Life-history Variation and Age at Maturity in Eurasian Perch (*Perca fluviatilis* L.)

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Abstract

Heibo, E. 2003. Life-history variation and age at maturity in Eurasian Perch (*Perca fluviatilis* L.)

This thesis deals with life-history variation in perch, with special focus on age at maturity. We conducted field studies to uncover the variation within short geographic distances and a literature review to study variation on a large geographic scale in order to reveal some factors affecting life-history. In two studies we discuss the relevance of predation risk and acidification, respectively, on age at maturity. With data from a large scale study (75 perch populations) covering a large range of the distribution area for perch we test life-history theory and optimality models. We found no effect of predation risk on age at maturity for five populations (3.6 – 4.5 years) in Northern Sweden, but predation risk was correlated with minimum size at maturity. There was no strong relationship between age at maturity in female perch and acidification in five lakes from southern Norway. However, age at maturity was lower for female perch from the most acidic lake (c. 2 years) compared with perch in the four other lakes (2.5 – 3.5 years). In the large scale study we found latitudinal effects on all life-history traits, except asymptotic body length. Generally, growth and mortality rates and reproductive investment decrease with latitude, whereas age and size at maturity and life span increased with latitude. There was a large variation in age at maturity with populations mean age at maturity span from 1 year in Lake Trasimeno in Italy southern Europe, to 6 years in Northern Yenisey in Siberia, Russia. Stunted (small-sized) populations had lower age and size at maturity and higher growth rate (K) compared to piscivorous populations. The life-history in southern populations with fast growth, high juvenile and adult mortality selects for early maturity and relatively large investment into reproduction. The opposite pattern was found for the northern populations. Roff's optimal age at maturity model gave good predictions for age at maturity in perch populations with data on growth and mortality rates. Mortality and age at maturity were negatively correlated, and growth coefficient (*K*) and age at maturity were also negatively correlated. In addition three other relationships showed invariance and all of them could therefore be termed as constants. Temperature differences, through latitude directly or indirectly, may to a large extent explain the variation found in life-history traits. In addition, different life-history trade-offs limit and constrains different traits. Reproduction constrains growth and survival. Age at maturity is constrained by the trade-off between growth and reproduction and the trade-off between survival and reproduction.

Key words: Life history, age at maturity, perch, *Perca fluviatilis*, trade-offs

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I.   Heibo, E. & Magnhagen, C. Variation in age and size at maturity in perch (*Perca fluviatilis*), compared across lakes with different predation risk. (Submitted manuscript)

II.   Heibo, E. & Vøllestad, L. A. 2002. Life-history variation in perch (*Perca fluviatilis* L.) in five neighbouring Norwegian lakes. Ecology of Freshwater Fish, **11**: 270-280.

III.   Heibo, E., Magnhagen, C. & Vøllestad, L. A. Latitudinal variation in life-history traits in Eurasian perch. (Manuscript)

IV.   Heibo, E. & Vøllestad, L. A. An analysis of life-history invariants in Eurasian perch (*Perca fluviatilis*). (Manuscript)

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Introduction

Distribution

Three species of the *Perca* genus are currently recognised, namely yellow perch (*P. flavescens* Mitchill), Eurasian perch (*P. fluviatilis* L.) and Balkhash perch (*P. schrenki* Kessler). Yellow perch is found in eastern North America (Weatherley, 1963) while Balkhash perch is confined to the Balkhash and Alakul' lakes system in the Asiatic highlands of eastern Kazakhstan (Berg, 1949; Collette & Banarescu, 1977). Eurasian perch (hereafter called perch) is the most common and widely distributed member of the perch family. It is widespread throughout Europe and Asia, but missing on the Iberian Peninsula (Weatherley, 1963). In Norway the distribution is bicentric with populations in south-east and north-east Norway, while it is mainly presented all over Sweden and Finland. It is found in the Baltic Sea basin, the White Sea basin, and the Arctic Ocean basin from the Kola to the Kolyma, but is absent from the Amur (Collette & Banarescu, 1977; Craig, 2000). In addition to the native distribution, the perch has been successfully introduced to other parts of the world mainly South Africa, Australia and New Zealand (Thorpe, 1977). The native distribution area of perch spans approximately in latitude from 40° to 70° N and perch thus make an excellent model organism in which to study the effect of latitude gradient on life-history variation.
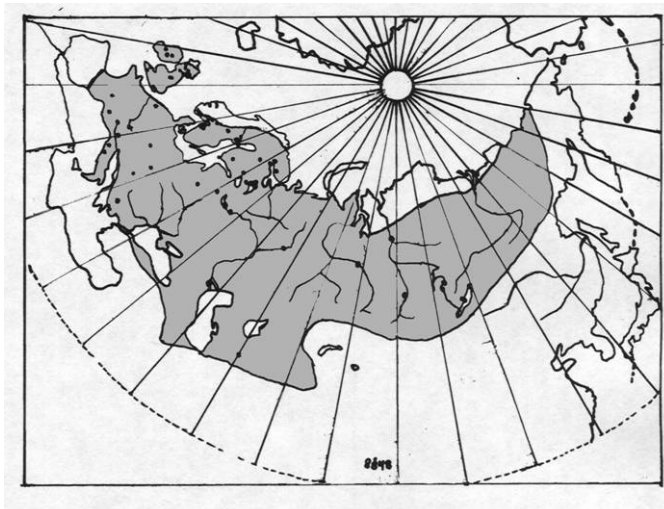
Figure 1. Map over east Palaearctic with the distribution area for Eurasian perch marked with dark grey. Spots show the location of populations that are used in the large scale study (75 perch populations) (distribution area of perch is taken from Collette & Banarescu, 1977).

General biology

Spawning takes place once a year in spring when temperature exceeds 7-8 °C. The event takes a few days in May or June in the northern regions, while it might span

from February to late April in the southern regions (Thorpe, 1977). Young-of-the-year (YOY) perch usually feed on zooplankton during their first weeks of life in the pelagic habitat. Depending on size and the density of one-year-old perch they shift habitat to the littoral zone in late summer (Byström *et al.*, 2003). If zooplankton density in the littoral zone in late summer is low, the YOY perch start earlier to feed on macroinvertebrates (Byström *et al.*, 1998; Persson *et al.*, 2000). Later, individual fish may perform a second ontogenetic niche shift changing from being benthivorous to being piscivorous. This niche shift is accompanied by an increased growth rate. If this niche shift does not occur, the perch remain small-sized (stunted), and often mature at a young age. A number of density-dependent interactions seem to influence an individuals probability of becoming piscivorous or not: predation, intra- interspecific competition (Ylikarjula *et al.*, 1999; Byström *et al.*, 1998; Persson *et al.*, 2000). Mortality is highly size-dependent and most intense on the smaller individuals (Byström *et al.*, 1998; Byström *et al.*, 2003), as it is for freshwater fish in general (Beverton, 1992; Chambers & Trippel, 1997).

Life history and age at maturity

A big diversity of life-history patterns has evolved in fish (Breder *et al.*, 1966). Some species reach sexual maturity within a few weeks after hatching and in others after several years. Some species spawn several times during their lifetime (iteroparity), while others only once in a lifetime (semelparity). Some species live for only a few weeks and other for decades. Even within species, there is a great variety of life-history patterns shown by different populations (**III**). Examples of life-history traits that can differ intraspecifically are growth pattern, age at maturity, size at maturity, number, size and sex ratio of offspring, age- and size-specific reproductive investments, age- and size-specific mortality schedules and life span (Stearns, 1992). These traits are bound together by numerous trade-offs, including those between: current reproduction and survival, current reproduction and future reproduction, number, size and sex of offspring. According to Stearns (1992), trade-offs are the linkages between traits that constrain the simultaneous evolution of two or more traits. A population exposed to environmental change may experience phenotypic change in a number of traits. Such phenotypic changes have two main sources: phenotypic plasticity and evolutionary change. If the change is solely due to phenotypic plasticity, no change in genotype composition has occurred. The observed phenotype characteristics are resulting from the mean population reaction norm. If evolution has taken place, the population genotype composition has changed and the resulting phenotypes are due to the new genotype composition. However, as genotype may differ in trait reaction norms, the observed phenotype change may also result from a combination of evolutionary change and phenotypic plasticity (see Schlichting & Pigliucci, 1998). Stearns (1983) showed genetic basis of differences in age and size at maturity among stocks of mosquitofish (*Gambusia affinis*) 75 years after an inplant. Belk (1995) showed phenotypic response in the bluegill sunfish (*Lepomis macrochirus*), where fish from populations with different predation pressures and life-history patterns matured at the same age in a common environment.

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Age at maturity is a very important factor influencing lifetime reproductive success, especially in animals with indeterminate growth and fecundity exponentially increasing with size (Stearns, 1992). Maturation has large implications for life-history traits such as growth, mortality and lifetime expectancy. When an individual decides to mature, energy that could be used for growth will instead be used for reproduction. This has an effect on survival if there is size-dependent mortality. A higher mortality risk could also be expressed as lower life time expectancy. From a demographic perspective, it would gain an individual to mature early to decrease time spent as juvenile, simply because it will increase chances of survival to maturation. Another argument is that organisms that mature earlier will also have higher fitness because their offspring are born earlier and start to reproduce sooner (Cole, 1954; Lewontin, 1965; Hamilton, 1966). Why then do some animals mature late? There are generally two factors favouring delayed maturation: First, delayed maturity permits further growth and thereby higher fecundity if fecundity and size is positively correlated. This factor increases the quantity of offspring born at each occasion. Second, if delaying maturity implies higher offspring quality, it will counteract high instantaneous juvenile mortality. This will improve offspring survival. The explanation for a late maturation may be a combination of the two factors. By delaying maturity the organism may live longer, grow larger, have more reproductive events, have higher fecundity later in life, have higher quality offspring, and gain in lifetime reproductive success by improving both quantity and quality of the offspring.

Factors affecting age at maturity in perch

Predators have negative effects on its prey and since the pike is gape-limited (Nilsson & Brönmark, 2000) only small-sized perch may be at great risk to be eaten. When reproduction begins resources that before only was used for growth is channelled into both growth and reproduction with the result of lower growth rate. If there is no size refuge for adults the individual's best solution is to mature earlier and consequently smaller to decrease time at predation risk as seen in the guppies (Reznick *et al.*, 1990). Since the timing of maturation affects the adult size there might be selection for postponing maturity till a certain size when there is a size refuge for prey like perch. We therefore suspect a relationship between age or size at maturity and predation risk.

One severe environmental problem due to anthropogenic activities which has escalated in contemporary time is acidification of inland waters especially in Scandinavia (Hesthagen *et al.*, 1999). Loss of fish populations is the most severe effect, but also decrease in population density either as a decrease in numbers of recruits (Beamish *et al.*, 1975) or a decrease in number of adults (Harvey, 1980) is a major problem. How will acidification affect a life history trait as age at maturity? Since we know that population density are experiencing a decrease we should find higher adult mortality, but also better growth due to less intra-specific competition. Thus according to life-history theory we would predict lower age at maturity in fish in waters with an acidification problem.

How and why species life histories vary with geography and environment are some of the most important questions in large-scale ecology (Gaston & Blackburn, 2000). Therefore we have collected several life-history variables to look at the effect of latitude on age at maturity and to test life-history theory in general. Temperature and latitude correlates well and therefore we predict a positive correlation between age at maturity and latitude.

Some patterns of variation in maturity, growth and mortality are called life history invariants and believed to be constant relationships (Beverton & Holt, 1959; Charnov, 1993; He & Stewart, 2001). We use data from 75 perch populations to test for invariance and also to test some life history models described for age at maturity and reproductive effort.

Objectives

In this thesis, I have studied life-history variation in Eurasian perch and some possible causes to this variation. I have studied life history in populations across the distribution range of perch to examine the effect of different factors influencing life history in perch and to test predictions derived from life-history theory. As fitness is very sensitive to changes in age at maturity, I have put special focus on this trait.

The main questions raised in this thesis are:

1. Do predation risk, acidification and latitude affect age and size at maturity?
2. Can life-history models based on life-history traits and population dynamic characteristics predict age at maturity and reproductive effort?
3. Do maturity related traits correlate with other life history traits in an invariant way?

Material and methods

Field data

Perch were sampled with gillnets prior to spawning in late April - early May in southern Norway (Breidtjern, Isebakketjern, Store Risen, Langtjern and Skinnarbutjern) 1992 and 1993 (**II**) and lake Ulvenvannet (Norway) in 1998, 1999 and 2000 (**III**). In five lakes in northern Sweden (Ängersjön, Stöcksjön, Bjennsjön, Trehörningen and Fisksjön), we also fished with gillnets prior to spawning in 1998, 1999 and 2000 (**I, III**). In order to increase the sample size of mature females in northern Sweden, we included fish sampled by recreational fishing in April (prior to ice-off and gillnet fishing). Data from a coastal population, in Norrbyn, were collected from commercial net catches in 1996 and recreational fishing during April 1998 (**III**). We measured natural tip length (**I, II, III**) and weight (g), and assigned sex and maturation stage following Kesteven (1960) and Treasurer & Holliday (1981). Age was determined from the opercular bone according to LeCren (1947). Female gonads in stage 5 (ripe/gravid) of maturity were weighed. Fecundity was estimated by counting the number of eggs in three sub-samples of each gonad with approximately 200 eggs. We used the mean estimated number of eggs/g for each gonad to estimate total fecundity. For the purpose of studying variation in age and size at maturity in perch in relation to predation risk, we also collected young of the year perch (YOY) in northern Sweden (Ängersjön, Stöcksjön, Bjännsjön, Trehörningen and Fisksjön). In September 1999 and 2000 YOY perch were collected using beach seining and electrofishing (only 1999) (**III**).

Literature data

We collected life-history data on 68 perch population from the literature (see Appendix, **III**), in addition to our own seven populations. Data on the various life-history traits were extracted from figures, tables or from the text of the publications. If data on female perch were not available we used pooled data for the sexes. The life-history parameters assembled was growth coefficient (K) and asymptotic body length (L_∞) of the von Bertalanffy growth equation (Bagenal, 1978), length at age 1 (L_1) and age 2 (L_2), specific juvenile growth rate (g), instantaneous adult mortality (Z_a), instantaneous juvenile mortality (Z_i), age (α) and length (L_α) at maturity, maximum age in population (T_{max}), reproductive life span (T), and reproductive investment (*GSI*) (Table 1). In some cases, only age and not length at maturity was available. In those cases, we estimated length at maturity using the von Bertalanffy growth model.

Table 1. *Glossary of terms and units used in this thesis.*

Symbol	Definition	Units
l_x	Probability to survive to age x	
m_x	Number of female daughters produced in age x	
r	Intrinsic rate of natural increase	
R_0	Fundamental net reproductive rate	
K	Growth coefficient	$year^{-1}$
L_∞	Asymptotic body length	mm
$L(t)$	Length at age t	mm
t	Age	year
h	Slope of the assumed trade-off between K and L_∞	
L_1	Length at age 1 (Back-calculated)	mm
L_2	Length at age 2 (Back-calculated)	mm
g	Specific juvenile growth rate	$year^{-1}$
Z_a	Instantaneous adult mortality	$year^{-1}$
Z_i	Instantaneous juvenile mortality	$year^{-1}$
S_a	Adult survival	$year^{-1}$
S_i	Juvenile survival	$year^{-1}$
α	Age (50%) at maturity	year
L_α	Length (50%) at maturity	mm
T	Reproductive life span (T_{max}- α)	year
T_{max}	Maximum age in population	year
γ	Intercept of the fecundity-length relationship	
β	Slope of the fecundity-length relationship	
Ew	Egg wet weight	mg
D	Diameter of egg	mm
RF	Relative Fecundity; number of eggs relative to weight	g^{-1}
B	Reproductive investment; estimated for Charnov's (1993) model	$year^{-1}$
GSI	Reproductive investment	$year^{-1}$

Estimation of life-history traits

Growth (length at age) was modelled using the simplified von Bertalanffy growth model (Bagenal, 1978; Roff, 1984). Back-calculated lengths from age 1 (L_1) and age 2 (L_2) from opercular measurements according to Lea's method (Bagenal, 1978) were used to calculate the specific growth rate for the second year of life ($g = \ln L_2 - \ln L_1$). Instantaneous adult mortality rates (Z_a) were estimated for the field data using standard catch curves (Ricker, 1975). Yearly survival (S) was calculated as $S = e^{-Z}$. All catch curves had slopes that significantly differed from zero ($P < 0.05$, simple linear regression test). Instantaneous juvenile mortality rates (Z_i) were estimated using estimated age and length at maturity and the parameter estimates of the fecundity - length relationship, in accordance with a model presented by Stearns & Crandall (1984). The model is based on the assumption that, a female perch at the age of mean population age at maturity will leave one female and one male descendant, given that the population is at equilibrium (*i.e. r* = 0). The relationship between the number of eggs produced by a female at mean population age at maturity and the two surviving progeny that

will reach maturity can be used to estimate instantaneous juvenile mortality (Z_i). We used logistic regression (Trippel & Harvey, 1991) with number of mature / number of immature as nominal category variable to estimate age and size at which 50% of the perch were mature. Estimates from literature data were mainly based on linear approximations with percentage of mature fish in each age group. Reproductive life span (T) was estimated as the observed maximum age in the population (T_{max}) minus the estimated age at maturity. We estimated the gonadosomatic index ($GSI_{somatic}$, %) as 100*(gonad wet mass / somatic wet mass). To standardise the length measurements, we converted all lengths to natural lengths. To transform these different length measurements into one standard metric, we collected the various length measurements from a large number of individual perch sampled in lakes the Umeå region. Using these data we established the relationships between the various measurements (**III**).

Predictive model

A population at equilibrium can be characterized by the classic Euler - Lotka equation, containing l_x (the probability to survive to age x), m_x (the number of female daughters produced at 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 age at maturity that maximises fundamental net reproductive rate (R_0) (Stearns, 1976; Gadgil & Bossert, 1970). Roff (1984) explored models that can be used to estimate age at maturity in animals with indeterminate growth. The models use R_o as 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, where K is the growth coefficient and L_∞ is the theoretical maximal length. Based on this, the optimal age (α) at maturity can be estimated:

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

Equation 1

where Z is instantaneous mortality rate.

Charnov (1993) has proposed a model (equation 2) which expresses optimal reproductive investment (B) of a fish. The model also covers other animals with indeterminate growth. It emerges ingrained in a two-stage growth model that can be related to von Bertalanffy growth model. First part goes from zero to age at maturity and is described by an equation in differential form. Next part goes from age at maturity to infinity and is described by another equation in differential form. The model is:

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

Equation 2

Results

Paper I.

We found no effect of predation risk on age at maturity for five populations in Northern Sweden. Age at maturation (3.6 – 4.5 years) was correlated with size of young-of-the-year (YOY) perch in the end of their first growth season, with the earliest maturation in those populations with the largest YOY perch. Length at maturation was correlated with L_∞ (asymptotic length when age is close to infinity) and K (growth rate coefficient) from von Bertalanffy growth model. Thus, fish from large-sized populations had also, on average, a large size at maturation. Predation risk from pike was correlated with minimum size at maturation. However, predation was probably more important in its effect on growth, with a high predation leading to a decrease in population density, decreased food competition, and as a consequence, higher growth rates. Instantaneous mortality rates did not affect maturation patterns when comparing across the five lakes. However, in the lake with the highest mortality rate perch matured early. No effects of adult growth (or mortality rates) on age at maturation were found.

Paper II.

There was no strong relationship between age at maturity in female perch and acidification. However, age at maturity was lower for female perch from the most acidic lake (c. 2 years) compared to perch in the four other lakes (2.5 – 3.5 years). Perch older than 10 years were missing in the acidified lakes. Estimated annual survival rates did not differ among populations. There was no relationship between acidification level and size-adjusted egg size, fecundity or reproductive investment (*GSI*; gonadosomatic index). Perch in the most acidified lake showed large variation in egg size, the lowest length-specific fecundity, the highest *GSI*, and the lowest age at maturity.

Paper III.

Age at maturity ranged from 1 to 6 years in its distribution area and was positively correlated with latitude. Size at maturity and life span also increased with latitude, while growth, mortality rates, and reproductive investment decreased with latitude. L_∞ was the only trait not significantly correlated with latitude. The populations could be grouped into two size categories based on variation in L_∞: stunted (small-sized) *vs*. piscivorous (large-sized) populations. Four trait – latitude relationships differed between these two groups: the growth coefficient (K) was larger and the specific growth rate, and age and length at maturity were lower in the stunted (2.9 year and 124 mm) populations compared with piscivorous (3.5 year and 178 mm) populations. Perch from southern populations in general grow fast, experience high juvenile and adult mortality. This selects for an early age and small size at maturity and relatively large investment into reproduction. The opposite pattern is found for northern populations.

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Paper IV.

Optimal age at maturity was predicted and Roff's model gave a good prediction for age at maturity in 49 perch populations with data on growth and mortality rates. We found no difference in population type (stunted or piscivore) in Roff's model and therefore we can say that both type of populations optimise their life history according to l_x and m_x theory even if they might have different approaches (strategies). In this study we also use data from 75 Eurasian perch populations to test for inter-trait invariance in perch. Mortality and age at maturity were negatively correlated and with a slope not significantly different from minus one. Growth rate and age at maturity were also negatively correlated and with a slope not significantly different from minus one. All together we found four of five suggested invariants to be true invariants and the last was invariant on within-population type level. Charnov's model of reproductive investment gave a good correlation between predicted and observed values, even if predicted values for stunted populations were significantly higher.

Discussion

Predation risk, acidification and latitude

Predation is one factor that may have large impact on prey and exert strong selection pressures on life-history traits (Endler, 1986; Abrams & Rowe, 1996). Since the main predator to perch, namely pike, is gape limited (Nilsson & Brönmark, 2000) the small perch will suffer the most. Predators can affect the perch either directly by eating them, or indirectly by changing their behaviour and growth conditions. If juvenile perch is consumed in large quantities there will be a thinning effect on the perch population (Persson *et al.*, 1996) and the survivors will experience better growth if resources are limited. Better growth is believed to select for lower age at maturity according life-history theory (Roff, 1992; Stearns, 1992). On the other hand, if there is a potential for further growth it will obviously gain the individual to postpone maturation until it has grown to a size experiencing low predation risk. This was seen in bluegill sunfish, coexisting with the piscivorous large-mouth bass (*Micropterus salmoides*) (Belk, 1995). In paper **I,** we found no relationship between mean age and size at maturity (50% probability) and predation risk, but predation risk had an effect on minimum size at maturation. In addition, the size of YOY perch was negatively correlated with age at maturation suggesting that rapid growth early in life induces early maturation. In a study by Persson (1990), perch populations in sympatry with roach matured later than allopatric perch, probably due to differences in food competition and growth in the early stages. Also within populations, as in Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.), and Arctic charr (*Salvelinus alpinus* L.) a rapid growth during the first year may lead to early maturation (Metcalfe *et al.*, 1988; Økland *et al.*, 1993; Forseth *et al.*, 1994). In our study lakes (**I**), it seems like predator abundance mainly affect maturation patterns through the effect on growth rate. This may arise from a high predation leading to a decrease in population density, decreased food competition, and as a consequence, higher growth rates. Alternatively, a fast-growing genotype could be selected for in populations with high predation. These two explanations can not be separated in our study. Predation is one factor affecting growth rates, but, in interaction with other factors (Holmgren & Appelberg, 2001). However, the fact that minimum size at maturation was correlated with predation risk indicates that the individual's risk of being eaten may also affect timing of maturation.

There was no relationship between acidification and age at maturity in female perch, but age at maturity was lower for female perch from Breidtjern (c. 2 years) compared to perch in the four other lakes (2.5 – 3.5 years). A low female age at maturity in perch may be a response to environmental stress [e.g. water level regulation (Stearns, 1983) or intense fishing (Haugen & Vøllestad, 2001)]. Linløkken *et al.* (1991) found lower age at maturity in female perch from the more acidified lake Gjerstadvann, compared to the less acidified lake Brøbørvann. High growth rate of juvenile perch, together with high density-independent and

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unpredictable juvenile mortality, will select for early maturation (Roff, 1992; Stearns, 1992). Based on life-history theory we would expect the perch in Breidtjern to mature at a relatively young age. Further, perch in Breidtjern, the most acidified lake, differed from the others by having low length-specific fecundity and the highest reproductive investment (*GSI*). Increased reproductive investment because of environmental stress does not need to be biased towards an increase in *GSI*. Rather, it is more likely that the fish seek an optimal combination of reproductive investment, egg size and fecundity (Hendry *et al.*, 2001; Hendry & Day, 2003).
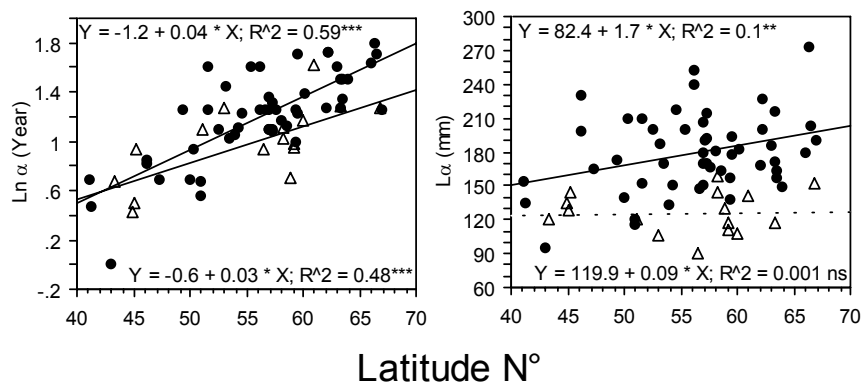

Figure 2. A. Age at maturity (left) and length at maturity (right) against latitude for 68 populations. Empty triangles are stunted populations while filled circles are piscivore populations. *** $P < 0.005$, ** $P < 0.05$, ns $P > 0.05$

Life-history traits have often been reported to have latitudinal clines (e.g. Mann *et al.*, 1984; Fleming & Gross, 1990; Vøllestad, 1992; Jonsson & L'Abée-Lund, 1993) and for age at maturity in special it has been shown to increase with latitude (Figure 2) (Colby & Nepszy, 1981; Vøllestad, 1992; Jonsson & L'Abée-Lund, 1993; **III**). In the Northern Swedish lakes (**I**), most males were mature at the age of two years, and thus matured earlier and at a smaller size, than did females. Further south in Southern Norway (**II**) males matured earlier than in north indicating a latitudinal cline in age at maturity for males. Commonly male perch mature one or two years earlier than females (Thorpe, 1977; Craig, 2000). We also found (**III**) that perch from stunted populations matured sexually at a younger age and smaller size than perch from piscivorous populations when latitude was accounted for (Figure 2). Similar results were found by Alm (1952) and Roff (1992), with individuals that had stunted growth usually maturing earlier at a smaller size, and having a shorter life span than the normal phenotype. On the contrary, we did not find any differences in maximum age in population between stunted or piscivorous populations, when the effect of latitude was used as a covariate. Taborsky *et al.* (2003) showed in their model that small changes in environmental conditions can lead to abrupt transitions in optimal life histories when size-dependent mortality is sufficiently strong. They predicted that stable

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conditions over time would lead to dominance by one distinct phenotype in the population, eg. early-maturing stunted or late-maturing piscivorous phenotype. For perch, we did not find any evidence that variation in mortality schedules influenced this transition, however our data can not discriminate between size-dependent or size-independent mortality. Usually, high growth rates lead to early transitions between life-history stages (Metcalfe *et al.,* 1988; Forseth *et al.,* 1994, Day & Rowe 2002), and for fish this has been found repeatedly for age and size at maturity (Alm, 1959; Reznick, 1993; Haugen, 2000). However, these studies are dealing with comparisons within populations, while the present study compares mean values across populations. For perch, the earlier maturation found in stunted compared to piscivorous populations indicates a trend opposite to the usual findings; that increased growth leads to postponement of age at maturity (see also Alm, 1959). With a low expectation of future growth and fecundity increase, early maturation may be the optimal life-history strategy for stunted populations. This has also been found in other fish species where stunted populations occur (reviewed in Alm, 1959). In addition, age at maturity was positively correlated with the ratio between juvenile and adult survival, irrespective of population type. This result is in accordance with earlier theoretical and empirical studies on life-history variation (Gadgil & Bossert, 1970; Schaffer, 1974; Hutchings, 1993).
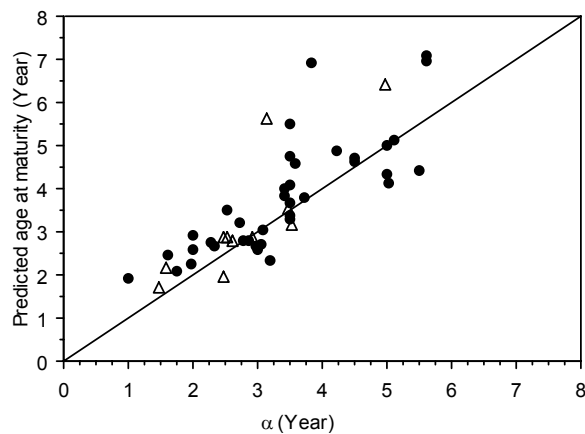

Figure 3. Predicted age at maturity against observed age at maturity for stunted (open triangles) and piscivorous (filled circles) perch populations. Line shows 1:1 relationship.

Predictive life-history models

Perch age and size at maturity can be predicted with high precision using the relatively simple life-history models developed by Roff (Figure 3). This is in accordance with earlier work (Roff, 1984; Mangel, 1996; Shuter, 1998). What is also noteworthy is that the precision was as high for stunted as for piscivorous populations, suggesting that the model is very robust to variation in growth rate and growth opportunity.

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We have a negative relationship between juvenile growth and maturity, with fast juvenile growth leading to early maturity (Figure 4D). This is the most common observed reaction norm for maturity-growth relations in fish. However, the good predictions for Roffs model do not make us able to discriminate between adaptive and plasticity reasons for the observed differentiation. Hence, we are unable to discriminate between if populations are only showing plasticity or if there are locally adapted reaction norms that spans a certain range in trait values. To resolve this issue one could estimate population-specific maturation reaction norms (sensu Heino *et al.*, 2002) or perform common-garden experiments (Roff, 2002), which includes reciprocal transplant experiments.
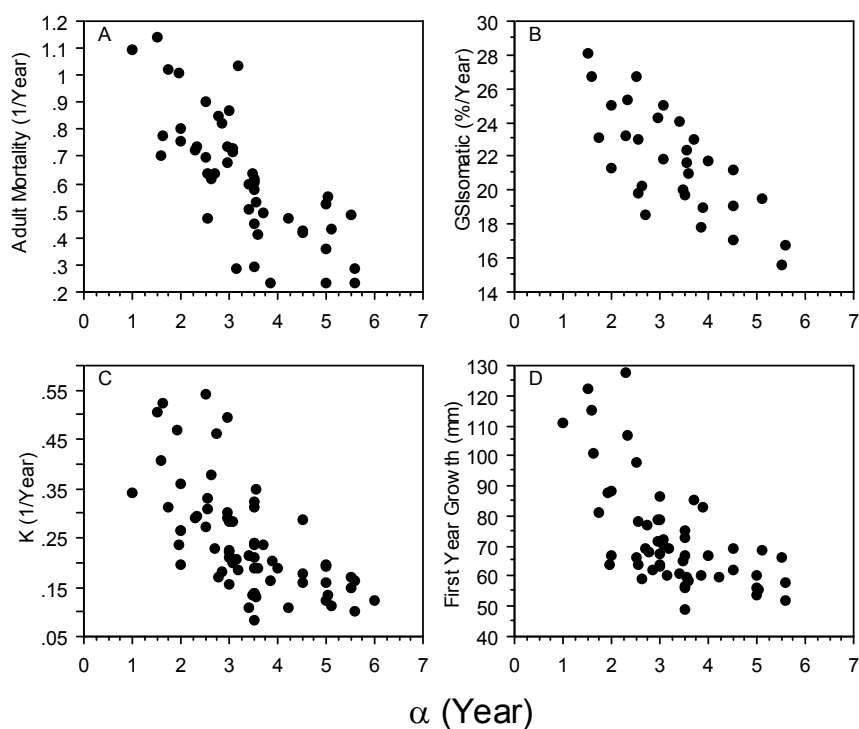

Figure 4. Life-history parameters (A: adult mortality, B: reproductive investment, C: growth coefficient *K* and D: length at age 1) vs. age at maturity for perch populations.

Charnov's (1993) model for reproductive investment predicted with reasonably high precision the investment into perch gonads (**IV**). 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 (C_3) (see Table 2 and equation 2), the main determinant of reproductive investment is the age at maturity. Reproductive investment should increase with decreasing age at maturity.

This is clearly the case for the perch data (Figure 4B). This is also predicted from general life-history theory. Interestingly, the predicted *vs.* observed values for reproductive investment differed strongly 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 values 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 population types, probably due to the large differences in growth opportunity for the two different population types. This again points to one very important inference, namely that growth opportunity and the cost of reproduction strongly influences life-history and allocation in fish and probably in all organisms.

Life-history trade-offs and Invariants

Trade-offs

Based on the assumption that natural selection acts on age-specific probabilities of producing future offspring, we can predict from adult and juvenile schedules of survival and fecundity that reproductive effort and age at maturity should covariate. When adult survival is low relative to juvenile survival early maturity and increased reproductive efforts is favoured (Gadgill & Bossert, 1970; Schaffer, 1974, Charlesworth, 1980). In our large scale study (**III**) with populations from different latitudes, we showed that juvenile survival (expressed as juvenile mortality in paper) decreased more than adult survival (expressed as adult mortality in paper) with decreasing latitude. We would therefore expect to find early age at maturity and high reproductive effort in south, while the opposite is expected in northern regions. Our findings are according to theory and not surprising since there is also a trade-off between age at maturity and reproductive effort (Figure 4B). Few studies have been able to test the theory so thoroughly, but there are exceptions. Reznick *et al.* (1990) studied guppies (*Poecilia reticulata*) with increasing predation on adult guppies leading to early maturation and increased reproductive allotment. Hutchings (1993) study on brook trout (*Salvelinus fontinalis*) also showed that high adult survival relative to juvenile survival rates favours low reproductive effort and delayed reproduction. Also other studies have been able to show the trade-off between age at maturity and reproductive effort on population level (Charnov, 1995; Clobert *et al.*, 1998).

Another prediction also gives a benefit for increased effort and early maturation under the assumption that natural selection acts on age-specific probabilities of producing future offspring. In fish, fecundity increases with age and size, and therefore fast juvenile growth in relation to adult growth will favour increased effort and early maturation (Schaffer & Elson, 1975; Hutchings, 1993). Since we did not find any relationship in asymptotic body length and latitude (**III**), but found a negative correlation with size at first year and latitude (**III**), we claim that there is a latitudinal cline with higher juvenile growth in relation to adult growth in south and opposite in north. In addition, we found a negative correlation

between YOY size of perch in the end of their first growth season and age at maturation (**I**). With data from large-scale study the negative relationship between length at age 1 and age at maturation became even more evident (Figure 4D).

Invariants

In paper **IV** we document that some so-called life-history invariants indeed may be useful for understanding the evolution of life-history traits within species. Further, we showed that some relatively simple models for predicting important life-history traits such as age and length at maturity and reproductive investment produced very good predictions.

Table 2. *Description of five dimensionless numbers believed to be constants or invariants. Predicted values are taken from Jensen, (1996, 1997).*

Invariant	Predicted	Description
$C_1 = z\alpha$	1.65	Relative life span, suggesting a trade-off between adult survival and age at maturity
$C_2 = z / K$	1.5	Growth-dependent mortality, suggesting a trade-off between survival and growth
$C_3 = L_\alpha / L_\infty$	0.66	Relative length at maturity, indicating that there is an inherent relationship between length at maturity and the maximum attainable length
$C_4 = L_\infty K^h$; $h = 0.4 - 0.8$	30	Relation between growth and size and is often called the growth trade-off
$C_5 = K\alpha$	1.1	Relationship between growth rate and age at maturity, showing the well-known result that increasing growth rate leads to an earlier age at maturity

Life-history invariant C_1 (the product of instantaneous mortality rate (z) and age at maturity (α)) was invariant for perch (III, Figure 4A), independent of population type. The estimated mean C_1 of 1.85 did not differ from the theoretical estimate of 1.66 obtained by Jensen (1996). Charnov (1993) report a typical range of this constant to be 1.75 to 2.2 for fish. However, estimates between 2.3 and 3.2 have also been reported (Beverton, 1987; Vøllestad *et al.*, 1993; Vøllestad & L'Abée-Lund, 1994). This large variability in parameter estimates argues against C_1 as being an invariant at high taxonomic levels like the species. However, 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 to occur. One is that reduced survival for large individuals will lead to selection 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 & Vøllestad, 2001). Further, according to classic life-history theory (Gadgil & Bossert, 1970) individuals maturing early should also have high reproductive output. This will lead to 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 estimates.

The ratio of length at maturity (L_α) to the length at infinity (L_∞) (C_2) was not a constant for perch in general, but within population types they were. The constant (L_α / L_∞) express the relative length at maturity, indicating that there is an inherent relationship between length at maturity and the maximum attainable length. Beverton & Holt (1959) and Charnov (1993) reported values of 0.4 to 0.8, which nicely enclose the value for stunted populations (0.61) and piscivorous perch (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 modeling approach by Stamps et al. (1998) does indicate that the 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 rates of adults of the same size will be positively related to their length at maturity.

For perch, the growth coefficient K and age at maturity (α) (C_5) were negatively correlated (Figure 4C), 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 & Rowe, 2002). Age at maturity is a very important life-history trait, as generation time is strongly determining intrinsic rate of increase. In determinate growers, growth stops after maturation. For such organisms we should therefore expect a very close link between K and α. 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 that the $K - \alpha$ relationship be less clear for the piscivorous perch populations as piscivorous perch maintain positive growth for a prolonged time period after maturation. We did observe that in stunted populations the observed $K\alpha$ values were close to the theoretically predicted values, whereas for piscivorous perch observed values were significantly different from the predicted values.

Conclusions

We found large variation in different life-history traits both on a large and a small geographic scale. The variation with latitude may partly be explained by abiotic factors, mainly temperature (under the assumption that latitude and average temperature correlate). Different life-history trade-offs limit and constrain different traits in a way that link nearly all traits together. Reproduction constrains growth and survival. Age at maturity is constrained by the trade-off between growth and reproductive effort and the trade-off between survival and reproductive effort. Age and size at maturity in female perch in five lakes in Northern Sweden, differing in predation risk seemed to be mainly influenced by factors affecting growth. Environmental stress, such as acidification, induces a number of changes to a lake community. It is therefore difficult to predict how acidification will influence the population dynamics and reproductive biology of a perch population. However, the highest reproductive effort and lowest age at maturity was found in the most acidified lake in the study with perch from five neighbouring lakes in southern Norway. In the large scale study, with assembled

life-history parameters from 75 perch population from the whole distribution area, age and size at maturity were strongly correlated with latitude. Perch from southern populations in general grow fast, experience high juvenile and adult mortality. This selects for an early age and small size at maturity and relatively large investment into reproduction. The opposite pattern is found for northern populations. Optimal age at maturity was predicted and Roff's model gave a good prediction for age at maturity in perch populations with data on growth and mortality rates. Test for invariance in perch showed that mortality and age at maturity were negatively correlated, with a slope not significantly different from minus one. Growth rate and age at maturity were also negatively correlated with a slope significantly different from minus one. All together we found four of five suggested invariants to be invariants and the last was invariant on with-in population type level. Charnov's model of reproductive investment gave a good correlation between predicted and observed values, even if predicted values for stunted populations were significantly higher. This may point to one very important inference, namely that growth opportunity and the cost of reproduction strongly influences life-history and allocation in fish and probably in all organisms.

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