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An analysis of life-history invariants in Eurasian perch, *Perca fluviatilis*

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ABSTRACT

Questions: Can life-history traits be aggregated into dimensionless and invariant indices? Can meaningful inferences be derived from such invariants? Can important life-history traits be predicted from simple measures of growth and mortality rates?

Organism: A medium-sized freshwater fish with a complex life history, Eurasian perch (*Perca fluviatilis*). Perch often display one of two growth types: slow growing and small-sized (stunted), or rapid growing and large-sized (often piscivorous).

Data used: Literature data from 75 populations spanning the natural distribution range of perch in Eurasia.

Conclusions: Most life-history traits are related through trade-offs, and covary in a predictable manner among populations. Suggested life-history invariants could be deemed as invariant using standard criteria. However, an observed difference between growth types suggests that evolutionary inference from invariants should be drawn with caution. On the other hand, simple optimality models based on information about growth and mortality schedules do predict age and size at maturity and reproductive investment with reasonably high precision.

Keywords: Beverton and Holt invariants, dimensionless numbers, life history, *Perca fluviatilis*, trade-offs.

INTRODUCTION

Life-history traits (e.g. age and size at maturity, mortality rate, adult life span, growth rate) that have the same unit may be aggregated into dimensionless numbers with parameter values that are more or less constant within taxa (Beverton, 1963; Charnov, 1993; Roff, 2002). These aggregated dimensionless numbers are often called 'life-history invariants'. The definition of what actually constitutes invariance is unfortunately not intuitive (Roff, 2002). However, if parameter values for such invariants differ among major taxa, general insight into how life-history traits evolve may result. A very useful research programme would then be to ask what processes lead to such invariants (Roff, 2002).

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One of the most studied life-history invariants is the product of adult life span (T_{max}, often estimated as z^{-1}, where z is the adult instantaneous mortality rate) and age at maturity (α), $(\alpha z)^{-1}$ (Charnov, 1993; Charnov *et al.*, 2001). Plots of α on z^{-1} show that the slopes differ strongly among taxonomic groups. The slopes for various vertebrate groups are 2.5 for birds, 1.4 for mammals, 0.8 for lizards and snakes, 0.6 for elasmobranches, and 0.5 for teleosts (Charnov and Berrigan, 1990; Frisk *et al.*, 2001). Even if the major groups separate nicely, there is large overlap among taxa. Some of this overlap may be due to measurement error, as some life-history traits are difficult to estimate with high precision (e.g. mortality rates). Furthermore, there may be large variation within taxonomic groups. For example, for two salmonid fish species, $(\alpha z)^{-1}$ was found not to be invariant for brown trout (*Salmo trutta*), whereas it was invariant for Arctic char (*Salvelinus alpinus*) (Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994).

A number of life-history invariants have been suggested based on general life-history theory (Beverton and Holt, 1959). Most studies on these invariants are based on comparisons among major taxa. At this scale, some clear and interesting assembly rules can be found. However, at the smaller among-population scale, it is evident that some of the suggested invariants are not so (Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994). Mangel (1996) explained the results for brown trout and Arctic char by suggesting that ontogenetic niche shifts (in both these species some individuals may change from benthivory to piscivory) violate the assumptions of the growth models used in the analyses. Most of the invariants are based on the assumption that individual growth trajectories can be described by the common von Bertalanffy growth equation. This may be too simple an assumption. When a niche shift occurs, growth trajectories may change dramatically.

Here, we study the relationship between various life-history traits in 75 Eurasian perch (*Perca fluviatilis*) populations from a broad geographic range covering the distribution area of the Eurasian perch. Eurasian perch are iteroparous, spawning annually during early spring (Thorpe, 1977; Craig, 2000). Perch usually feed on zooplankton during their first year of life, then shift to feeding on benthos mainly in the littoral zone (Byström *et al.*, 2003). Some perch go through a second niche shift, changing from being benthivorous to being piscivorous. However, in many populations this second niche shift does not occur, probably due to strong density-dependent interactions (Ylikarjula *et al.*, 1999; Claessen *et al.*, 2000) or low availability of one or more prey components within their diet [the trophic bottleneck hypothesis (Heath and Roff, 1996)]. Populations containing almost exclusively slow-growing and small-sized (stunted) individuals may be the result. In this study, we analyse a number of life-history indices and test if they are invariant as suggested by theory (see Charnov, 1993). In particular, we explore if the invariants are influenced by population type – that is, if the population is stunted or not. We also use this large data set to test some general models (Roff, 1984; Charnov, 1993) predicting important life-history traits, such as reproductive investment and age at maturity, based on information about growth and mortality rates.

MATERIALS AND METHODS

The data

The data analysed in this paper are described in detail in the Electronic Appendix (see also Heibo *et al.*, 2005). Briefly, parameter values for several life-history traits (defined in Table 1) were collected from the literature. The data consist of the growth coefficient (K) and asymptotic length (L_∞) estimated for the simplified von Bertalanffy growth model, the

Table 1. Definitions of symbols used in this study

Symbol	Definition
l_x	Probability to survive to age x
m_x	Number of daughters produced in age x
r	Intrinsic rate of natural increase
R_0	Fundamental net reproductive rate
α	Age at maturity; when 50% of the individuals in an age class within a population is mature
L_α	Length at maturity; length corresponding to the estimated age at maturity
L_∞	Length at infinity (asymptotic length); estimated using the von Bertalanffy growth model
K	The growth rate coefficient estimated from the von Bertalanffy growth model
h	Slope of the assumed trade-off between K and L_∞
z	Instantaneous mortality rate
GSI	Reproductive investment (%); gonad mass relative to somatic mass
B	Reproductive investment; estimated from Charnov's (1993) model
T_{max}	Lifespan (years); age of the oldest individual in the population

instantaneous adult mortality rate (z), age (α) and length (L_α) at maturity, and reproductive investment estimated as the gonadosomatic index (GSI). The GSI was defined as the gonad weight relative to somatic weight. Populations with estimated $L_\infty \leq 250$ mm were classified as stunted, whereas populations with $L_\infty > 250$ mm were classified as piscivorous [for details about the data and sampling procedure, see Heibo and Vøllestad (2002) and Heibo *et al.* (2005)].

Life-history invariants

Beverton and Holt (1959) and Charnov (1993) proposed that a number of aggregate life-history traits are constant within taxa. These so-called life-history invariants were derived from life-history theory, as described by Beverton and Holt (1959), Charnov (1993), Jensen (1996, 1997) and He and Stewart (2001). Here, the different life-history invariants are summarized.

$z\alpha$ is a suggested life-history invariant that expresses the relative life span and suggests that there is a trade-off between adult survival and age at maturity. Originally, this invariant used T_{max} as an estimator of z.

z/K expresses that mortality is growth-dependent, suggesting a trade-off between survival and growth.

L_α/L_∞ expresses the relative length at maturity. This life-history invariant indicates that there is an inherent relationship between length at maturity and the maximum attainable length (Beverton, 1963). Beverton and Holt (1959) suggest that short-living species have, on average, the higher L_α/L_∞ values and thus mature at a relatively late stage in their growth cycle.

$L_\infty K^h$ expresses the relation between growth and asymptotic length and is often called the growth trade-off. The constant h is the slope of the assumed trade-off between K and L_∞. Charnov (1993) proposed that the relationship between asymptotic length and the growth coefficient might be the result of a constraint on growth.

$K\alpha$ expresses the relationship between the growth coefficient and age at maturity, showing the well-known result that increasing growth rate leads to an earlier age at maturity (see Alm,

1959). This constant is closely related to the relative length at maturity through the von Bertalanffy growth equation, and species/populations with the same value for L_α/L_∞ also have the same $K\alpha$ value.

Predictive life-history models

A population at equilibrium can be characterized by the classic Euler-Lotka equation, containing l_x (the probability of surviving to age x), m_x (the number of daughters produced in age x) and the intrinsic rate of increase r. Maturation should occur at or before the peak in the $l_x m_x$ curve, because natural selection favours an age at maturity that maximizes fundamental net reproductive rate (R_0) (Stearns, 1976; Gadgil and Bossert, 1970). Roff (1984, 1986) explored models that can be used to estimate age and length at maturity in animals with indeterminate growth. The models use R_0 as a fitness estimator. Fecundity is assumed to vary as a power function of length (power 3) and growth is described by the von Bertalanffy growth function. Based on this, the optimal age (α) and length (L_α) at maturity can be estimated as:

$$\alpha = \left(\frac{1}{K}\right) \ln\left(\frac{3K+z}{z}\right) \tag{1}$$

$$L_\alpha = L_\infty \left(\frac{1}{1+\left(\frac{z}{3K}\right)}\right) \tag{2}$$

Charnov (1993) proposed a model for predicting the optimal reproductive investment (B) of a fish. It is based on a two-stage growth model that can be related to the von Bertalanffy growth model. Prior to reproduction, growth is a power function of body weight, with an exponent close to 2/3. After sexual maturation, the individual allocates some proportion (B) of its resources to reproduction. After some recombination, it is found that B can be a simple relationship between age and length at maturity and asymptotic length:

$$B = \left(\frac{3L_\alpha}{\alpha L_\infty}\right) \tag{3}$$

RESULTS

Life-history invariants

In this paper, we evaluate five proposed life-history invariants. Before analysing the parameter estimates, it is necessary to determine whether these relationships are indeed invariant. The common way to test for invariance is to test the slope between the two involved parameters on a log–log scale (see Gardner *et al.*, 2005). If the relationship is invariant, we should expect a slope not significantly different from ± 1 (tested using t-test). We would also expect variance to be small, and analyse this by estimating the coefficient of variation (CV) of each suggested invariant. Since both variables are subject to measurement error, we used geometric mean (GM) regression (Sokal and Rohlf, 1981; Ricker, 1973) to estimate slopes and associated confidence intervals. For the total material, the GM regression slope was significantly different from 1 for L_α/L_∞ (Fig. 1, Table 2). For the other suggested invariants,

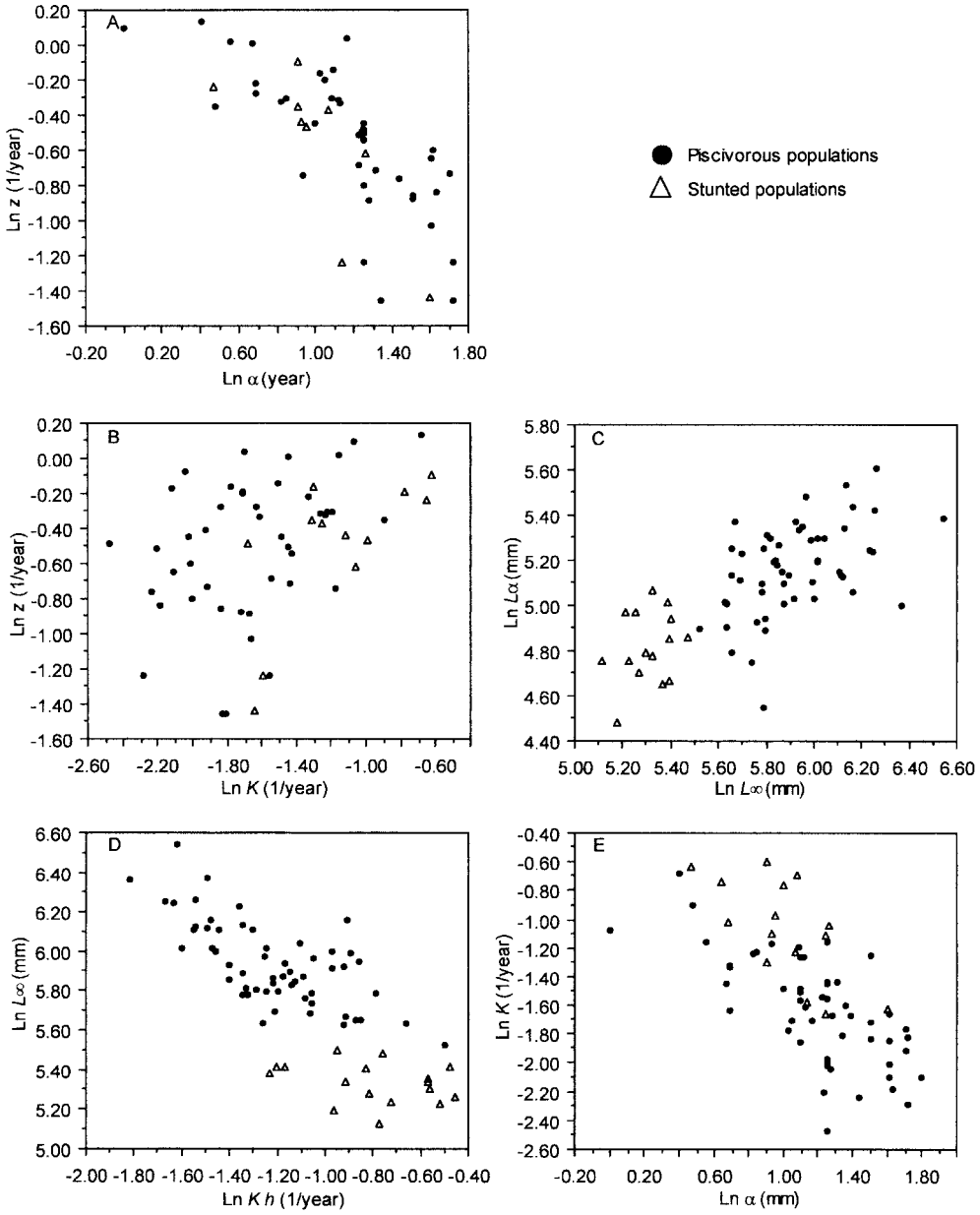

Fig. 1. Relationship between various life-history traits, on a log–log scale for 75 perch populations. Related statistics are given in Table 2. (A) Instantaneous mortality rate (z) versus age at maturity (α). (B) Instantaneous mortality rate (z) versus the von Bertalanffy growth exponent (K). (C) Length at maturity (L_α) versus asymptotic length (L_∞). (D) Asymptotic length (L_∞) versus the von Bertalanffy growth exponent (K^h). (E) The von Bertalanffy growth exponent (K) versus age at maturity (α).

Table 2. Estimated slopes (± 95% confidence limits), correlation coefficients (r), statistical significance (P) for the functional regressions between life-history traits, and observed mean index (with CV; standard deviation/mean)

	Pooled	Piscivorous	Stunted
ln z vs. ln α			
Slope	−1.079 (± 0.216)	−1.026 (± 0.227)	−1.443 (± 0.796)
r (n)	−0.731 (49)	−0.746 (39)	−0.736 (10)
P	<0.0001	<0.0001	0.01
Mean $z\alpha$ (CV)	1.85 (0.27)	1.90[a] (0.27)	1.66[a] (0.26)
ln z vs. ln K			
Slope	0.909 (± 0.229)	1.010 (± 0.290)	1.135 (± 0.585)
r (n)	0.386 (56)	0.387 (44)	0.683 (12)
P	0.003	0.0094	0.0144
Mean z/K (CV)	3.16 (0.48)	3.48[a] (0.44)	1.99[b] (0.33)
ln L_α vs. ln L_∞			
Slope	**0.758 (± 0.132)**	0.941 (± 0.232)	1.601 (± 0.922)
r (n)	0.704 (68)	0.480 (53)	0.275 (15)
P	<0.0001	0.0003	0.321
Mean L_α/L_∞ (CV)	0.51 (0.22)	0.48[a] (0.20)	0.61[b] (0.16)
ln L_∞ vs. ln K^h			
Slope	−1.000 (± 0.149)	−0.999 (± 0.190)	−1.000 (± 0.526)
h	0.732	0.577	0.297
r (n)	−0.768 (75)	−0.705 (58)	−0.296 (17)
P	<0.0001	<0.0001	0.248
Mean $L_\infty K^h$ (CV)	11.04 (0.22)	14.71[a] (0.17)	15.05[a] (0.12)
ln K vs. ln α			
Slope	−1.205 (± 0.220)	−1.008 (± 0.206)	−1.263 (± 0.570)
r (n)	−0.669 (68)	−0.685 (53)	−0.657 (15)
P	<0.0001	<0.0001	0.0077
Mean $K\alpha$ (CV)	0.74 (0.33)	0.67[a] (0.29)	0.97[b] (0.28)

Note: Estimates are given for all populations together, and separately for the two population types (stunted, piscivorous). Slope estimates given in **bold** are significantly different from ±1 (t-test, $P < 0.05$), and mean parameter estimates sharing the same letter are not significantly different ($\alpha = 0.05$).

the slopes were not significantly different from ±1. The variance for each suggested invariant was relatively high (CV = 0.12–0.48). Based on this, only $z\alpha$, $K\alpha$ and $L_\infty K^h$ could be deemed as invariants. For the relationship between L_α and L_∞, we further tested if the relationship differed between stunted and piscivorous populations. However, the data for the two population types did not overlap, so we tested if the slopes of within-group GM regressions differed using a t-test. The slopes did not differ ($t_{64} = 0.126$, $P > 0.5$). Furthermore, for three of five invariants the parameter values differed significantly between stunted and piscivorous populations (Table 2).

Predictive life-history models

Observed age at maturity (α) varied between 1 and 6 years (mean ± standard deviation: 3.36 ± 1.13) and was strongly positively correlated with that predicted by Roff's basic model ($R^2 = 0.65$, $P < 0.0001$; Fig. 2). The slope of the relationship between observed and predicted values, using GM regression, was 1.202 ± 0.208 (95% confidence interval), and was not significantly different from 1 ($t_{47} = 1.961$, $P = 0.058$). Observed age at maturity did not differ among population types (ANOVA: $F_{1,66} = 3.609$, $P = 0.062$), and the slope of the relationship between observed and predicted values did not differ between stunted and piscivorous populations (ANCOVA: $F_{1,45} = 1.326$, $P = 0.256$).

Observed length at maturity (L_α) varied between 87.9 and 272.8 mm (166.2 ± 39.2) and was strongly positively correlated with predicted values ($R^2 = 0.68$, $P < 0.0001$; Fig. 2). The slope of the relationship was estimated as 1.100 ± 0.182, and was not significantly different from 1 ($t_{47} = 1.120$, $P = 0.282$). Observed length at maturity differed significantly among population types (stunted: 124.2 ± 8.3 (standard error); piscivorous: 178.2 ± 4.4; ANOVA: $F_{1,66} = 32.790$, $P < 0.001$), but the slope of the relationship between observed and predicted values did not differ between stunted and piscivorous populations (ANCOVA: $F_{1,45} = 0.016$, $P = 0.899$).

Observed female reproductive investment (*GSI*) varied between 15.6 and 28.1%, and was significantly positively correlated with the reproductive investment (*B*) predicted from Charnov's model (Fig. 3; $R^2 = 0.521$, $P < 0.0001$, $n = 31$). The observed mean *GSI* did not differ among population types (ANOVA: $F_{1,29} = 0.006$, $P = 0.941$). However, there was a significant effect of population type on the relationship between *B* and *GSI* (ANCOVA: $F_{1,28} = 16.39$, $P = 0.0004$), but the slopes did not differ between the two population types (ANCOVA: $F_{1,27} = 0.420$, $P = 0.522$). The least squares mean values for *B* were higher for stunted (0.708 ± 0.047) than for piscivorous (0.496 ± 0.023) populations.

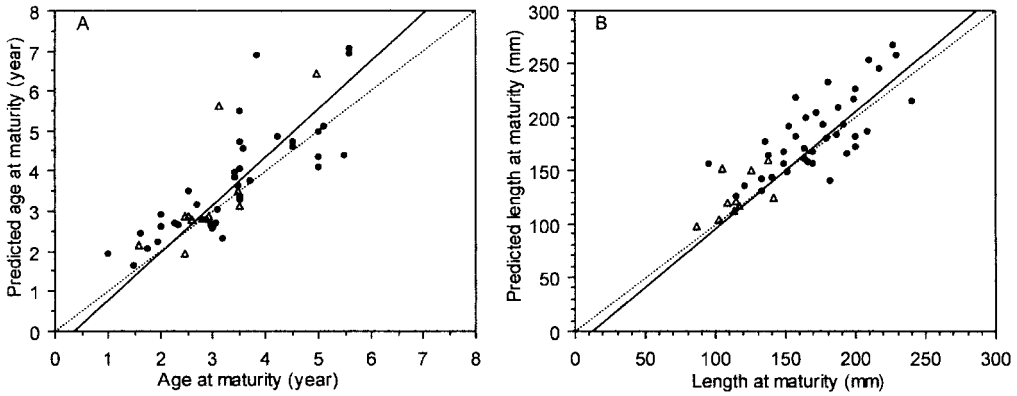

Fig. 2. Predicted versus observed age (A) and length (B) at maturity for stunted (triangles) and piscivorous (circles) perch populations. The 1:1 line (dotted line) is given for comparison with the calculated functional regression.

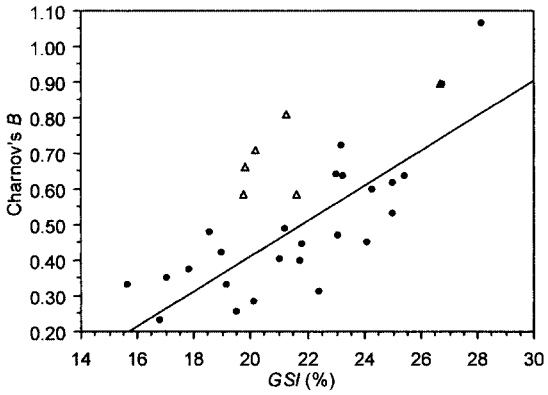

Fig. 3. Predicted reproductive investment (Charnov's *B*) versus observed reproductive investment (*GSI*) for stunted (triangles) and piscivorous (circles) perch populations. Linear regression is presented for the piscivorous population type only, since the linear regression for the stunted population was not significant.

DISCUSSION

Life-history invariants

Only one of five suggested life-history invariants analysed here did not show invariance, when defining invariance as a slope for the relationship between the traits not different from ±1 on the log–log scale. When analysing the invariants for the population types (stunted, piscivorous) separately, all were invariant. However, for two of the suggested invariants (z/K, $L_\infty K^h$) variance was very large, indicating that they are less useful for inferring any specific evolutionary process causing this pattern. Usually, invariance has been found when looked for (Charnov, 1993), even if there are exceptions (Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994).

The product of instantaneous mortality rate (z) and age at maturity (α) was invariant for perch, independent of population type. Charnov (1993) reported the typical range of this constant to be 1.75–2.2 for fish. However, values between 2.3 and 3.2 have also been reported (Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994). This large variability in parameter values argues against the index as being invariant at higher taxonomic levels than the species. This life-history invariant is of great interest as it is thought to express the relative life span, and it suggests that there is a trade-off between adult survival and age at maturity. There may be various reasons for this trade-off. One important reason is that reduced survival for large individuals will select for reduced age at maturity. This is a trend predicted from general life-history theory (Stearns, 1992; Roff, 2002), and also documented in studies on the effect of size-selective harvest (Haugen and Vøllestad, 2001; Olsen *et al.*, 2004). Furthermore, according to classic life-history theory (Gadgil and Bossert, 1970), individuals maturing early should also have high reproductive output. This will lead to an increased cost of reproduction, and increased mortality. Thus, the trade-off may occur through different pathways, and opposing selection may easily lead to large variation in parameter values.

Also, the ratio between the instantaneous mortality rate (z) and the von Bertalanffy growth coefficient (K) was invariant for perch, indicating a trade-off between adult

mortality and growth. The mean parameter value for the total perch material (3.16) was rather high and so was its variance. In the literature, a large range of z/K ratios is reported for fish. Interestingly, parameter values seem to differ according to habitat. Marine species of teleosts and elasmobranchs usually have z/K ratios between 1 and 2 (Beverton and Holt, 1959; Pauly, 1980; Frisk *et al.*, 2001). On the other hand, freshwater species seem to have parameter values varying between 2 and 3.55 (Craig, 1982; Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994; present study). Why do parameter values differ between freshwater and marine fish species? It is likely that adult mortality (especially for larger individuals) in general is higher and also more variable in marine habitats than in freshwater ones. Obviously, there are more and larger predators in the marine environment. Furthermore, when we estimated parameter values for z/K for stunted and piscivorous perch populations separately, the parameter value for the stunted populations (1.99 ± 0.42) was significantly different from the mean value for piscivorous populations (3.48 ± 0.47). These last values were close to the values observed for walleye (*Stizostedion vitreum*), brown trout and Arctic charr (Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994). The incidence of high values, together with the deviation from the suggested invariance in some freshwater species, has been argued to originate from individuals escaping a size ceiling [e.g. by switching from planktivory to piscivory (Mangel, 1996)]. When analysing the z/K relationship within species, some populations may have extremely high values leading to a strongly skewed distribution. More precisely, high values for z/K may be the result of low values of the growth rate K in some piscivorous populations. It is important to keep in mind that K indicates how fast the asymptotic size is reached and not growth rate as such. For species or populations that undergo ontogenetic niche shifts from benthivory or planktivory to piscivory, growth will be better described using a set of von Bertalanffy growth curves, and K may be underestimated. Le Cren (1992) described the growth trajectory of exceptionally large perch from Lake Windermere to be like a 'double' von Bertalanffy growth curve, and suggested that it is caused by a shift to piscivory after a period of reduced growth. Persson *et al.* (2000) showed that larger perch surviving die-offs in an allopatric population gained substantial energy from cannibalism in years with strong recruitment. This led to increased growth rates and may give rise to 'double' von Bertalanffy growth trajectories. Not all large perch, however, exhibit the double growth curve (Thorpe, 1977; Le Cren, 1992).

The ratio of length at maturity (L_α) to length at infinity (L_∞) was not a constant for perch in general, but within population types it was. The constant (L_α/L_∞) expresses the relative length at maturity, indicating that there is an inherent relationship between length at maturity and the maximum attainable length. Beverton and Holt (1959) and Charnov (1993) reported values ranging from 0.4 to 0.8, which enclose the values for both stunted (0.61) and piscivorous populations (0.48). The lower value for the piscivorous perch means that growth is maintained at a high level even after age at maturity is attained. A modelling approach by Stamps *et al.* (1998) indicated that a positive correlation between size at maturity and asymptotic size is predicted if growth costs of reproduction are inversely related to size at maturity. One very interesting but largely untested assumption of their model is that the instantaneous growth rate of adults of the same size will be positively related to their length at maturity.

In a population having a large asymptotic size, K is often small. For the perch data, these two parameters (L_∞ and K) were significantly negatively correlated ($R^2 = -0.496$, $n = 75$, $P < 0.001$). This means that perch that attain a large body size take a relatively long time to reach that size, whereas small-sized fish rapidly reach their maximum size. However, for

bloater (*Coregonus hoyi*) a positive correlation between L_∞ and K has been reported (Szalai *et al.*, 2003). Sometimes a positive relationship may occur when a negative one is expected, because the trait values do not span a large enough range (von Noordwijk and de Jong, 1986; Stearns, 1992). Furthermore, the large variability in this index indicates that the evolutionary inference that might be drawn is limited.

For perch, the growth coefficient (K) and age at maturity (α) were significantly negatively correlated, suggesting that K and α are intrinsically linked. One reason for this is that most life-history transitions are growth dependent in that more rapid growth leads to earlier stage transitions (Alm, 1959; Day and Rowe, 2002). Age at maturity is a very important life-history trait, as generation time strongly determines intrinsic rate of increase. For determinate growers, growth stops after maturation. For such organisms a close link between K and α is expected. For indeterminate growers such as fish, these two traits may be less tightly linked, especially if the growth opportunity for mature individuals is good. We would therefore expect the K–α relationship to be less clear for the piscivorous than for the stunted perch populations, since piscivorous perch maintain positive growth for a prolonged period after maturation.

Predictive life-history models

Age and size at maturity can be predicted with high precision for perch by using the relatively simple life-history models developed by Roff (Fig 2). This is in accordance with earlier work (Roff, 1984; Mangel, 1996; Shuter *et al.*, 1998). What is also noteworthy is that the precision was as high for stunted as for piscivorous populations, suggesting that the models are very robust to variation in growth rate and growth opportunity.

Charnov's (1993) model for reproductive investment predicted with reasonably high precision the investment in perch gonads. This indicates that reproductive investment is closely linked to growth and age at maturity. Based on the general assumption that the ratio between length at maturity and asymptotic length is invariant (see earlier discussion), the main determinant of reproductive investment is age at maturity. Reproductive investment should increase with decreasing age at maturity. This is clearly the case for the perch data ($r_{31} = -0.860$, $P < 0.001$), and is also predicted from general life-history theory. Interestingly, the predicted versus observed values for reproductive investment differed markedly between perch belonging to the two different population types (stunted, piscivorous). The observed distribution of *GSI* values did not differ among population types, but the model consistently predicted higher reproductive investment for stunted than for piscivorous populations. The main reason for this difference is probably that the relationship between length at maturity and asymptotic length differs among the two population types, probably due to the large differences in growth opportunity they experience. This again points to one very important inference, namely that growth opportunity and the cost of reproduction strongly influence life-history choices and allocation decisions in fish and probably in all organisms.

In this study, we document that some so-called life-history invariants indeed may be useful for understanding the evolution of life-history traits within species. However, we also show that a crucial assumption has to be fulfilled for the life-history invariants to be useful – growth must adequately be modelled using the von Bertalanffy growth model. If growth is better explained by more complex models so as to incorporate ontogenetic niche shifts, then it becomes less clear whether the life-history invariants are useful. Furthermore,

we show that some relatively simple models for predicting important life-history traits such as age and length at maturity and reproductive investment indeed produce very good predictions.

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