper and Smith 1981).

Results

Parameter estimates and goodness-of-fit criteria for the alternative models (eq. 6) are given in Table 2. Models 2 and 3, based on a generalised allometry with variable M_r , provide the best fit. The estimate of c in model 2 is -1.12 , close to the value of -1 assumed a priori in model 3. Model 3 provides the best fit overall, with the reduction in the number of parameters to be estimated outweighing the slight increase in SSQ compared with model 2. Models 4 and 5, assuming

constant M_r and variable or constant allometric exponent c , perform far worse than the others. Overall, these results indicate that, while the allometric exponent c can be generalised across experiments, M_r is too variable to be generalised.

A goodness-of-fit profile for the allometric exponent c is shown in Fig. 1. The approximate 95% confidence interval for c is $(-1.66$ to $-0.62)$ and the profile is fairly flat between -1.3 and -1.0 .

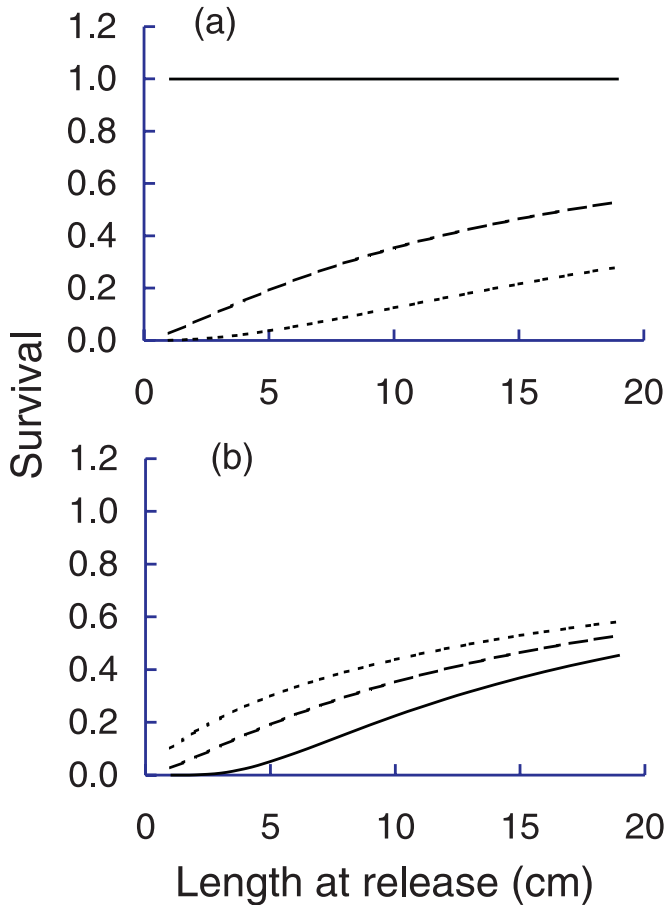
Model 3, with $c = -1$, is therefore selected as the best-performing model. A comparison of observed survival and model 3 predictions for the seven studies is shown in Fig. 2. Note that, because periods at large, t , vary between stocking events, data and model predictions do not form a smooth curve. In most studies, there is close correspondence between observed and predicted patterns. Relatively large deviations in experiments C and F reflect strong interannual variation in survival.

In Fig. 3, residuals of model 3 are plotted against predicted survival and the independent variables. No systematic patterns are apparent, apart from a small cluster of mainly positive residuals for periods at large between 0.2 and 0.6 years in Fig. 3c.

Discussion

Results from the present analysis show that stocking experiments with fish of different release sizes can be analysed and interpreted on the basis of allometric mortality-size relationships, with a constant allometric scaling and population-specific mortality at reference size. This result lends further support to the existence of a fundamental allometry of

Fig. 4. Relationships between release size and survival for different mortalities at reference length (M_r ; solid line, $M_r = 0/\text{year}$; dashed line, $M_r = 1/\text{year}$; dotted line, $M_r = 2/\text{year}$) (a) and different growth rates (u ; solid line, $u = 0 \text{ cm/year}$; dashed line, $u = 10 \text{ cm/year}$; dotted line, $u = 20 \text{ cm/year}$) (b). All predictions are based on model 3 ($c = -1$), with $u = 10 \text{ cm/year}$ in a and $M_r = 1/\text{year}$ in b. The dashed line is identical in the two graphs.



mortality that applies to stocked as well as wild fish in natural ecosystems. The allometric exponent is far more stable between populations than the overall level of mortality. Moreover, the simple assumption that mortality is inversely related to fish length, corresponding to a weight exponent of $-1/3$, was found to be adequate for the analysis of release size. This relationship is mathematically convenient, because it leads to relatively simple survival equations for stocked fish.

The dynamics of survival in relation to release size implied by model 3 ($c = -1$) with different levels of M_r is illustrated in Fig. 4. Figure 4a shows the effect on survival of different M_r (0, 1, and 2/year) at a constant growth rate, u , of 10 cm/year. Note that the relative size dependence of survival increases with M_r , i.e., constant allometry of mortality does not imply constant relative survival at different release sizes. The higher the overall level of mortality (M_r), the greater the relative survival advantage of large release sizes, a prediction consistent with the observation that high levels of predation require large seed fish for stocking (e.g., Heidinger 1999). Figure 4b shows the effect on survival of

different linear-growth rates, u (0, 10, and 20 cm/year), for constant M_r (1/year). Survival increases with increasing growth rate, but the effect is far less pronounced than that of differences in M_r (Fig. 4a). Note that, in the seven studies analysed, estimates of M_r ranged from 0.7 to 33/year (a range far wider than the 0–2/year plotted in Fig. 4a), while estimates of the average growth rate, u , ranged from 5 to 20 cm/year (less than the range of 0–20 cm/year plotted in Fig. 4b). Hence, variation in the overall level of mortality (measured by M_r) is likely to play a more important role in determining optimal stocking size and the viability of enhancements than variation in growth.

Results of the present study indicate that survival models based on allometric mortality–length relationships with $c = -1$ and population-specific M_r provide practical tools for assessing optimal release size in stocking programmes. A linear length growth model was used in the analysis, because periods at large were short and fish were small relative to the asymptotic sizes reported for the respective species. However, when using allometric mortality models to predict survival over longer time periods, linear-growth models may no longer be adequate. Exponential and von Bertalanffy growth models may be substituted into eq. 3 and, in the case of $c = 1$, integration leads to the fairly simple survival equations given in Table 3. The application of these survival models to the analysis and prediction of stocking outcomes requires an estimate of M_r in the population in question (as well as the growth parameters). Estimation of M_r requires data on the absolute post-stocking abundance of the stocked fish; an indicator of relative survival such as the recapture rate, which reflects a combination of survival and harvesting effort, is not sufficient. If absolute-survival data are available from stocking with a particular release size, the use of the equations in Table 3 to assess the survival of alternative sizes is straightforward.

If only recapture (rather than absolute survival) has been estimated, there is a range of possible responses in recapture to changes in release size, which is dependent on the underlying true survival. To illustrate this in a simple example, assume that the recapture rate from a brief fishing event at time t after release is available. Recapture R_t is then the product of survival to time t and the proportional harvest rate H :

$$(10) \quad R_t = S_t H$$

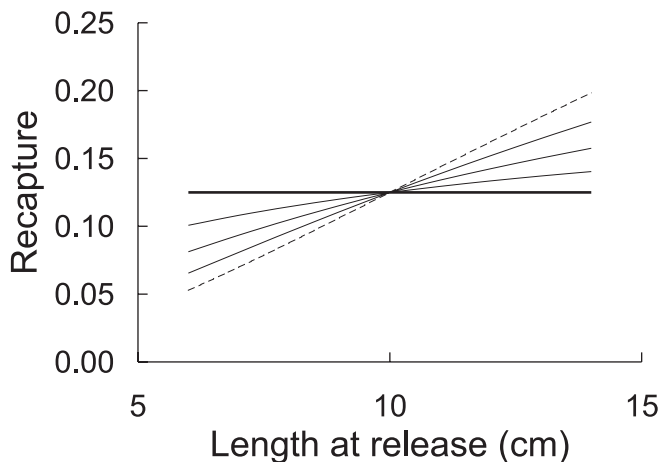
For a given R_t , absolute survival S_t must be between 1 (no natural mortality, $R_t = H$) and R_t (complete harvesting, $R_t = S_t$). These extremes define the range of possible responses to changes in release size, from size-independent survival at $S_t = 1$ (and therefore $M_r = 0$) to the most strongly size-dependent survival at $S_t = R_t$. This is illustrated in an example (Fig. 5) for a known recapture of $R_t = 0.125$ for 10-cm seed fish ($t = 1 \text{ year}$, $u = 10 \text{ cm/year}$). The range of possible responses is bounded by the extreme cases of $S = 1$ and $S = 0.125$. Although the exact response cannot be predicted without knowledge of M_r , even a bounded range of possibilities may aid management decision making and the design of experiments to resolve the remaining uncertainty. Moreover, it may often be possible to identify a likely range for the harvest rates in a fishery and, therefore, narrow down the range of possibilities. However, in practice, the analysis of

Table 3. Equations to predict the survival of stocked fish to time t after release (S_t) for $c = -1$ (mortality inversely proportional to length), and linear, exponential, and von Bertalanffy growth models.

Growth model	Growth equation	Survival equation
Linear	$l_t = l_0 + ut$	$S_t = \left(\frac{l_0}{l_0 + ut} \right)^{\frac{M_r l_r}{u}}$
Exponential	$l_t = l_0 e^{Gt}$	$S_t = e^{-\frac{M_r l_r (e^{Gt} - 1)}{l_0 G}}$
von Bertalanffy	$l_t = l_\infty - (l_\infty - l_0)e^{-kt}$	$S_t = \left(\frac{l_0}{l_0 + l_\infty (e^{kt} - 1)} \right)^{\frac{M_r l_r}{l_\infty k}}$

Note: l_t , length at time t ; l_0 , length at stocking; u , linear-length growth rate; G , exponential-length growth rate; l_∞ , asymptotic length; k , von Bertalanffy growth rate; M_r , mortality rate at reference length l_r .

Fig. 5. Possible responses in recapture (R) to changes in release size, when recapture is known for a single release size but absolute survival is not known. The extreme cases of $S = 1$ (thick solid line) and $S = R$ (thick dashed line) define the boundaries of possible relationships, with examples of intermediate relationships shown as thin solid lines. In this example, $R = 0.125$ for l_0 (release size) = 10 cm and $u = 10$ cm/year, and the extreme values of mortality are $M_r = 0$ /year (solid line, $S = 1$) and $M_r = 2$ /year (dashed line, $S = 0.125$).



recaptures for a range of release sizes may also be complicated further by differences in harvest rates (related to, for example, differential size and habitat use at the time of harvesting). Differences in harvest rates are implicitly accounted for when absolute-abundance estimates are used, but may be difficult to separate from true differences in survival when only recapture data are available.

Although the studies analysed are unlikely to be representative of stocking programmes, and the levels of mortality should not be taken as indicative of the survival of stocked fish in general, it is interesting to compare the M_r estimates with values measured in natural populations. Based on length–weight relationships given in Carlander (1953, 1969), the approximate weight at a length of 15 cm is 15 g for *Esox*

masquinongi and 35 g for *Oncorhynchus mykiss* and *Stizostedion vitreum*. Substituting these values into the empirical natural mortality – weight relationship for natural fish populations, $M = 3W^{-0.29}$ (Lorenzen 1996), gives expected values of M_r (at 15 cm) of 1.4 and 1.1 for natural populations of *E. masquinongi* and of *O. mykiss* and *S. vitreum*, respectively. Hence the estimated M_r values for stocked fish are 3 to 30 times higher than expected for natural populations in the experiments using *E. masquinongi* and *S. vitreum*, but slightly lower than expected for wild fish in the *O. mykiss* experiments. These values indicate that the mortality of stocked fish is highly variable and can be substantially higher, as well as lower, than expected for natural fish populations.

In the survival models developed in the present study, mortality is a continuous function of body size. Detailed ecological studies suggest that distinct threshold sizes for mortality may exist in some populations, for example, when fish outgrow predation by key piscivores and shift habitat use (Mittelbach and Chesson 1987). The consistency of empirical mortality – body size relationships across ecosystems and levels of organisation (McGurk 1986; Lorenzen 1996; this study) suggests that such thresholds do not in general lead to significant departures from the allometric mortality relationship. Nonetheless, departures from the continuous power relationship may occur at certain points in the ontogeny of stocked fish and, where this is the case, the detection of thresholds through experimental studies may allow further improvements in stocking regimes.

Detailed ecological studies (e.g., Wahl et al. 1995; Szendrey and Wahl 1996) are required to improve understanding of the mechanisms underlying differences in M_r , and to identify measures to reduce M_r in stocked fishes. The allometric survival models derived in the present study can aid in assessing release size under a given mortality regime and, thereby, contribute to improved management of stocked fisheries. Furthermore, the allometric relationship provides a basis for the comparison of mortalities between stocking experiments. Widespread use of this approach may lead to a substantial data base that would provide much information for appraisal and evaluation of stocking programmes.

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