

Using population models to assess culture-based fisheries: a brief review with an application to the analysis of stocking experiments

Kai Lorenzen

T H Huxley School of Environment, Earth Sciences and Engineering
Imperial College of Science, Technology and Medicine
Prince Consort Road, London SW7 2BP, United Kingdom
Tel: (+44) 171 594 9312; Fax: (+44) 171 589 5319
E-mail: k.lorenzen@ic.ac.uk

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Abstract: Population dynamics models are powerful tools for the analysis of culture-based fisheries and the optimisation of stocking and harvesting regimes. Key population

processes and the resulting dynamics of culture-based fisheries are briefly reviewed, and approaches to the practical assessment of management regimes are outlined. A model is developed for the analysis of stocking experiments, and applied to mrigal (*Cirrhinus mrigala*) stocking in Huay Luang reservoir, Thailand.

1 Introduction

Culture-based fisheries are fisheries based mainly or entirely on the recapture of farm-produced seed fish (Lorenzen 1995). Culture based fisheries are widespread in the developed and developing world, operating on the largest scale in Chinese reservoirs (Welcomme & Bartley 1998). Yields and technical efficiency measures vary widely between culture-based fisheries, but the underlying reasons are poorly understood and the predictability of outcomes remains limited. There is therefore an urgent need for rigorous evaluation and analysis culture-based fisheries. Such analyses must go beyond merely diagnosing success or failure of particular fisheries: they must pinpoint underlying reasons, and identify improvement in management regimes where such potential exists.

In culture-based fisheries, hatchery-reared fish are released into waterbodies not primarily managed for fish production, and recaptured upon reaching a desirable size. Mortality and growth of the stocked fish are dependent on the natural conditions of the stocked water body, and a key technological management problem is therefore to identify stocking and harvesting regimes that make the best possible use of the given conditions.

The approaches used to identify optimal management regimes differ greatly between aquaculture and capture fisheries, being based largely on experimentation in the former, and on the use of stock assessment models in the latter. In culture-based fisheries, the scope for controlled experimentation is far lower than in aquaculture, yet the conventional assessment models for capture fisheries are inadequate to address the management problems posed by stocked fisheries. The development of models that capture the dynamics of culture-based fisheries adequately is therefore a key step towards

the optimisation of management regimes. Conventional fisheries models divide the life cycle of fish into recruited phase where mortality is constant and growth independent of population density, and a pre-recruit phase where non-specified density-dependent processes give rise to a stock-recruitment relationship. In culture-based fisheries, fish are stocked at an intermediate stage of the pre-recruit phase, and population density can be manipulated to an extent that elicits strong compensatory responses even in the recruited stock. Hence the size- and density-dependent processes in the juvenile and adult phases of the life cycle must be considered explicitly to evaluate management options.

In this paper, process models for mortality and growth applicable to culture-based fisheries, and the resulting dynamics of stocking and harvesting are briefly reviewed. The process of assessing culture-based fisheries is described, and an example application to the analysis of stocking experiments is provided. Finally, the potential for comparative analyses is discussed.

2 Population process models for culture-based fisheries

Key population processes in culture-based fisheries are density-dependent growth and size-dependent mortality.

2.1 Density-dependent growth

Density-dependent growth is well documented in wild fish populations (e.g. Beverton and Holt, 1957; Le Cren, 1958; Backiel and Le Cren, 1978; Hanson and Leggett, 1985; Salojaervi and Mutenia, 1994) and in extensive aquaculture (Walter, 1934; Swingle and Smith, 1942; van Someren and Whitehead 1959). Building on earlier work by Beverton and Holt (1957), Lorenzen (1996a) developed a von Bertalanffy growth model for density dependent growth. In the model, asymptotic length is assumed to decline linearly with population biomass density. This leads to the following expression for asymptotic weight:

$$W_{\infty B} = (W_{\infty L}^{1/3} - c B)^3 \quad (2)$$

where $W_{\infty B}$ is the asymptotic weight at biomass B and $W_{\infty L}$ is the limiting asymptotic weight when biomass approaches zero. The competition coefficient c describes how steeply asymptotic weight declines with increasing biomass. For a given species, the limiting asymptotic weight $W_{\infty L}$ is related to properties of the waterbody stocked, and in general $W_{\infty L}$ is likely to be positively correlated with the productivity of the waterbody. Generalisations about the competition coefficient c are difficult to make at present, but are likely to emerge from comparative studies once the model has been applied to a wider range of populations.

2.2 Size-dependent mortality

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

$$M_W = M_u W^{-b} \quad (1)$$

where M_W is natural mortality at weight W , M_u is mortality at unit weight, and b is the allometric exponent. Lorenzen (1996b) shows that mortality of fish in natural ecosystems is governed by a consistent allometric relationship with parameters $b=-0.3$ and $M_u=3/\text{year}$.

A meta-analysis of stocking experiments (Lorenzen unpublished) shows that average release size-survival relationships are well described by models based on allometric mortality with constant b , and that the mathematically convenient assumption of $b=-1/3$ is adequate for the analysis of release size. M_u was found to be highly variable between experiments. Hence in practical assessment work, b can be fixed at $-1/3$ a priori, while M_u has to be estimated separately for each fishery.

3 Population dynamics of culture-based fisheries

The population dynamics of culture-based fisheries governed by density-dependent growth and size-dependent mortality have been investigated by Lorenzen (1995). Key results of this analysis can be summarised as follows.

The optimal stocking regime is dependent on the harvesting regime and vice versa. This is illustrated schematically in Figure 1 where production is shown as a function stocking density and fishing effort. High fishing effort calls for high stocking densities and vice versa. High stocking densities combined with low fishing effort lead to overstocking, with low production due to slow growth and low survival from stocking to harvest. Conversely, low stocking rates combined with high fishing effort lead to overfishing. Note that both overstocking and overfishing can be alleviated by changes in either stocking density or fishing effort.

Potential production from stocked fisheries is inversely related to the size at which fish are harvested. Hence in combination with the overall ecological productivity of the waterbody, the minimum size at which fish are marketable effectively limits the production that can be achieved from stocking. Where large fish are desired, stocking densities should be low and overall production will also be low. Where small fish are marketable, high production levels can be achieved when stocking densities are high and fish are harvested at the smallest marketable size. Where fish are marketable below their normal size at maturity, culture-based fisheries can achieve higher levels of production than wild stocks of the same species because large and somatically unproductive spawners can be replaced by a large number of small and somatically productive fish.

A wide range of different stocking sizes can be used to achieve similar levels of production, but the numbers that need to be stocked decrease in a non-linear way as size increases (Figure 2). This is a consequence of the allometric mortality-size relationship, and the fact that larger seed fish require less time to reach a harvestable size. The biomass of seed that needs to be stocked to achieve a given level of yield increases with increasing seed size, and so does the cost of producing the individual seed fish.

The above provides general rules that apply to a wide range of culture-based fisheries. Where natural reproduction is an important source of recruitment or there is strongly density-dependent mortality after stocking, there are further considerations.

4 Assessment of management regimes in practice

Population models incorporating the key processes of size-dependent mortality and density-dependent growth can be used in a variety of practical assessment situations. This section provides a brief overview of data requirements and assessment procedures.

4.1 Data requirements

For a full assessment of management regimes, it is necessary to estimate natural and fishing mortality rates as well as parameters of the density-dependent growth model. A single stocking experiment is sufficient to obtain preliminary estimates of all parameters except the degree of density-dependence in growth (i.e. the competition coefficient c), which can only be established if growth data are available for a range of biomass densities.

The data required from a stocking experiment are the number and size of fish released, and the recaptures of stocked fish over time (numbers as well as individual weight and/or length). The temporal dimension of recaptures is crucial to the analysis and must be recorded, for example as numbers of fish recaptured per month and their average weight and/or length. If only total recaptures in numbers or weight are recorded, it is not possible to estimate model parameters.

As a general rule, the best data will be obtained if the stocked seed fish are batch-marked (individual identification is not required for this application). Using marked seed fish has the advantage that the temporal dimension of recaptures and growth is determined even when fish can not be aged directly (as is the case in many tropical situations), and that any possible natural recruitment of the species does not lead to bias in the parameter

estimates. Where fish can be aged from hard parts and the possibility of natural recruitment can be excluded, age-structured catch data will provide the same information as batch mark-recapture.

Where no mark-recapture or age-based data are available, analysis of catch-length data may provide information on growth and total mortality in the recruited size classes (see e.g. Pauly and Morgan 1987). Such information may be used to estimate model parameters, but the precision of these estimates is likely to be lower than achievable from mark-recapture or age-based data.

4.2 Assessment procedure

A full assessment of management options in culture-based fisheries requires the following steps (Lorenzen et al. 1997):

- (1) Estimation of natural and fishing mortality rates and reconstruct the stocked cohort(s).
In culture-based fisheries (where initial cohort numbers are known), the full information is obtained from a single analysis to which there are two different approaches: cohort analysis and statistical catch-at-age analysis (Hilborn and Walters 1992). An example of the use of cohort (or virtual population) analysis in culture-based fisheries is given in Lorenzen et al. (1997), while catch at age analysis is illustrated in Section 5 of this paper.
- (2) Estimation of density-dependent growth parameters. The growth model is fitted to weight or length-at-age data, using the reconstructed population biomass as an independent variable (see Lorenzen et al. 1997). This analysis is possible only if growth data are available for several cohorts, under conditions of varying biomass density.
- (3) Project catches and other variables of interest (e.g. size of harvested fish) for different possible management regimes. This step requires a forward projection model such as that used in statistical catch-at-age analysis (see section 5). For a full analysis accounting for the effects of density dependent growth, the model must involve a

feedback loop between growth and biomass. Lorenzen et al (1997) used an equilibrium model for the evaluation of management options, but dynamic models can be constructed in a similar way.

Where data on density-dependent growth are lacking, it is still possible to carry out a more restricted analysis of the present management regime. It must be remembered, however, that density-dependent growth will affect the outcomes of all management interventions that involve changes in biomass density.

5 Example: preliminary assessment based on a single stocking experiment

5.1 The stocking experiment

Siripunt et al. (1989) carried out a stocking experiment with batch-marked seed fish in Huay Luang reservoir (3100 ha), Northeast Thailand. Three differently marked cohorts of mrigal (*Cirrhinus mrigala*) were released at large (10 cm), medium (7cm) and small (5cm) size at the end of November 1987. Recaptures over the following 11 months were recorded on a monthly basis. The data are summarised in Table 1.

Information on the growth of stocked fish is summarised in Fig. 1. The large and medium cohorts show a similar growth pattern, described well by a von Bertalanffy growth function

$$W_t = (W_\infty^{1/3} - (W_\infty^{1/3} - W_{t-1}^{1/3}) \exp(-K))^3 \quad (3)$$

with parameters $W_\infty = 58,000\text{g}$ and $K=0.034/\text{month}$. Growth in the cohort stocked at small size appeared to be far lower than in the others, with fish reaching only about 350g on average as compared to about 2000g for fish stocked at larger size. However, the very low recapture of the small cohort limits information on growth. In the following analysis

the measured mean weights are used, except in the case of the small cohort where an “eye fit” von Bertalanffy growth function with $W_{\infty} = 10,000\text{g}$ and $K=0.034/\text{month}$ has been used to predict overall recapture.

5.2 Population model and parameter estimation

Under the simplifying assumption that recaptures occur at the end of each monthly period (rather than continuously throughout the month), a discrete time population model can be developed. Furthermore, it may be assumed that the allometric scaling of mortality is $b=-1/3$ (cf. section 2.1), and that gear selectivity is described by a logistic curve based on weight (Lorenzen et al. 1997).

The population model to project cohort abundance and catch over time is then:

$$N_t = (N_{t-1} - C_{t-1}) \exp(-M_u((W_t + W_{t-1})/2)^{-1/3} \Delta t) \quad (4)$$

$$F_t = F' / (1 + \exp(p (W_c - W_t))) \quad (5)$$

$$C_t = N_t (1 - \exp(-F_t \Delta t)) \quad (6)$$

$$Y_t = C_t W_t \quad (7)$$

Where N is the number of fish alive, F is the fishing mortality rate, C is the catch in numbers, Y is the yield (catch in weight), and Δt is the time difference between $t-1$ and t . The parameters of the logistic selectivity model (Equation 5) are the fishing mortality rate at full selection F' , the weight at 50% selection W_c , and the slope of the selection curve q .

The model was implemented in a spreadsheet as shown in Table 2. Parameters were estimated as the set that minimised the sum of squared residuals (SSQ) between the log transformed observed and predicted catches:

$$SSQ = \sum (\log(C_{\text{observed}}) - \log(C_{\text{predicted}}))^2 \quad (8)$$

Minimisation was performed numerically using the optimisation tool in the spreadsheet.

Following parameter estimation, the model was used to predict the effects of changes in stocking and harvesting regimes on recapture rates and yield per stocked fingerling.

5.3 Results

The model was fitted simultaneously to recapture data for the large and medium cohorts. Initially, a joint set of parameters was estimated for both cohorts. However, examination of residuals showed substantial inconsistencies between predicted and observed recaptures in the first three months, which suggested a difference in selection patterns for the two cohorts. Parameters were therefore allowed to vary between cohorts. Estimation of separate values for q (slope of the selection curve) for the two cohorts removed the discrepancies in residuals and drastically reduced the SSQ (from 0.94 to 0.38). Hence the final model (Table 2), is based on joint estimates of all parameters except for q , which was allowed to vary between cohorts.

The estimated parameters, numbers alive and predicted as well as observed catches are shown in Table 2. Observed and predicted catches are shown graphically in Figure 4. The estimated natural mortality rate at unit weight $M_u=2.27/\text{month}$ (27.2/year) is extremely high. Fishing mortality is also high at $F'=0.19/\text{month}$ (2.3/year). Combined with a weight of entry into the fishery of $W_c=126\text{g}$, this implies very high fishing pressure even on small fish.

The predicted and observed recapture rates (total recaptures as proportion of fish stocked) for the three release sizes are shown in Figure 5. The prediction for the small seed fish (1.5g) is based on the selectivity pattern estimated for the middle group and the indicative growth curve for the small cohort (see Fig. 3).

The predicted effects of changes in the harvesting regime (fishing mortality rate F and weight of entry into the fishery W_c) or the level of natural mortality M_u of the stocked

fish are shown in Figure 6. The present harvesting regime ($F'=0.19/\text{month}$, $W_c=126\text{g}$) is close to the optimum in terms of yield per fingerling, although recapture in numbers could be increased by harvesting at higher F' and lower W_c . Yields per fingerling are, however, very low at less than 18g, and changes in the harvesting regime will not lead to any substantial improvements. The key factor limiting returns is the high level of natural mortality in the stocked fish, and any reduction in M_u is predicted to result in substantial improvements.

5.4 Discussion

The population model provides a good fit to the observed catches (Fig. 4), and predicts the recapture rates achieved for different release sizes well (Fig. 5). Differences in overall recapture rates between release sizes are related primarily to the allometry of natural mortality, but are exacerbated by low growth in the cohort stocked at small size, and a more gradual entry into the fishery of the cohort stocked at large size.

The harvesting regime is characterised by high fishing mortality and a low size of entry into the fishery. However, high fishing pressure is not the primary cause of low returns, and no significant benefits could be derived from optimising exploitation patterns in this case.

The level of natural mortality in the stocked fish was extremely high at $M_u=27.2/\text{year}$, compared to a wild stock average of 3.0/year (Lorenzen 1996b) or the value of 2.1/year determined for bighead carp in a Chinese reservoir (Lorenzen et al. 1997). The high level of mortality is the primary cause of low recapture and yield per fingerling in the experiment, and any management measures to reduce M_u would yield substantial improvements. This may be achieved by optimising rearing and release techniques, which have been shown to influence survival of stocked fish (Berg & Joergensen 1991; Berg & Joergensen 1994; Cowx 1994; Carlstein 1997). Any reductions in M_u would lead to increased biomass (unless stocking is reduced or fishing intensified), and a density-dependent growth response. The actual benefits of reduced mortality are therefore likely

to be lower than predicted here, but the exact magnitude of this compensatory effect can not be predicted without information on the degree of density dependence in growth.

6 The need for comparative analyses

At present, most of the population model parameters have to be estimated for each particular fishery. An exception is the allometric scaling factor b of natural mortality, which has been found to be highly consistent in comparative analyses, and may therefore be considered known *a priori*. Other key parameters such as the competition coefficient c or the limiting asymptotic weight $W_{\infty L}$ are likely to be related to the species concerned and to characteristics of the waterbody stocked. Once these parameters have been determined for a range of fisheries, comparative analyses may lead to empirical generalisations that would greatly improve the predictability of outcomes of culture-based fisheries. Hence more widespread use of population models in the assessment of culture-based fisheries would lead to synergistic benefits in addition to the immediate benefits to the fishery assessed.

6 Conclusions

Population models with explicit representation of the key processes of density-dependent growth and size-dependent mortality are powerful tools for the assessment of stocking and harvesting regimes in culture-based fisheries. Population models provide insights into the factors underlying observed outcomes, and allow a quantitative evaluation of management options. Such models also aid comparative studies because they allow estimation of parameters that can be compared between widely different fisheries, such as M_u or the asymptotic size for a standardised biomass density.

Widespread use of population models will allow comparative analyses to identify relationships between population model parameters and waterbody characteristics, which

would further reduce data requirements for individual fisheries and provide a better basis for pre-stocking appraisal.

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Table 1. Stocking and recapture data for the *Cirrhinus mrigala* stocking experiment in Huay Luang reservoir (from Siripunt et al. 1989).

Stocking size	Large		Medium		Small		
Number stocked	18941		20759		17370		
Recaptures	W[g]	C	W[g]	C	W[g]	C	
Time [months]							
0		10.4		4.3		1.5	
1		36	185	18	8		
2		78	192	54	27		
3		132	222	132	222	32	2
4		332	541	216	170	95	2
5		471	200	394	125		
6		732	141	621	110		
7		1180	102	982	31		
8		1559	50	1313	18	1	1500
9		2100	33	1622	27		
10		2300	40	1905	19	9	346
11		2032	20	2309	9		

Table 2. Spreadsheet layout used in the analysis of the stocking experiment. The parameter estimates in cells C1-C5 were obtained by minimising the SSQ in cell F6.

	A	B	C	D	E	F
1	M at 1g		2.27			
2	F		0.19			
3	Wc		126			
4	p (7cm)		0.047			
5	p (10cm)		0.024			
6	SSQ					0.384
7						
8	Time	W[g]	N	C pred	C obs	SQ diff
9	Cohort 7cm					
10	0	4.3	20759			
11	1	18	7495	8	8	0.001
12	2	54	3757	23	27	0.004
13	3	132	2260	229	222	0.000
14	4	216	1350	229	170	0.016
15	5	394	799	137	125	0.001
16	6	621	497	85	110	0.011
17	7	982	322	55	31	0.064
18	8	1313	215	36	18	0.097
19	9	1622	145	25	27	0.001
20	10	1905	100	17	19	0.001
21	11	2309	69	11	9	0.014
22	Cohort 10 cm					
23	0	10.4	18941			
24	1	36	8528	167	185	0.001
25	2	78	4628	206	192	0.000
26	3	132	2729	261	222	0.005
27	4	332	1703	291	541	0.072
28	5	471	1037	178	200	0.002
29	6	732	656	112	141	0.009
30	7	1180	431	74	102	0.019
31	8	1559	290	50	50	0.000
32	9	2100	200	34	33	0.000
33	10	2300	139	23	40	0.050
34	11	2032	96	16	20	0.006

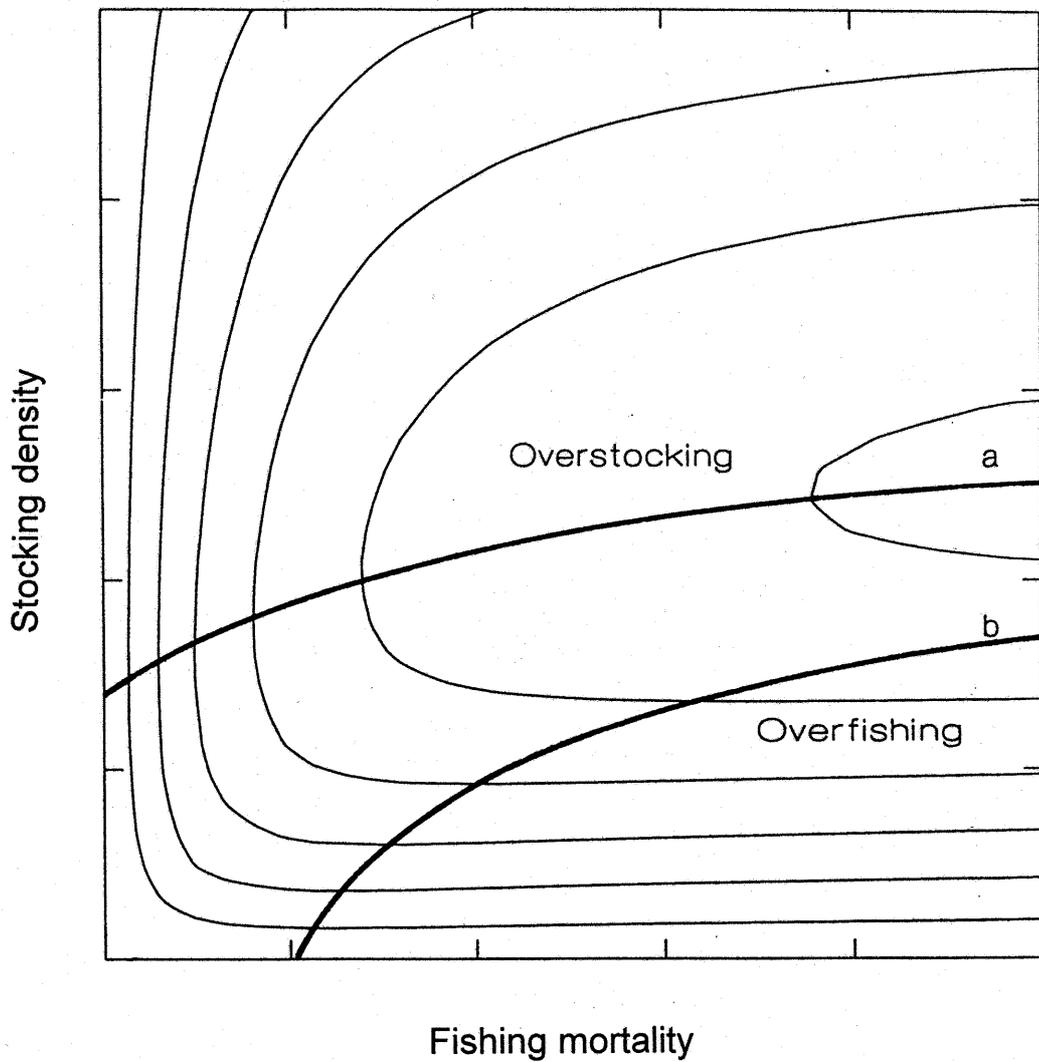


Fig.1. Production as a function of stocking density and fishing mortality (effort) in a culture-based fishery. Modified from Lorenzen (1995).

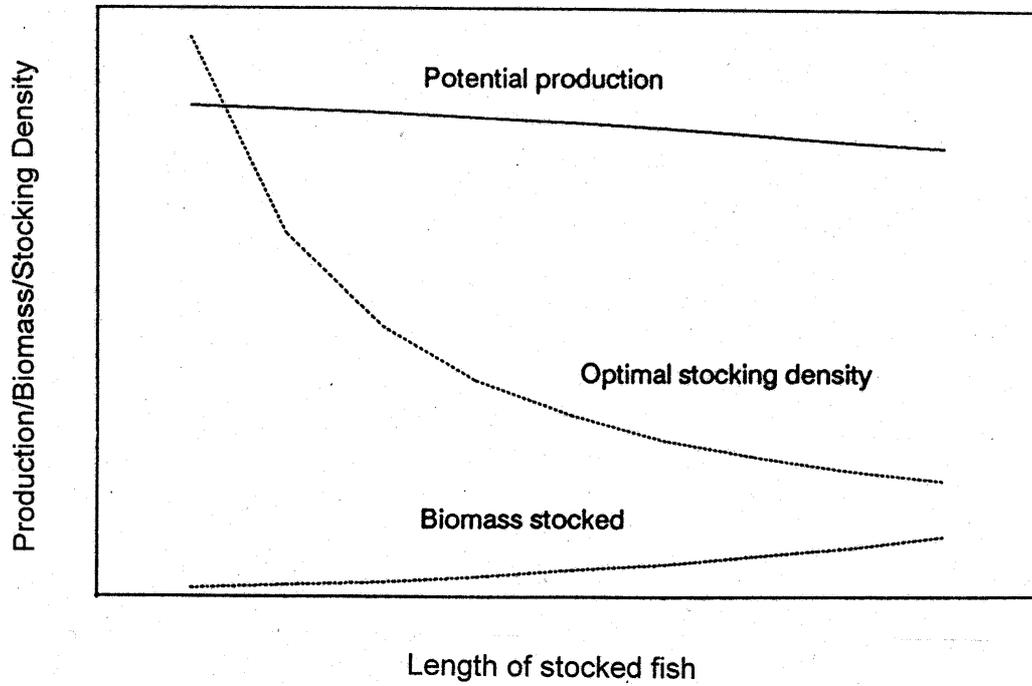


Fig. 2. Maximum production and the corresponding optimal stocking density and weight stocked as a function of the length of seed fish. Modified from Lorenzen (1995).

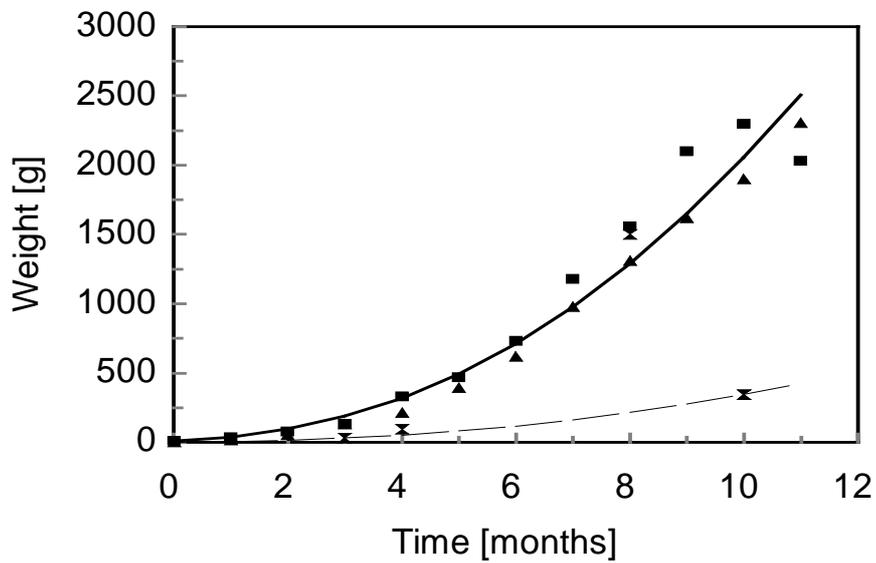


Fig. 3. Growth of stocked *C. mrigala* in Huay Luang: The cohorts stocked at large (squares) and medium (triangles) size show similar growth patterns that can be described by a von Bertalanffy growth function with $W_{\infty} = 58,000\text{g}$ and $K=0.034/\text{month}$ (solid line). Growth appears to be much slower in the cohort stocked at 5 cm (hourglass). The data are not sufficient to fit a growth model, but the dashed line ($W_{\infty} = 10,000\text{g}$ and $K=0.034/\text{month}$) provides a reasonable “eye fit”.

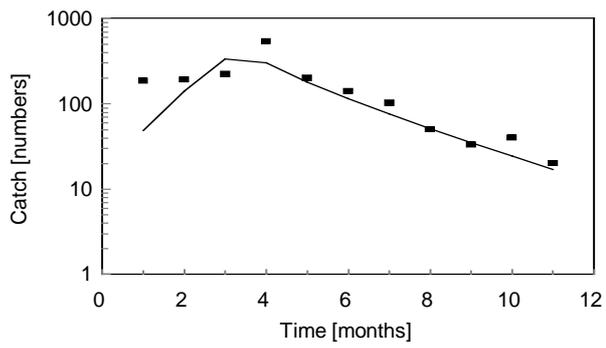
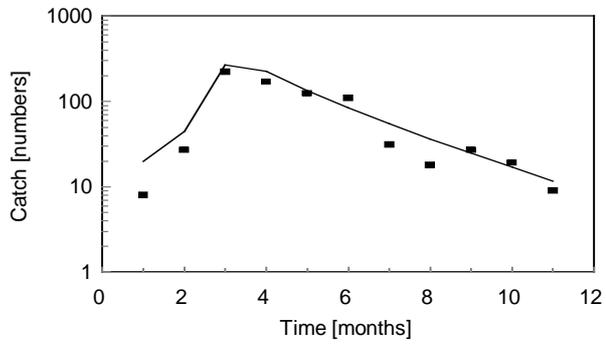


Fig. 4. Observed (squares) and predicted (lines) catches over the period of the stocking experiment. Medium (top) and large (bottom) size at stocking.

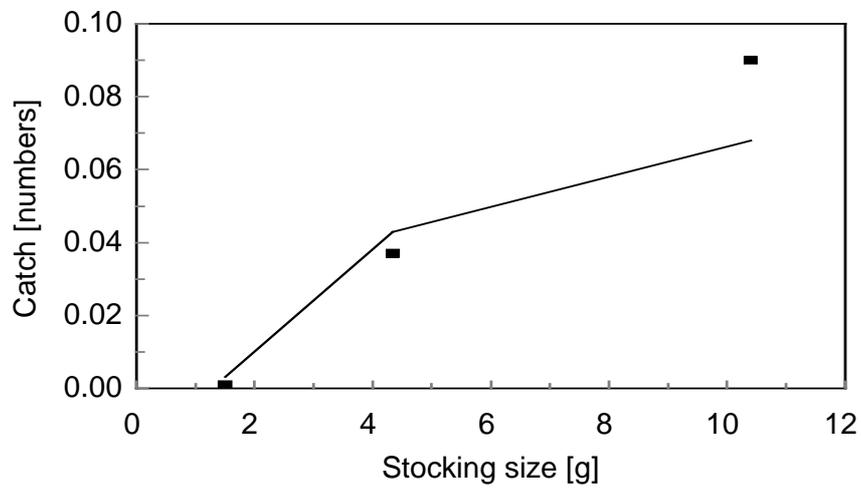


Fig. 5. Observed (squares) and predicted (lines) recapture of stocked fish in relation to weight at release. The prediction for the small seed fish (1.5g) is based on the selectivity pattern estimated for the middle group and the indicative growth curve for small seed (see Fig. 3).

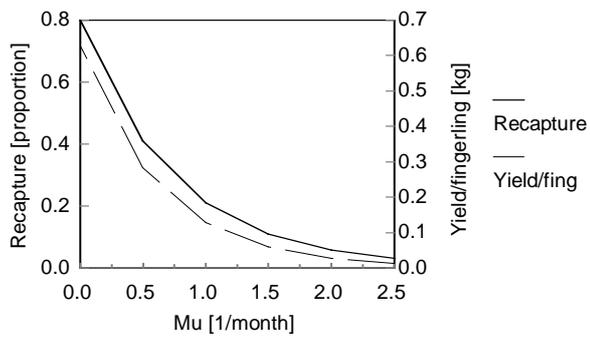
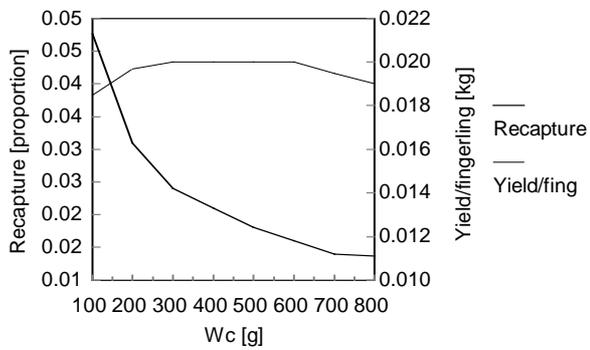
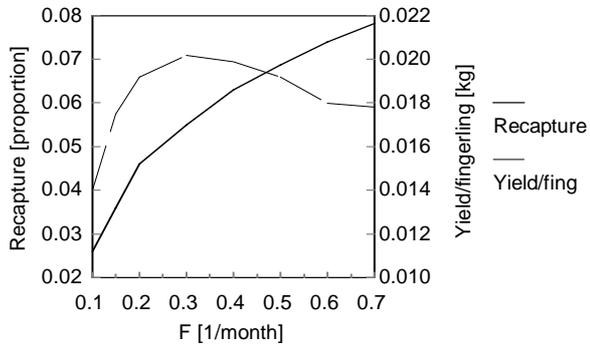


Fig. 6. Predicted effect on recapture and yield per fingerling of changes in fishing mortality F (top), gear selection length (centre) or the level of natural mortality (bottom). All predictions for the middle size group.