

Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality¹

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Abstract: Life history variation among 60 Ontario populations of lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*), cisco (*Coregonus artedii*), and yellow perch (*Perca flavescens*) is presented and interpreted using a biphasic model of individual growth that specifically accounts for the significant shift in energy allocation that accompanies sexual maturity. We show that the constraints imposed on life history variation by the character of the biphasic growth model are such that optimal life histories will exhibit associations among growth parameters, reproductive investment, and mortality that are largely consistent with associations evident in both our data set and earlier empirical studies; the von Bertalanffy growth parameter k varies with reproductive investment, and both k and investment vary with adult mortality. Our analysis suggests that within a food web, life history parameters will shift in a predictable fashion with the decreases in mortality expected as one moves from primary consumers up toward top predators. This expectation is supported by the differences in life history parameters that we observe between the two top predators in our data set (lake trout and walleye) and the two mid-trophic level consumers (cisco and yellow perch).

Résumé : Nous présentons les variations dans les cycles biologiques de 60 populations ontariennes de touladis (*Salvelinus namaycush*), de dorés (*Sander vitreus*), de ciscos de lac (*Coregonus artedii*) et de perchaudes (*Perca flavescens*) et les interprétons à l'aide d'un modèle biphasique de croissance individuelle qui tient compte spécifiquement du changement significatif d'allocation de l'énergie qui accompagne la maturité sexuelle. Nous démontrons que les contraintes imposées à la variation du cycle biologique par les caractéristiques du modèle de croissance biphasique sont telles que les cycles biologiques optimaux montrent des associations entre les paramètres de croissance, l'investissement reproductif et la mortalité qui sont en grande partie compatibles avec les associations présentes dans nos données et celles d'études empiriques antérieures: le paramètre de croissance de von Bertalanffy k varie en fonction de l'investissement reproductif et tant k que l'investissement varient en fonction de la mortalité des adultes. Notre analyse indique qu'à l'intérieur d'un réseau alimentaire, les paramètres démographiques vont se déplacer dans un sens prévisible en fonction du déclin de la mortalité attendu lorsqu'on passe des consommateurs primaires aux prédateurs supérieurs. Cette prédiction se réalise dans les différences observées dans les paramètres démographiques entre, d'une part, les deux prédateurs supérieurs (touladis, dorés) et, d'autre part, les deux consommateurs de niveau intermédiaire (ciscos, perchaudes).

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Introduction

The von Bertalanffy growth model has been used by many authors as a vehicle for summarizing empirical variation in the life history of fish and for developing theory to account

for that variation. This use continues in spite of strong criticism (e.g., Day and Taylor 1997) that the equation is, in principle, a flawed instrument that hides, within a fixed formal structure, the significant changes in energy allocation that characterize sexual maturation and that are the primary

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subject matter of life history theory. Recently, more realistic models have been developed. Charnov et al. (2001) presented an analysis of life history variation based on a biphasic growth model that explicitly represents the consequences for somatic growth and future reproduction produced by the reallocation of energy to reproduction. Lester et al. (2004), in a related study, showed that a small set of empirically justifiable, simplifying assumptions was sufficient to develop a new model of lifetime somatic growth for fish, with the following useful attributes: (i) the lifetime growth pattern is biphasic, thus more accurately reflecting the shift in energy allocation that occurs with maturity; (ii) adult somatic growth is exactly represented by a von Bertalanffy growth equation with parameters that provide explicit information on the amount of energy allocated to reproduction; (iii) under the assumption that life histories are shaped by selection to maximize lifetime reproductive output, the model makes simple and explicit quantitative predictions of the relationships expected among age at maturity, reproductive investment, and total mortality that match observed relationships based on interspecific comparisons of freshwater fish.

In this paper, we use the biphasic model of Lester et al. (2004) to analyse an extensive new database that documents intraspecific variation in the life histories of four species of freshwater fishes: two species that typically fill the role of top predator (walleye (*Sander vitreus*) and lake trout (*Salvelinus namaycush*)) in their food webs and two species (cisco or lake herring (*Coregonus artedii*) and yellow perch (*Perca flavescens*)) that typically occupy a middle position in their respective food webs. We then assess the ability of the biphasic model to both describe and account for this variation. For each species, we proceed as follows: (i) we assess the validity of each of the primary simplifying assumptions that underpin the structure of the biphasic model; (ii) we assess the validity of the prediction that the parameters of the adult growth curve provide an indirect measure of reproductive investment; (iii) we assess the degree to which intra- and inter-specific variation in age at maturity, reproductive investment, and mortality follow the simple inter-relationships (Lester et al. 2004) generated by applying optimal life history theory to the biphasic model. Our analysis is restricted to female growth and reproductive investment, since for our four species, female investment in gonadal development is measurable and is likely to represent most of the reproductive investment made by individual females.

The biphasic von Bertalanffy growth model: a summary

When using the biphasic model to describe the somatic growth pattern typical of a particular population, we assume the following: (i) for all individuals, $W_s = aL^{3.0}$, where W_s is somatic weight (i.e., total weight less gonad weight), L is length, and a is a population-specific constant; (ii) for ages $t \geq T$, the age at which allocation of energy to reproduction begins, the surplus energy production by an individual of somatic weight W_s equals $(c_1 - c_2)W^{0.67}$, where c_1 is a constant defining the weight-specific rate of energy assimilation, and c_2 is a constant defining the weight-specific rate of energy expenditure on both maintenance and active metabolism; (iii) c_1 and c_2 can vary as a function of abiotic factors, such as temperature; (iv) for ages $t < T$, systematic changes in $(c_1 - c_2)$ can arise, depending on the character of the prey

and predator fields experienced by the younger members of the population. Under these assumptions, potential somatic growth for age t fish (where t is in the neighbourhood of T) is given by

$$(1) \quad L_t = h(t - t_1)$$

where L_t is length at age t , $h = (c_1 - c_2)/3a^{1/3}$, and the parameter t_1 captures, in a very simple fashion, the influence of both predator and prey fields on the early ($t \ll T$) growth of the focal organism: (i) $t_1 = 0$ if predators are absent and there are abundant prey species that vary widely in size so that the focal organism can shift smoothly from smaller to larger prey as it grows; (ii) $t_1 > 0$ if the presence of predators suppresses risky feeding behaviour (and therefore growth) in the focal organism until it grows beyond a critical size; (iii) $t_1 < 0$ if the prey field is truncated so that the availability of prey of suitable size does not keep pace with the increasing size of the growing focal organism, leading to a drop in somatic growth rate later in juvenile life. For females of age $t \geq T$, we assume: (i) investment of energy in reproduction begins in year T , and first spawning occurs a year later at age $T + 1$; (ii) $R = gW_s^{1.0}$, where R is the investment of energy in reproduction (i.e., eggs and gonadal tissue) by a typical mature female, measured in somatic wet weight units, and g is a population-specific constant; (iii) W_g , the wet weight of the mature female gonad at spawning, equals R/δ , where δ is the ratio of gonad energy density to soma energy density, on a wet weight basis. Under these assumptions, the realized somatic growth for a female aged $t > T$ is given by

$$(2) \quad L_t = L_\infty [1 - e^{k(t-t_0)}]$$

where $L_\infty = 3h/g$, $k = \ln(1 + g/3)$, and $t_0 = T + \{\ln[1 - g(T - t_1)/3]/\ln(1 + g/3)\}$.

Next, we link investment in reproduction to fecundity (F) by assuming fecundity $F = W_g/W_e$, where W_e is the wet weight of a typical ripe egg and is assumed to be a species-specific constant. This permits us to use eq. 2 to calculate the lifetime reproductive output of a typical female given values for g and T . If we assume that differences in total adult mortality rate (Z) will select for T and g values that maximize the lifetime output of offspring by a typical female (e.g., Charlesworth 1994) and use the biphasic growth model to evaluate the consequences of such evolutionary effects, we generate the following predicted relationships among T , g , and Z :

$$(3) \quad T \approx 1.95 \frac{1}{e^Z - 1} + t_1$$

$$(4) \quad g \approx 1.18 \frac{e^Z - 1}{e^Z}$$

These functions are least squares fits to exact values obtained by numerical optimization (Lester et al. 2004). For Z in the range (0.05, 1.0), the difference between the exact value of T and the value given by eq. 3 is $<0.3 \cdot \text{year}^{-1}$, and the difference between the exact value of g and the value given by eq. 4 is $<0.02 \cdot \text{year}^{-1}$. These discrepancies are small relative to the changes in g and T expected (0.1–0.7 and 14–1, respectively), given a shift in Z from 0.05 to 1.0.

Table 1. Summary of population life history statistics.

Character*	Species			
	Lake trout	Walleye	Cisco	Perch
h (cm·year ⁻¹)	5.4 (3.2, 9.0), $n = 15$	6.4 (3.5, 8.2), $n = 18$	4.0 (3.5, 6.0), $n = 10$	6.2 (4.2, 9.9), $n = 17$
T (year)	8.2 (5.9, 11.1), $n = 15$	4.8 (3.6, 7.2), $n = 18$	3.4 (2.4, 4.1), $n = 10$	2.0 (1.1, 3.8), $n = 17$
L_T (cm)	47.0 (30.0, 65.1), $n = 15$	40.0 (31.1, 44.2), $n = 18$	23.4 (17.0, 30.3), $n = 10$	11.6 (6.1, 16.5), $n = 17$
L_∞ (cm)	76.3 (52.2, 106.4), $n = 15$	85.8 (62.1, 123.5), $n = 18$	33.7 (23.5, 41.0), $n = 10$	34.9 (24.0, 46.6), $n = 17$
W_e (mg)	69.4	2.8	5.3	2.1
g (year ⁻¹)	0.21 (0.12, 0.30), $n = 15$	0.23 (0.14, 0.35), $n = 18$	0.40 (0.28, 0.50), $n = 10$	0.54 (0.29, 0.76), $n = 17$
Z (year ⁻¹)	0.22 (0.15, 0.30), $n = 15$	0.25 (0.17, 0.40), $n = 18$	0.38 (0.23, 0.55), $n = 10$	0.55 (0.34, 0.73), $n = 15$

Note: Data are mean, range (in parentheses), and number of populations. Egg weights for lake trout, cisco, and perch were derived as follows: egg volume was calculated from egg diameter and converted to weight, assuming a specific gravity of 1.0. Sources for egg diameter estimates for each species are as follows: lake trout, 5.1 mm (direct measurement of ripe eggs from two populations, mean of several population values in Martin and Olver 1980); cisco, 2.1 mm (mean of values in Brooke (1970), Henault and Fortin (1991), Scott and Crossman (1973)); perch, 1.5 mm (Craig (2000)). The egg weight for walleye was derived from dry weight values given in Johnston and Leggett (2002) and converted to wet weight assuming a conversion factor of 3.15. All populations are found within the region bounded by 43°N–53°N latitude and 75°W–95°W longitude.

* h , potential somatic growth rate just prior to age T ; T , age at which allocation to reproduction begins; L_T , fork length at age T ; L_∞ , maximum female size; W_e , egg wet weight; g , annual investment in reproduction by a mature female; Z , instantaneous mortality rate suffered by mature females.

The following is a brief summary of the parameters that we use in this paper (Table 1): T (years), age at which allocation to reproduction begins; $T + 1$ (years), age of first spawning; h (cm·year⁻¹), potential somatic growth rate just prior to age T ; L_T (cm), fork length at age T ; L_∞ (cm), maximum female size, estimated by fitting a von Bertalanffy curve to the growth pattern of mature females; W_e (mg), egg wet weight; g (year⁻¹), annual investment in reproduction by a mature female, measured as the proportion of her somatic weight that is energetically equivalent to her investment in eggs, gonadal tissue, and reproductive behaviours; Z (year⁻¹), instantaneous mortality rate suffered by mature females.

Methods

Field sampling

Sampling for walleye, perch, and cisco was carried out in the fall of the years from 2000 through 2002 as part of a survey program sponsored by the Ontario Ministry of Natural Resources. Multipaneled sinking gill nets with mesh sizes ranging from 25 to 152 mm were randomly set throughout the lakes at depth strata of 2–5 m and 5–15 m. Additional samples were obtained from a few populations using similar methods by university researchers. Fish were measured for fork length and round weight. A subsample of the catch was assessed for sex and maturity. Gonads were weighed and preserved in ethanol for later determination of fecundity. Fecundity was estimated by counting all of the eggs in a weighed subsample (~10% of total gonad weight) of tissue taken from the centre of the gonad. Ages were determined from otoliths.

Sampling for lake trout was carried out in the spring and summer of years 1980 to 2002, under a variety of survey programs sponsored by Ontario Ministry of Natural Resources (Shuter et al. 1998; Payne et al. 1990). Gear and sampling protocols varied among populations (i.e., methods used included gill and trap net surveys and creel surveys) but were always designed to give a representative sample of both mature fish and older immature fish. Sampling for fecundity was rarely done. Fall sampling of spawning fish in two lakes (Louisa and Opeongo) was carried out to obtain

more extensive estimates of egg size and fecundity. This was supplemented with values reported by Trippel (1993) and Peck (1986). Growth and maturity data from the long-term lake trout monitoring program on Lake Opeongo (see Shuter et al. 1987 for study details) were also included in this analysis.

Estimating individual characteristics

Sex was determined by internal examination of gonads. Categorization of female maturation was based on the presence of developing eggs. Total potential fecundity (F) was estimated by counting the number of eggs in a weighed sample of gonad tissue to estimate eggs per gram, and then multiplying this estimate by the total gonad weight for the animal. For lake trout, walleye, and perch, the weight of the female gonad at spawning was calculated as

$$W_g = FW_e$$

where W_e is the average wet weight of a ripe egg (Table 1). Egg weights for lake trout, cisco, and yellow perch were calculated from egg diameters, assuming a spherical shape and a specific gravity of 1.0. In the absence of direct measurements for each species, this is a reasonable approximation given Kamler's (1992) compendium of data on fish egg composition. Her data demonstrates that a typical egg is 61% water, 26% protein, and 7.5% lipid. The remaining 5% is a mixture of carbohydrate and ash. The estimated specific gravity of such an egg is 1.05, assuming the water, protein, and lipid proportions listed above, plus specific gravity values of 1.0, 1.2, and 0.95 (Lehninger 1970) for water, protein, and lipid, respectively. Walleye egg weight was taken directly from dry weight values reported in Johnston and Leggett (2002). For cisco, fecundity was estimated for only a small subset (six) of all the populations in the study, but gonad weights were recorded for all populations at about 4–6 weeks prior to spawning. These values were used to estimate fecundity by dividing them by the average number of eggs (538) per gram of gonad tissue determined from the six populations with fecundity estimates. Ripe gonad weight was then estimated from this fecundity estimate by multiplying by the W_e value for cisco (Table 1). For all species, re-

Table 2. Exponent estimates in the critical allometric relationships for each species.

Species	Somatic weight \propto (fork length) ^b	Fecundity \propto (somatic weight) ^c
Lake trout	3.20 (3.05, 3.36), $n = 12$	1.17 (0.69, 1.57), $n = 8$
Walleye	3.13 (2.96, 3.42), $n = 22$	1.10 (0.88, 1.75), $n = 22$
Cisco	3.05 (2.82, 3.36), $n = 18$	0.90 (0.80, 0.99), $n = 4$
Perch	3.16 (2.88, 3.31), $n = 20$	1.05 (0.87, 1.20), $n = 20$

Note: Data are mean, range (in parentheses), and number of populations (e.g., mean b value for lake trout = 3.20; mean c value = 1.17).

productive investment was estimated from ripe gonad weight by multiplying by a conversion factor (δ) to correct for energy density differences between eggs and somatic tissue. For perch and walleye, values for this energy conversion factor were 1.24 (derived from data in Henderson et al. (2000)) and 1.41 (from Henderson and Nepszy (1994)), respectively. For lake trout and cisco, values were 1.52 (from Jonsson et al. (1991)) and 1.75 (from Lahti and Muje (1991)), respectively. The latter three values all fall close to the median value (1.6) reported by Gunderson and Dygert (1988) in their review of reproductive investment in marine species. Egg-soma energy density ratios based on wet weights will generally be significantly larger than energy density ratios based on dry weights, because fish egg tissue tends to have a lower water content than fish soma tissue. For example, in Kamler's (1992) summary of egg composition data, the water content of a typical egg is 61% compared with 82% for soma.

Estimating population characteristics

Logistic regression (StatSoft 1994) was used to estimate the relationships linking the fraction of mature females to age and to length. These relationships were then used to estimate both the age (T) and length (L_T) at which females begin to allocate energy to reproduction. Adult mortality was estimated from the maximum observed age of fish in each population using Hoenig's (1983) empirical formula: $Z = 4.22(\text{maximum observed age})^{-0.982}$. The lifetime growth pattern for each population was characterized as follows. The pre-maturation somatic growth rate was estimated using standard linear regression on the length-at-age data for immature fish. Changes in net production during the pre- and immediate post-maturation periods were assessed by examining somatic growth rates of immature fish prior to, and just after, the population age at maturity. Significant systematic shifts in pre-maturation growth rate were reflected by non-zero t_1 values. The postmaturation growth curve was estimated using nonlinear regression to fit eq. 2 to length-at-age data for ages $t \geq T$. The fit provided by eq. 2 depends on four parameters: h , t_1 , T , and g . We searched for the value of g that would best describe the growth of mature females, given a value for T based on the maturation schedule and values for h and t_1 based on the growth of immature fish in the neighbourhood of T .

Results

We described growth characteristics of 15 lake trout, 18 walleye, 10 cisco and 17 yellow perch populations (Table 1). All 60 populations are spread across the relatively large geographic area of Ontario (Table 1). Intraspecific variation for

many population characteristics is quite large and the inter-specific variation is even larger.

Are the assumptions regarding size-dependence met?

The biphasic model makes several assumptions regarding the length-dependence of somatic weight and the somatic weight-dependence of both mature gonad weight and fecundity. These relationships were evaluated for each population (Table 2), and we found that (i) for all four species, the assumption that weight varies as the cube of length was closely adhered to; and (ii) the assumption that fecundity varies with somatic weight was closely adhered to, and hence the assumption that mature gonad weight varies with somatic weight was met, given fixed ripe egg size.

Does the biphasic growth model provide a good description of lifetime growth pattern?

The biphasic model successfully described the range of growth patterns seen in the four species of fish (Fig. 1). The examples shown clearly demonstrate a switch from linear to asymptotic growth at the age of maturity. For lake trout, walleye, and cisco, somatic growth rate during the first year of life usually exceeded the average somatic growth rate for the rest of the pre-maturation period. Because the growth rate just prior to maturity was relatively constant (Fig. 1), this aspect of the pre-maturity growth pattern was adequately captured by including estimated t_1 values that were significantly less than 0 (see Lester et al. 2004 for details). For yellow perch, growth rate from birth to maturity was relatively constant, and thus we could set t_1 to zero for all populations.

Does adult growth reflect reproductive investment?

Given that g values estimated from the lifetime growth pattern should reflect relative investment averaged over the entire reproductive life cycle, we characterized the reproductive investment typical for each population as the value of W_g/W_s for a female midway through her reproductive lifespan and characterized by a length $L_{\text{mid}} = (L_T + L_\infty)/2$, where L_T and L_∞ are population-specific values. Values for W_g and W_s were estimated from L_{mid} using population-specific weight and fecundity regression relationships. We then compared this direct estimate of reproductive investment with our g estimate derived from the growth pattern of mature females (Fig. 2).

Within species, the median values and ranges for our direct and indirect estimates of reproductive investment were very similar (Table 3). We found significant positive associations between our direct measure of reproductive investment and the estimates of g derived from the lifetime somatic growth pattern for walleye (Spearman's $R = 0.65$, one-sided $p < 0.003$) and for perch (Spearman's $R = 0.48$, one-sided

Fig. 1. Sample prereproductive (open circles, observed values; broken line, fitted relationship) and postreproductive (solid circles, observed values; solid line, fitted relationship) growth patterns for (a) lake trout (*Salvelinus namaycush*, Squeers Lake), (b) walleye (*Sander vitreus*, Wakami Lake), (c) lake herring (*Coregonus artedii*, Red Cedar Lake), and (d) yellow perch (*Perca flavescens*, Nagagamis Lake). The two fitted relationships, which characterize each phase of the overall growth trajectory, have been drawn over a broad range of ages to emphasize the contrast between the phases. Fitted values for h (prereproductive somatic growth rate) and g (reproductive investment) are given for each curve.

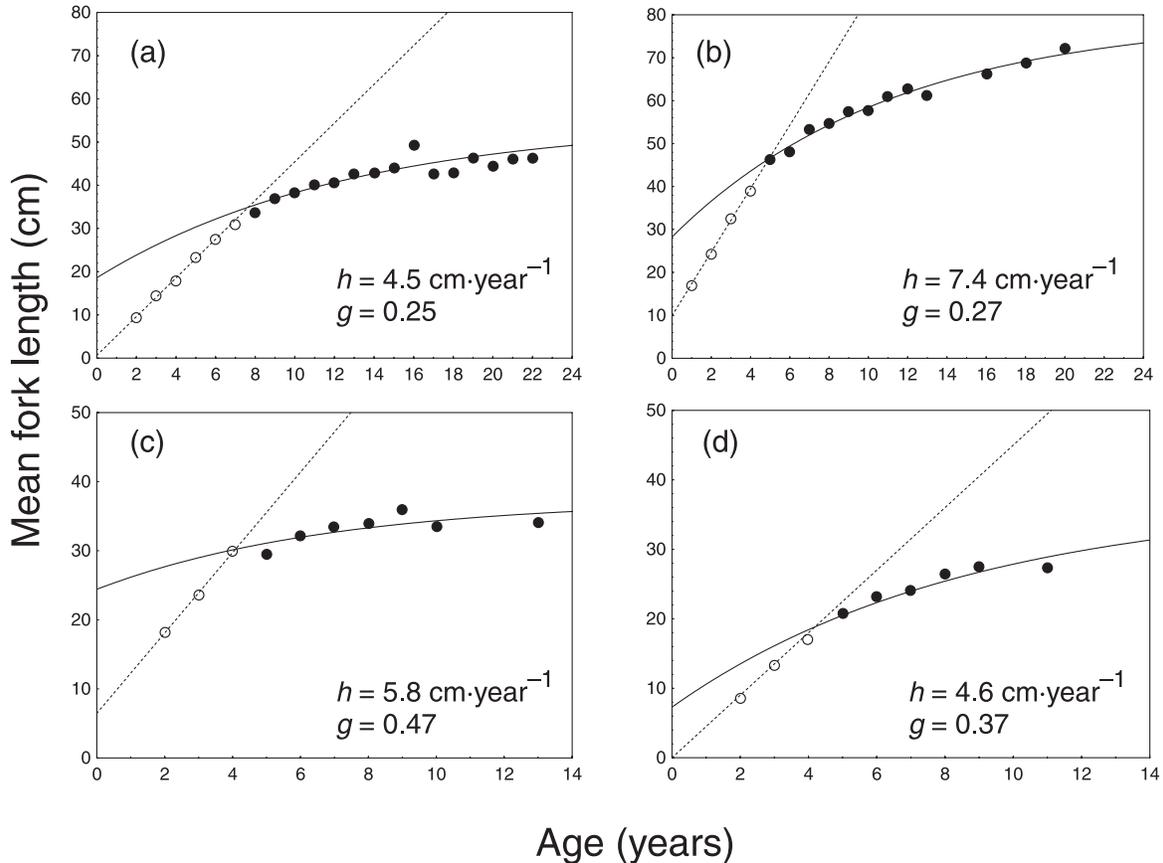
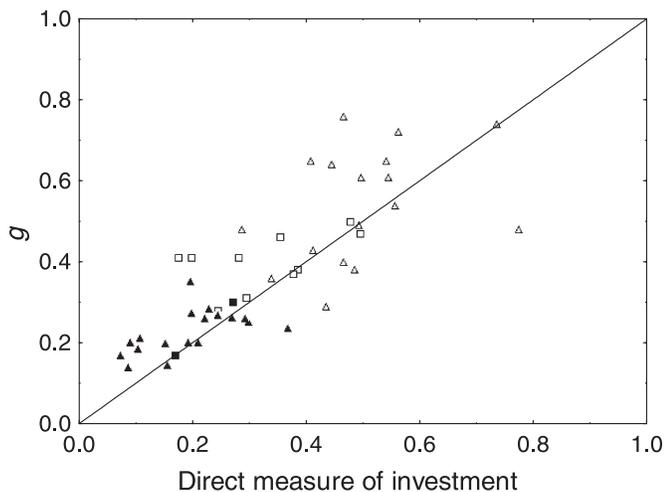


Fig. 2. Comparison between direct estimates of reproductive investment, based on measured female gonad weight, and indirect estimates of reproductive investment, obtained by estimating g from a von Bertalanffy fit to the somatic growth trajectory of mature females. The solid line is the 1:1 line. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedii*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



$p < 0.04$). There were not enough populations in the lake trout data set to permit a meaningful assessment of association. For cisco, the association between the two measures was not statistically significant (Spearman's $R = 0.08$).

Are reproduction and adult mortality linked as predicted by life history theory?

Observed variation in T , g , and Z for each of our four species is summarized (Table 1 and Fig. 3). Intraspecific variation for most parameters is relatively high, with the maximum observed value typically 2–3 times the minimum observed value. Total mortality values are higher for the mid-trophic-level species. T and g estimates appear to vary with total mortality in accordance with eqs. 3 and 4 (Fig. 3).

Discussion

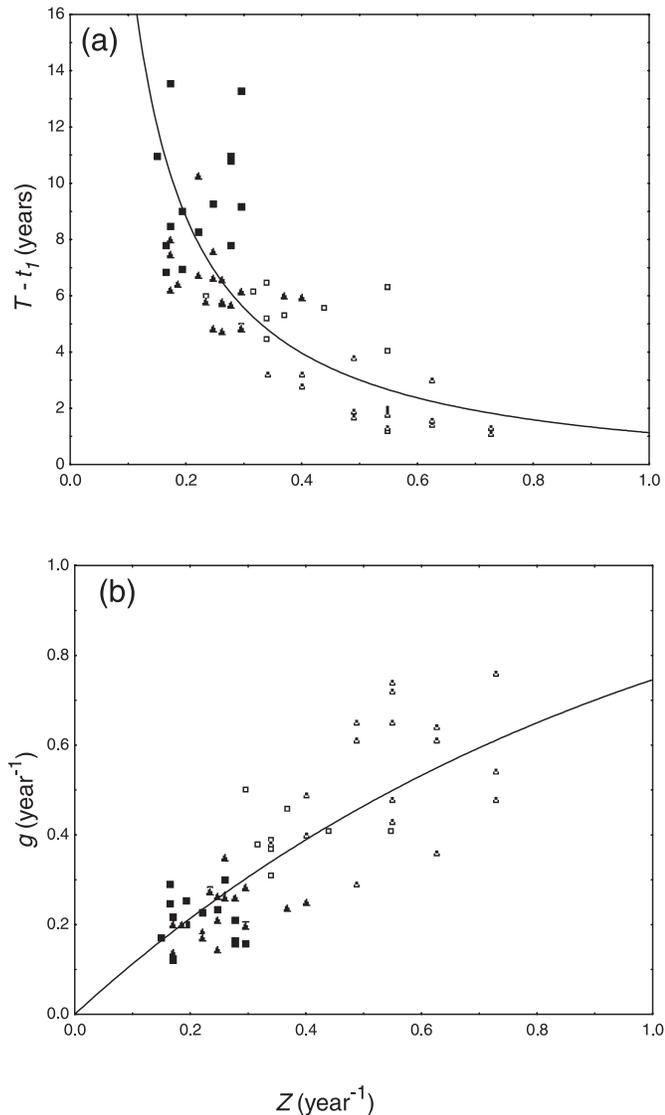
For the four species in this study, the primary assumptions that underlie the biphasic growth model are largely met, and the model is capable of providing a good description of observed lifetime growth patterns. For long-lived species with relatively late maturation ages (e.g., lake trout), the biphasic character of the growth pattern is clearly demonstrated. The fact that growth-based g values are similar to direct measures of reproductive investment supports the premise that

Table 3. Comparison of direct and indirect estimates of reproductive investment.

Species	Measure of investment	
	Direct	Indirect
Lake trout	0.21, (0.18–0.22), $n = 2$	0.21, (0.12–0.30), $n = 15$
Walleye	0.24, (0.09–0.44), $n = 18$	0.22, (0.14–0.35), $n = 18$
Cisco	0.32, (0.17–0.48), $n = 10$	0.41, (0.16–0.55), $n = 10$
Perch	0.49, (0.29–0.78), $n = 17$	0.54, (0.29–0.76), $n = 17$

Note: Data are median, range (in parentheses), and number of populations. Direct estimates of investment were derived from measurements of gonadal development in mature females; indirect estimates were obtained from fitting the biphasic growth curve to length-at-age data from mature females.

Fig. 3. Comparison between observed and predicted values for $(T - t_1)$ and reproductive investment (g). Each point represents the observed values for a particular population. The solid lines are the predicted values derived from eqs. 3 and 4, respectively. Z is total adult mortality rate. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedii*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



female adult growth pattern is shaped by reproductive investment. For all four species, the median values for both the direct and indirect measures of reproductive investment were similar; however, only two of the three intraspecific comparisons exhibited statistically significant positive associations between these two measures. The weakness of these intraspecific associations may stem from the fact that population data (rather than individual data) were used to derive each of the measures — the growth trajectory-based g values came from mean length-at-age data and the direct measures of reproductive investment came from mean fecundity – somatic weight data. These data averaged over cohorts, were frequently based on different subsamples of fish, and thus may only loosely reflect the close connection between somatic growth and reproduction that is assumed to exist for individuals, as represented in the biphasic growth model. This suggests that a more exacting test of this model should be based on growth and reproductive investment data derived concurrently from the same individuals.

Since the observed associations among T , g , and Z match the relationships predicted by applying simple life history theory to the biphasic growth model, we conclude that a significant portion of the demographic variation exhibited among populations of these four species can be attributed to the shaping of life histories to match ambient mortality rates by some combination of selection and phenotypic plasticity. For mid-trophic-level species (cisco and perch), these ambient mortality rates are natural rates in the sense that they do not contain a component that is driven directly by human activities, such as fishing. For the top predators (lake trout and walleye), the ambient rates do contain a fishing component. However, the populations in our data set have been subjected to moderate levels of fishing for several generations and, as is evident from other papers in this symposium (e.g., Munch et al. 2005; Olsen et al. 2005; Reznick and Ghalambor 2005), selection imposed by fishing can operate rather quickly to alter the reproductive characters of adults. Thus, it is at least possible that selection may be the primary force underlying the correspondence between observed and predicted values of T and g shown in this study.

In our earlier paper (Lester et al. 2004), we showed that these predicted associations among T , g , and Z were also consistent with patterns of interspecific demographic variation evident in a large sample of North American freshwater fish. If we assume that this theory has some validity for fish generally, then it provides a simple, mechanistic account of the frequently observed empirical association between the parameters of the von Bertalanffy growth curve and mortality (e.g., Beverton 1963; Pauly 1980; Charnov 1993) and

Table 4. Comparison of observed and predicted values for the quantities identified by Charnov (1993) as life history invariants.

Quantity	Nominal value or range cited in Charnov (1993)	Predicted value*
$(T + 1)Z$	(1.75, 2.20)	(1.95, 2.10)
L_{T+1}/L_{∞}	0.65	(0.42, 0.73)
Z/k	(1.65, 2.10)	(2.6, 4.5)
ϕ^{\dagger}	(-0.8, -0.4)	-1

*Predicted values are generated from applying eqs. 3 and 4 to the biphasic growth model for a range of Z values from 0.05 to 1.0.

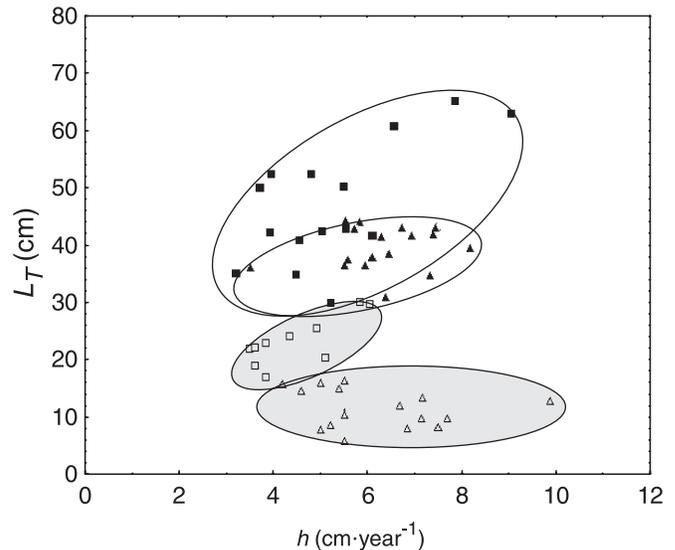
$\dagger \ln L_{\infty} \propto k^{\phi}$.

also of the empirical association between direct measures of reproductive investment (e.g., female gonadosomatic index) and mortality (Gunderson and Dygert 1988; Gunderson 1997). Optimization of demographic characters that are constrained by the biphasic growth model “naturally” produces associations among growth parameters, reproductive investment, and mortality, which are largely consistent with the empirical associations documented in these earlier studies. Fits of the von Bertalanffy equation ($L_t = L_{\infty}[1 - e^{-k(t-t_0)}]$) to observed adult growth patterns yield values for k that vary with reproductive investment (since $k = \ln(1+g/3)$), and reproductive investment (as measured directly through the gonadosomatic index or indirectly through k) will vary with mortality (see eq. 4).

Charnov (1993) summarized various empirical associations among life history parameters and mortality in terms of four quantities that he termed “life history invariants” — dimensionless quantities that appeared to be relatively constant when estimated for a variety of species, living under a wide range of environmental conditions (Table 4). Our theoretical analysis of life history variation yields predictions for these quantities that can be compared with Charnov’s summary (his Chapter 4, our Table 4).

Our analysis predicts that the first quantity ($(T + 1)Z$) is essentially invariant under a wide range of mortality rates, with a value very similar to that given by Charnov (1993). The second quantity (L_{T+1}/L_{∞}) varies with mortality, but the range of variation is less than twofold for mortality rates between 0.05 and 1.0, and Charnov’s nominal value sits close to the middle of that range. However, our analysis, unlike Charnov’s, predicts a systematic decline in L_{T+1}/L_{∞} with increasing mortality. Our predictions for the third (Z/k) invariant differ somewhat from Charnov’s summary. Our analysis predicts that Z/k will increase with mortality, giving a range of values that is just above the range cited by Charnov as “typical”, but is well within the overall range defined by the Pauly (1980) data set (0.60 to 4.6 is the 90% range), which was Charnov’s primary source. This discrepancy could stem in part from a systematic bias in the estimate of k that can arise when a single von Bertalanffy equation is used to describe the entire lifetime growth trajectory. We simulated this situation (B.J. Shuter, unpublished data) by using a non-linear least squares (S-Plus 2001) procedure to fit a single von Bertalanffy function ($L_T = L_{\infty}(1 - e^{-kt})$) to the optimal (as specified by eqs. 3 and 4) biphasic growth curves for Z values ranging from 0.1 to 1.0. We found that the least squares estimate of k was always higher than the true value, with the ratio of the biased to the true value declining from

Fig. 4. Observed values for length at maturity (L_T) and pre-reproductive somatic growth rate (h). Values for each species have been enclosed with an ellipse. The ellipses for the two mid-trophic-level species have been shaded to distinguish them from the two top predators. Lake trout (*Salvelinus namaycush*), solid squares; cisco (*Coregonus artedii*), open squares; yellow perch (*Perca flavescens*), open triangles; walleye (*Sander vitreus*), solid triangles.



1.5 toward 1.0 as Z increased from 0.1 to 1.0. When we substituted this biased estimate of k for the true value in Charnov’s third invariant (Z/k) we found very similar values (1.78, 2.8) to those cited as “typical” by Charnov for $Z \in (0.1, 0.5)$ and somewhat larger values (3.1, 4.1) for $Z \in (0.6, 1.0)$.

Our model predicts that the fourth quantity (ϕ in $L_{\infty} \propto k^{\phi}$) should be truly invariant with a value (-1) that is just below the range (-0.8 to -0.4) cited by Charnov as typical. The positive bias in k estimates mentioned above cannot account for this discrepancy; however, one factor that might be responsible is density-dependent plasticity in growth. This effect is omitted from our model and from Charnov’s models (Charnov 1993; Charnov et al. 2001). In our model, $L_{\infty} = 3h/g$ and $k = \ln(1 + g/3)$. This implies that L_{∞} is approximately proportional to hk^{-1} , and thus the relationship between L_{∞} and k will be affected by systematic changes in growth rate (h). The increase in ϕ comes about if we assume that higher Z , and consequently higher k values, are associated with relatively low-density populations, where typical adults enjoy higher surplus energy production and hence higher h values. The rate of decline in L_{∞} with increasing k , which is inherent in our basic model, would be ameliorated by this effect, resulting in an estimate for ϕ that is greater than -1 and therefore closer to the typical range cited by Charnov (Table 4). Trends in our data are consistent with the existence of this effect; within each species, growth rate was positively related to reproductive investment.

Given that the theoretical predictions summarized in eqs. 3 and 4 have some general validity, we would expect that within a food web, life history parameters will shift in a predictable fashion with the decreases in mortality expected as one moves from primary consumers up toward top predat-

tors. This expectation is born out by the observed differences in both mortality and life history characteristics between our two mid-trophic-level consumers and our two top predators. The top predator species mature at older ages and larger sizes, invest less in reproduction, and attain larger asymptotic sizes. The observed differences in g and T are expected, given that mortality rates are lower for top predator species. In the following arguments, we show that larger L_∞ and L_T (Fig. 4) values among the top predators can also be interpreted as consequences of smaller g and Z values. According to the biphasic growth model, $L_\infty = 3h/g$ and thus variation in L_∞ is potentially explained by variation in pre-maturation somatic growth rate (h) and (or) reproductive investment (g). With our four species, the pre-maturation growth rates of mid-trophic-level species and top predator are very similar (Fig. 4), while the g values for top predators are roughly half the g values for mid-trophic-level species. Thus, the higher L_∞ values among the top predators are explained mainly by the lower investment in reproduction associated with lower mortality rates. Similarly, the higher sizes at maturity (L_T) among top predators (Fig. 4) can also be interpreted as a consequence of lower mortality rates. Given (i) that L_T varies with hT (eq. 1), (ii) that T is given by eq. 3, then L_T will vary with $h/(e^Z - 1)$, and (iii) since values of h are independent of trophic position but values of Z decline with increasing trophic position, then increases in L_T with increases in trophic position are expected and are observed (Fig. 4).

Our results suggest that in an unexploited food web, the life histories of the resident fish species will be shaped by the progressive decline in adult mortality that accompanies the relaxation of predation pressure experienced by primary, secondary, and tertiary consumers. This set of interdependent mortality rates will have shaped the life histories of the fish in the web and thus will have determined, to a significant degree, their responses to increasing rates of exploitation. When directed exploitation raises the mortality rate for one species, it will produce a cascade of changes in the mortality rates experienced by species at successive trophic levels below that of the harvested species. Over time, these changes will promote the evolution of a new suite of life history traits among the fish species of the web, with a variety of consequences for their population dynamics. Raising fishing mortality rates to levels that are high relative to the natural rates for the exploited species in the web will exaggerate both the magnitude and extent of this cascade, with consequences that are currently unpredictable and possibly undesirable.

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