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Analysing extensive fish culture systems by transparent population modelling: bighead carp, *Aristichthys nobilis* (Richardson 1845), culture in a Chinese reservoir

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Abstract

A transparent population modelling approach is used to analyse a large-scale extensive fish culture system, the bighead carp, *Aristichthys nobilis* (Richardson 1845), fishery in a Chinese reservoir. The population model incorporates explicit sub-models for density-dependent growth and size-dependent mortality, and allows the assessment of stocking density, seed fish size, fishing mortality (fishing effort), and gear selectivity. The process of model building and parameter estimation from stocking and catch data is described in detail. The full analysis is carried out in computer spreadsheets where all model components are visible and can easily be modified to take account of specific conditions, or to explore different assumptions. The practical use of the model in management decision making is discussed, together with data requirements and the possible need for experimental management.

Introduction

In extensive aquaculture seed fish are stocked, left to utilize natural aquatic production for growth, and recaptured upon reaching a desired size. Management in extensive culture is thus concerned with the development of stocking and harvesting regimes that make efficient use of a given natural productivity. Quantitative analysis and modelling of the culture system can aid management decision making in two ways: the process of analysis improves the understanding of the interactions between management actions and natural processes, and the derived model may be used to evaluate different management options. To realize this potential, the analysis and modelling framework must be transparent and flexible to allow constructive interaction between decision makers and analysts. This paper describes the process of analysing and modelling a large-scale culture system in a Chinese reservoir, using a spreadsheet-based transparent population model.

Extensive fish culture in Dongfeng reservoir, China

Extensive fish culture is a widespread practice in Chinese reservoirs and lakes, with a total production estimated at 0.3–0.6 million t year^{-1} (Lu 1992; Wang & Li 1995). The culture system analysed in the present study operates in a multi-purpose reservoir in Zhejiang Province, in the temperate region of China. Dongfeng is a medium-size reservoir with an average surface area of 100 ha and a mean depth of 7 m. Managed comprehensively by a reservoir bureau, Dongfeng is used for extensive carp culture in a common Chinese system described by De Silva, Yu & Xiang (1991) and Li & Xu (1995). The reservoir is stocked around the end of each year with large (12 cm) fingerlings of bighead carp *Aristichthys nobilis* (Richardson 1845), silver carp *Hypophthalmichthys molitrix* (Cuvier & Valenciennes 1840), and small numbers of other carp species. Harvesting takes place only once a year around December and January, using the 'combined fishing method'. In the combined method, seine nets and blocking nets are used to drive fish into a large stationary trap net. Only fish of marketable size are harvested, selected by the gear but also by hand. The total production from Dongfeng reservoir is about 750 kg ha^{-1} $year^{-1}$, comprising 60% bighead carp, 32% silver carp, and 8% other carp species. Bighead and silver carp do not reproduce naturally in the reservoir, and their yield is based entirely on regular stocking.

The present management regime of Dongfeng reservoir was established in an experimental study conducted from 1974 to 1978. During the experiment, stocking densities were increased over previous levels and stabilized at a total 2700 ha^{-1} $year^{-1}$, with 1700 ha^{-1} $year^{-1}$ of bighead carp fingerlings. The age distribution and weight at age of fish in the catch were determined regularly, and the number and body weight of seed fish recorded. These data are used here to illustrate the process of model development and analysis. The management of Dongfeng reservoir has not changed greatly since the experiment, but no detailed data have been collected since 1978.

Analysis and model development

The population dynamics of fish in extensive culture are determined by the management actions of stocking and harvesting, in interaction with the natural processes of individual growth and mortality. Lorenzen (1995) developed a size-structured population model for culture-based fisheries and extensive fish culture, incorporating explicit sub-models for the processes of density-dependent growth and size-dependent mortality. In the present paper the model is reformulated in an age-structured framework. The model is implemented in computer spreadsheets, together with tools for the estimation of model parameters from stocking and catch data.

The individual growth of fish is described by a density-dependent version of the von Bertalanffy growth function (VBGF), described in Lorenzen (1996a). In the model, asymptotic weight $W_{\infty B}$ is defined as a function of population biomass:

$$W_{\infty B} = (W_{\infty r}^{1/3} - c\ (B - B_r))^3 \qquad (1)$$

where B is the actual population biomass, $W_{\infty r}$ is the asymptotic weight at reference biomass B_r, and c is the competition coefficient which describes the decline in asymptotic weight with increasing biomass. Mortality is described by a power function of weight in accordance with theoretical and empirical studies of fish mortality (Peterson & Wroblewski 1984; McGurk 1986; Gulland 1987; Lorenzen 1996b):

$$M_w = M_r \left(\frac{W}{W_r}\right)^b \qquad (2)$$

where M_W is the natural mortality rate at weight W, M_r is the mortality rate at reference weight W_r, and b is the allometric scaling factor of natural mortality.

The analysis of the fish culture system is conducted in four steps. First, cohort analysis is used to estimate fishing and natural mortality rates, and to reconstruct the population biomass dynamics over the period of the experiment. Second, the information on biomass dynamics is used to estimate parameters of the density-dependent growth model. Third, a size-based selectivity model is fitted to predict the effects of density-dependent growth on fishing mortality rates. Finally, an equilibrium yield model is constructed and used to predict the response of the culture system to changes in stocking and harvesting patterns. All analyses are carried out in computer spreadsheets which are illustrated in Tables 1, 2 and 3. Details of the spreadsheet construction and analysis procedures are given in the Appendix.

Cohort analysis

The reconstruction of the population and estimation of mortality rates is conducted by means of cohort analysis (also known as virtual population analysis, for a general account see Hilborn & Walters 1992). Cohort analysis reconstructs individual cohorts (year classes) of fish from the catches taken from that cohort over its lifetime. The analysis starts at the terminal age group of the cohort, i.e. the last age group that has contributed to the catch. Terminal

Table 1 Cohort analysis spreadsheet for bighead carp in Dongfeng reservoir (experiment 1974–78)

	A	B	C	D	E	F	G	H
1	Cohort analysis for extensive fish culture							
2								
3	Year	Age (years)	0	1	2	3	4	
4								
5	Body weight (g)							
6								
7	1974		15	355	655	3150	5250	
8	1975		15	265	960	1320	4050	
9	1976		15	235	635	2190	3090	
10	1977		15	190	655	1410	3320	
11	1978		15	175	665	1075	2090	
12								
13	Catch (ha^{-1})							
14								
15	1974		0.0	61.2	340.0	7.6	0.3	
16	1975		0.0	61.9	161.0	158.9	0.3	
17	1976		0.0	8.8	175.0	47.4	14.5	
18	1977		0.0	19.0	231.0	90.6	9.8	
19	1978		0.0	1.0	121.0	169.7	5.9	
20								
21	Population (ha^{-1})							
22		Stocking No.						
23	1974	850	865.3	387.9	576.4	8.0	0.3	
24	1975	1407	1437.7	494.8	238.8	179.7	0.3	
25	1976	1715	1748.9	810.2	305.2	61.2	16.8	
26	1977	1554	1574.4	959.9	563.1	99.2	11.3	
27	1978	1703	1703.0	855.2	655.7	250.1	6.8	
28								
29	Natural mortality							
30	b =	–0.3						
31	M_r =	0.27 year^{-1}						
32	W_r =	1000 g						
33								
34	Fishing mortality (year^{-1})							
								Average 3,4
35								
36	1974		0.000	0.172	0.891	2.956	2.000	2.478
37	1975		0.000	0.134	1.121	2.155	2.000	2.078
38	1976		0.000	0.011	0.852	1.487	2.000	1.744
39	1977		0.000	0.020	0.528	2.447	2.000	2.224
40	1978		0.000	0.001	0.204	1.135	2.000	1.568
41	Average 1974–78		0.000	0.067	0.719	2.036	2.000	
42								
43	Population biomass (kg ha^{-1})							
44		Total						
45	1974	554	13	137	377	25	2	
46	1975	619	22	130	229	237	1	
47	1976	594	26	189	193	134	52	
48	1977	750	24	181	368	140	38	
49	1978	894	26	149	436	269	14	

Table 2 Spreadsheet layout for the estimation of growth parameters. Parameters have been estimated by minimizing the sum of squared differences (SSQ) between the observed and expected weights

	A	B	C	D	E	F	G	H
1	Estimation of density-dependent VBGF parameters							
2								
3	Year	Age (years)		0	1	2	3	4
4								
5	Observed weights (g)							
6								
7	1974			15	355	655	3150	5250
8	1975			15	265	960	1320	4050
9	1976			15	235	635	2190	3090
10	1977			15	190	655	1410	3320
11	1978			15	175	665	1075	2090
12								
13	Model parameters							
14								
15	$W_{\infty r}$ =		10525 g					
16	K =		0.20 year^{-1}					
17	c =		0.012 g$^{1/3}$ ha kg^{-1}					
18	B_r =		714 kg ha^{-1}					
19								
20	Predicted weights (g)							
21								
22		B (kg ha^{-1})	$W_{\infty B}$ (g)					
23	1974							
24	1975	619	12194		234	985	1430	4223
25	1976	594	12661		240	847	1854	2295
26	1977	750	9935		205	712	1302	3060
27	1978	894	7822		175	569	1223	2082
28	Average	714						
29								
30	Squared differences of the log transformed observed and expected weights							
31								
32	1974							
33	1975				0.0028	0.0001	0.0012	0.0003
34	1976				0.0001	0.0157	0.0052	0.0167
35	1977				0.0010	0.0013	0.0012	0.0013
36	1978				0.0000	0.0046	0.0031	0.0000
37								
38	SSQ =	0.055						

age groups are the oldest age groups in cohorts that no longer contribute to the catch, and all the age groups in the most recent year included in the analysis.

In Dongfeng, fishing mortality occurs in a single annual event (during which natural mortality is negligible), while natural mortality acts throughout the year. Hence the number of fish alive in the terminal age group prior to fishing equals the number caught, divided by the proportion of fish harvested. If the proportion harvested is expressed as an exponential fishing mortality rate $F_{a,t}$, then the terminal numbers alive $N_{a,t}$ (at age a and time t) are given by

$$N_{a,t} = \frac{C_{a,t}}{1 - \exp(-F_{a,t})} \tag{3}$$

where $C_{a,t}$ is the terminal catch. The younger age groups in the cohort are reconstructed by successively working backwards from the terminal group. The

Table 3 Equilibrium yield model spreadsheet

	A	B	C	D	E	F	G	H	I
1	Equilibrium yield model								
2									
3	Growth parameters			Mortality parameters			Fishing parameters		
4									
5	W_{∞_r} = 10525 g				b = –0.3			F = 2.1 year^{-1}	
6	K = 0.2 year^{-1}				M_r = 0.27 year^{-1}			W_c = 880 g	
7	c = 0.012 g$^{1/3}$ ha kg^{-1}							p = 0.005 g^{-1}	
8	B_r = 714 kg ha^{-1}				W_r = 1000 g				
9									
10	Age (years)		0	1	2	3	4	5	
11									
12	W (g)		15	173	533	1057	1680	2343	
13	F (year^{-1})		0.033	0.068	0.334	1.471	2.056	2.098	
14	N (ha^{-1})		1700	891	569	304	55	6	
15	B (kg ha^{-1})		26	154	303	322	92	13	
16	C (ha^{-1})		54	59	162	234	48	5	
17	Y (kg ha^{-1})		1	10	86	248	80	12	
18									
19	Biomass				Summary				
20									
21			Assumed = 909 kg ha^{-1}			Yield = 436 kg ha^{-1}			
22			Calculated = 909 kg ha^{-1}			Mean weight = 777 g			
23			Absolute difference = 0 kg ha^{-1}						
24									
25			$W_{\infty B}$ = 7503						

number alive $N_{a-1,t-1}$ in the previous year is defined as the number $N_{a,t}$ divided by the survival rate (expressed here in terms of the exponential natural mortality rate), plus the catch $C_{a-1,t-1}$:

$$N_{a-1,t-1} = C_{a-1,t-1} \frac{N_{a,t}}{\exp(-M_W)} \quad (4)$$

where M_W is the (weight-dependent) natural mortality rate corresponding to the weight at mean length during the period:

$$M_W = M_r \left(\frac{W_{a-1,t-1}^{1/3} + W_{a,t}^{1/3}}{2\ W_r^{1/3}} \right)^{3b} \quad (5)$$

The exponential fishing mortality rates $F_{a,t}$ on the non-terminal groups are calculated from:

$$F_{a,t} = -\ln \left(1 - \frac{C_{a,t}}{N_{a,t}} \right) \quad (6)$$

Exponential fishing mortality rates are proportional to the effort expended on fishing, and to the selectivity of fishing gear for the respective age (size) group.

Cohort analysis requires the input of the natural mortality parameters M_r and b, and of the terminal fishing mortalities $F_{a,t}$ for all cohorts in the population. The natural mortality parameters are assumed to be constant over the period of the experiment (the validity of this assumption is examined later on). Comparative empirical studies indicate that the value of the allometric scaling factor b is fairly invariant between populations, and may therefore be fixed *a priori* in situations where no specific information exists (Lorenzen 1996b). The natural mortality rate M_r and the terminal fishing mortality rates are initially set to arbitrary values and then adjusted in the analysis in the following manner. In complete cohorts that have been observed from stocking until they have expired (i.e. no longer appear in the catch), M_r and the terminal $F_{a,t}$ are adjusted until the reconstructed initial numbers correspond to the stocking densities, and the terminal fishing mortalities are consistent with values estimated for younger but fully selected age groups. Complete cohorts provide the best estimates of M_r because the reconstructed initial numbers are insensitive to the assumed terminal $F_{a,t}$. Expired cohorts that have been observed only during their later years are reconstructed in a similar way, using the M_r estimate from the complete cohorts. In active cohorts which contribute to the catch in the most recent year, terminal $F_{a,t}$ assumptions have a major impact on the reconstructed numbers and therefore require careful consideration. Terminal $F_{a,t}$ values may be set to correspond to the values estimated for the same age group in previous years, assuming that fishing mortality at age has remained constant over time. Alternatively, terminal fishing mortalities may be set so that reconstructed initial numbers correspond to stocking densities, allowing fishing mortalities to vary over time. If the two approaches lead to different results, then either fishing or natural mortality rates have changed over time, and further information and judgement are necessary to decide which is the case. If the question cannot be resolved, both assumptions should be carried through the full analysis, including the assessment of management options.

Once all cohorts have been reconstructed, total population biomass B_t in year t is calculated as:

$$B_t = \sum_{a=0}^{a_{\max}} N_{a,t}\ W_{a,t} \quad (7)$$

Statistical confidence limits for results of the cohort analysis are difficult to obtain due to the use of external information and subjective judgement, and it is therefore important to assess the sensitivity of results to different assumptions. Erroneous assumptions lead to systematic errors which can not be detected by statistical analyses, while random variation in fishing mortality is reflected in $F_{a,t}$ estimates and can be quantified by fitting a selectivity model as described later.

Growth model estimation

The density-dependent VBGF predicts the mean individual weight $W_{a,t}$ as a function of $W_{a-1,t-1}$ (the cohort's mean individual weight in the previous year), and of $W_{\infty B}$:

$$W_{a,t} = ((W_{\infty B}^{1/3} - (W_{\infty B}^{1/3} - W_{a-1,t-1}^{1/3})\ \exp(-K))^3 \quad (8)$$

The asymptotic weight $W_{\infty B}$ is a function of population biomass as defined in equation 1. It is assumed here that the weights $W_{a,t}$ in year t reflect the population biomass B_t at the same instant in time.

If weight at age data are available and the population biomass dynamics have been reconstructed, then the parameters of the density-dependent VBGF can be estimated as follows. For each observed weight $Wo_{a-1,t-1}$, the predicted weight $Wp_{a,t}$ in the following year is calculated from equation 8, subject to B_t. The best estimates of the growth model parameters are the values that minimizes the sum of squared differences (SSQ) between the observed and expected weights, $Wo_{a,t}$ and $Wp_{a,t}$. Applying a logarithmic transformation, the SSQ is calculated as

$$SSQ = \sum_{a=0,\, t=t_{\min}}^{a_{\max},\, t_{\max}} (\log(Wo_{a,t}) - \log(Wp_{a,t}))^2 \quad (9)$$

The parameter set that minimizes SSQ is found by numerical search, as described in the Appendix. Approximate confidence limits for the estimates are given by the parameter values that satisfy

$$SSQ(W_{\infty r}, K, c) = SSQ(\hat{W}_{\infty r}, \hat{K}, \hat{c}) \left(1 + \frac{3}{n-3} F(3, n-3, 1-q)\right) \quad (10)$$

where $\hat{W}_{\infty r}$, $\hat{K}$ and $\hat{c}$ are the best estimates, and F is the value of the cumulative F-distribution for n observations and significance level q (Draper & Smith 1981). These confidence limits are approximate and may underestimate the true uncertainty in parameter values for two reasons. Most data points occur twice, in the independent and in the dependent variable, which may lead to bias in both the point and variance estimates of parameters. Also, the reconstructed biomass may be subject to systematic errors which are not reflected in the confidence limits of the growth model parameters. Nevertheless, the derived confidence limits provide a useful indication of the uncertainty in parameter estimates and their approximate nature can be accounted for by using wider limits in the uncertainty analysis of management options.

Selectivity model estimation

In the cohort analysis, fishing mortality has been treated as an age-related parameter. However, fish are selected for harvesting by size not age, and density-dependent changes in growth lead to changes in fishing mortality at age. It is therefore necessary to express F as a function of individual weight, here in the form of a logistic relationship:

$$F_{a,t} = \frac{F'_t}{1 + \exp(p\,(W_c - W_{a,t})} \quad (11)$$

where F'_t is the fishing mortality on the fully selected size-groups, W_c is the mean selection weight, and p indicates the steepness of the logistic curve. Selectivity parameters are estimated analogous to growth parameters, by determining the values that minimize the SSQ between the $F_{a,t}$-values determined in the cohort analysis and the values predicted by equation 11. Approximate confidence limits can be determined in the same way as for the growth model parameters.

Equilibrium yield prediction, sensitivity and uncertainty analysis

At equilibrium, population structure, biomass and yield are constant and independent of time, and a cross-section of the population is equivalent to following a cohort over its lifetime. Equilibrium yield is calculated by following a cohort of stocked fish over its lifetime, using the growth and mortality equations derived above. A complication arises because growth is dependent on biomass, which in turn depends on growth. Hence the equilibrium population structure is found by solving the equation

$$B^* = \sum_{a=0}^{a_{max}} N(B^*)_a \; W(B^*)_a \quad (12)$$

for the equilibrium biomass B^* subject to the model parameters, and the stocking density and body weight of seed fish (N_0 and W_0, respectively). The population $N(B^*)_a$ at age is given by

$$N(B^*)_a = N(B^*)_{a-1} \exp(-F_{a-1}) \exp(-M_W) \quad (13)$$

where F_{a-1} is the fishing mortality rate defined as a logistic function (equation 11) of weight $W(B^*)_{a-1}$. The natural mortality rate M_W is given by equation 5. Weights $W(B^*)_a$ are given by equation 8, with $W_{\infty B}$ defined by equation 1.

Once the equilibrium population has been found by solving equation 12, the corresponding catches C_a are calculated from:

$$C(B^*)_a = N(B^*)_a\,(1 - \exp(-F_a)) \quad (14)$$

Total equilibrium yield Y^* is then:

$$Y^* = \sum_{a=0}^{a_{max}} C(B^*)_a \; W(B^*)_a \quad (15)$$

The model does not necessarily have an equilibrium solution for all possible parameter values and conditions, but in general a solution exists for the parameter values and conditions of practical interest.

An uncertainty analysis is carried out on the absolute level of equilibrium yield, as well as on the relative response in yield to changes in management. The analysis identifies key uncertainties which must be considered in the analysis of management options.

Results

All analyses were carried out using *a priori* values for the allometric exponent of natural mortality b consistent with the empirical results of Lorenzen (1996b). The standard value of b was set at –0.3, while values of –0.2 and –0.5 were used in order to assess the uncertainty in predictions resulting from the uncertainty about the true value of b for the population.

Cohort analysis

The cohort analysis spreadsheet with the final results of the analysis is shown in Table 1 (see the Appendix for details of implementation). The natural mortality rate at reference weight W_r = 1000 g has been estimated as $M_r = 0.27$ year^{-1}, given the standard value of $b = -0.3$. The natural mortality rates for the other assumed values of b are $M_r = 0.32$ year^{-1} for $b = -0.2$, and $M_r = 0.19$ year^{-1} for $b = -0.5$. Terminal fishing mortalities in the active cohorts have been adjusted so that their initial numbers correspond to the known stocking densities, allowing for changes in $F_{a,t}$ over time. The estimated $F_{a,t}$ rise steeply from age 0 to 3 years, reflecting the increasing selection by the fishing gear. Over time, fishing mortalities in ages 3 and 4 years are relatively stable, while there is a sharp decline in F at age 1 year, and to a lesser extent at age 2 years. The actual and reconstructed stocking numbers are shown in Fig. 1, for the estimated rate of natural mortality and a 10% variation in this rate. Also shown are the stocking numbers obtained by setting the terminal $F_{a,t}$ values to their averages over the preceding years. Stocking numbers reconstructed using this criterion are far below the actual numbers in 1976 and 1977, indicating that $F_{a,t}$ must have changed over time as described above. The decline in reconstructed stocking numbers could also be attributed to an increase in natural

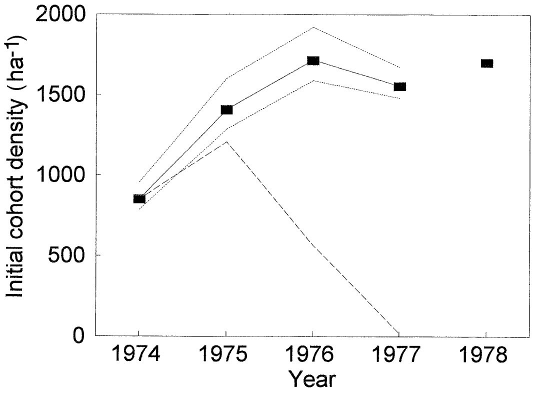

Figure 1 Actual and reconstructed initial cohort densities during the experiment. The actual stocking densities are denoted by squares. The solid line indicates initial cohort densities obtained by adjusting the terminal $F_{a,1978}$ to reconstruct actual stocking densities. Dotted lines indicate the sensitivity of reconstructed initial densities to a 10% variation in the natural mortality rate M_r. The dashed line indicates initial cohort densities obtained by setting the $F_{a,1978}$ to the average $F_{a,1974–78}$.

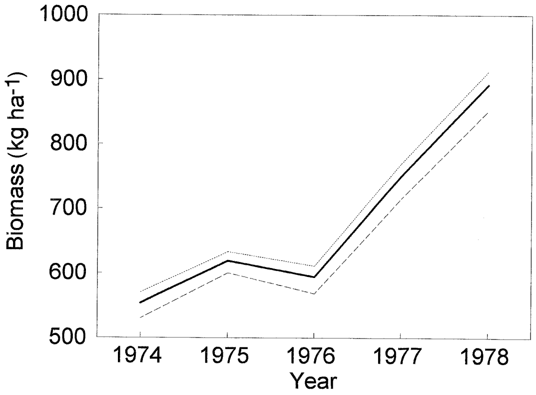

Figure 2 Reconstructed biomass of bighead carp during the experiment. The solid line indicates biomass for the default value of $b = -0.3$. Also shown are the results for $b = -0.5$ (dashed line) and $b = -0.2$ (dotted line).

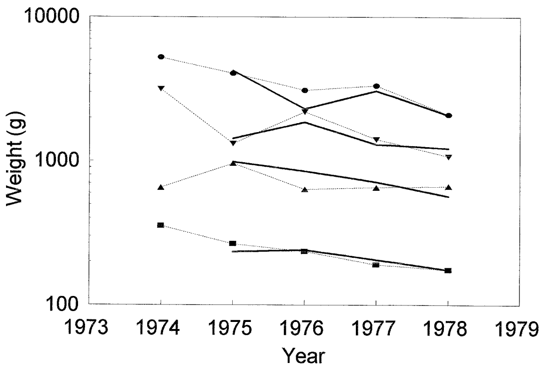

Figure 3 Observed (solid lines) and predicted (heavy solid lines) weights at age 1 (■), 2 (▲), 3 (▼) and 4(●) years during the period of the experiment. Predictions represent the best fit of the growth model (Table 2).

mortality rates to 0.58 year^{-1} in the 1976, and 2.2 year^{-1} in the 1977 cohorts. However, such an increase in M_r would imply reduced yields in the years following the experiment, which is not borne out in the actual data (cf. Fig 5). Hence declining fishing mortality in the younger age groups due to density-dependent growth reduction is the most plausible explanation of the observed patterns. This is also supported by the results of fitting the weight-based selectivity model (see below).

The population biomass is dominated by ages 1 to 3. The reconstructed total biomass is shown in Fig. 2, for the different assumed values of *b*. Biomass rises sharply (from about 550 to 900 kg ha^{-1}) over the period, particularly after 1976 when the strong cohorts stocked from 1975 onwards have reached significant biomass (Table 1). The assumed value of *b* has only a minor influence on the absolute level of the reconstructed biomass, and even less impact on the relative change in biomass over time.

Growth model estimation

The spreadsheet used for growth model estimation is shown in Table 2. Based on the biomass reconstruction for $b = -0.3$, the density-dependent growth parameters, together with their approximate 95% confidence limits (in brackets) are $W_{\infty r} = 10525$ (7530, 14700) g, $K = 0.2$ (0.17, 0.23) year^{-1} and $c = 0.012$ (–0.009, 0.031) g$^{1/3}$ ha kg^{-1}, for a reference biomass of $B_r = 714$ kg ha^{-1} (the average biomass in 1975–78). The same set of growth parameters is estimated using the biomass reconstructions for other values of *b* when the reference biomass is set to the respective averages ($B_r = 732$ kg ha^{-1} for $b = -0.2$ and $B_r = 684$ for $b = -0.5$). The observed and predicted weight at age over the period are illustrated in Fig. 3. The approximate confidence limits of the competition coefficient *c* are very wide, and include negative values. Negative values of *c* imply a positive effect of population density on growth, which contradicts biological knowledge and management experience.

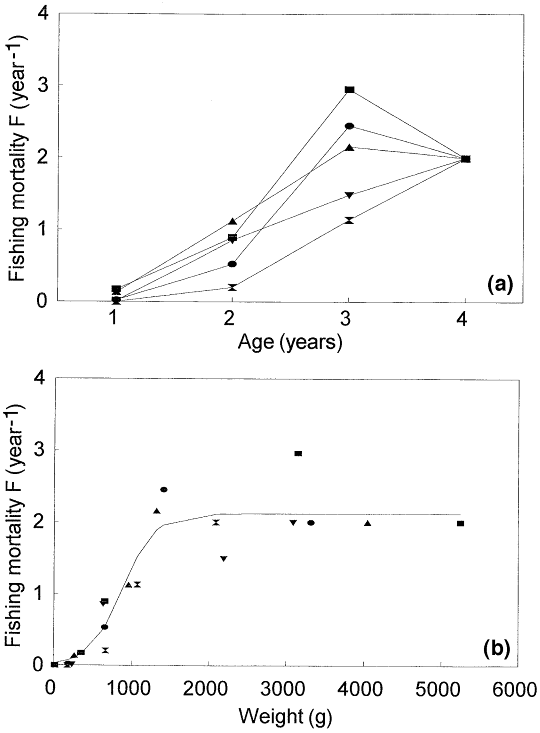

Figure 4 Fishing mortality $F_{a,t}$ patterns estimated in the cohort analysis; (a) Fishing mortality at age in different years, (b) Fishing mortality in relation to weight, with the fitted weight-dependent selectivity model (heavy solid line). The different years are denoted by symbols (■) 1974 (▲) 1975 (▼) 1976 (●) 1977 (⧗) 1978.

Hence in the analysis of management options, $c = 0$ is considered the lowest possible value. (If negative density-dependence is strongly apparent in the analysis, this may indicate a change in $W_{\infty r}$ over time which would require a structural alteration in the model.)

Selectivity model estimation

The spreadsheet used to estimate the selectivity model parameters is similar to that used for the growth model, and is not shown here. The selectivity parameters with approximate 95% confidence limits were estimated as $F = 2.1$ (1.8, 2.4) year^{-1}, $W_c = 880$ (700, 1080) g, and $p = 0.0048$ (0.0026, 0.0100) g^{-1}. An overview of the $F_{a,t}$ patterns reconstructed in the cohort analysis is given in Fig. 4a, while Fig. 4b shows the reconstructed fishing mortalities in relation to weight, together with the fitted selectivity model. The reconstructed fishing mortalities are well described by the weight-based selectivity model.

Equilibrium yield predictions

The yield model spreadsheet is reproduced in Table 3, showing the equilibrium solution for the best parameter estimates and the end of experiment management regime. The equilibrium biomass is 909 kg ha^{-1}, and the equilibrium yield is 436 kg ha^{-1} year^{-1} with an average body weight of 777 g. Catches and yield are dominated by fish of age 3 years, hence the production cycle of the culture system is effectively 3 years. The mortality and growth parameters derived for alternative values of b (–0.2 and –0.5) result in the same equilibrium yield as the standard set, albeit at slightly different values of equilibrium biomass.

The actual stocking density and yield of bighead carp in Dongfeng reservoir from 1974 to 1980 are shown in Fig. 5, together with the stocking density and predicted yield of the end-of-experiment equilibrium solution. Stocking density has been approximately 1700 ha^{-1} per year since 1976, and the actual yield approaches the predicted equilibrium yield 3 years later, in 1979. Equilibrium model predictions correspond well to the observed yield.

The results of the uncertainty analysis of yield and yield response to changes in management (50% reduction in stocking density, 50% reduction in fishing mortality, and 67% reduction in fingerling body weight) are given in Table 4. The parameter uncertainties are based on the approximate confidence intervals for growth and selectivity parameters, and on external information and critical judgement for the natural mortality parameters. Uncertainty in b is based on the comparative study of Lorenzen (1996b), while uncertainty in M_r was determined by assuming a maximum error of 20% in the recorded stocking data and calculating the corresponding error in M_r. The single-most uncertain parameter is the competition coefficient c, followed by the steepness parameter p of the selectivity model. Overall, the predictions are fairly insensitive to variation in parameters; all parameter uncertainties result in smaller relative uncertainties in the yield predictions. The growth parameters are the greatest source of uncertainty about the absolute value of yield, and the competition coefficient c is by far the greatest source of uncertainty in the yield response to changes in management. The analysis of

Table 4 Uncertainty analysis of the equilibrium yield model. Given are the uncertainty in parameter values and the corresponding sensitivity of predicted yield and yield response to changes in management. The alternative management scenarios are a 50% reduction in fishing mortality ($F \times 0.5$), a 50% reduction in stocking density (SD × 0.5) and a 67% reduction in the weight of seed fish ($W_0 \times 0.33$).

Parameter	Uncertainty %	Sensitivity of yield (%)	Sensitivity of relative change in yield (%) due to		
			$F \times 0.5$	SD × 0.5	$W_0 \times 0.33$
$W_{\infty r}$	35	19	4	2	0
K	16	14	2	3	2
c	130	22	28	34	12
b	55	9	10	6	7
M_r	23	9	6	5	3
F	15	2	5	3	2
W_c	22	5	10	11	4
p	80	9	7	9	4

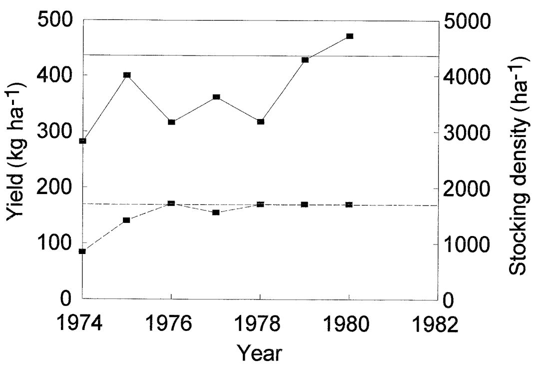

Figure 5 Stocking density (dashed line) and yield (solid line) during the experiment and the following two years. Lines with solid squares indicate the actual values. The corresponding horizontal lines without symbols indicate the end-of-experiment density, and predicted equilibrium yield.

management options must therefore account for uncertainty primarily with respect to the value of c.

Analysis of management options

The equilibrium solution of the model for the standard parameter set and end-of-experiment conditions was used as a benchmark for the evaluation of management options. This benchmark solution (which corresponds well to the observed yield after 1978; Fig. 5) was treated as known, and made independent of the value of c by setting the reference biomass and corresponding asymptotic weight of the growth model to the equilibrium values.

The predicted responses in yield to changes in stocking density and fishing mortality are shown in Fig. 6, for the standard value of $c = 0.012$ g$^{1/3}$ ha kg^{-1} and the extreme values of $c = 0$ g$^{1/3}$ ha kg^{-1} and $c = 0.031$ g$^{1/3}$ ha kg^{-1}. Arrows indicate the status at the end of the experiment. The analysis indicates that the end-of-experiment stocking and harvesting regimes are near optimal, unless the true value of c is very different from the best estimate.

The predicted effect of changing the body weight of stocked fingerlings is shown in Fig. 7, for the standard and extreme values of both c and b. Uncertainty in c has a greater overall effect on predicted yield than uncertainty in b. For the best estimate of c, yield is fairly insensitive to fingerling weight. In the absence of density dependence, a reduction in fingerling weight would result in a more marked loss of yield. Under extremely high density dependence, a reduction in fingerling weight would actually increase yield. The use of smaller seed fish is equivalent to a reduction in stocking density which, under high density dependence, would increase yield (cf. Fig. 6a). The effect of fingerling weight on yield is most sensitive to the value of b (i.e. the degree of size dependence in mortality) when density-dependence in growth is weak and therefore does not compensate for changes in mortality. The analysis indicates that substantial reductions in seed size may be possible without significantly reducing yield.

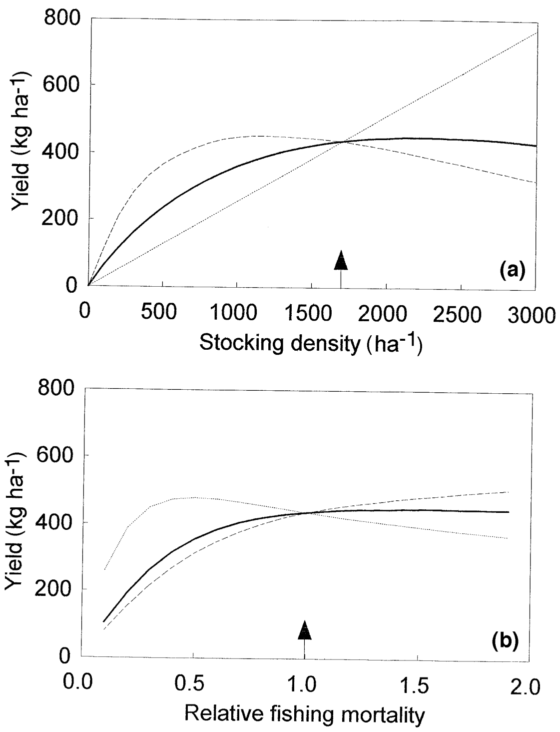

Figure 6 Response of predicted equilibrium yield to changes in stocking density (a) and relative fishing mortality (b). The baseline (end-of-experiment) management is indicated by arrows. Predictions are given for the standard value of $c = 0.012$ $g^{1/3}$ ha kg^{-1} (solid line), and for the extreme values of $c = 0$ $g^{1/3}$ ha kg^{-1} (dotted line) and $c = 0.031$ $g^{1/3}$ ha kg^{-1} (dashed line).

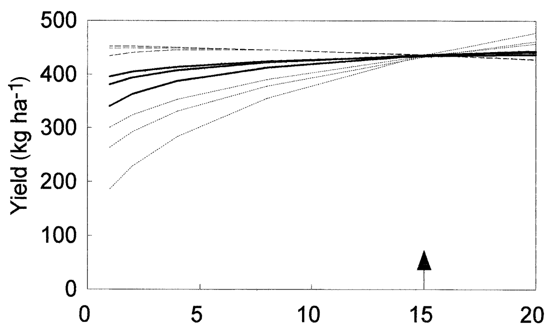

Figure 7 Equilibrium yield predictions for different weights of seed fish, stocked at the baseline stocking density of 1700 ha^{-1} per year. Predictions are given for the standard value of $c = 0.012$ $g^{1/3}$ ha kg^{-1} (solid line), and the extreme values of $c = 0$ $g^{1/3}$ ha kg^{-1} (dotted line) and $c = 0.031$ $g^{1/3}$ ha kg^{-1} (dashed line). For each value of c, predictions are shown for mortality weight exponents of $b = -0.2$, $b = -0.3$, and $b = -0.5$.

Model predictions were obtained for various management options, including scenarios in which several conditions are changed simultaneously. The results are summarized in a decision table (Table 5), which shows the predicted yield for each option given different assumptions about the true value of c. Of the options considered, only a combined increase in stocking density and fishing mortality is virtually certain to increase yield, regardless of the true value of c. All other options may lead to an increase or a decrease in yield, depending on the true value of c. Options with uncertain outcomes may be adopted if the expected benefit outweighs the associated risk. In the present case, however, none of the uncertain options promises substantial increases in yield for any values of c. The 'certain' options of combined increases in stocking density and fishing mortality by 20 or 40% are expected to result in only moderate yield increases of 6 or 10%, respectively. Overall this suggests that the bighead culture system in Dongfeng operates slightly below its optimum for yield, and probably close to its optimum for efficiency (i.e. utilization of inputs).

Discussion

The analysis may be carried out by a technical specialist who should liaise closely with managers and others who have detailed knowledge of the particular culture system. This is important to ensure that the system is adequately represented in the model, and that the analysis is transparent, relevant and credible to decision makers. Also, the manager's perception of uncertainties and attitude to risk must be taken into account in the evaluation of management options. If potentially beneficial management options are identified and considered for implementation, it is important to remember that the expected benefits may not be realized immediately. The change from one equilibrium state to another may occur slowly, and may involve temporary loss of yield.

Details of the model and analysis may need to be adapted to each particular culture system, and will also depend on the availability of data. The model may be modified to include natural recruitment (e.g. by defining the initial cohort number as the number stocked plus a natural contribution that may depend on population biomass), or density-dependent mortality (e.g. by making M_r dependent on population biomass). Information on such processes

Table 5 Decision table of management options, showing the predicted effects of changes in fishing mortality (F) and stocking density (SD) on yield (kg ha^{-1} $year^{-1}$), for different values of the competition coefficient c

Management option	**Value of *c* ($g^{1/3}$ ha kg^{-1})**		
	0.000	**0.012**	**0.031**
Baseline (end-of-experiment regime)	437	437	437
20% reduction in *F*	457*	420	401
20% increase in *F*	418	445*	459*
20% reduction in SD	350	410	449*
20% increase in SD	524*	448*	411
20% reduction in both *F* and SD	361	402	442*
20% increase in both *F* and SD	497*	462*	441*
40% increase in both *F* and SD	560*	481*	441*

*, indicates a predicted increase in yield over that achieved by the end-of-experiment management regime.

is often very limited, and different assumptions need to be considered and their implications explored.

The analysis uses stocking and catch data, including age-related data on catch composition and body weight, which may be obtained either by ageing fish from hard parts, or by batch marking of seed fish. When sampling catches, random samples must be taken for the estimation of age composition. Additional targeted sampling of large fish should be carried out for the estimation of mean weight at age, because large and old fish provide important information on growth but will not be strongly represented in random samples.

In culture systems under equilibrium conditions (i.e. stable management and environment), a single age-related sample may be sufficient to estimate all model parameters except for those describing density-dependent effects. Such parameters (e.g. the competition coefficient c) can be estimated only if data are available for different population densities. Variation in population density often occurs naturally due to factors beyond management control, but may also be induced deliberately in management experiments. If no specific data on density effects are available, it may still be possible to infer likely ranges of relevant parameter values from analyses of similar culture systems. This information may then be used to assess the possible benefits obtainable from management experiments, as well as the risks involved. Further guidance on the design of experimental (adaptive) management systems is given in Hilborn & Walters (1992).

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Appendix: Implementation of the spreadsheet models and analyses

Cohort analysis (Table 1)

Spreadsheet construction:
C3..G3; Age to which the data relate.
A7..A49; Time to which the data relate.
C7..G11; Observed body weights $W_{a,t}$.
C15..G19; Observed catches $C_{a,t}$.
B23..B27; Stocking numbers.
C23..F26; Cohort analysis equation 4 (incorporating equation 5) to determine $N_{a,t}$.
G23..G27; Cohort analysis equation 3 to determine terminal $N_{a,t}$.
C27..F27; Cohort analysis equation 3 to determine terminal $N_{a,t}$.
B30..B32; Natural mortality parameters.
C36..F39; Cohort analysis equation 6 to determine $F_{a,t}$.
G36..G40; Terminal $F_{a,t}$ entered by the user.
C40..F40; Terminal $F_{a,t}$ entered by the user.
H36..H40; Average $F_{a,t}$ age 3 and 4 years.
C41..G41; Average $F_{a,t}$ years 1974–78.

C45..G49; Biomass at age ($N_{a,t} \times W_{a,t}/1000$).
B45..B49; Eqn 7 to calculate total biomass.
Analysis:
(1) The only complete cohort (stocked in 1974 and running diagonally through the table) was reconstructed using arbitrary initial guesses of the terminal $F_{4,1978}$ and of the natural mortality rate M_r.
(2) The terminal $F_{4,1978}$ was adjusted to a value close to the estimated $F_{3,1977}$, reflecting the assumption that all fish of age 3 years and over are fully selected by the fishing gear and therefore subject to the same fishing mortality.
(3) The natural mortality rate M_r was adjusted to make the reconstructed $N_{0,1974}$ equal to the number stocked in 1974.
(4) The cohorts stocked prior to 1974 were reconstructed by setting the all terminal $F_{4,t}$ to the value of $F_{4,1978}$. The sensitivity of cohort sizes to adjustments in the terminal $F_{4,t}$-values was assessed and found to be very small.
(5) The terminal $F_{a,1978}$ values of cohorts stocked after 1974 were set so that the reconstructed cohort numbers $N_{0,t}$ equal the corresponding stocking numbers.

Growth model estimation (Table 2)

Spreadsheet construction:
D3..H3; Age to which the data relate.
A7..A36; Time to which the data relate.
D7..H11; Observed weights $Wo_{a,t}$
B15..B18; Model parameter values.
B24..B27; Population biomass reconstructed in the cohort analysis.
B28; Average biomass over the period 1974–78.
C24..C27; Equation 1 to calculate $W_{\infty B}$ subject to the given parameters and biomass.
E24..H27; Equation 8 to predict weights $Wp_{a,t}$ from observed weights $Wo_{a-1,t-1}$ in the previous year, subject to $W_{\infty B}$ in year t (C24..C27), and K (B16).
E33..H33; Squared differences between the (log-transformed) observed and predicted weights.
B38; Equation 9 to calculate the sum of squared differences (SSQ).
Analysis:
(1) The competition coefficient was set to $c = 0$, and initial values for $W_{\infty r}$ and K identified by manually varying their values until a good correspondence of observed and predicted weights was achieved.
(2) The optimizer facility was used to find the values of $W_{\infty r}$ and K that minimize SSQ, with c fixed at zero.
(3) The optimizer was used again to minimize SSQ, this time allowing c to vary.
(4) Minimization was repeated from different starting values to check for multiple minima in SSQ.
(5) Approximate confidence limits were determined for each parameter by finding the values above and below the best estimate that resulted in the critical SSQ at confidence level q, calculated from equation 10.

Equilibrium yield model (Table 3)

Spreadsheet construction:
A5..I8; Model parameter values.
C10..H10; Age to which the data relate.
C12; Body weight of seed fish W_0.
D12..H12; Equation 8 to calculate weights W_a from W_{a-1}, subject to the assumed biomass (C21) and the corresponding asymptotic weight $W_{\infty B}$ (C25).
C13..H13; Equation 11 to calculate F_a based on the fishing parameters and weights $W_{a,t}$.
C14; Stocking density N_0.
D14..H14; Equation 13 to predict population numbers N_a.
C15..H15; Biomass at age.
C16..H16; Equation 14 to calculate catches C_a, from F_a and N_a.
C17..H17; Yield at age Y_a ($C_a \times W_a/1000$).
C21; Assumed total biomass, which is adjusted to equal calculated biomass in order to find the equilibrium solution.
C22; Calculated total biomass (sum of cells C15..H15).
C23; Absolute difference between the assumed and calculated biomass, which is minimized using the optimizer in order to solve the model.
G21; Total yield (sum of cells C17..H17).
G22; Mean weight, i.e. total yield divided by total catch (sum of cells C16..H16).
Analysis:
The equilibrium solution of the model is found by adjusting the assumed biomass until it equals the predicted value, either manually or by using the optimizer facility. Use of the optimizer is more convenient but may fail to find an equilibrium even though it exists and may be found by manual search. The model must be solved again after every change in parameters or conditions.

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