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A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*)

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Abstract

A simple model for density-dependent growth is described, and applied to the analysis of carp growth in extensive aquaculture. The model is based on a von Bertalanffy growth function, with the asymptotic length a linear declining function of population biomass. The model provides a good description of carp growth both in mixed-age populations and in single cohorts, and the model parameters can be interpreted biologically. It is concluded that the density-dependent extension of the von Bertalanffy growth function provides a useful conceptual framework for the analysis of fish growth in extensive aquaculture. The model is a potentially valuable tool for the quantitative assessment of extensive aquaculture systems, and of culture-based fisheries.

Keywords: Aquaculture; Density-dependence; Growth; Model

1. Introduction

Fish are renowned for their extreme plasticity in individual growth (Wootton, 1990). One aspect of this plasticity is the dependence of growth on population density, which is well documented in wild 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; Pillay, 1990). Density-dependent growth in natural populations and extensive culture is the result of intraspecific competition, mainly for food.

Density-dependent growth is a key process in the dynamics of extensive aquaculture systems. Where such systems operate on a large scale as culture-based fisheries, a

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mathematical model for density-dependent growth is an important tool for the assessment of stocking and harvesting regimes (Lorenzen, 1995). Yet there is at present no conventional way of describing density-dependent growth mathematically, and this problem has received little attention since the study by Beverton and Holt published in 1957.

Beverton and Holt (1957) analyzed empirically the growth response in North Sea plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) to changes in population density. They concluded that the observed variations in growth could be well described by a von Bertalanffy growth function (VBGF) with the asymptotic length L_∞ defined as a linear declining function of population density. A linear relationship between asymptotic length or length at age and population density or biomass has also been found in other studies of natural and laboratory populations (Foerster, 1968; Barlow, 1992; Salojaervi and Mutenia, 1994). However, Beverton and Holt's simple model has rarely been applied, least of all in an aquaculture context.

In the present study, the von Bertalanffy model for density-dependent growth first proposed by Beverton and Holt (1957) is developed further with respect to extensive aquaculture. The model is then applied to the analysis of carp growth experiments.

2. Material and methods

2.1. Formulation of the growth model

In the von Bertalanffy growth function (VBGF), growth is defined as the net result of the processes of anabolism and catabolism (Bertalanffy, 1957; Beverton and Holt, 1957). In the form of the VBGF commonly used to describe the growth rate in length L of fish,

$$\frac{dL}{dt} = -K(L - L_\infty) \tag{1}$$

the parameter K is a measure of the catabolic activity, while the asymptotic length L_∞ is related to anabolism. Catabolism, the breakdown of body materials, is largely independent of population density. Anabolism, the building up of body materials, is clearly dependent on the food resources available to individual fish. Hence L_∞ must be expressed as a function of population density in order to account for density-dependence in growth.

The model proposed here assumes that total population biomass density is a good predictor of competition effects on the growth of individuals, regardless of their size or age. This implies a high degree of overlap in the resources utilized by different individuals in the population. The asymptotic length is expressed as a linear decreasing function of population biomass density (biomass per unit area or volume):

$$L_{\infty B} = L_{\infty L} - gB \tag{2}$$

where $L_{\infty B}$ is the asymptotic length at biomass density B. The new parameter $L_{\infty L}$ is the limiting asymptotic length of the growth curve in the absence of competition. In the absence of competition, anabolism is still dependent on the available food resources. Consequently, the limiting asymptotic length $L_{\infty L}$ is dependent on the productivity of the water body in which the population lives. The second parameter g is the competition coefficient, and equals the amount by which $L_{\infty B}$ decreases per unit of biomass density. Hence g relates to the degree of overlap in the resource requirements of individuals in the population. The degree of overlap in turn primarily reflects the population structure and ontogenic changes in diet.

Assuming isometric growth, the expression equivalent to Eq. (2) for the asymptotic weight $W_{\infty B}$ is:

$$W_{\infty B} = \left(W_{\infty \mathrm{L}}^{1/3} - cB\right)^3 \tag{3}$$

where $W_{\infty \mathrm{L}}$ is the limiting asymptotic weight. The competition coefficient for weight, c, is related to g by

$$c = ga^{1/3} \tag{4}$$

where a is the coefficient of the isometric length–weight relationship:

$$W = aL^3 \tag{5}$$

Substitution of Eqs. (2) and (3) for L_∞ and W_∞ in the differential VBGF results in the following expressions for growth in length:

$$\frac{\mathrm{d}L_t}{\mathrm{d}t} = -K(L_t - L_{\infty \mathrm{L}} + \mathrm{d}B_t) \tag{6}$$

and in weight:

$$\frac{\mathrm{d}W_t}{\mathrm{d}t} = -3KW_t\left(1 - \frac{W_{\infty \mathrm{L}}^{1/3} - cB_t}{W_t^{1/3}}\right) \tag{7}$$

The model predicts the instantaneous growth rate of individuals as a function of current size and population biomass density. The parameters of the growth model have clear biological interpretations: K is a measure of metabolism (a physiological parameter), $L_{\infty \mathrm{L}}$ (or $W_{\infty \mathrm{L}}$) is a measure of the productivity of the habitat, and c (or g) is a measure of the intensity of intraspecific competition.

The growth curves predicted by the model can have various forms, depending on the dynamics of population biomass. Two cases of population biomass dynamics are of particular interest both conceptually and in practice. Populations consisting of several cohorts are often characterized by approximately constant biomass. In the single-cohort populations common in aquaculture, biomass increases greatly during the production period, often by more than an order of magnitude.

For mixed-age populations with constant biomass density B, it follows from Eqs. (2) and (3) that $L_{\infty B}$ and $W_{\infty B}$ are also constant, and therefore growth curves follow a conventional VBGF pattern.

In single cohorts, $L_{\infty B}$ and $W_{\infty B}$ decrease as fish grow and biomass density increases. Hence the density-dependent model predicts single-cohort growth curves that are mathematically different from conventional VBGF curves (with constant asymptotic length or weight). It will be shown later, however, that the predicted single-cohort growth curves can always be approximated very closely by a conventional VBGF.

The growth model for single cohorts is derived as follows. Since the biomass density B_t of a cohort is given by its numerical density N_t times the mean weight of individuals

W_t, the growth rate in weight of individuals can be written as a function of weight and numerical density:

$$\frac{dW_t}{dt} = -3KW_t\left(1 - \frac{W_{\infty L}^{1/3} - cN_tW_t}{W_t^{1/3}}\right) \tag{8}$$

The equivalent expression to Eq. (8) for length growth is derived in a similar way by substituting N_tW_t for B_t in Eq. (6). Unfortunately, Eq. (8) cannot be integrated analytically to give weight as a function of time, and it must be solved numerically.

The asymptotic weight $W_{\infty N}$ approached by individuals in a cohort of density N is obtained by setting Eq. (8) to zero, which gives

$$W_{\infty N}^{1/3} + cNW_{\infty N} = W_{\infty L}^{1/3} \tag{9}$$

This equation has three solutions, but only one for which $0 < W_{\infty N} < W_{\infty L}$ holds true. The solution can be found numerically, or calculated from a rather awkward formula.

2.2. Walter's experiments on common carp growth in extensive aquaculture

In a comprehensive study on the growth and production of common carp (*Cyprinus carpio*) in extensive pond culture, Walter (1934) conducted stocking experiments with different population structures and pond treatments. The results of these experiments provide an excellent opportunity to test the growth model and the biological interpretation of its parameters.

Walter stocked mixed-age populations as well as single cohorts, thereby covering both special cases of biomass dynamics identified above: approximately constant biomass, and continuously increasing biomass in the single cohort. Population biomass in the experiments increased on average by a factor of 1.7 (max. 2.5) in the mixed-age populations, and by a factor of 8 (max. 20) in single cohorts. The experiments were conducted over periods of about 6 months, which represent the full annual growth period under central European conditions.

In the mixed-age experiments, Walter stocked 1- to 4-year-old carp in approximately constant proportions at two different densities, each in unfertilized ponds and in ponds fertilized with inorganic phosphate and liquid manure. Total stocking densities were 115 and 345 ha^{-1} in the fertilized ponds, and 110 and 325 ha^{-1} in the unfertilized ponds. The ratios between age groups 1, 2, 3 and 4 at stocking were approximately 4:3:3:1 in numbers, and 1:10:35:25 in weight, respectively. The numbers and mean weights at stocking and at harvesting for each age-group were calculated from Walter's data for individual fish, and are given in Appendix A (Table A1). No information was available on mortalities, and hence numerical densities in the mixed-age experiments were assumed to be constant.

The results of the mixed-age experiments are illustrated here as Ford–Walford plots (see e.g. Ricker, 1973) in Fig. 1. A Ford–Walford plot is a convenient visual way first of checking whether a growth curve can be described by a conventional VBGF, and second of estimating and comparing VBGF parameter values. If growth follows a VBGF, the Ford–Walford plot of final length versus initial length will show a straight line, with slope $-\ln K$, intersecting the unit line at L_∞. In Fig. 1, lines were fitted by eye, subject to the constraint that their slopes (i.e. values of K) must be identical within

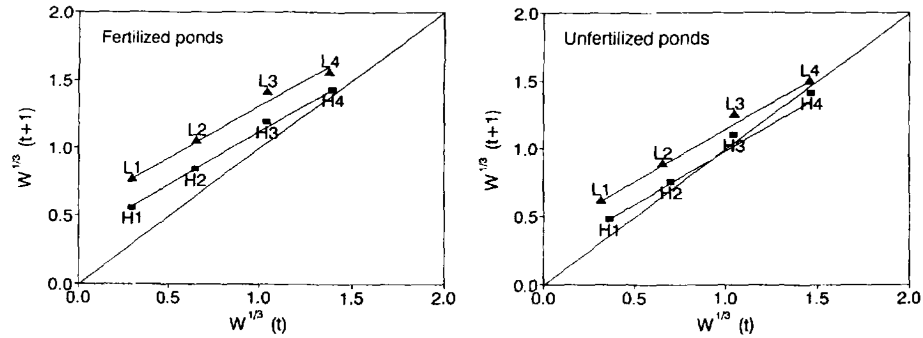

Fig. 1. Ford–Walford plots of Walter's mixed-age stocking experiments in fertilized and unfertilized ponds. The cube root of the final mean weight is plotted against the cube root of the initial mean weight for each age group. Labels denote high or low stocking density (H, L) and the age group of the carp (1–4 summers). Lines were fitted by eye for illustration purposes only.

each fertilizer treatment. Growth in all mixed-age populations is therefore described well by a conventional VBGF with similar K, in line with the theoretical basis of the density-dependent VBGF. The intercepts of the lines, and hence the asymptotic weights W_∞, differ between populations in response to population density and pond productivity (fertilization). Within each pond treatment, W_∞ is higher at low stocking density. For similar stocking densities, W_∞ is higher in the fertilized (more productive) ponds. In the unfertilized pond at high density, the weight at stocking of 4-year-old carp was higher than the asymptotic weight W_∞ for that population. Consequently, 4-year-old carp lost weight during the growth period, while the smaller size groups in the same population did show a positive growth rate.

In the single-cohort experiments, Walter stocked separate populations of 1- and 2-year-old carp in ponds fertilized with inorganic phosphates. The numbers and mean weights at stocking and at harvesting as given in Walter (1934) are reproduced in Appendix A (Table A2). Both initial and final numbers are available, allowing mortality rates to be calculated for each cohort. The results of the experiments are summarized in Fig. 2, where each line represents the weight and density change of one cohort. Three of the cohorts were stocked at a mean weight at or above the asymptotic weight for their density and did not grow; two of them even lost weight. Cohorts stocked at a small size and high density, shown in the lower right-hand region of the graph, suffered a slightly higher mortality (decrease in density) than the cohorts stocked at larger size and lower density. Interestingly, however, the three cohorts stocked at or above their asymptotic weight did not show any signs of mortality.

2.3. Parameter estimation from Walter's data

The growth model predicts instantaneous length or weight growth rates as a function of current size and population biomass density. This differential equation has explicit solutions only in certain special cases, such as that of constant population biomass. Hence a relatively complex procedure is required to estimate parameters if the population biomass changes during the experiment due to growth and mortality. In this study,

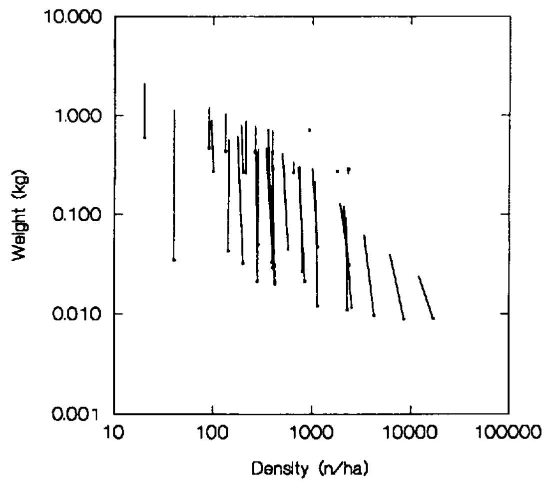

Fig. 2. Summary illustration of Walter's single-cohort experiments. Development of weight and density in individual cohorts. Note logarithmic scaling of density axis.

the mean weight of fish at stocking and their numerical density were taken as the independent variables, and the mean weight at harvesting was predicted by numerically solving the growth and population models described in Appendix B. The parameters of the growth function were estimated using a non-linear optimization procedure, as the combination which minimized the difference between the log-transformed observed and predicted weights at harvesting. The logarithmic transformation was applied in order to ensure homogeneity of variance. Goodness of fit was assessed on the basis of residual plots.

The parameters of the growth model are correlated, i.e. various combinations of K, $W_{\infty L}$ and c fit the data equally well, making it difficult to interpret variation in $W_{\infty L}$ and c between the experiments. This problem can be alleviated by fixing the value of K, which on theoretical grounds is expected not to vary between experiments. Hence parameter estimation was performed in two steps. First, all parameters were estimated independently for all experiments. K was then fixed at a value consistent with the estimates, and $W_{\infty L}$ and c were estimated again subject to the fixed value of K.

The time interval between stocking and harvesting was assumed to be 1 year, thereby averaging out seasonality in growth. Setting the time interval only affects the estimate of K. If an interval of half a year (the true duration of the experiments) was assumed, K would be twice the annual value, and would describe growth during the summer period only.

3. Results

3.1. Parameter estimation

The parameter values estimated for Walter's experiments are given in Table 1. Both the independent estimates of all parameters, and the estimates for fixed K are shown.

Table 1
Parameters of the density-dependent VBGF growth model, estimated from Walter's experiments

	All parameters estimated			K fixed		
	K (per year)	$W_{\infty L}$ (kg)	c (ha kg$^{-2/3}$)	K (per year)	$W_{\infty L}$ (kg)	c (ha kg$^{-2/3}$)
Mixed age, fertilized	0.23	44.10	0.0068	0.25	35.7	0.0063
Mixed age, unfertilized	0.19	22.92	0.0073	0.25	12.8	0.0059
Cohort	0.27	23.60	0.0096	0.25	28.5	0.0095

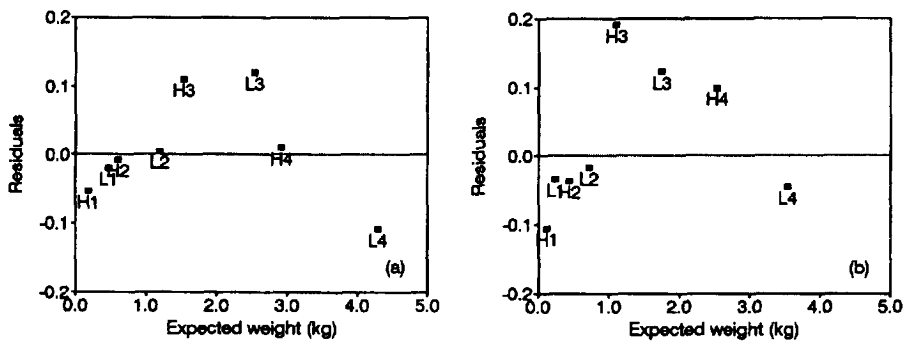

Fig. 3. Residuals (log observed weight minus log expected weight) of the VBGF growth model fitted to Walter's mixed-age data. (a) Fertilized ponds. (b) Unfertilized ponds. Labels denote high or low stocking density (H, L) and the age group of the carp (1–4 summers).

The independent estimates of K vary between 0.19 and 0.27 year^{-1}, and K is fixed at 0.25 year^{-1}. Residual plots are shown in Fig. 3 for the mixed-age experiments, and in Fig. 4 for the cohort experiments.

The residuals of the mixed-age experiments show a systematic pattern for all four populations (Fig. 3). The same pattern (H3 and L3 higher, and L4 lower, than expected) and can be detected in the Ford–Walford plots (Fig. 1), indicating that it represents a

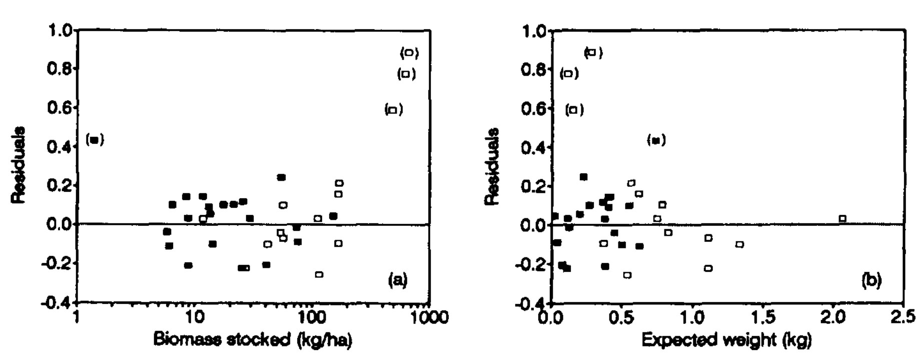

Fig. 4. Residuals (log observed weight minus log expected weight) of the VBGF growth model fitted to Walter's single-cohort stocking data, plotted against (a) biomass stocked and (b) expected weight. Data points in parentheses have been excluded from the fit. Carp were in their first (■) or second (□) summer.

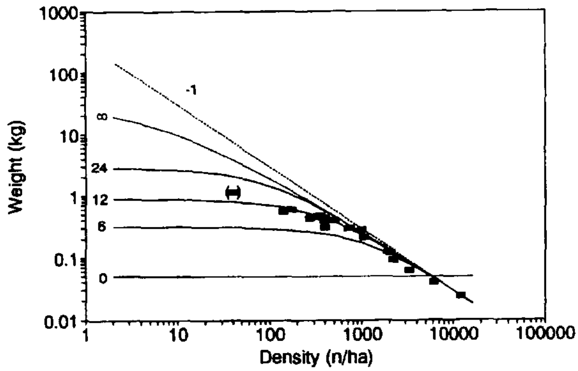

Fig. 5. Predicted weight of carp in single-cohort culture, after 6, 12, and 24 months, and W_∞ as a function of stocking density. Initial weight at Time 0 was 0.05 kg. No mortality. Note logarithmic scaling on both axes. A straight line of slope -1 denotes constant final biomass density. Data points indicate the observed weight at harvesting of 1-year-old carp in Walter's experiments. Parameter values: $K = 0.25$ year^{-1}; $W_{\infty L} = 28.5$ kg; $c = 0.0095$ ha kg$^{-2/3}$.

mild deviation from the basic VBGF rather than a problem of the density-dependent model.

In Fig. 4, residuals for the cohort experiments are plotted against the biomass stocked and against the predicted weight. The residuals are small and apparently random over a wide range of biomass. Growth at the extremes of biomass density is not described well by the model, and the corresponding experiments have been excluded from the parameter estimation.

In the mixed-age experiments, $W_{\infty L}$ is 35.7 kg in the fertilized ponds, and much lower (12.8 kg) in the unfertilized ponds (Table 1). The value of $W_{\infty L}$ in the cohort experiments is at an intermediate 28.5 kg. The competition coefficients c are very similar for the mixed-age stocking experiments (0.0063 and 0.0059 ha kg$^{-2/3}$). In contrast, the competition coefficient for the single-cohort experiments is 0.0095 ha kg$^{-2/3}$, about 50% higher than for mixed-age stocks.

3.2. Predicted growth in single-cohort culture

The model predictions for growth in Walter's single-cohort populations are now explored further. For simplicity, mortality is assumed to be zero. The predicted growth response to different stocking densities is illustrated in Fig. 5. Both density and weight are displayed on logarithmic scales, following a procedure common in plant yield–density studies (Kira et al., 1953; Harper, 1977). Weight at stocking (Time 0 line) is assumed to be 0.05 kg. Solid lines show the predicted weights after 6, 12 and 24 months of growth, and the asymptotic weight $W_{\infty N}$ as a function of density. A line of slope -1 indicates combinations of weight and density resulting in the same total biomass.

Over a range of low densities, predicted weight-at-age changes little and is therefore almost independent of density. At higher densities, weight-at-age declines rapidly as density increases, approaching the line of slope -1 at high densities. This means that

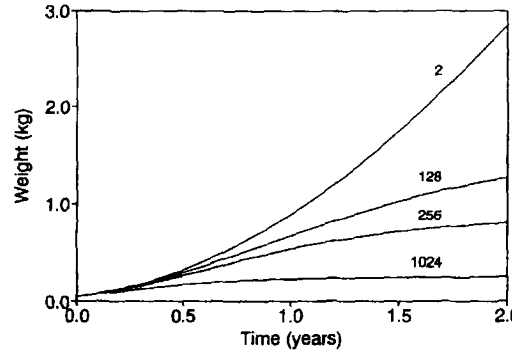

Fig. 6. Predicted growth curves of carp in single-cohort culture at various stocking densities. Labels indicate stocking density in numbers per hectare. Initial weight 0.05 kg. No mortality. Parameter values: $K = 0.25$ year^{-1}; $W_{\infty L} = 28.5$ kg; $c = 0.0095$ ha kg$^{-2/3}$.

under strong competition, individual weight is inversely proportional to cohort density in numbers, and that total biomass is constant.

The observed weights of 1-year-old carp in Walter's experiments correspond well to the predicted weights for stocking densities given above 100 ha^{-1} (Fig. 5) The observed weight at a stocking density of 40 ha^{-1}, which was omitted from parameter estimation as an outlier at very low biomass density (Fig. 4), illustrates the limits of validity of the given set of parameter values. Consequently it does not correspond well to the predictions shown in Fig. 5, and serves as a reminder that the model is realistic only for a limited range of densities.

Predicted growth curves for single-cohort populations of different density, obtained as initial-value solutions of Eq. (8), are shown in Fig. 6. At a low density of two fish per

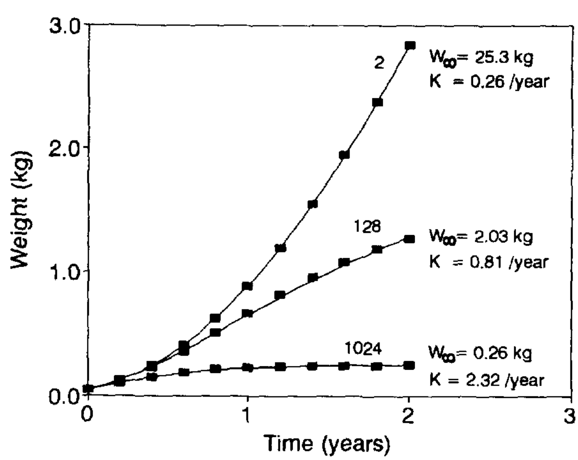

Fig. 7. Conventional VBGF approximations to single-cohort growth curves predicted by the density-dependent model. Symbols (■) denote the growth curves predicted for cohorts of 2, 128 or 1024 fish ha^{-1}, as indicated by the labels. Lines denote the conventional VBGF approximations. The respective parameter values of the approximations are given in the graph.

hectare, weight continues to increase even 2 years after stocking. At a density of 128 ha^{-1}, growth continues at the end of the second year, but at a lower rate. Finally, at the higher densities of 256 and 1024 ha^{-1}, asymptotic weight is approached within less than 2 years.

The predicted single-cohort growth curves can be approximated very closely by a conventional VBGF, resulting in a different set of the parameters K and W_∞ for each density. This is shown in Fig. 7, where the symbols indicate predicted growth for densities of 2, 128 and 1024 ha^{-1}, and the lines indicate fitted conventional VBGF growth curves. The estimated conventional VBGF parameter values are also shown in the graph. With increasing density, the estimated W_∞ decreases. The estimated K, however, increases with density as the low asymptotic weight is approached more quickly.

4. Discussion

A density-dependent growth model on the basis of the von Bertalanffy growth function was first proposed by Beverton and Holt (1957). Their model is based on a linear relationship between asymptotic length and population density, for which they provided both empirical evidence and a theoretical explanation. A number of subsequent empirical studies also support such a relationship (Foerster, 1968; Barlow, 1992; Salojaervi and Mutenia, 1994). In the present study, the model of Beverton and Holt is interpreted and developed further with respect to extensive aquaculture.

Analysis of Walter's carp pond experiments (Walter, 1934) by means of the density-dependent von Bertalanffy model shows first, that the model provides a good description of fish growth in this extensive culture system, and second, that the theoretical interpretation of the model parameters is consistent with empirical data. The growth rate parameter K is expected on theoretical grounds to be independent of population density, population structure and the productivity of the water body. This is born out by the fact that all of Walter's experiments can be described by the model with a common value of K. The limiting infinite weight $W_{\infty L}$ is expected to reflect the natural productivity of a water body, and indeed the analysis of Walter's experiments shows that $W_{\infty L}$ is highest in the mixed-age ponds fertilized with phosphates and manure, lowest in the unfertilized mixed-age ponds, and intermediate in the single-cohort ponds fertilized with phosphates only. The competition coefficient c is expected to reflect the intensity of competition in a population, which is related to the degree of overlap in the resource requirements of individuals. Again, analysis of Walter's experiments supports this interpretation: similar values of c have been estimated for mixed-age populations stocked in ponds of different productivity, while a much higher value of c was estimated for single-cohort populations. For a given biomass density, competition is more severe in populations of individuals of the same size than in populations comprising individuals of a wide range of sizes.

The growth curves predicted by the density-dependent VBGF model for single-cohort populations in extensive culture are mathematically different from conventional VBGF growth curves. However, the predicted growth patterns can be approximated very closely by conventional VBGF curves, with W_∞ declining and K increasing with increasing cohort density. Hence, fish kept at high densities in extensive culture are expected to grow to a low W_∞ at high K, while the same fish kept in intensive culture, where feeding reduces competition for food, should grow to a high W_∞ at low K. Prein (1990) noticed this effect in his empirical study of tilapia growth in different culture systems.

Walter (1934) only provides initial and final mean weights, and it is therefore not possible to test how well the model describes the true growth patterns of cohorts during the experiments, between stocking and harvesting.

Backiel and Le Cren (1978) have derived a simple empirical model for density-dependent growth from Walter's experiments on single cohorts of 1-year-old carp. The density-dependent VBGF model provides a unified framework for the analysis of all of Walter's carp growth experiments under extensive conditions.

The model should be tested on a range of data sets in order to determine the limits of its applicability. It is likely that the model can be refined to make it applicable to a wider range of densities or sizes. However, if such refinements involve the introduction of additional parameters into the model, even more comprehensive data from well-designed experiments will be required to estimate the full set of parameters.

4.1. Practical application of the model

This simple von Bertalanffy model for density-dependent growth is a potentially useful tool for the analysis and modelling of extensive aquaculture systems and culture-based fisheries. The model has only three parameters, which can be estimated from pond-stocking experiments or from stocking and catch data for culture-based fisheries. However, the full set of parameters can only be estimated from data covering a range of densities and individual sizes. When such complete data are not available, one or two of the parameters need to be fixed a priori for the model to be used. Predictions obtained from such a model must be treated with extreme caution, but may nevertheless provide useful indications in certain management situations.

The theoretical basis and biological interpretation of the model parameters indicate which parameter(s) can be estimated a priori in any given situation. An estimate of the parameter K can be obtained easily by fitting a conventional VBGF to growth data from the same species under similar environmental conditions in a situation of constant competition, i.e. a mixed-age population, a cohort in extensive culture at low density, or a cohort in intensive culture with feeding. Both $W_{\infty L}$ and c can only be estimated from data involving a range of biomass densities. However, the value of c is expected to be dependent on the population structure, and once a number of experiments have been analyzed using the model, it may be possible to predict the likely range of c for a given species and population structure.

The most common population structure in extensive pond aquaculture is the single cohort. The density-dependent model predicts a growth curve for single cohorts which is different from a conventional VBGF curve, but can nevertheless be approximated very closely by a conventional VBGF. The estimation of a density-dependent VBGF model is worthwhile and possible only if data are available for a range of stocking densities. If the aim is to describe the growth of a cohort at one particular density only, the density-dependent model does not offer any advantage over a conventional VBGF.

Indeed, the conventional model would be preferable because its two parameters can be estimated from a single observed growth curve, while a priori assumptions would have to be made on the values of at least one of the three parameters of the density-dependent model.

The use of the density-dependent VBGF is advantageous in situations where explicit consideration of density effects on growth is crucial to management. When stocking and/or harvesting regimes are complex, for example in culture-based fisheries, the density-dependent growth model offers a valuable tool for the quantitative assessment of management options (Lorenzen, 1995).

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Appendix A. Carp growth data from Walter (1934)

Table A1
Carp growth in the mixed-age experiments. Numbers and mean weights have been calculated from data given in Table 6 in Walter (1934)

Fertilization	Density	Age	Number ($1\ ha^{-1}$)	Initial weight (kg)	Final weight (kg)
Unfertilized	Low	1	35	0.031	0.245
		2	35	0.281	0.710
		3	10	3.115	3.385
		4	30	1.158	1.978
	High	1	130	0.047	0.113
		2	70	0.343	0.432
		3	30	3.168	2.798
		4	95	1.143	1.337
Fertilized	Low	1	40	0.026	0.466
		2	35	0.279	1.195
		3	10	2.625	3.850
		4	30	1.142	2.866
	High	1	120	0.025	0.176
		2	100	0.270	0.602
		3	30	2.713	2.948
		4	95	1.122	1.707

Table A2
Carp growth in single-cohort experiments, From Tables 34 and 35 in Walter (1934)

Age	Initial number ($l\ ha^{-1}$)	Final number ($l\ ha^{-1}$)	Initial weight (kg)	Final weight (kg)
1	40	40	0.035	1.134
1	142	142	0.043	0.563
1	200	175	0.032	0.611
1	280	270	0.021	0.433
1	284	284	0.050	0.458
1	420	340	0.020	0.459
1	400	360	0.029	0.478
1	420	390	0.021	0.396
1	420	395	0.021	0.310
1	396	396	0.033	0.445
1	568	497	0.045	0.409
1	840	715	0.021	0.298
1	800	740	0.027	0.302
1	1136	994	0.047	0.289
1	1136	1065	0.012	0.213
1	2376	1914	0.031	0.126
1	2520	2080	0.012	0.121
1	2272	2201	0.011	0.092
1	4260	3337	0.010	0.063
1	8520	6106	0.009	0.040
1	17040	12070	0.009	0.024
2	20	20	0.590	2.117
2	90	90	0.467	1.211
2	100	95	0.270	0.889
2	132	132	0.430	1.040
2	200	190	0.267	0.797
2	213	213	0.263	0.867
2	264	264	0.425	0.777
2	360	355	0.462	0.722
2	400	390	0.286	0.420
2	396	396	0.423	0.700
2	639	639	0.263	0.337
2	924	924	0.714	0.690
2	1782	1782	0.270	0.272
2	2310	2310	0.286	0.256

Appendix B. Estimation of parameters of the density-dependent VBGF

The growth in mixed-age populations with constant numerical density was described by a set of four identical differential equations, one for each age group.

$$\frac{dW_i}{dt} = -3KW_i\left(1 - \frac{W_{\infty L}^{1/3} - c\,\Sigma N_i W_i}{W_i^{1/3}}\right) \tag{B1}$$

The mean weights at harvesting of the four age groups were predicted by solving the set of equations subject to the initial densities N_i and mean weights W_i ($i = 1 - 4$).

For a single cohort subject to a constant mortality rate M, the development of numbers N and mean weight W over time was described by the following system of differential equations:

$$\frac{dN}{dt} = -MN \tag{B2}$$

$$\frac{dW}{dt} = -3KW\left(1 - \frac{W_{\infty L}^{1/3} - cNW}{W^{1/3}}\right) \tag{B3}$$

The mean weight at harvesting of the cohort was predicted by solving the system of equations subject to the initial density N_0 and mean weight W_0. The predictions used the actual mortality rate for each cohort, as calculated from the numbers stocked and harvested.

Growth parameters were estimated as the combination which minimized the sum of squared differences between the log-transformed observed and expected weights. Minimization was performed using the downhill simplex method as implemented in the AMOEBA routine from *Numerical Recipes* (Press et al., 1986).

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