

Life-history evolution in grayling:
evidence for adaptive phenotypic divergence
during 8–28 generations

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PREFACE

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ABSTRACT

Most organisms show phenotypic variation among populations inhabiting different habitats. A central inquiry in biology has been, ever since Darwin's hypothesis of evolution through natural selection, to explain to what extent such variation can be attributed to local adaptation. In this thesis, I study phenotypic divergence in life-history traits between five populations of grayling *Thymallus thymallus* resulting from 8–28 generations of segregation. Qualitative predictions of phenotypic levels are made from general life-history models, and I interpret correlations with observed values as indication of adaptation. Furthermore, quantitative genetic experiments are used to partition genetical and environmental sources of the phenotypic variation.

Important fitness related traits like early development rates, growth rate during first period of feeding, and survival during early life stages, were found to vary among the populations in field experiments. This pattern remained even after adjusting for important environmental variables. As this result suggest that genetic differences may occur among the populations, I conducted a common-garden experiment that involved different temperatures. This experiment revealed genetic differences among the populations. In addition, significant additive genetic variance for early life-history traits was found and the populations differed in temperature reaction norms for the same traits. For all populations, survival during the first feeding period was best in the temperature mimicing the natal temperature. I therefore suggest that temperature adaptation seems likely to occur during this early life stage for the study populations.

Significant among-population differences in adult mortality rates, age at maturity, growth pattern and reproductive traits (egg size, fecundity and gonad size) were documented. An age-specific mortality hypothesis gave good predictions of age at maturity and reproductive investment levels, as age at maturity decreased with adult mortality and gonad

size increased with adult mortality. The populations had different maturation norms with respect to differences in growth pattern, and the degree of maturation plasticity was found to be negatively associated with adult mortality rate. Among-population differences in fishery-induced mortalities is suggested as a selective agent causing the adult mortality differences. Body-size adjusted egg size varied among the populations. I suggest that differences in intensity of density-dependent regulation in early life stages may cause the egg-size difference.

In this thesis, I have demonstrated that adaptive phenotypic divergence in life-history traits has occurred during less than 28 generations. Estimated rates of divergence and evolution (in haldane and darwin) are among the highest ever reported, thus it may be concluded that evolution of life-history traits can proceed rapidly in grayling.

LIST OF PAPERS

Paper I:

HAUGEN, T. O. (2000). EARLY SURVIVAL AND GROWTH IN POPULATIONS OF GRAYLING WITH RECENT COMMON ANCESTORS—FIELD EXPERIMENTS. *JOURNAL OF FISH BIOLOGY* 56: 1173–1191.

Paper II:

HAUGEN, T. O. (2000). GROWTH AND SURVIVAL EFFECTS ON MATURATION PATTERN IN POPULATIONS OF GRAYLING WITH RECENT COMMON ANCESTORS. *OIKOS* 90(1): 107–118

Paper III:

HAUGEN, T. O. & VØLLESTAD, L. A. (2000) POPULATION DIFFERENCES IN EARLY LIFE-HISTORY TRAITS IN GRAYLING. *JOURNAL OF EVOLUTIONARY BIOLOGY* 13(6): 000–000.

Paper IV:

HAUGEN, T. O. DIVERGENCE IN REPRODUCTIVE TRAITS IN POPULATIONS OF GRAYLING WITH RECENT COMMON ANCESTORS. (*MANUSCRIPT*).

INTRODUCTION

Phenotypic evolution has been shown to progress rapidly in many organisms (reviewed in Hendry & Kinnison, 1999). Darwin's finches (particularly *Gospiza fortis*) in the Galápagos Islands constitute a famous example where evolution of beak dimensions and body size was found to evolve rapidly in response to changes in the availability of small seeds. In years with heavy rain falls (El Niño events), the abundance of small seeds increased, and the relative fitness of finches with small beaks also increased (Grant & Grant, 1995). As a consequence, the population mean beak size dropped. Due to the large drop in mean trait values and the short time span, estimates of evolutionary rates were very high in this study. Another vertebrate example is the Anolis lizard *Anolis sagrei* which was introduced to small islands in the Caribbean and surveyed ten years later. The populations diverged in a manner correlated with the amount the vegetation deviated from the vegetation found in the source area (Losos *et al.*, 1997). Recently, Huey *et al.* (2000) showed that a latitudinal cline in wing size in *Drosophila subobscura* that exists in Europe, evolved and largely converged on the ancestral line after two decades following the introduction to America.

A central challenge in biology is to document whether changes in phenotypes within populations or differences in phenotypes among populations may be attributed to local adaptation, *i.e.* have resulted from natural selection, or merely is caused by environmental variation, *i.e.* phenotypic plasticity. In the two vertebrate examples above, the genetic basis for differences in the investigated traits was unknown, and thus it is not possible to quantify the genetic and environmental contribution to the phenotypic differences.

Some of most the successful studies showing rapid genetically based phenotypic evolution are from freshwater fish systems. These studies show significant divergence in life-history traits to occur within less than 30 generations in very different freshwater species like guppies in Trinidad (Reznick *et al.*, 1990; Reznick *et al.*, 1997) and pacific salmon in

USA and New Zealand (Hendry *et al.*, 1998; Kinnison *et al.*, 1998a; Kinnison *et al.*, 1998b). Salmonids are good study organisms of adaptation, as they form local populations across a diversity of environments (Taylor, 1991). Furthermore, they are easily reared under artificial conditions, which facilitates experimental studies used to assess genetic effects. Finally, life-history traits vary considerably both among species and within species (see short review in Elliott, 1994). For instance, most species of the genus *Oncorhynchus* are semelparous, whereas most species in other salmonid genera are iteroparous. Population-specific mean smolt ages ranges between 1 to 8 years in Atlantic salmon *Salmo salar* (Thorpe, 1990), and within-population range of fecundities may range from 100 to 2000 in brown trout *Salmo trutta* (Elliott, 1994).

The study organism of this thesis is the European grayling *Thymallus thymallus*. As for other salmonids, this species exhibits large among-population variation in life-history traits (reviewed in Northcote, 1995). Most of the populations presented in this thesis had never previously been studied, but as the lake properties are very different, large among-population phenotypic differences were expected.

Phenotypic variation, at any level of organisation, has two sources; genetic and environmental (Falconer & Mackay, 1996). Studies on phenotypic evolution are concerned with the relationship between these two sources, *i.e.* how they add and how they interact to produce the final phenotype. A typical study of local adaptation has three main components (Endler, 1986). First, phenotypic variance must be documented for the populations in their natural environment. Second, experiments under controlled conditions are conducted to document heritable components of the traits under study. Finally, documentation of links between trait values and fitness components (survival, growth, fecundity) need to be shown. Populations introduced to new habitats provide unique opportunities to study the process and speed of local adaptation. When organisms are introduced into novel environmental conditions they will experience new selection regimes, and consequently, phenotypes

different from the ones in the original system may be favoured by natural selection. As such, introduction of organisms into novel habitats constitute experiments of local adaptation (Reznick & Travis, 1996). However, in most cases, the introductions are not performed in order to test specific adaptation hypothesis, and therefore, environmental factors are not under control. Consequently, most often environmental and genetic factors are confounded in trait values deriving from individuals sampled in the wild (Endler, 1986). There are two procedures by which the two sources of variance may be separated: by performing reciprocal transplants (individuals from all populations are introduced into all habitats) or by rearing families from the different populations in controlled common environments (common gardens).

The goal of most adaptation studies is not only to document its existence, but also to get further insight into the ultimate factors that have *caused* the phenotypic results. There are two approaches prevailing in the construction of life-history trait predictions: the optimization approach, and the quantitative genetics approach (Roff, 1992; Stearns, 1992). Optimization theory is often used in theoretical phenotypic evolution studies as it focuses on *processes* causing different selection pressures, and thus the resulting phenotypes. Most life-history models aiming at predicting trait values are based on optimization criteria (Roff, 1992; Stearns, 1992). The generated predictions show the optimal phenotype that should evolve under specified constraints and trade-offs (see Section 1. on p. 8). Even though this approach has been criticized (recently reviewed in Schlichting & Pigliucci, 1998), its relative simplicity and success in predicting empirical data (Roff, 1992; Stearns, 1992) advocates its further use (Seeger & Stubblefield, 1996). The other theoretical approach producing testable predictions for life-history systems is quantitative genetic modelling. This theory combines information on selection intensity and heritability of phenotypic traits to produce predictions on phenotypic values (Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998). This

approach was initially developed for artificial selection programs. Its use in phenotypic evolution studies under natural conditions (*e.g.* Lande & Arnold, 1983; Via & Lande, 1985; Lande, 1988) has been subject to discussion (see reviews in Endler, 1986; Schlichting & Pigliucci, 1998). One of the major concerns is that this technique does not provide any information about the factors *causing* the selection, but rather illuminates the magnitude and direction of the selection intensity. When the two approaches are compared, it is often found that they produce similar predictions (Charlesworth, 1990; Abrams *et al.*, 1993).

In this thesis, I have used optimization theory to generate predictions of adaptive life-history trait values. Agreement between predictions and empirical data will be interpreted as an indication of natural selection in action on the studied traits, and that they are evolving in an adaptive manner. This is not the same as stating that the populations are perfectly adapted to their environment, but rather that they are in a process of adaptation (Seger & Stubblefield, 1996).

Objectives

The main objectives of this thesis has been to 1) document significant divergence in life-history traits among grayling populations with recent (8–28 generations) common ancestors and 2) to test qualitative predictions of adaptive trait values. I have used life-history theory applied on age-structured populations to qualitatively predict how the populations should differ in mean trait values and in plasticity responses.

The main objectives were accomplished by attaining information on age/stage specific mortality together with abiotic environmental conditions (Paper I & II). This information was used to generate qualitative predictions of age at maturity (Paper II) and reproductive traits (Paper IV), and finally, evidence of genetic differentiation in trait values and the existence of significant additive variance was assessed by performing quantitative genetic experiments (Paper III).

SYNOPSIS

1. Life-history theory and evolution of life-history traits

Life-history theory provides a tool for the analysis and understanding of the evolution of life-history traits. Using this theoretical framework, it is possible to predict trait values that are optimal under different environmental and demographic settings. Life-history traits are generally coupled with fitness, and due to functional constraints, trade-offs exist among several of the traits (Partridge & Sibly, 1991; Stearns, 1992). Life-history predictions are therefore, directly or indirectly, based on finding optimal trade-off solutions under different constraining environments. For instance, if egg size is under strong directional selection in favour of large eggs, the optimal egg size will have to be traded against fitness loss due to reduced fecundity (Bell, 1980). The fecundity *vs* egg size trade-off is most intense for young (*i.e.* small) individuals as they have less resources and smaller body cavities than older and larger individuals. It may therefore be optimal to delay maturation to gain larger size. Delayed maturation must in turn be traded against survival probability and growth potentials. Clearly, this small example (which is more thoroughly discussed in Paper IV) illustrates the complexity of life-history evolution.

Predictions from life-history theory are most often generated by applying optimization models (Roff, 1992; Stearns, 1992). The optimization criterion is fitness, but no general measure of fitness exists (Charlesworth, 1994). Therefore, every life-history study will have to define the appropriate fitness measure (Kozlowski, 1993). Here, one should distinguish between local and global fitness measures. Local measures assume that maximization of a fitness component will also maximize the overall fitness. Survival during a critical life stage or net rate of energy intake may serve examples (examples in Roff, 1992). Global measures

involve all critical life-history components and their inter-relations. Typical examples of global measures are the net reproductive rate (R_0) and the intrinsic rate of increase (r). Both include the product of age/stage (x) specific fecundity (m_x) and survival (l_x):

$$1 = \sum_{x=\alpha}^{\omega} e^{-rx} l_x m_x, \quad (1)$$

$$R_0 = \sum_{x=\alpha}^{\omega} l_x m_x, \quad (2)$$

where α is age at maturity and ω is expected age at death.

The usefulness of the different fitness measures is under discussion (Stearns, 1992; Mylius & Diekmann, 1995), but there is general consensus that selection on life-history traits acts through maximization of global fitness measures (Roff, 1992; Stearns, 1992; Charlesworth, 1994) and that aspects of fecundity and survival are important parts of these measures. Critical aspects that affect the choice of fitness measure are environmental- and demographic stability, density-dependent population regulation, and frequency dependent evolution of strategies (Roff, 1992; Stearns, 1992; Charlesworth, 1994). One important aspect of density dependence is that population growth may be regulated by density-dependent factors, whereas selection on genotypes may be density independent within such populations (Prout, 1980; Stearns, 1992).

1.1. Life-history evolution in stable, predictable environments

Most life-history models have been developed for populations experiencing stable (*i.e.* predictable) environments. The assumption of stable environments makes things easier with respect to stable population structures (Charlesworth, 1994), and is often a feasible first approximation to the real world (Roff, 1992). As environmental conditions are constant, the optimal phenotypes will also remain constant, at least if the spread of genotypes within the population is density independent (Roff, 1992; Stearns, 1992). The choice of fitness measures

under such conditions depends on whether the population is growing or constant, where r may be used in both cases, but R_0 is preferred in the last as it is easier to estimate (Kozlowski, 1993). When density dependence is occurring, both measurements may still be used. However, which measure used depends on *how* the density dependence acts on the demographic rates (Mylius & Diekmann, 1995). For instance, Mylius & Diekmann (1995) found that if density-dependent factors reduce the life-time offspring production, R_0 is the correct fitness measure. If mortality increases uniformly across age classes as a result of density-dependent forces, then r is the optimal fitness measure. Clearly, information on such details in natural populations is rarely available, thus, more or less justified assumptions must be made in order to estimate fitness for natural populations.

From simple optimization models (assuming stable age structures, density independence and equilibrium conditions) it can be concluded that differences/changes in age-specific mortality will have huge impact on important life-history traits like age at maturity and reproductive effort (Gadgil & Bossert, 1970; Law, 1979; Michod, 1979, see also Charlesworth, 1994). Such models predict that an increase in adult mortality rate relative to the juvenile mortality rate select for a decrease in age at maturity and an increase in reproductive effort. This so-called age-specific mortality hypothesis has received strong empirical support (Reznick, 1982; Hutchings, 1993a; Hutchings, 1993b; Reznick *et al.*, 1996). Motivated by Gadgil & Bossert (1970), who suggested that the optimal age at maturity to be predicted from the largest age specific product of l_x and m_x , Roff (1984) derived a general model for optimal maturation age in fish. By substituting parameters from the frequently used von Bertalanffy growth function (see Eqn. 2 in Paper II) into the $l_x m_x$ -equation the age at maturity (α) could be estimated as:

$$\alpha = \frac{1}{k} \ln \left(\frac{3k}{M} + 1 \right), \quad (3)$$

where M is the constant natural mortality and k is the growth constant in the von Bertalanffy equation. Even though this model predicts empirical data very well (Roff, 1984), it does not predict optimal ages at maturity as fitness consequences of different ages at maturity are not considered (Stearns, 1992). To assess *optimal* ages at maturity, costs (increased mortality, reduced growth, reduced future fecundity) and benefits (survival to reproduction) of different maturation ages should be considered under assumptions of maximizing some sort of global fitness measure (usually r or R_0). Several studies have analysed the sensitivity of fitness to changes in different cost and benefit relationships (reviewed in Roff, 1992; Stearns, 1992). Typically, some analysed the effect of changing the size vs fecundity relation (Bell, 1980; Roff, 1984; Kozłowski & Wiegert, 1987), whereas others analysed the effect of different survival probabilities to maturation (Stearns & Crandall, 1981; Stearns & Koella, 1986).

1.2. Life-history evolution in variable environments

In natural systems, environmental conditions are rarely stable. Rather, they may vary both in time and space, which in turn will affect the demography of the populations (the demographic environment (Charlesworth, 1994)). Non-seasonal temporal variation has a larger impact on life-history traits than spatial variation; the former affecting the entire population, whereas the latter only affects proportions of the population (Roff, 1992). Generating predictions of optimal phenotypic values in stochastic systems is not as straightforward as in stable systems. Other fitness measures than those applied in stable systems will have to be used due to varying demographic rates (Orzack & Tuljapurkar, 1989; Metz *et al.*, 1992; Charlesworth, 1994). By dividing the population growth history into different periods, period-specific finite rates of increase ($\lambda(t) = e^{r(t)}$) may be estimated. Cohen (1966) suggested that for situations where populations experience stochastic environments, the

geometric mean of the $\lambda(t)$ s should be maximized, and this approach has produced robust general predictions (Cohen, 1966; Roff, 1992). Slatkin (1974) utilized this approach when predicting that organisms experiencing unavoidable environmental variation should evolve a bet-hedging strategy, *i.e.* spreading risks (*e.g.* by evolving iteroparity).

In a stochastic environment, the direction of selection may vary in time and space, leading to different optimal solutions to the same problem (Via & Lande, 1985; Hutchings, 1996). It has therefore been suggested that the object of selection is neither specific genes nor the discrete phenotypes produced in different environments, but rather the capacity of organisms to deal with environmental continua (Travis, 1994; McNamara & Houston, 1996; Schlichting & Pigliucci, 1998). Consequently, if selection acts on the systematic change of the genotype's alteration of its phenotype across environmental gradients (*i.e.* the reaction norm), adaptive reaction norms are expected to evolve (Schmalhausen, 1949; Stearns & Koella, 1986). By applying life-history theory on systems with environmental variability, optimal trait values may be assessed under different environmental settings. Predictions from such optimal reaction norms show that genotypes experiencing highly variable environmental conditions often attain higher fitness by evolving phenotypic plasticity (environmental variability hypothesis, (Stearns, 1992; Hutchings, 1996)), and adaptive phenotypic plasticity will evolve (Via & Lande, 1985; Stearns & Koella, 1986; Scheiner, 1993). Laboratory studies have documented additive genetic variation in reaction norms, and it has also been demonstrated that they can respond to selection (McKenzie *et al.*, 1983; Gebhardt & Stearns, 1988; Gebhardt & Stearns, 1993).

Due to differences in growth conditions between years and spatial variation in habitat qualities, the growth patterns may vary among individuals with common genotypes. As growth has a decisive impact on important fitness components like age-specific fecundity (Thorpe *et al.*, 1984; Hutchings, 1993b) and survival (reviewed in Conover & Schultz, 1997)

in most fish, life-history strategies should evolve to cope with variability in growth patterns. Theoretical models show that mortality influences both shape and position of maturation reaction norms (Stearns & Koella, 1986; Perrin & Rubin, 1990; Kawecki & Stearns, 1993)]. Stearns and Koella (1986) investigated effects of different growth-dependent mortality responses on maturation reaction norms. For any combination of mortality responses to growth pattern, all resulting reaction norms predicted rapid growers to mature earlier than slow growers. Abrams *et al.* (1996) claims that the use of maturation reaction norms with respect to varying juvenile growth pattern may be erroneous. Growth is not an environmental variable, and many environmental settings (e.g. many predators or little food) may produce the same growth pattern. Thus, by using growth as an environmental cue, real environmental effects may be obscured.

1.3. Life-history evolution under density-dependence—emphasize on early life

As mentioned previously, global fitness measures also exist under density-dependent conditions, and thus predictions of optimal trait values may be assessed under such conditions as well (Mylius & Diekmann, 1995). The most obvious factor causing density-dependence are limited food resources. Here, interactions among the individuals are expected to occur. Egg size has been predicted to increase with decreasing resource abundance (Smith & Fretwell, 1974; Sibly & Carlow, 1983). This hypothesis is based on the assumption that density-dependent factors are the most predominating factors affecting resource availability. Most fish studies testing the resource-abundance theory have been performed on salmonid fishes where females invest a great deal into the individual offspring (large eggs, nest digging, nest guarding) and where intensive interactions occur among the offspring after emergence (Kalleberg, 1958; Abbott *et al.*, 1985; Abbott & Dill, 1989). By producing large eggs, the resulting offspring will also be large. Large offspring (fry) often

have higher survival probabilities due to better competitive capacities, better starvation tolerance, and a greater ability to utilize a wide size-spectrum of prey items (Conover & Schultz, 1997). The optimal egg size might not be as large as the one producing the highest mean offspring survival probability. An increase in egg size involves decreased fecundity (trade-off) and this fecundity cost must be considered in order to determine the optimal egg size (Bell, 1980). In addition, an increase in egg size may conflict with abiotic constraints like incubation temperature and oxygen availability (Chapman, 1988). In species where offspring are not territorial, selection in favour of large eggs may be relaxed as access to territories is removed as an interaction factor. Similarly, in small populations that have large nursery areas, food availability may not be limiting, and thus few interactions among the offspring may be expected and selection for larger eggs is relaxed.

2. The European grayling and the study system

The European grayling is widely distributed in Europe and extends in the east to the Ural Mountains (Northcote, 1995). In Norway, grayling is naturally distributed in the eastern parts of Finmark, northern Norway, and in larger river systems in south-eastern Norway (Pethon, 1985). In addition, grayling has been introduced to neighbouring watersheds of the natural inhabited ones, also including the study system for this thesis (see below).

A review of the general grayling life cycle is available in Northcote (1995). The grayling belongs to the family Salmonidae, but is atypical in being a spring spawner. Spawners from most lentic grayling populations migrate into streams and rivers after ice break. During the spawning act (see Fabricius & Gustafson, 1955) the eggs are deposited a few centimetres below the gravel surface, however no nest digging or nest protection takes place as in many other salmonids. Hatching occurs within the gravel after about 130–140 degree-days, and the yolk-sac larvae stay within the gravel until the yolk is resorbed (about

130 degree-days). The larva then emerges from the gravel (an action called swim-up), fills its swim-bladder with air and, for a period, stays in small shoals in a mid-water position. After a few days, the fry take position closer to the bottom and the shoals reduce to small groups or single individuals (Bardonnet & Gaudin, 1991). Within the rest of the first growth season (in the present study systems within one to one and a half month), the fry migrate/drift down-stream into the lake. When maturing, the grayling returns to its natal stream with high precision to spawn (Kristiansen & Døving, 1996). The grayling is typically iteroparous (Northcote, 1995).

Grayling from Lesjaskogsvatn in central Norway (a population that was established in the late 1880s) were released into Hårrtjønn and Øvre Mærrabottvatn in 1910 (Fig. 1). Individuals eventually dispersed downstream into Aursjøen (in the 1920s) and further into Osbu- and Holbumagasinet (1950s). All lakes are located within a range of 40 km, and are therefore assumed to be affected by the same macroenvironmental conditions. However, as the lakes and their tributaries differ in a number of attributes, local environmental conditions may vary considerably (see Table 1&2 in Paper I and Table 1 in Paper II). The grayling lives sympatrically with brown trout in all the lakes. Minnows *Phoxinus phoxinus* are only present in Lesjaskogsvatn. The grayling:trout biomass ratio varies among the lakes. Trout and grayling generally feed on different prey, probably due to differences in mouth morphology (Bellamy, 1983; Woolland, 1988; Haugen & Rygg, 1996). From this, I assume that interspecific interactions do not significantly affect the evolution of the life history in grayling in the present study system.

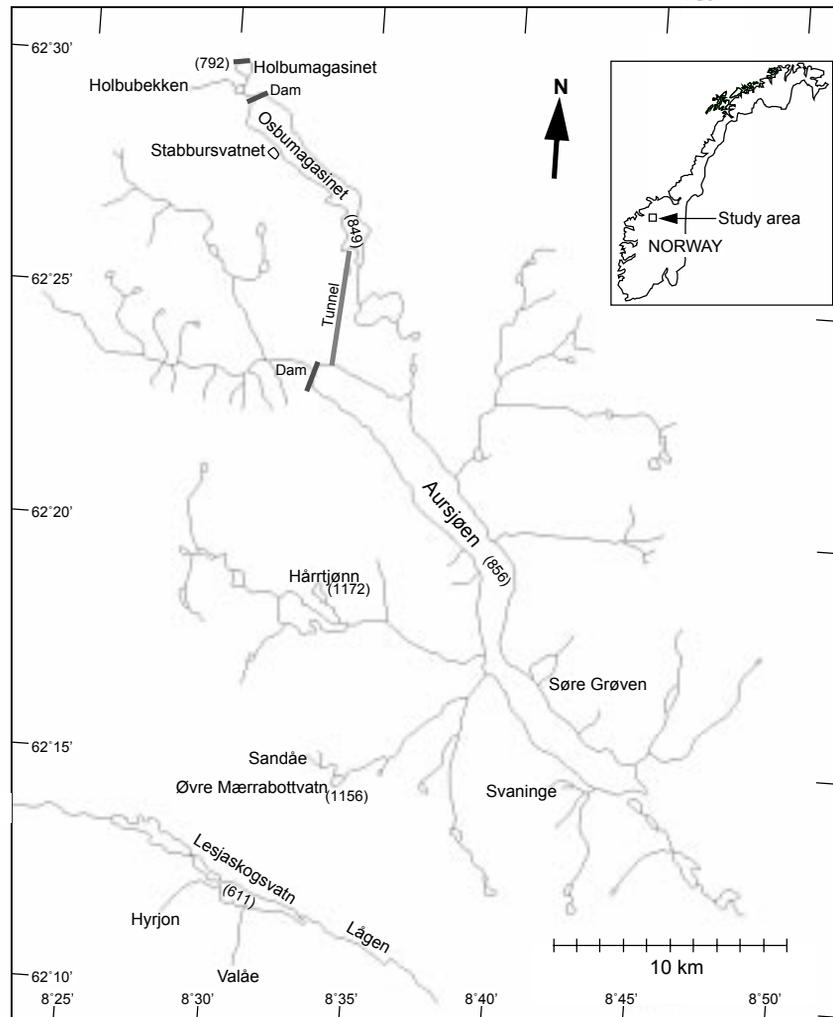


FIG. 1. The study area and its surroundings. Numbers in parentheses are altitude in metres. Only names on localities involved in the thesis are given.

The catchment areas of the lakes are mostly located at high altitudes with pre-cambrian granitic and granodioritic gneisses as the dominating rocks. This produces low-ionic water ($8\text{--}18 \mu\text{S}\cdot\text{cm}^{-1}$), with large Secchi-depths ($7\text{--}10 \text{ m}$; *i.e.* clear water) and pH between $6.2\text{--}7.0$. The main environmental differences between the lakes seem to be a) differences in altitude (*i.e.* length and predictability of length of growth season), b) differences in surface area (spatial variation) and c) differences in fishing pressure (summarized in Table I).

TABLE I. Qualitative assessments of important environmental factors for the five study lakes.

Lake	Spawning and nursery area			Fishing pressure	Lake area	
	Spawning sites	Nursery area	Growth season		Habitat numbers	Growth season
Lesjaskogsvatn	Many	Intermediate	Long	High	Many	Long
Øvre Mærrabottvatn	Few	Intermediate	Unpredictable Intermediate	Very high	Few	Unpredictable Intermediate
Hårrtjønn	Very few	Small	Unpredictable Short	Low	Few	Unpredictable Short
Aursjøen	Many	Large	Intermediate	Low	Many	Intermediate
Osbumagasinet	Many	Large	Short	Intermediate	Many	Short

3. Qualitative predictions

From the general knowledge of the grayling life cycle and expected differences among populations in mortality regimes and environmental variability (both temporal and spatial), qualitative predictions of directions of mean trait values, trade-offs and plasticity responses can be made from life-history theory:

- 1) Populations with low adult mortalities compared to early mortalities will:
 - a) delay maturation
 - b) have low reproductive investments
- 2) Populations with environment-induced variability in growth pattern show
 - a) early maturation for rapid growers
 - b) reduced maturation plasticity with increasing adult mortality rate
- 3) In populations which are regulated by density-dependent factors in early life stages
 - a) egg size should be large
 - b) egg size vs fecundity trade-off should be large
 - c) egg size should be positively correlated with body size

4. Summary of the results—do they fit the predictions?

In this section, I summarize and comment on the main results in light of the predictions made in the previous section. I begin by summarizing results that concern the environmental settings (demography and growth pattern) of the different systems, then differences in important mean traits will be treated, before differences in plasticity responses to differences in growth pattern (adult traits) and temperature (juvenile traits) are presented. Finally, I present and discuss fitness consequences of different maturation ages with respect to variation in survival costs and fitness consequences of different egg sizes at varying body sizes.

4.1. Differences in demographic rates and growth pattern—the environmental frames

Survival during the period from fertilization to swim-up (called early survival, S_{SU}) was measured by use of field experiments (Paper I) and under artificial conditions (Paper III). The field experiments revealed that survival during this period was high in all populations ($\bar{S}_{SU}=0.86-0.93$) except the two most elevated ones, Hårrtjønn and Øvre Mærrabottvatn ($\bar{S}_{SU}=0.54$ and 0.22 respectively). The population differences in survival remained after adjusting for important biotic and abiotic variables, which I suggest to be indicative of genetic differentiation. This hypothesis was strengthened by results from experiments under controlled temperature regimes (though survival was generally lower for all populations). Survival during the first period of external feeding (S_{EF}) was estimated under artificial conditions with *ad libitum* feeding (Paper III). During this period (180 degree-days), the S_{EF} was significantly different among populations within temperature regimes, and the populations had different survival responses towards temperature. S_{EF} was highest in the temperature regime that simulated the prevailing temperature under natural conditions. I suggest this to be due to temperature adaptations.

Instantaneous total mortality rates for individuals older than three or four years (called adult mortalities, Z) were estimated by use of catch curves (Paper II). The mortality pattern differed among populations, being constant over age (t) for Lesjaskogsvatn ($Z = 0.49$) and Hårrtjønn (0.36), increasing with age in Aursjøen ($0.060t - 0.001$), and decreasing with age in Osbumagasinet ($3.33e^{-0.26t}$, Fig. 3, Paper II). As no individuals older than six years were caught in Øvre Mærrabottvatn, mortality rate was obviously high in this population (0.77). Maximum ages in the other populations varied from 15 years in Lesjaskogsvatn and Osbumagasinet to 27 years in Hårrtjønn.

Size allometries of fecundity varied slightly among the populations, as all but Øvre Mærrabottvatn had similar length vs fecundity regressions (see Table 3 and Fig. 2, Paper IV). Size-specific fecundity was far higher in Øvre Mærrabottvatn than in the other populations. As growth pattern varied among the populations, age-specific fecundities were very different.

Growth varied among the populations throughout the life-span. During the first period of external feeding (*i.e.* in the tributaries), a field survey showed that mean specific growth rates varied between 1.2 to 2.0% day⁻¹, being lowest in Lesjaskogsvatn and highest in Aursjøen (Paper I). These mean growth rates were not correlated with temperature, as might be expected. This lack of temperature effect could be due to genetic differences caused by temperature adaptation, or might simply reflect differences in *e.g.* food availability. In order to assess environmental and genetic effects on early growth rates, experiments under controlled temperature and feeding regimes were conducted by using three populations that covered the entire temperature- and altitude range (Paper III). These common-garden experiments revealed that the populations differed significantly in temperature reaction norms for early growth rates, and that the populations either had equal growth rates at all temperatures (7.9–11.2°C) or grew better under the temperature regime that simulated the

one prevailing in their natural environment.

Population-specific life-time growth trajectories were described by fitting von Bertalanffy growth functions (see Eqn. 2 in Paper II) to age-specific otolith radii. All populations differed in von Bertalanffy growth pattern. Aursjøen and Hårrtjønn grayling had larger maximum sizes than the other populations, and Aursjøen differed from Hårrtjønn in having larger growth constants. Lesjaskogsvatn grayling had similar maximum size as grayling from Osbumagasinet, but larger growth constants. Growth functions were difficult to fit for Øvre Mærrabottvatn grayling due to lack of older individuals and corresponding growth stagnation. However, growth to maturation was very rapid in this population (see Table 1 in Paper IV). By defining the von Bertalanffy growth equations as the expected population-specific growth pattern, it was possible to assess individual deviations from the expected size at age (Δ_{vonB}). This metric was used to assess differences in population-specific maturation reaction-norms with respect to growth pattern (Paper II).

By performing among-lake comparisons of the magnitude of variation in age-specific otolith radii for different cohorts, differences in individual growth conditions were assessed (Fig. 4 in Paper II). In all age classes but age one, Hårrtjønn grayling had the highest variation in growth rates. The three large lakes grouped in a mid position and Øvre Mærrabottvatn most often had the lowest variation. The high variation in Hårrtjønn was suggested to be due to inter-annual variation in growth conditions. Spatial variation caused by many habitat types was suggested as the main source of variation in the three large lakes.

4.2. Differences in mean life-history traits, allometric relations and trade-offs

Mean age at maturity (α_L) varied between 2.9 to 6.2 years among the populations (Paper II). The lowest α_L was found in Øvre Mærrabottvatn, and the two highest α_L were found in Hårrtjønn and Aursjøen. Similarly, large differences in mean size-adjusted egg

weights and gonad weights were documented (Paper IV). Øvre Mærrabottvatn grayling had by far the smallest eggs and the largest size-specific gonad weights, which produced a very high relative fecundity. Size-specific egg sizes were also small in Aursjøen, but as gonad sizes were generally small, fecundity was similar as in the other populations. In Lesjaskogsvatn, both egg size and gonad weights were large. Egg size increased with body size in Hårrtjønn and Lesjaskogsvatn. Egg size increased slowly with body-size in Aursjøen grayling. In the two remaining populations, no correlation was found. Gonad weight vs body size allometries were very similar among the populations. However, I found a small additive effect of population due to large and small size-adjusted gonads in Øvre Mærrabottvatn and Aursjøen, respectively.

Adult survival rates were positively correlated ($r_{sp} = 0.90$) with mean age at maturity (Paper II) and negatively correlated ($r_{sp} = -0.98$) with gonad investments (Paper IV). This is in accordance with predictions made from the age-specific mortality hypothesis (prediction 1a) and b)). Even though no measure of density-dependent interactions have been performed in this study, inferences can be made from Table I. The Hårrtjønn and Lesjaskogsvatn populations are the most likely candidates in which to find density-dependent population regulation in early life. This is due to large spawning stocks compared to size of nursery area. The other populations are probably less influenced by density-dependent regulation as spawning stocks are small compared to the nursery area. Provided that these considerations are right, prediction 3a) that larger egg-sizes are favoured in populations with density-dependent regulation is supported. The predictions 3b) and c) follows from the fact that gonad size is constrained by the body size, so that larger (older) individuals will have less fecundity costs of an increase in egg size (Elgar, 1990). If selection favours large eggs, the egg size-fecundity trade-off for a given size should increase in magnitude, as found in Paper IV (Table 4).

4.3. Differences in plastic responses

Differences in temperature reaction norms were found for development rate to hatching, early growth rate, and early survival among the three populations involved in the Paper III-study. Temperature has a pervasive influence on all developmental traits of poikilotherms like grayling, and adaptation to local temperature regimes are regularly documented (Taylor, 1991). As mentioned, survival was best at natural temperature regimes for all three populations involved in this experiment. Furthermore, Hårrtjønn fry grew clearly best under the natal temperature regime (11.2°C), whereas temperature had little effect on growth rate in the two other populations. Even more interesting, the Hårrtjønn fry did not grow at all under the cold regime (7.9°C) (Fig. 5 in Paper III). Assuming that the families used in this experiment is representative for all populations and no experimental artefacts influence the results, the Hårrtjønn population seems to have less growth plasticity than the other two populations. As this population lives at a high altitude (1172 m.a.s.l.), temperatures below 7.9 °C in August are likely to occur from time to time, and thus the observed temperature reaction norm may seem maladaptive. Lack of genetic variability, *e.g.* due to founder effects following the introductions in 1910, may be one explanation to this phenomena, though it still remains an open question.

Differences in growth reaction norms for age at maturity (Paper II) and size-adjusted egg size and gonad size (Paper IV) were found. The maturation reaction norms were in accordance with prediction 2a), showing that rapid growers within a population matured earlier and at larger sizes than slow growers. I found a negative correlation between slopes describing maturation plasticity and the corresponding adult mortality rate, and in the population with the highest adult mortality (Øvre Mærrabottvatn) no maturation plasticity was found as all individuals matured at age 3. This result supports prediction 2b).

4.4. Evidence of genetic differentiation and additive genetic variance

In this thesis, all phenotypic measures performed in the field are confounded with environmental variation, and thus inferences on genetic differentiation in these traits may not be drawn (Endler, 1986). In order to test for eventual genetic differentiation, I therefore conducted quantitative genetic experiments where individuals from three of the populations were raised in common environments (Paper III). The results from these experiments showed that the three populations differed significantly in temperature reaction norms for early development rate, growth rate and survival. Clearly, these results must be interpreted as being due to genetic differences. Even though inferences of genetic differentiation can be drawn for the studied traits only, this result also strengthens the expectation that the differences found for other traits have a genetic basis.

4.5. Are the observed trait values adaptive?—fitness considerations

In Paper II, predictions derived from the maturation model of Roff (1984) (Eqn 3) were compared with data from my study systems. The model predicted the same qualitative result as the empirical data, however it generally underestimated the actual age at maturity. I suggest that age/size-related costs are higher than assumed in the model. As pointed out by Stearns (1992), this model does not predict the optimal age at maturity since it does not consider cost and benefits of different ages at maturity. In order to test effects of maturation cost over varying ages at maturity, I can use information available from Paper II & IV. I found that rapid growers matured earlier than slow growers (see Fig. 5&6 in Paper II). Once the maturation of the gonads has started, resources will have to be allocated into the eggs. As resources are limited, this allocation will be traded against the somatic growth, and consequently future fecundity (growth costs (Bell, 1980)). I found growth costs of maturation to vary over age at maturity and among populations (see Fig. 4 in Paper IV). By

using this information on size at maturity and growth costs during gonad development, age specific fecundities could be estimated for different maturation ages for all populations. I have not been able to estimate survival costs of maturation (*e.g.* Hutchings, 1993a). I therefore test the sensitivity of fitness to different survival costs at varying age at maturity (assuming juvenile survival to be equal for all strategies). By assuming a stable demographic environment (global $r \approx 0$), R_0 can be used as a fitness measure (Kozłowski, 1993). The result of the fitness simulation is visualised in Fig. 2. It is evident that the difference in survival between mature and immature individuals must be larger than 30% in all populations in order to have optimal age at maturity at the observed level (α_L). In Aursjøen and Osbumagasinet, the two populations with highest growth costs of maturation (see Fig. 4 in Paper IV) the difference should be close to 50%. These values are in accordance with values found by *e.g.* Hutchings (1993a) as he documented survival differences to be between 31% and 58% in brook trout *Salvelinus fontinalis*. Clearly, such high costs of maturation will favour a delay in maturation age in order to gain high first-reproduction fecundity, and this may explain why the Roff-model underestimated age at maturity.

In Øvre Mærrabottvatn, age at maturity should be larger than four years for the survival difference to be $\geq 30\%$. However, estimated age at maturity is 2.9 years in this population, indicating small differences in survival between mature and immature fish. In Øvre Mærrabottvatn, an intense gill-net fishery induces a strong size-selective mortality on large fish, and this effect probably overrules the effects of maturation survival costs.

Large egg size has a positive effect on early survival in both Hårrtjønn and Lesjaskogsvatn grayling, whereas no effect was documented in Aursjøen grayling (Paper III). These results suggest that selection may favour larger eggs in these two populations compared to Aursjøen, probably due to more intense density-dependence in early life (discussed in Paper IV). Maternal fitness (w) may be estimated from the product of juvenile

survival and the number of offspring produced at a given reproductive occasion (Hutchings, 1991; Charlesworth, 1994):

$$w_{ijk} = \sum_i m_j \cdot l_k, \quad (4)$$

where for an egg size i , m_j is the expected fecundity that could be produced in a gonad of size j , and l_k is the survival for the same egg size at temperature k . The egg-size and temperature dependent survival probabilities are given in Table 6 in Paper III. Notice that in the Aursjøen population, egg size had no effect on the survival probabilities. Fitness isopleths are shown as functions of i and j at given k s in Fig. 3. Selection should favour small eggs in Aursjøen as the isopleths have positive slopes. As small eggs are favoured, an increase in egg size with gonad size is not expected, which corresponds to the field data (shaded areas in the figures). In Hårrtjønn, fitness values are generally highest in the warm environment, and egg size should increase with gonad size (optimal w_k values are where $\frac{\partial w_k}{\partial i} = \frac{\partial w_k}{\partial j}$, corresponding to isopleth slopes equal to -1 when similar scales of i and j (-66.7 in Fig. 3), see *e.g.* Perrin & Sibly, 1993). This prediction is supported by empirical data for this population. In Lesjaskogsvatn the highest fitness values are predicted for the medium temperature, and the prediction is that egg size should only increase slightly with increasing gonad size, which is also supported by the field data. It can therefore be concluded that the differences in mean egg size and egg size vs body size allometries are in accordance with predictions made from Eqn 4, and thus should be adaptive. One caution must be added; the relation between early survival and egg size has been derived from laboratory conditions with good food supplies, and thus may give a spurious picture on this relationship for natural conditions. Conover & Schultz (1997) uses another approach where local adaptation is used to test theory. By adapting this approach, predictions of differences in mature and immature survival rates (as they appear in Fig. 2) could be tested in the present study systems, for instance by use of capture-mark-recapture methodology (Nichols *et al.*, 1994).

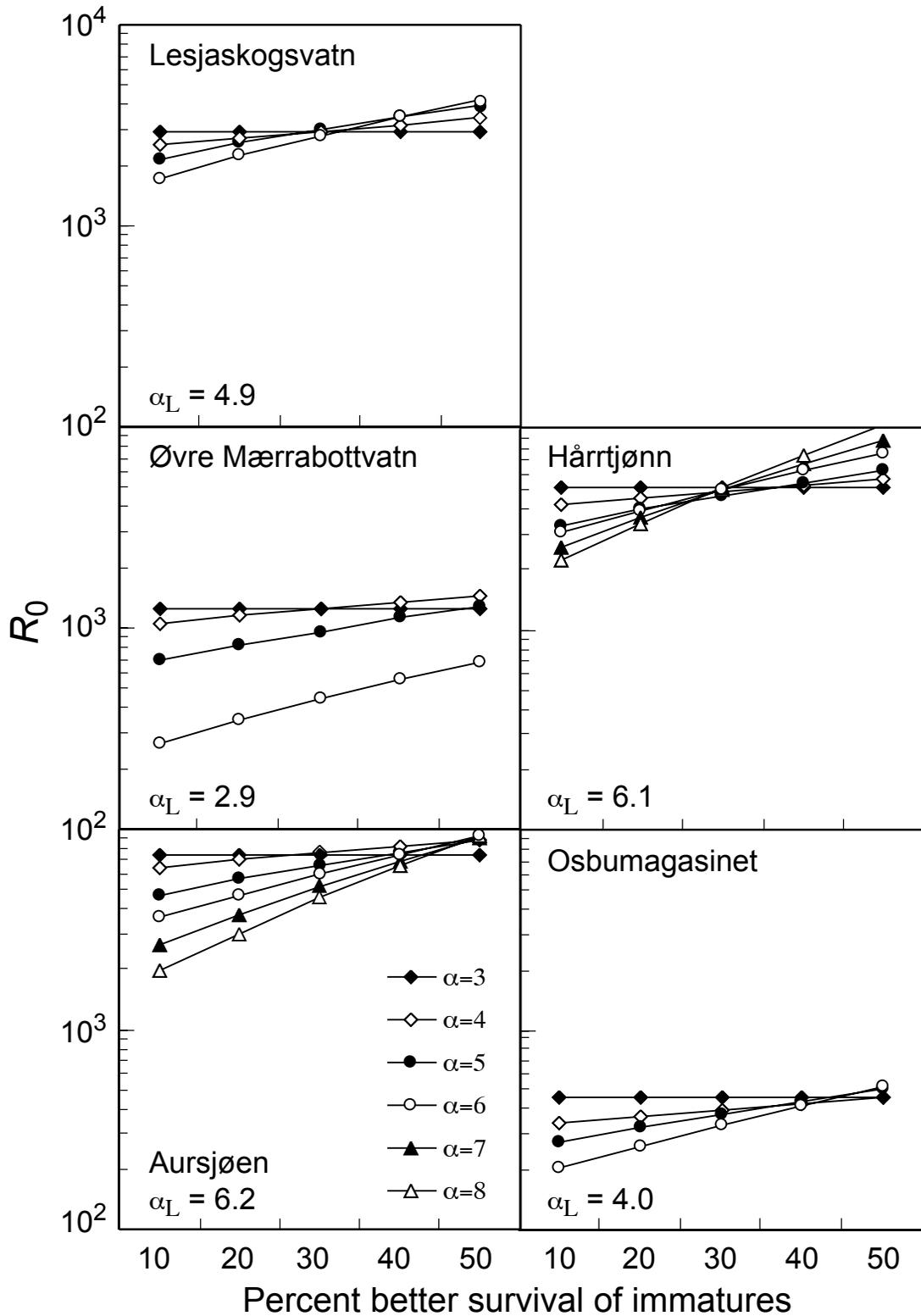


FIG. 2. Sensitivity of fitness (R_0 , Eqn 2) to differences in age-specific survival rates of mature and immature individuals. The difference in survival between mature and immature individuals is assumed to be constant with age. α is age at maturity, and α_L = mean age at maturity derived from field data (Paper II).

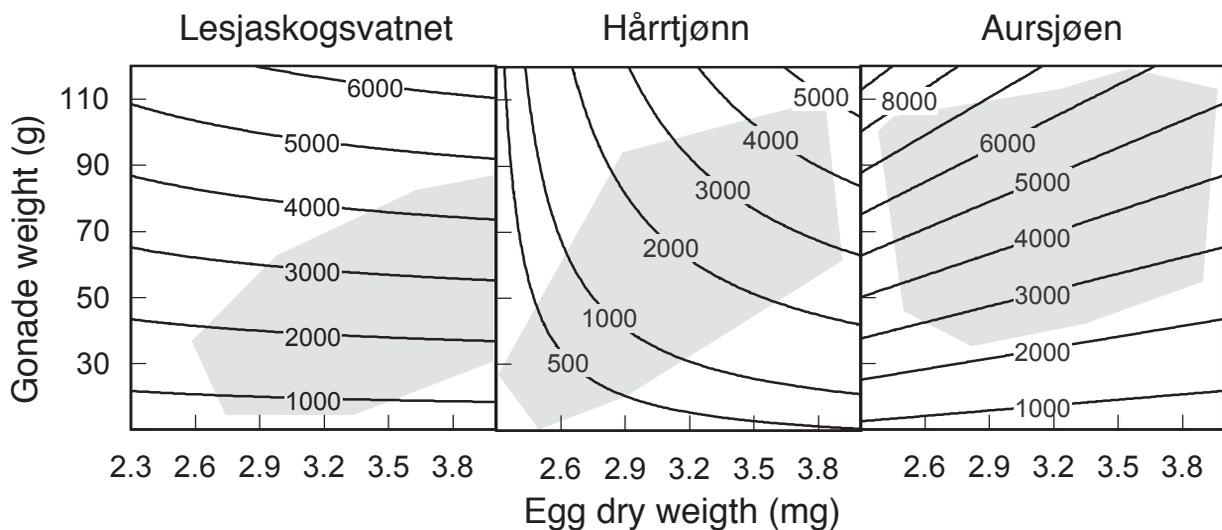


FIG. 3. Maternal fitness isopleths as function of egg size and gonad size. Fitness was estimated by using Eqn 4, and only fitness isopleths for natal temperature regimes are displayed (*i.e.* at highest fitness values). Shaded areas are values covered by empirical data (Paper IV).

5. How rapid may life-history evolution proceed?

The evolution of life-history traits is expected to proceed quickly, as these traits are closely coupled with fitness (Charlesworth, 1994). Significant divergence in life-history traits has been shown to occur within 8–28 generations in several fish species (Hendry & Quinn, 1997; Reznick *et al.*, 1997; Hendry *et al.*, 1998; Kinnison *et al.*, 1998a). In most of these studies, the evolution has been termed as rapid. However, in an extensive review of several microevolution studies (Hendry & Kinnison, 1999) show that most estimated levels of evolution- and divergence rates (estimated as darwin and/or haldane, see Paper I) are within the same range. They therefore suggest that “rapid evolution” is the norm when populations are introduced into novel environments. In Table II, rates of evolution (size at age five and minimum size at maturation in Lesjaskogsvatn) and rates of divergence have been estimated for the present study systems. In general, rates based on phenotypic studies

are larger than the genotypic ones, showing that environmental factors confound these estimates. Furthermore, rates for adult traits are larger than the juvenile traits, which may be due to larger environmental influence or due to higher selection pressures on adult traits. Nonetheless, most of the estimated rates are, after adjustment for the generation length or time of segregation, within the range of values found in other studies of micro-evolutionary rates. The values found for growth rates and all adult traits are clearly in the upper range of values reported, especially when compared to other studies of life-history traits. It can therefore be concluded that the divergence and evolution of many of the measured life-history traits has been rapid. Will this high rate of evolution proceed into the future? Most comparisons of evolutionary rates between palaeontological data and microevolution studies show that evolutionary rates are far higher in the latter ones (more than $10^3\times$ (assuming one generation per year)) (Kirkpatrick, 1996). The response to selection (R), which is related to the darwin metric (d), is estimated as the ratio of the mean change in phenotypic value of a trait ($\Delta\bar{z}$) on the mean population value (\bar{z}) per generation. It can be shown that R depends on the relative phenotypic variance (CV_p), the heritability of the trait, and the standardized selection gradient ($\tilde{\beta}$), so that (Falconer & Mackay, 1996; Kirkpatrick, 1996):

$$d \times 10^{-6} = R = \frac{\Delta\bar{z}}{\bar{z}} = CV_p h^2 \tilde{\beta} \quad (5)$$

This equation suggests that adaptation ceases if selection ceases ($\tilde{\beta} \rightarrow 0$) or if variation is exhausted ($CV_p \rightarrow 0$). In fitness-related traits, like most life-history traits, phenotypic variation may clearly get exhausted, though factors such as environmental variability (Paper I & II), over-lapping generations (Paper II) and G×E-interactions (Paper I, II & III) are known to preserve phenotypic variation (Roff, 1997; Lynch & Walsh, 1998). Most palaeontological studies focus on morphological traits that probably are under very weak selection with small effects on fitness (Kirkpatrick, 1996). On the other hand, a trait like body size may have a huge impact on fitness, but no evidence of reduced variation nor selection is

available for the palaeontological data for this trait. Gingerich (1983) suggests that during a larger time span the direction of selection may change, and due to this the mean evolutionary rate may be reduced.

TABLE II. Rates of divergence (synchronic) and rate of evolution (allochronic) for grayling populations in the Lesja region, central Norway. “Type” is either genetic (G) or phenotypic (P), where phenotypic values are derived from common garden experiments and field surveys, respectively. Rates are given as absolute values in synchronic studies, whereas the sign is given in the allochronic study in order to evaluate the direction of the evolution.

Trait	Type	Synchronic		Allochronic
		Darwin	Haldane	Darwin
Time to 50% hatching ^a	G	0.55±0.26	0.004±0.003	
Size at hatching ^a	G	0.52±0.39	0.067±0.039	
Yolk-sac volume ^a	G	0.21±0.10	0.073±0.058	
°D to first swim-up ^b	P	0.69±0.41	0.027±0.020	
Size at swim-up ^a	G	0.32±0.23	0.039±0.029	
Size at 180 °D ^a	G	1.00±0.99	0.056±0.047	
Early growth rate ^a	G	1.98±1.25	0.056±0.047	
Early growth rate ^b	P	5.18±1.05	0.157±0.082	
Size at age 5 ^c	P			-5.56±11.11
Min. size at maturity ^d	P			1.64±12.08
Size at maturity ^e	P	2.79±1.32	0.233±0.108	
St. egg dry weight ^f	P	2.38±1.55	0.152±0.084	
Rel. fecundity ^f	P	3.93±4.01	0.121±0.101	
GSI ^f	P	2.15±1.28	0.102±0.071	

a. Paper III.

b. Paper I.

c. From data in Gammelsrud (1982) and Paper II. The values are from studies performed in 1923, 1930, 1951, 1964, 1967, 1981, 1991 and 1997.

d. From data in Gammelsrud (1982) and Paper II. The values are from studies performed in 1904, 1930, 1981 and 1995.

e. Paper II.

f. Paper IV.

6. Suggestions of selection factors

John A. Endler (1986) states in his extensive review of natural selection in the wild that “a demonstration of natural selection is not really complete unless the biological reasons for selection are discovered” (page 94). Thus, it is not sufficient to demonstrate that traits are affected by natural selection. In order to gain knowledge of why natural selection affects the evolution of phenotypic traits, causal factors will have to be documented and manipulated (Reznick & Bryga, 1987). Selective agents that have been shown to rapidly affect fitness-related life-history traits are predator or fishery induced differences in age/size specific survival (Hutchings, 1993a; Policansky, 1993; Reznick *et al.*, 1996) and variation in environmental predictability (Stearns, 1983, but see also Newman, 1988). As the intensity of gill-net fisheries varied among the populations, this selection factor turns out to be a candidate in causing age-specific mortality variation among the populations. In order to test this, experiments with relaxed gill-net fisheries must be performed (Reznick & Travis, 1996).

The difference in egg size among populations is suggested to be due to variation in degree of density-dependent population regulation in early life among the populations. If density dependence is more pronounced in populations with large eggs, one might expect behavioural differences to evolve with individuals from large-egg populations being more aggressive than those in small-egg populations. Perhaps this may explain why the populations had different survival responses to egg size in Paper **III**. In order to test this hypothesis, fry from the different populations should be raised together (competition experiments) under varying density- and food conditions.

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