

Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons

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It is generally assumed that fish populations are regulated primarily in the juvenile (pre-recruit) phase of the life cycle, although density dependence in growth and reproductive parameters within the recruited phase has been widely reported. Here we present evidence to suggest that density-dependent growth in the recruited phase is a key process in the regulation of many fish populations. We analyse 16 fish populations with long-term records of size-at-age and biomass data, and detect significant density-dependent growth in nine. Among-population comparisons show a close, inverse relationship between the estimated decline in asymptotic length per unit biomass density, and the long-term average biomass density of populations. A simple population model demonstrates that regulation by density-dependent growth alone is sufficient to generate the observed relationship. Density-dependent growth should be accounted for in fisheries' assessments, and the empirical relationship established here can provide indicative estimates of the density-dependent growth parameter where population-specific data are lacking.

Keywords: fish; population dynamics; regulation; growth; density dependence; fisheries management

1. INTRODUCTION

Understanding the mechanisms by which the abundance of fish populations is regulated is of fundamental importance to the management of fisheries. In general, density-dependent survival in the juvenile phase is believed to be of key importance in regulating fish populations (e.g. Rothchild 1986). This view is embodied in most age-structured fisheries assessment models where regulation is effected through a stock-recruitment relationship while mortality, growth and reproductive parameters in the recruited population are assumed to be density independent (Hilborn & Walters 1992; Rochet 2000).

Density-dependent growth as a result of competition for food in recruited (late juvenile and adult) fishes has been described for many populations (e.g. Beverton & Holt 1957; Rochet 1998; Post *et al.* 1999; Jenkins *et al.* 1999; and references therein), but the generality of the mechanism and its importance in the regulation of fish populations remain little appreciated. Here we present results from among-population comparisons and a population model which suggests that density-dependent growth is a common and important mechanism in the regulation of fish populations.

A comparative study requires a common model to describe density-dependent growth in the different study populations. Here we use a density-dependent extension of the von Bertalanffy growth function, the model most widely used to describe growth in fishes. Based on the physiological concepts underlying the von Bertalanffy growth function, Beverton & Holt (1957) show that density-dependent growth mediated by competition for

food is expected to affect the asymptotic size (L_∞ or W_∞) of fishes, but not the growth rate (K) at which this size is approached. Subsequent work by Walters & Post (1993), Lorenzen (1996) and Shin & Rochet (1998) has provided further theoretical and empirical support for this result. Lorenzen (1996, 2000) shows that a simple model where asymptotic length is defined as a linear function of population biomass density provides a good description of density-dependent growth in various pond experiments. This model is also used in the present study. Asymptotic length $L_{\infty B}$ is defined as a linear declining function of population biomass density:

$$L_{\infty B} = L_{\infty L} - gB, \quad (1.1)$$

where the competition coefficient g describes the decline in asymptotic length per unit of biomass density, and $L_{\infty L}$ is the limiting asymptotic length as B approaches 0.

The present study is concerned with the parameter g (the growth response to changes in biomass density), and its relationship to the long-term average biomass density (carrying capacity) of the population. The factors determining the value of g in a particular population are likely to be complex, combining attributes of the study organism such as preferred diet and flexibility in diet choice, and attributes of the environment such as production responses in prey populations (Beverton & Holt 1957; Walters & Post 1993). We do not explore these biological factors further, but focus instead on the implications of given values of g for the biomass dynamics of the respective populations. As a result and in reversal of the underlying causal relationship, we also develop a simple empirical relationship to predict the degree of density dependence in growth from average population biomass, i.e. without reference to the biological factors determining g .

Our analysis is carried out in three steps. First, we

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estimate the parameters of the density-dependent growth model for 16 fish populations (representing 13 species in 9 teleost families). Second, we establish a close inverse relationship between the density-dependent growth parameter g and average biomass density \bar{B} among the populations exhibiting significant density dependence in growth. Finally, we use a simple population model to show that this pattern is consistent with the hypothesis that these populations are regulated primarily by density-dependent growth, and that the value of g determines the equilibrium biomass density (carrying capacity).

2. MATERIAL AND METHODS

(a) *Growth and biomass data*

Long-term growth and biomass data for 16 wild fish populations (seven freshwater and nine marine populations) were identified from the literature. Inclusion in the study was determined by data availability in the case of freshwater populations. The marine populations represent a subset of the North Atlantic herring, North Sea demersal, and Baltic stocks assessed by working groups of the International Council for the Exploration of the Sea (ICES), supplemented by one dataset from the primary literature. There was no intentional selection for populations known to exhibit density-dependent growth. However, inadvertent selection cannot be ruled out in the case of datasets gleaned from the primary literature (mainly freshwater populations), because data may be more likely to be published if they exhibit ecologically significant patterns. An overview of the datasets analysed is given in table 1.

The growth data consisted of time series of annual mean length or weight at age for several age groups and years. In most cases, these data were derived from direct measurement and ageing of catch samples, but a minority of datasets ((d), (j) and (n)) are based on back-calculated lengths from scale readings. Where only weight data were available, these were converted to length using length–weight relationships for the study populations.

Biomass data were based on stock reconstruction from catch-at-age data (using virtual population analysis or related approaches, Hilborn & Walters (1992)), or on direct sampling in the case of some freshwater populations. In the latter cases, biomass densities were measured directly in kg ha^{-1} . In studies where total stock biomass was reconstructed, this was expressed as biomass density, by dividing biomass by the water body area in the case of lakes, or by the relevant statistical area in the case of marine stocks. As the distribution of most populations is spatially heterogeneous, the biomass-density estimates are in effect averages over relatively large areas.

(b) *Estimation of growth parameters*

A von Bertalanffy growth model was used to predict mean length $L_{\text{pred},a,t}$ of age group a at time t from the observed mean length of the cohort in the previous year ($L_{\text{obs},a-1,t-1}$):

$$L_{\text{pred},a,t} = L_{\infty B} - (L_{\infty B} - L_{\text{obs},a-1,t-1}) \exp(-K), \quad (2.1)$$

where $L_{\infty B}$ is the asymptotic length at the average observed (or reconstructed) biomass density B during the year ($t-1$ to t):

$$L_{\infty B} = L_{\infty L} - g \left(\frac{B_{t-1} + B_t}{2} \right). \quad (2.2)$$

The model was fitted to growth data by the method of least squares where the sum of squares (SSQ) is defined as

$$\text{SSQ} = \sum_a \sum_t (L_{\text{obs},a,t} - L_{\text{pred},a,t})^2. \quad (2.3)$$

A numerical search was used to identify the set of growth parameters K , $L_{\infty L}$ and g that minimizes SSQ. Goodness-of-fit profiles (Hilborn & Mangel 1997) were generated for the competition coefficients g . Approximate confidence bounds for g were determined using the F criterion (Kimura 1980; Draper & Smith 1981). Diagnostic plots were used to check for systematic patterns in residuals.

(c) *Among-population comparisons*

The purpose of among-population comparisons was to establish relationships between the estimated competition coefficient g , average population biomass density \bar{B} , and other growth parameters in populations where significant density dependence in growth had been established. Populations with estimates of g not significantly different from 0 (7 out of 16) were excluded from this analysis. Single and multiple regression analysis of logarithmically transformed variables for the remaining populations was used to establish relationships.

(d) *Population model*

A population model was used to explore the relationship between the competition coefficient g and the resulting equilibrium biomass B^* that would be expected in populations regulated exclusively by density-dependent growth in the recruited stock. For this purpose we constructed a discrete age-structured population model, incorporating density dependence in growth, but no other regulatory mechanisms.

Growth in the recruited stock was described by the density-dependent von Bertalanffy model defined in equations (1.1) and (2.1), starting with a constant length at recruitment $L_{1,t}$. Population numbers $N_{a,t}$ at age a and time t were given by

$$N_{a,t} = N_{a-1,t-1} e^{-M}, \quad (2.4)$$

where M is the annual mortality rate. Maturity was described as a length-dependent knife-edge process so that the proportion mature, $P_{a,t}$, is defined by:

$$P_{a,t} = \begin{cases} 0 & \text{if } L_{a,t} < L_m \\ 1 & \text{if } L_{a,t} \geq L_m \end{cases}, \quad (2.5)$$

where L_m is the constant length at maturity. The population is assumed to be regulated only through density-dependent growth in adults, so that recruitment is a linear function of spawning stock biomass:

$$N_{1,t} = RS = R \sum_a P_{a,t-1} \alpha L_{a,t-1}^\beta N_{a,t-1}, \quad (2.6)$$

where R is the number of recruits per unit of spawning stock biomass S , and α and β are parameters of the length–weight relationship. Total population biomass is then:

$$B_t = \sum_a \alpha L_{a,t}^\beta N_{a,t}. \quad (2.7)$$

The model was solved for equilibrium population biomass B^* .

The model parameter values were chosen so that the growth parameters correspond to the median values in the populations with significant density dependence (table 1). Mortality rate M and length at maturity L_m were set in order to satisfy the empirical ‘Beverton & Holt invariants’ $M/K = 1.75$ and $L_m/L_{\infty} = 0.65$ (Charnov 1993). This led to the following set of parameter values: $L_{\infty L} = 32$ cm, $K = 0.3 \text{ yr}^{-1}$, $L_{1,t} = 10$ cm, $\alpha = 0.01 \text{ g cm}^{-3}$,

Table 1. Synopsis of studies analysed and the estimated growth parameters. (Location also indicates freshwater (F) and marine (M) environments.)

study	species	location	B range (kg ha ⁻¹)	\bar{B} (kg ha ⁻¹)	K (yr ⁻¹)	$L_{\infty L}$ (cm)	$L_{\infty B}$ (cm)	$\frac{L_{\infty B}}{L_{\infty L}}$	g [95% CI] (cm ha ⁻¹ kg ⁻¹)	source(s) of data
(a)	<i>Clupea harengus</i>	Celtic Sea (M)	1.1–3.5	2.6	0.32	35.8	32.2	0.90	1.390 [0.970, 1.700]	ICES (2000a)
(b)	<i>Clupea harengus</i>	North Sea (M)	19–60	43	0.52	33.0	32.1	0.97	0.029 [0.002, 0.055]	ICES (2000a)
(c)	<i>Coregonus hoyi</i>	Lake Michigan (F)	1–33	8.8	0.21	53.3	50.0	0.94	0.378 [0.105, 0.711]	Brown <i>et al.</i> (1987)
(d)	<i>Coregonus lavaretus</i>	Lake Oulujaervi (F)	0.6–1.3	0.9	0.54	33.5	30.0	0.90	3.890 [1.200, 6.500]	Salojärvi (1992)
(e)	<i>Coregonus lavaretus</i>	Lake Inari (F)	1.2–3.9	2.7	0.32	40.6	37.1	0.91	1.296 [0.140, 2.240]	Salojärvi & Mutenia (1994)
(f)	<i>Esox lucius</i>	Lake Windermere (F)	3.0–5.3	4.1	0.33	90.9	86.2	0.95	1.150 [–0.500, 2.800]	Frost & Kipling (1967); Le Cren <i>et al.</i> (1977)
(g)	<i>Gadus morhua</i>	North Sea (M)	6–17	9.8	0.23	121.7	119.0	0.98	0.281 [–0.300, 0.870]	ICES (2000b)
(h)	<i>Melanogrammus aeglefinus</i>	North Sea (M)	5–104	20	0.08	94.3	98.1	1.04	–0.196 [–0.510, 0.039]	ICES (2000b)
(i)	<i>Merluccius bilinearis</i>	Gulf of Maine (M)	5–69	27	0.26	42.5	38.4	0.90	0.156 [0.070, 0.371]	Ross & Almeida (1986); Helsler & Almeida (1997)
(j)	<i>Perca fluviatilis</i>	Klicava Reservoir (F)	8–70	30	0.18	22.6	25.0	1.10	–0.081 [–0.275, 0.037]	Pivnicka & Svatoria (1988)
(k)	<i>Perca fluviatilis</i>	Lake Windermere (F)	92–246	119	0.42	23.7	20.4	0.86	0.028 [0.009, 0.047]	Le Cren (1958); Le Cren <i>et al.</i> (1977)
(l)	<i>Platichthys flesus</i>	Baltic (M)	3–6	4.3	0.30	38.0	35.9	0.94	0.490 [–0.550, 1.540]	ICES (2000c)
(m)	<i>Pleuronectes platessius</i>	North Sea (M)	5–11	8.5	0.07	60.0	57.0	1.05	–0.350 [–1.580, 0.820]	ICES (2000b)
(n)	<i>Rutilus rutilus</i>	Klicava Reservoir (F)	41–218	141	0.21	31.9	27.4	0.86	0.032 [0.013, 0.077]	Pivnicka & Svatoria (1988)
(o)	<i>Solea solea</i>	North Sea (M)	0.4–2.4	1	0.26	44.3	46.8	0.94	2.791 [1.180, 4.370]	ICES (2000b)
(p)	<i>Trisopterus esmarkii</i>	North Sea (M)	9–30	16	0.87	19.8	21.5	0.92	0.108 [–0.060, 0.280]	ICES (2000b)

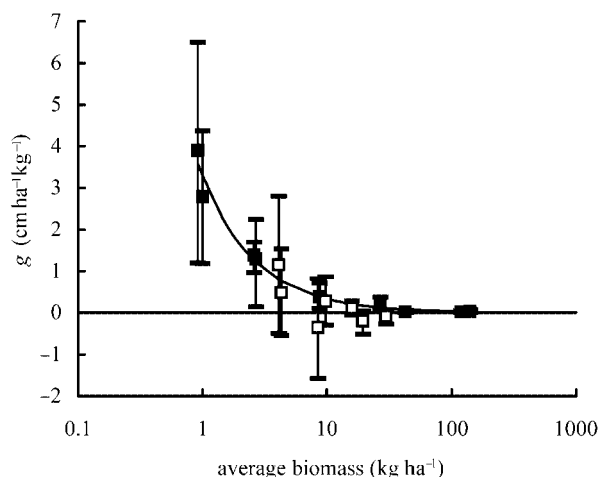


Figure 1. Relationship between the competition coefficient g (estimates shown with 95% CI) and average population biomass density \bar{B} . The solid line indicates the relationship $g = 3.3 \bar{B}^{-1.0}$ estimated for populations with significant density dependence in growth (solid squares). Populations with estimates of g not significantly different from 0 (open squares) were excluded from the analysis.

$\beta = 3$, $M = 0.5 \text{ yr}^{-1}$ and $L_m = 21 \text{ cm}$. Predictions were obtained for several different values of R (number of recruits per unit of biomass density). Note that the model serves merely to explore the general relationship between g and equilibrium biomass B^* in populations regulated by density-dependent growth; it is not intended to predict average biomass for specific study populations.

3. RESULTS

Growth-parameter estimates for all populations are given in table 1. In addition to K , g and $L_{\infty L}$, table 1 lists the asymptotic length $L_{\infty \bar{B}}$ at average biomass \bar{B} over the observation period, equivalent to the average asymptotic length during that period. Residual analysis provided no indication of model misspecification, i.e. the linear relationship between asymptotic length and biomass was adequate to describe density-dependent growth in the 16 study populations. Density dependence in growth was significant (i.e. g was significantly higher than 0) in 9 out of the 16 populations. Negative point estimates of g were obtained for three populations ((h), (j) and (m)), but the estimates were not significantly different from 0.

Comparisons among the nine populations where significant density dependence in growth had been detected showed a close inverse relationship between the competition coefficient g and average population biomass density \bar{B} (figure 1). Regression analysis demonstrated a highly significant ($p < 0.001$) relationship of the form $g = 3.3 \bar{B}^{-1.0}$, which is indicated by a solid line in figure 1. No relationships were established between g and the other growth parameters (K or $L_{\infty \bar{B}}$), even when the dominant relationship between g and \bar{B} was accounted for.

The population model predicts the relationship between the competition coefficient g and the equilibrium biomass density B^* based on the assumption that populations are regulated exclusively by density-dependent growth in the recruited phase. Model predictions of equilibrium biomass

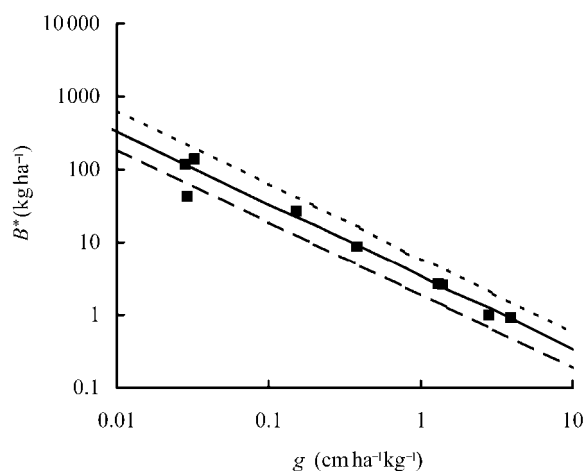


Figure 2. Model predictions of equilibrium biomass B^* as a function of the competition coefficient g , for different values of the parameter R (numbers of recruits per unit of spawning stock biomass): $R = 12 \text{ kg}^{-1}$ (dashed line), $R = 15 \text{ kg}^{-1}$ (solid line) and $R = 30 \text{ kg}^{-1}$ (dotted line). Other parameters are as given in the text. The observed relationship between g and \bar{B} among populations with significant density dependence in growth (solid squares), is also shown for comparison.

density B^* as a function of g are shown in figure 2, for different values of the parameter R (recruits per unit of spawning stock biomass). The model predicts an inverse relationship between g and B^* for all values of R large enough to sustain a population (i.e. allowing non-trivial equilibria, $B^* > 0$). The observed relationship among populations with significant density dependence in growth is consistent with model predictions, and therefore with the hypothesis that these populations are regulated primarily by density-dependent growth.

4. DISCUSSION

Significant density dependence in growth was detected in the majority (9 out of 16) of the study populations. Four other populations where density dependence was not statistically significant showed point estimates of g consistent with the among-population relationship between g and \bar{B} . Only three populations ((h), (j) and (m)) departed notably from the relationship and showed negative point estimates of g . In all three cases, the departures are likely to reflect population and time-specific factors rather than fundamental life-history patterns, as other studies have demonstrated the occurrence of density-dependent growth in the species concerned (e.g. population (k) of the present study for *Perca fluviatilis*; Rijnsdorp & Van Leeuwen (1996) for *Pleuronectes platessa*; Marshall & Frank (1999) for *Melanogrammus aeglefinus*). Apparent density independence or negative density dependence may arise, for example, when variation in environmental conditions affects growth as well as overall biomass density. In this case, accounting for environmental factors in the growth model may help to separate density dependence from variation in carrying capacity, as demonstrated by Rijnsdorp & Van Leeuwen (1996) for the North Sea plaice (*P. platessa*) population.

The fact that the majority of study populations showed significant density dependence in growth suggests that the

process is common, but not necessarily that it is an important regulatory mechanism. However, evidence for the latter is provided by the close, inverse relationship between g and \bar{B} among populations, and the model predictions (figure 2) which show that this relationship is to be expected in populations regulated primarily by density-dependent growth.

The compensatory nature of density-dependent growth implies that where the process is significant, yield and biomass responses to changes in exploitation are less pronounced than predicted from conventional dynamic pool models assuming density-independent growth (Beverton & Holt 1957; Rochet 2000). Hence disregarding density-dependent growth would lead to conservative reference points for underexploited stocks, but would give rise to over-optimistic assessments of the effectiveness of conservation measures for overexploited stocks. Explicit consideration of density-dependent growth is also, and perhaps most important in aquaculture-based and enhanced fisheries where population densities are manipulated directly by stocking (Petermann 1991; Salojärvi 1992; Lorenzen 1995).

Assessment models accounting for density-dependent growth have been developed for both capture fisheries (e.g. Beverton & Holt 1957; Patterson 1997; Helser & Brodziak 1998; Shin & Rochet 1998) and for aquaculture-based fisheries (Lorenzen 1995; Lorenzen *et al.* 1997). However, population-specific data on density dependence in growth are available only for a limited set of the most well-studied populations. The present study identifies the first empirical relationship that may be used to obtain indicative information on the degree of density dependence in growth for populations where specific data are not available. Comparative analyses of larger datasets may lead to relationships of greater predictive power. However, predictors based on average biomass density will always be subject to uncertainty resulting from the variability of fish population biomass itself, and the consequent difficulty in defining average biomass.

The existence of an inverse relationship between g and \bar{B} implies that a given relative change in B (as a proportion of \bar{B}) will result in the same absolute change in L_{∞} regardless of average populations' biomass density \bar{B} . In the case of the populations with significant density-dependent growth analysed here, the absolute change in L_{∞} is 3.3 cm for a 100% change in B from \bar{B} . Given a median $L_{\infty\bar{B}}$ for these populations, of 32 cm, this implies a 10% change in L_{∞} for a 100% change in B . This provides a simple rule of thumb for fisheries assessments where specific data on density-dependent growth are not available. The rule applies to fish stocks with an $L_{\infty\bar{B}}$ in the range of ca. 20–45 cm (the range represented among the study populations with significant density dependence in growth), but it is unclear whether and how it can be extrapolated to populations with values of $L_{\infty\bar{B}}$ outside of this range.

The results presented here suggest that density-dependent growth should be recognized as a key process in the regulation of fish populations, and accounted for in fisheries assessments. The results also suggest simple rules of thumb that can aid assessments where specific data on density dependence in growth are not available.

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