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Population management in fisheries enhancement: Gaining key information from release experiments through use of a size-dependent mortality model

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Abstract

Population management, the optimisation of release and harvesting regimes, is a key element of effective fisheries stock enhancement. Population dynamics theory and assessment methods are becoming available to support management decision-making in enhanced fisheries. To apply such approaches in practice, it is necessary to estimate growth and mortality parameters for the target fishery. Here I show how this information can be extracted from release experiments through use of a size-dependent mortality model. The model, which describes natural mortality as an inverse function of fish length, has been derived in an earlier study and enjoys strong empirical support. Analysis of release experiments using this model provides direct estimates of size-dependent natural and fishing mortality patterns, which can be used to predict recapture and yield under alternative release and harvesting regimes. Furthermore, by expressing size-dependent mortality in terms of a single parameter, the mortality rate M_r at reference length L_r, the model facilitates comparative analyses of data from experiments in which mortality rates have been measured for different fish sizes. A preliminary comparative analysis shows that natural mortality is more variable, and substantially higher on average, in released hatchery-reared fish (median $M_r = 13.3\ \text{year}^{-1}$) than in wild fish (median $M_r = 3.3\ \text{year}^{-1}$) for the same reference length ($L_r = 5\ \text{cm}$). Such comparative information provides a benchmark against which the effectiveness of releases may be evaluated. Application of the approach is illustrated through the analysis of published data from a cod (*Gadus morhua*) release experiment in Norway.

Keywords: Fishing mortality; Released hatchery fish; Cod; *Gadus morhua*

1. Introduction

Releases of cultured fish into natural ecosystems are widely practiced for a range of purposes, including creation of culture-based fisheries, and enhancement or restoration of natural fish stocks (Cowx, 1994; Blankenship and Leber, 1995; Munro and Bell, 1997; Travis et al., 1998; Lorenzen et al., 2001). The biological effectiveness of such measures relies strongly on both post-release performance of hatchery-reared fish and on the management of stocked populations through adequate stocking and harvesting regimes (Olla et al., 1998; Lorenzen, 2005). Whereas the importance of cultured fish quality and certain aspects of the release regime (e.g., size at release and release habitat) have been widely appreciated and much researched, population management aspects have long been addressed only in broad qualitative terms. However, recent years have seen rapid developments in this area with population dynamics theory and fisheries assessment methods being extended to aquaculture-enhanced fisheries (Lorenzen, 1995, 2005; Walters and Martell, 2004).

Lorenzen (2005) extends the dynamic pool theory of fishing as developed by Beverton and Holt (1957) to the analysis of enhancements by "unpacking" the stock-recruitment relationship into size-based stages, accounting for population regulation in the recruited phase of the life cycle, and considering developmental and genetically based performance differences between released cultured fish and wild individuals. Arguably the most important biological extension of the original dynamic pool model is a size-dependent model of natural mortality. This model assumes that natural mortality is inversely proportional to length throughout the juvenile and adult stages of the fish life cycle. The length-inverse

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mortality model has been proposed independently by several authors (e.g., Beyer, 1989), and is supported by extensive empirical analyses (Lorenzen, 1996, 2000). Of particular relevance to the present study is Lorenzen's (2000) analysis of release experiments, which demonstrated that the length-inverse mortality pattern holds for a wide range of overall levels of natural mortality.

Population dynamics provides a powerful and general tool for the evaluation of stock enhancement programmes, from early planning to full-scale operation (Lorenzen, 2005). To apply such assessment methods to particular fisheries, it is necessary to estimate population model parameters pertaining to body growth, natural and fishing mortality rates, and (where relevant) reproduction. Such parameters may be estimated from three principal sources: (1) quantitative assessments of the wild stock, (2) release experiments with marked fish, and (3) comparative empirical studies and meta-analyses. Stock assessments can provide information on most parameters relating to the wild stock, including density-dependent processes if data show sufficient contrast (Hilborn and Walters, 1992). Release experiments can provide very precise estimates of post-release growth and mortality parameters, and also allow separation of natural and fishing mortality rates. Where no such stock-specific data are available, comparative studies can provide invaluable a priori information on parameter values, including those of the stock–recruitment relationship (Myers, 2001), size-dependent mortality in wild and released hatchery fish (Lorenzen, 1996, 2000); density-dependent growth in the recruited phase (Lorenzen and Enberg, 2002); and the relative performance of wild and hatchery fish (Fleming and Petersson, 2001).

Release experiments are carried out in many stock enhancement programmes, but are rarely analysed beyond a purely statistical treatment of recapture ratios. This is unfortunate because much useful management information remains hidden unless experiments are analysed within a population dynamics framework. Where such analyses have been carried out, they often involve ad hoc assumptions to deal with the problem that natural mortality rates vary over the duration of the experiment. This problem may be overcome, and the analysis simplified and unified through use of a size-dependent mortality model. Such a model has two main functions. First, it allows us to model the survival and recapture of a released cohort throughout its lifetime even if fish are released as juveniles. Second, it unifies the analysis of cohorts released at different sizes, which are linked through a common mortality process. The analysis provides direct estimates of size-dependent natural mortality and fishing mortality patterns, which can then be used to predict recaptures and yield under alternative release and harvesting regimes. Furthermore, the size-dependent natural mortality parameter allows comparative analyses of post-release performance between experiments that differ in release size and fishing patterns.

In this paper, I describe a method for analysing release experiments using the size-dependent mortality model. I also provide an example application to published data, and close with a discussion of possible further developments.

2. Methods

Release experiments typically involve the stocking of individually or batch-marked fish. Recaptures of marked fish in the fishery are recorded over a period after release. Data on individual recaptures normally comprise the date and place of recapture, and the length and/or weight of the fish. Often this information is reported in aggregated form: as the number and mean length or weight of fish recaptured within consecutive periods of duration Δt (e.g., months, quarters or years) after release. The analysis approach presented here is designed for such aggregated data. It is the temporal pattern of size and recaptures post-release that contains information on population dynamics, hence the temporal dimension of the data must be preserved (where data are aggregated into overall totals, the analysis can not be carried out).

2.1. Growth model estimation

Both natural and fishing mortality rates are size-dependent, and it is thus necessary to model growth as a basis for modelling the mortality processes. Growth is often well described by a von Bertalanffy model predicting mean length $L(t_i)$ at time t_i from mean length of the cohort at the time of release $L(t_1)$:

$$L(t_i) = L_\infty - (L_\infty - L(t_1))\exp(-Kt) \tag{1}$$

where L_∞ is the asymptotic length and K is the growth rate.

As data have been aggregated over intervals of time, mean length during each interval is used to fit the model to data, and cazulate the length-dependent natural and fishing mortality rates for that interval. Mean length $\bar{L}(t_i)$ during the interval preceding t_i is given by

$$\bar{L}(t_i) = \frac{L(t_{i-1}) + L(t_i)}{2} \tag{2}$$

The maximum likelihood estimate of the growth parameters L_∞ and K is obtained by minimizing the negative log likelihood $\mathbf{L}$ of the observed length data given the model. Assuming a normal error distribution, and ignoring an additive constant, the log likelihood is $\mathbf{L}$ given by:

$$\mathbf{L} = \frac{n}{2}\log\left(\frac{\sum_{i=1}^{i\max}\left(\bar{L}(t_i)_{\text{obs}} - \bar{L}(t_i)_{\text{pred}}\right)^2}{n}\right) \tag{3}$$

The parameter values that minimize L may be found using numerical search routines such as the SOLVER tool in Excel. Confidence limits for model parameters can be constructed from their likelihood profiles (Hilborn and Mangel, 1997).

Likelihoods of independent data sets predicted by the same model can be combined. Thus, if several independent releases have been conducted and the resulting data are predicted by a joint model, the negative log likelihoods **L** of all experiments given the joint model may be combined additively.

2.2. Population model estimation

The population analysis is based on modelling the probability of recapturing marked fish over time, and fitting the model to observed recapture data. It broadly follows established methods for analysing recapture data (Lebreton et al., 1992; Julliard et al., 2001), but incorporates the size-dependent mortality model and is formulated specifically for fitting to aggregated data. Assuming that recapture monitoring covers the full area of distribution, the probability of a marked fish being recaptured and reported in any particular period depends on the natural and fishing mortality processes that have acted since the time of release, the rate at which tags are lost from live fish, and the proportion of recovered tags that are reported.

Both natural and fishing mortality rates are size dependent. Following the results of Lorenzen (1996, 2000), natural mortality is assumed to be inversely proportional to length:

$$M(\bar{L}) = M_r \frac{L_r}{\bar{L}} \qquad (4)$$

where $M(\bar{L})$ is the natural mortality rate at mean length, and M_r is the mortality rate at reference length L_r. The relationship between size and fishing mortality depends on the gear types used in the fishery, but is often well described by a logistic function of length:

$$F(\bar{L}) = \frac{F_\infty}{1 + \exp(q(\bar{L} - L_c))} \qquad (5)$$

where F_∞ is the fishing mortality at fully selected length, L_c the length at 50% gear selection and q describes the steepness of the selectivity curve (Gulland, 1981).

Using the size-dependent natural and fishing mortality models and assuming that tag loss is a size-independent rate process, the probability $Q(t_i)$ of a tagged fish surviving to time t_i and retaining its tag can be calculated from $Q(t_{i-1})$ by:

$$Q(t_i) = Q(t_{i-1}) \exp(-(M(\bar{L}(t_i)) + F(\bar{L}(t_i)) + \varphi)\Delta t) \qquad (6)$$

where φ is the rate of tag loss. This model assumes that all captured fish are retained rather than re-released, as is the case in most commercial fisheries. Finally, the probability $P(t_i)$ of a tagged fish being recaptured and reported in period t_{i-1} to t_i is given by:

$$P(t_i) = \rho Q(t_{i-1}) \frac{F(\bar{L}(t_i))}{M(\bar{L}(t_i)) + F(\bar{L}(t_i)) + \varphi} \times \left(1 - \exp(-(M(\bar{L}(t_i)) + F(\bar{L}(t_i)) + \varphi)t)\right) \qquad (7)$$

where ρ is the probability of a tag recapture being reported. Using this model it is possible to predict the probability of a tag being reported for all periods monitored.

Parameter estimation is again by maximum likelihood. Ignoring an additive multinomial term independent of the parameters, the negative log likelihood **L** of the observed data is given by:

$$\mathbf{L} = -\sum_{i=1}^{i\max} C(t_i) \ln(P(t_i)) - \left(R - \sum_{i=1}^{i\max} C(t_i)\right) \ln\left(1 - \sum_{i=1}^{i\max} P(t_i)\right) \qquad (8)$$

where R is the number of tagged fish released, and $C(t_i)$ is the number of recaptures actually reported in the period t_{i-1} to t_i. The maximum likelihood estimate of the model parameters is obtained by finding the parameter values that minimize **L** through numerical search.

The population model described here is relatively complex. It contains a total of six free parameters (M_r, F_∞, q, L_c, φ and ρ), which may be difficult to estimate from data sets that are small or of low contrast. It may thus be necessary to fix certain parameters a priori at values estimated in independent studies. The tag loss rate φ in particular can be estimated independently using double-marked fish (Seber, 1982).

2.3. Comparative analysis and benchmarking

By expressing size-dependent mortality in terms of a single parameter (M_r at an arbitrarily defined reference length L_r), the length-inverse mortality model facilitates comparative analyses of data from experiments in which mortality rates have been measured for different fish sizes. Such comparisons are based on the premise that the length-inverse mortality model holds regardless of the overall level of mortality, a result explicitly derived in Lorenzen (2000) for released hatchery fish, and also supported by an earlier analysis of the allometry of mortality in wild fish (Lorenzen, 1996).

There is extensive information on size-dependent mortality rates for wild fish. Lorenzen (1996) compiled data on natural mortality rates $M(W^*)$ of wild fish in relation to weight W^* at mean length during the period for which M was estimated. From each such data point, the corresponding M_r at reference weight W_r may be calculated as:

$$M_r = M(W^*) \left(\frac{W^*}{W_r}\right)^b \qquad (9)$$

Assuming the length-inverse natural mortality model and an isometric length–weight relationship, $b = -0.33$. On average in fish, a body weight of 1 g is equivalent to a length of 5 cm, hence choosing $W_r = 1$ g provides M_r for a reference length of $L_r = 5$ cm. Estimates of natural mortality rates (as opposed to recapture ratios) of released hatchery fish are relatively scarce. However, published data from release experiments

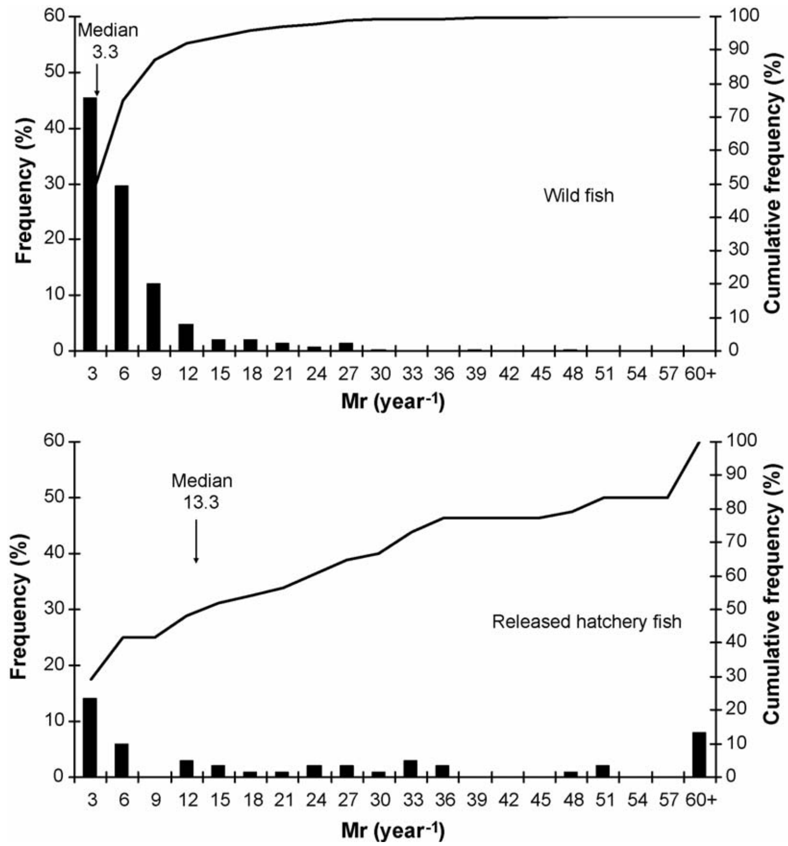

Fig. 1. Distribution of mortality M_r at reference length $L_r = 5$ cm for natural populations (top), and released hatchery-reared fish (bottom). From data compiled by Lorenzen (1996, 2000).

collated by Lorenzen (2000) provide 22 independent estimates of M_r.

The distributions of M_r (at $W_r = 1$ g or $L_r = 5$ cm) for wild and released hatchery fish are shown in Fig. 1. The distribution of M_r for wild fish is skewed (approximately log-normal) with a median of 3.3 year^{-1}. The cumulative distribution shows that 75% of M_r values in wild fish are below 6 year^{-1}, while 90% are below 11 year^{-1}. The distribution of M_r in released hatchery fish extends far to the right of that for wild fish, with a median of 13.3 year^{-1} and 25% of estimates greater than 35 year^{-1}. Thus post-release performance of hatchery fish may be similar to that of wild fish, but is often much lower. As further estimates of M_r for released hatchery fish become available, the distribution will become increasingly informative and provide a good basis for risk assessment of stock enhancement. More extensive comparative data will also allow quantifying the benefits of measures aimed at improving post-release mortality such as habitat enrichment, life skills training or artificial selection (Jonasson et al., 1997; Olla et al., 1998; Brown and Dey, 2002; Mahnken et al., 2004).

Comparative data on mortality rates in wild and released hatchery fish provide a benchmark against which the performance of released fish can be judged. The distribution of M_r in wild fish indicates what may be expected if hatchery fish were produced in such a way that their performance in the wild was similar to that of wild fish. It thus provides an 'upper limit' of what may be achievable with the best genetic and developmental management under hatchery conditions. Conversely, the distribution of M_r in released hatchery fish allows us to measure performance against what has been achieved in other stock enhancement programmes.

2.4. *Evaluating effects of population management options*

Growth and mortality parameters estimated from the release experiment may be used in complex and fairly comprehensive models for enhanced fisheries such as that described by Lorenzen (2005). Usually this will require additional information from stock assessments and comparative studies. In the first instance, however, much management information may be gained by using the same underlying population model as described above to explore recapture and yield per stocked fish under alternative management scenarios: release size, fishing mortality rate, gear selectivity parameters, or performance (natural mortality rate) of released fish.

Removing the terms for tag loss and reporting rates, the equations describing numbers of released fish $N(t_i)$ and harvest $H(t_i)$ of stocked fish over time become

$$N(t_i) = N(t_{i-1}) \exp(-(M(\bar{L}(t_i)) + F(\bar{L}(t_i)))\Delta t) \quad (10)$$

and

$$H(t_i) = N(t_{i-1}) \frac{F(\bar{L}(t_i))}{M(\bar{L}(t_i)) + F(\bar{L}(t_i))} \times \left(1 - \exp(-(M(\bar{L}(t_i)) + F(\bar{L}(t_i)))\Delta t)\right) \quad (11)$$

Total harvest from a stocked cohort is then

$$T = \sum_{i=1}^{i\,\max} H(t_i) \quad (12)$$

while total yield is given by

$$Y = \sum_{i=1}^{i\,\max} \alpha \bar{l}(t_i)^{\beta} C(t_i) \quad (13)$$

where α and β are parameters of the length–weight relationship. Dividing T and Y by the number of fish released R gives recapture ratio and yield per released fish.

This simple population model does not account for density-dependent processes in mortality or growth. Such processes are likely to become important if management variables such as stocking density, fishing effort or post-release performance are modified substantially from those found during the release experiment. Hence the model will provide good predictions of the effects of moderate changes in variables, but will tend to over-predict the effects of large changes (which will be moderated by compensatory density-dependence).

3. Example application

To illustrate the approach, I analyze a published data set on experimental releases of hatchery-reared cod in the Øygarden archipelago off central Norway. Kristiansen et al. (2000) provide aggregated growth and recapture data for a total of 62,777 hatchery-reared cod released in the area between 1991 and 1996. The released fish are grouped by season and size at release, resulting in nine groups: winter, spring and summer releases of small, medium and large fish each (Table 1). For each of the groups, the total number of fish released and mean length at release are reported. Recaptures are reported in quarterly intervals after release, giving the number recaptured and the mean length of fish recaptured in each interval.

Table 1
Release and recapture data for reared cod in Øygarden

	Release group								
	A $Ø_{wi}$ S	B $Ø_{wi}$ M	C $Ø_{wi}$ L	D $Ø_{sp}$ S	E $Ø_{sp}$ M	F $Ø_{sp}$ L	G $Ø_{su}$ S	H $Ø_{su}$ M	I $Ø_{su}$ L
Number released	6982	15381	4958	5022	9320	4431	3752	8275	4656
Recaptured in quarter									
1	23	82	40	21	74	54	44	143	224
2	22	101	93	51	137	112	17	81	76
3	26	109	34	18	50	34	19	102	78
4	33	61	23	30	72	49	16	93	102
5	36	76	39	21	62	63	38	131	73
6	46	83	38	37	65	45	11	38	25
7	30	56	19	13	25	14	20	45	42
8	15	38	7	16	44	25	12	31	12
9	12	38	11	7	17	8	10	18	10
10	7	15	6	4	10	9	5	9	3
11	6	9	3						
Length at release (cm)	22.4	25.9	29.1	23.6	28.0	31.3	24.0	29.0	34.0
Mean length (cm) in quarter									
1	22.4	26.8	29.7	26.2	29.9	32.5	24.9	29.3	34.8
2	24.0	29.1	31.8	29.0	31.9	33.0	26.8	31.2	34.4
3	28.9	31.6	33.8	35.9	38.6	40.2	32.7	36.9	39.3
4	35.7	38.5	41.7	40.2	42.3	44.0	37.5	40.8	42.9
5	39.7	42.7	43.5	43.0	44.8	47.3	41.1	44.3	46.8
6	42.0	45.7	46.1	42.1	47.1	51.1	40.8	45.5	47.5
7	43.1	43.9	44.7	49.3	51.1	55.8	47.1	51.3	57.1
8	47.2	50.7	57.6	53.8	57.1	57.0	53.5	53.0	54.8
9	51.4	54.8	57.2	61.8	54.0	59.0	51.0	56.2	63.8
10	63.0	57.8	61.0	58.8	61.8	58.3	53.4	56.8	62.3
11	50.0	57.0	57.5						

From Tables IV and VI in Kristiansen et al. (2000). Release group codes are retained form the original paper and denote location: Ø (Øygarden); season: wi (winter), sp (spring), su (summer); size: S (small), M (medium), L (large).

Table 2
Parameter values set or estimated

Parameter	Value [95% CI]	Source
VBGF, L_∞	122 [95,234] cm	Estimated
VBGF, K	0.16 [0.07, 0.24] year^{-1}	Estimated
Reference length, L_r	5 cm	Set (arbitrary)
Tag loss rate, φ	0.1 year^{-1}	Set (see text)
Tag reporting, ρ	0.68 [0.55, 0.90]	Estimate
Natural mortality at L_r, M_r	12.8 [11.9, 13.7] year^{-1}	Estimate
Fishing mortality, F	1.8 [1.0, 3.9] year^{-1}	Estimate
Length at 50% selectivity, L_c	49.5 [45.0, 55.7] cm	Estimate
Slope of selection curve, q	0.16 [0.14, 0.18] cm^{-1}	Estimate

Estimates with 95% confidence limits. VBGF: von Bertalannfy growth function.

3.1. Parameter estimation

A von Bertalanffy growth model was fitted to the mean length at recapture data as described in Section 2.1. A joint set of parameters was estimated for all release groups by additively combining the individual **L** values and finding the overall maximum likelihood estimate. The estimated parameter values are shown in Table 2, and predicted mean length is plotted against observed mean length in Fig. 2. The model provides a good description of observed growth patterns and parameter estimates consistent with others for the same species (FishBase, 2004). This growth model was used as a basis for the subsequent population analysis.

Population model parameters were estimated as described in Section 2.2. The tag loss rate φ was not estimated from the data, but set at 0.1 year^{-1} a priori in accordance with previous independent estimates (Kristiansen et al., 2000; Julliard et al., 2001). The model predicted observed recaptures well in all nine release groups (Fig. 3). The parameter estimates are shown in Table 2. The length-dependent natural and fishing mortality rates are illustrated in Fig. 4. Natural mortality declines with the inverse of length, from about 2.8 year^{-1} at the smallest release size to 1 year^{-1} at 60 cm. Fishing mortality increases gradually over the length range. The length at 50% selection is estimated at $L_c = 49.5$ cm, hence the actual fishing mortality suffered by the largest fish within the observed length range is about 1 year^{-1}, just over half the theoretical maximum for fully selected fish ($F_\infty = 1.8$ year^{-1}). The fitted model provides a good description of the observed relationship between length at release and recapture ratio (Fig. 5). The model thus describes both within and between group variation in recaptures based on a simple, unified relationship between mortality and size.

3.2. Benchmarking with comparative information

The comparative data summarized in Fig. 1 provide benchmarks against which the performance of released cod can be judged. The size-dependent natural mortality rate of released cod has been estimated at $M_r = 12.8$ year^{-1}, at a reference length of $L_r = 5$ cm (Table 2). Comparison with the distributions in Fig. 1 shows that this is very high relative to wild fish, but within the mid-range for released hatchery fish. Hatchery cod in this experiment thus perform broadly as expected for the released hatchery fish.

3.3. Exploration of management options

The information on growth, natural and fishing mortality patterns derived from the release experiment allows assessment of a wide range of possible modifications to the release and harvesting regimes. As an example, I consider interactions between two aspects of the release regime subject to management intervention: post-release mortality M_r and size at release (Fig. 4). Post-release mortality M_r may be improved through adoption of hatchery practices that promote good performance in the wild, within limits as indicated

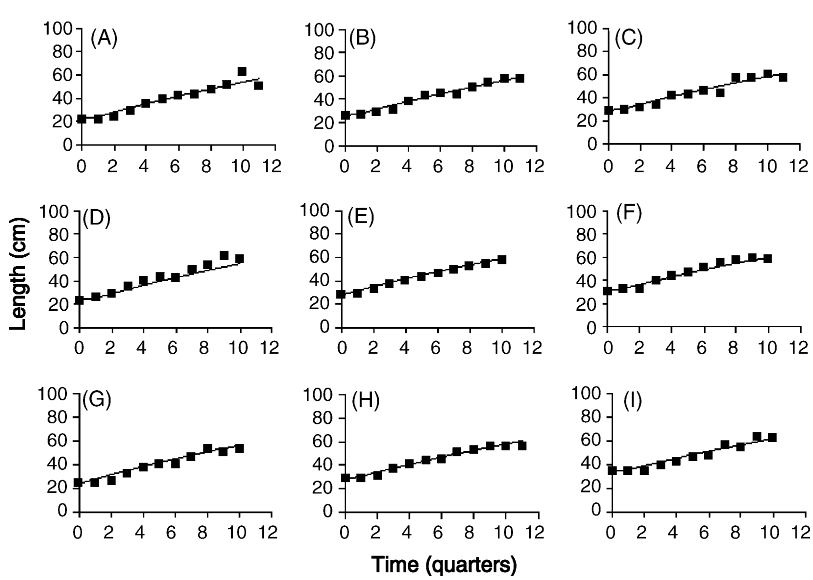

Fig. 2. Predicted and observed mean lengths for all release groups (see Table 1 for details). Predicted length is based on the fitted von Bertalanffy growth model.

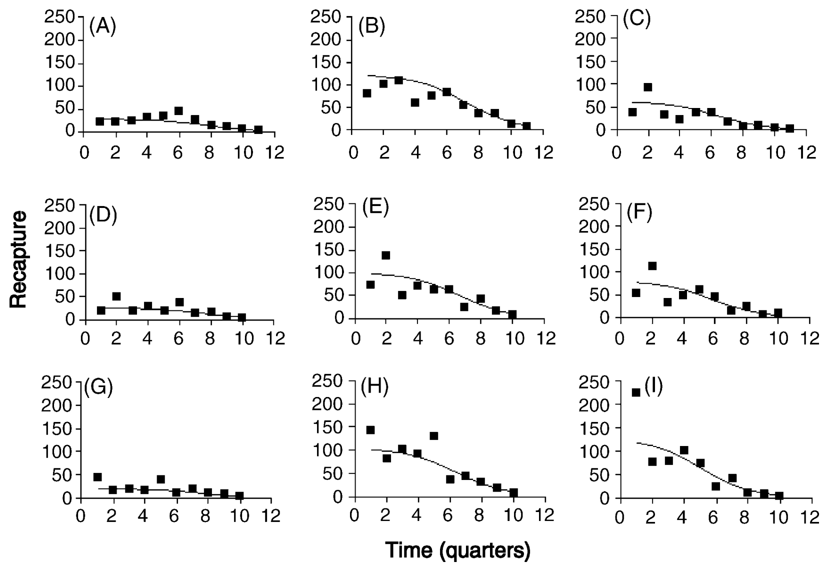

Fig. 3. Predicted and observed number of recaptures for the nine release groups (see Table 1 for details).

by the wild fish M_r distribution. Recapture ratios and yield per released fish increase with increasing length at release, and with reduced mortality (Fig. 6a and b). At $M_r = 12$ year^{-1}, approximately the rate estimated from the release experiment, yield per fish remains lower than body weight at release throughout (Fig. 6b). If post-release mortality was reduced to $M_r = 7.5$ year^{-1}, yield would equal weight at release for smaller fish, but remains below release weight for fish >25 cm at release. A reduction of post-release mortality to the wild fish average of $M_r = 3.0$ year^{-1} would provide a yield greater than the weight at release throughout the length range considered. Net biomass production as a proportion of biomass released (Fig. 6c) again shows that mortality must be reduced to below $M_r = 7.5$ year^{-1} for positive production to occur. It also shows that if M_r can be reduced to a level where positive biomass production is achieved, net production is maximised by releasing relatively small fish. The analysis thus indicates that optimal release size is highly sensitive to the overall level of size-dependent natural mortality suffered after release. Such insights provide important directions for the further development of stock enhancement programmes. Whereas it might seem logical to produce larger fish for release in order to boost recapture ratios, it is clear in this case that this strategy would fail to produce adequate returns. Rather, the focus should be on producing small fish capable of performing well in the wild, with size-dependent post-release mortality not exceeding about $M_r = 7.5$ year^{-1}. Whether this is technically possible and economically feasible, only experiments can

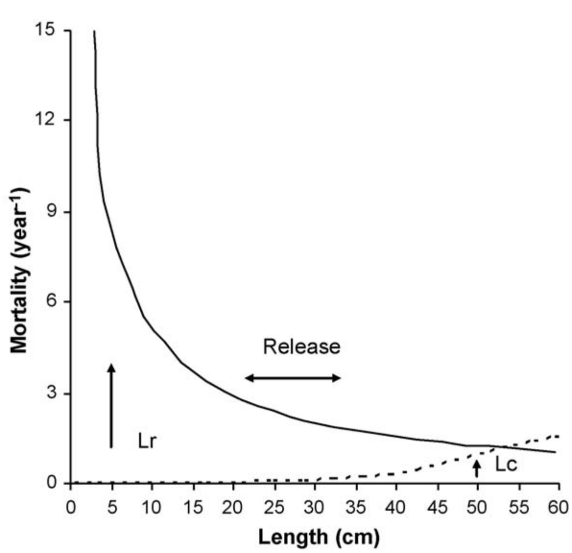

Fig. 4. Estimated length-dependent rates of natural mortality M (solid line) and fishing mortality F (dashed line). Also indicated are the reference length ($L_r = 5$ cm, arbitrarily set) for natural mortality, the gear selection length ($L_c = 49.5$ cm, estimated), and the range of lengths at release (release) in the experiment.

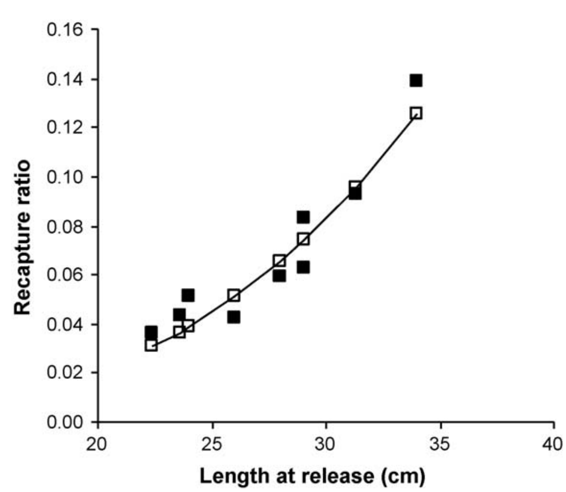

Fig. 5. Predicted (open squares) and observed (solid squares) total recapture ratio (total recaptures divided by number released, T/R) as a function of length at release.

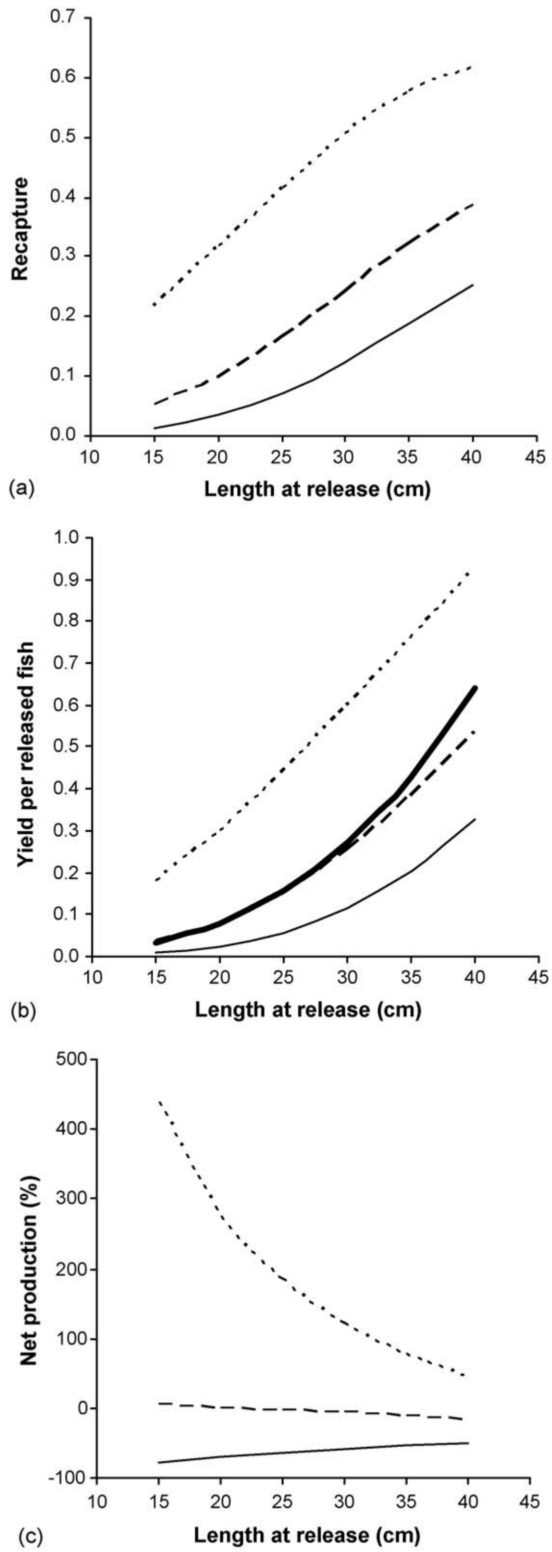

Fig. 6. Predicted recapture ratio (a), yield (b) and net biomass production (c) as a function of length at release, for different values of natural mortality M_r (at reference length $L_r = 5$ cm): 12 year^{-1} (solid line), 7.5 year^{-1} (dashed line) and 3.0 year^{-1} (dotted line). Also shown in (b) is body weight at release (heavy solid line).

show. It should also be borne in mind that large improvements in post-release performance will lead to equivalent increases in population density and may precipitate compensatory density-dependent responses and thus, lower gains than predicted here. The predictions of biological returns derived here are easily combined with information on the costs of producing fish for release at different sizes to conduct an economic analysis of optimal release size.

4. Discussion

The approach developed here provides a simple, unified and robust framework for the analysis of release experiments. It provides direct estimates of size-dependent natural and fishing mortality patterns, which can then be used to predict recaptures and yield under alternative release and harvesting regimes. The size-dependent natural mortality parameter M_r facilitates comparative analyses of post-release performance between experiments that differ in release size and fishing patterns.

The model as formulated here will be adequate for many stock enhancement applications. It may be simplified where availability of data is very limited, for example, by assuming knife-edge selection rather than a general logistic function for fishing mortality. Also, several parameters may be fixed or constrained on the basis of prior information. Conversely, where data are extensive and informative, the model may be improved by allowing for seasonal or cohort effects. Lebreton et al. (1992) provide a general framework for capture-recapture modelling into which the size-dependent mortality model is easily integrated.

The model used here does not account for density-dependent processes. Quantifying such processes in both the juvenile and adult life stages is crucial to the assessment of operational-scale stock enhancement (Peterman, 1991; Lorenzen, 2005). Release experiments have the potential to provide very precise information on density-dependent processes, but only if there is temporal and/or spatial variation in release densities. In most experiments, however, density variation is too small to allow density-dependent parameters to be estimated. Lorenzen (2005) provides an approach for gauging density dependence in juvenile mortality rates from knowledge of the stock-recruitment relationships. The same approach can be used to estimate density-dependent parameters from release experiments where there is sufficient contrast in the densities at release.

The simple size-dependent mortality model upon which the methodology developed here is based enjoys substantial empirical support (Lorenzen, 1996, 2000). Nonetheless, the wider application of this approach to a variety of stock enhancement systems is required to assess the robustness of the model and the reliability of its predictions. At the very least, however, the model provides a first quantitative generalisation about post-release mortality of hatchery-reared fish against which empirical observations and future generalisations can be measured. It will thus allow the study of release strategies to move from an empirical case by case approach towards an analytical framework and quantitative generalisations.

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