

Invader population speeds up life history during colonization

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Abstract We explore the long-term developments in population biology and life history during the invasion and establishment of the fish species vendace *Coregonus albula* in a subarctic watercourse by comparing life-history traits and molecular genetic estimates between the source and the colonist population. The two populations exhibited highly contrasting life-history strategies. Relative to the source population, the colonist population was characterized by slower somatic growth rates, earlier sexual maturation at smaller individual size, higher mortality rates and a shorter life span. The two populations could also be significantly discriminated by the genetic markers.

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Limited founder effects were detected from heterozygote deficit and reduced allelic richness in the colonist population, but both populations were associated with relatively high genetic diversity. The study reveals that the invasion into a new environment induced large changes in life-history strategy, with typical *r*-selected traits being more prominent in the colonist than in the source population. We discuss the mechanisms that may explain the observed life-history differences between the source and the colonist population, and argue that the accelerated life history of the colonist population represents an adaptive pioneer strategy aimed at fast population increase during colonization and establishment.

Keywords Invasion · Growth · Sexual maturation · Adaptation · Phenotypic plasticity · *r*- and *K*-selection

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Introduction

Invasions may provide excellent opportunities to study basic processes in population biology and the plasticity of life-history traits (Sakai et al. 2001; Shea and Chesson 2002), and may be considered natural experiments in this respect, often inducing ecological processes far more expeditious than those in undisturbed systems (Sakai et al. 2001). Few investigations have, however, addressed the population ecology and life history of the invading species during establishment (Williamson 1999). The invasion of a species into a new environment may generate rapid changes in population biology, life-history strategies and genetic structure of the invader (e.g. Reznick and Ghalambor 2001; Lee 2002; Lambrinos 2004). Ecological and evolutionary processes may influence the development of the invader through (1) founder effects (Tsutsui et al. 2000; Dlugosch and Parker 2008), (2) adaptations to the native ecological community with its new predator–prey relationships and competitive interactions (Shea and Chesson 2002; Lockwood et al. 2007), and (3) phenotypic adjustments to the new environment (Sandlund 1992; Huey et al. 2000). Based on these three often linked responses, invading species may adopt a pioneer life-history strategy facilitating rapid population increase and expansion during the invasion process (McMahon 2002; Ruesink 2005). A colonist population may therefore display a life-history strategy that is deviant from its source population, but studies comparing population biology and life-history strategies of the source and colonist populations during an invasion are lacking.

The present study addresses the invasion of a non-native fish, vendace *Coregonus albula*, in the subarctic Inari–Pasvik watershed in northern Europe. Vendace was introduced in Lake Inari, Finland, around 1960 (Mutenia and Salonen 1992), established a dense population and colonised downstream lakes in the Pasvik watercourse, Norway and Russia, where the species was observed for the first time in 1989 (Amundsen et al. 1999). In Lake Vaggatem, Norway, in the upstream part of the Pasvik watercourse, the invader rapidly became the dominant pelagic fish species (Bøhn et al. 2004, 2008). Long-term investigations with annual sampling of vendace have been carried out in Lake Inari since 1985 (Salonen 1998, 2004) and in Lake Vaggatem since 1991 (Amundsen et al. 1999; Bøhn et al. 2008). Here we perform a

combined analysis of these time-series in order to compare the population biology and life-history strategies of the source (Lake Inari) and colonist (Lake Vaggatem) populations of the invader species prior to and following the downstream invasion and establishment. The genetic diversity, variability and divergence between the two populations were also examined to evaluate whether any population differences were solely a consequence of phenotypic plasticity in life history traits or a combination of both phenotypic and genetic responses.

Most fish species have indeterminate somatic growth trajectories and may show plasticity in growth rate and other life-history characteristics (Stearns and Koella 1986; Wootton 1998). Plastic responses and selection on relevant traits may quickly modify phenotypes in periods of rapid population growth (Reznick et al. 1997; Hendry et al. 2000). Vendace is a specialist with a narrow ecological niche in terms of food and habitat choice (Svårdson 1976; Bøhn and Amundsen 2001; Kahilainen et al. 2011), but is known to exhibit substantial variation in life-history parameters such as growth rate, age and size at maturity, individual fecundity, and number of spawnings during their lifetime (Sandlund 1992; Sarvala and Helminen 1995; Bøhn et al. 2004). Hence, following the invasion into a new environment, vendace could potentially undergo rapid changes in life-history strategy. We therefore hypothesized that the colonist and source population would exhibit distinct differences in population biology; the colonist population having more rapid life-history characteristics, including earlier sexual maturation, reduced somatic growth and increased mortality rates due to larger reproductive investments, representing phenotypic and adaptive responses facilitating the invasion of a new ecological environment.

Study area

Three countries share the Inari-Pasvik watershed. Lake Inari (1,102 km²) in Finland is the largest lake in the watershed, draining north into the Pasvik watercourse which firstly runs into Russia for about 30 km. Thereafter, the watercourse forms the border between Norway and Russia over a distance of about 120 km before entering into the Arctic Ocean (Fig. 1). The total catchment area of the watershed covers

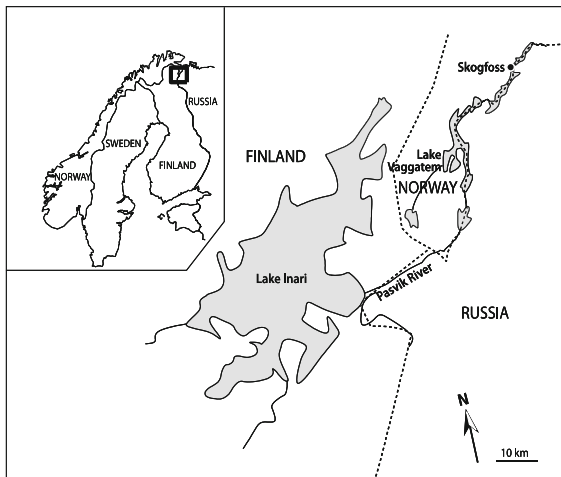


Fig. 1 Map of the study area with the two lake localities indicated

18,403 km²; mainly located on Finnish territory. The Norwegian–Russian section of the watercourse has a total area of 142 km², restricted to a quite narrow zone in the Pasvik valley along the borderline of the two countries. The mean annual water flow is about 175 m³ s⁻¹. The Vaggatem reservoir (referred to as Lake Vaggatem) is the largest lake in the upstream part of this section and covers 34 km². In total, there are seven hydropower impoundments in the Pasvik watercourse, which has caused most natural rapids and waterfalls to disappear. Four dams are situated between Lake Inari and Lake Vaggatem. Hence, the present water system primarily consists of a series of lakes and reservoirs linked by slow-flowing river sections. Both Lake Inari and Lake Vaggatem are affected by the water regulations, but the regulation amplitude of both reservoirs are usually less than 1.5 m. In both lakes the ice-free season normally lasts from May–June to October–November and they have similar water chemistry (Table 1). The lakes also have similar fish communities with European whitefish *Coregonus lavaretus* (L.) as the dominant native species in both systems (see Mutenia and Salonen 1992 and Amundsen et al. 1999 for details).

The invasion of vendace from Lake Inari to the downstream Pasvik watercourse occurred in the late 1980s (Amundsen et al. 1999). At this time period, the source population in Lake Inari was at a peak abundance (Salonen 1998, 2004; Salonen et al. 2007), suggesting that a high number of individuals may have emigrated from the lake and downstream

Table 1 Abiotic background data for the two lake localities

	Lake Inari	Lake Vaggatem
Latitude (°N)	69°00'	69°13'
Longitude (°W)	28°50'	29°14'
Country	Finland	Norway
Surface area (km ²)	1102	34
Altitude (m.a.s.l.)	114	52
Max depth (m)	96	50
Mean depth (m)	14	8
pH	7.01 (6.76–7.13)	6.86 (6.17–7.10)
Color (mg Pt/l)	10 (10–11)	15 (10–23)
Cond (µS/cm)	29 (28–30)	27 (20–32)
HCO ₃ (mg/l)	11.4 (11.0–11.8)	9.9 (5.7–12.1)
Ca (mg/l)	2.79 (2.65–2.91)	2.28 (1.41–2.62)
Mg (mg/l)	0.94 (0.86–1.05)	0.82 (0.50–1.01)
Na (mg/l)	0.94 (0.86–1.05)	1.59 (1.33–1.90)
K (mg/l)	0.39 (0.36–0.44)	0.43 (0.35–0.55)
SO ₄ (mg/l)	2.7 (2.6–2.9)	2.2 (1.6–2.6)
Cl (mg/l)	1.3 (1.0–1.9)	1.4 (1.1–1.9)
Tot P (µl)	10 (4–25)	15 (5–39)
Tot N (µl)	154 (114–212)	254 (116–574)

into the Pasvik watercourse. The invasion proceeded rapidly down the watercourse, apparently facilitated by a concurrent overflow of the dam constructions (Amundsen et al. 1999). Vendace was observed in Lake Vaggatem for the first time in 1991 and had by 1995 established populations along the whole Pasvik system (Amundsen et al. 1999). In Lake Vaggatem, the species also rapidly became the dominant species in gill net catches from the pelagic zone (Amundsen et al. 1999), relegating whitefish from this habitat and the associated zooplankton food resources (Bøhn and Amundsen 2001; Bøhn et al. 2008).

Materials and methods

Field sampling and population structure analysis

In both study lakes, vendace were sampled from the upper part of the pelagic zone. Vendace samples from Lake Inari were collected from trawl catches, whereas samples from Lake Vaggatem were collected using gill net series with mesh sizes from 8 to 35 mm. In both lake localities the sampling is assumed to be non-selective for vendace > 10 cm (see Salonen 1998 and

Bøhn et al. 2004 for sampling details). Relative fish density has been estimated from catch per unit effort in both systems (see Salonen 1998; Salonen et al. 2007; Bøhn et al. 2008), but unfortunately based on different types of catch data, thus preventing the use of fish density as an independent variable in the analysis of life-history variation between the two systems. All fish were measured in mm [total length (T_L) in Lake Inari, fork length (T_F) in Pasvik, but here adjusted to total length by the equation: $T_L = 1.085 * T_F - 0.277$, based on measurements of both T_L and T_F from a subsample of fish ($N = 86$, $R^2 = 0.999$)] and weighed in grams. Sex and stage of maturity were determined (see Salonen 1998; Bøhn et al. 2004 for further details on the sampling procedures). The age of the fish was determined from scales in Lake Inari and from surface readings of otoliths in Lake Vaggatem. Scale reading of coregonids may underestimate the age of older fish, but closely resembles reading from otoliths in young fish (Raitaniemi et al. 1998). Since most of the fish sampled for the present study were younger than 5 years, the different methods for aging are unlikely to cause any bias. Samples have in general been collected annually from 1987 to 2007 in Lake Inari and from 1991 to 2007 in Lake Vaggatem. The data have been compiled into five consecutive time periods, including 1987–1990 (period 1), 1991–1994 (period 2), 1995–1998 (period 3), 1999–2002 (period 4) and 2003–2007 (period 5). The total material includes 16 315 and 4 950 vendace from Lake Inari and Lake Vaggatem, respectively.

Maturation

We used logistic regression (Agresti 2002) with immature and mature fish as the nominal categorical response variable to estimate the probability of maturation as a function of the predictor populations (source or colonist) and length in one model, and as a function of the predictor populations and age in a separate model. From these models, the length and size where the probability of maturation was 50% were extracted and denoted L_{m50} and age A_{m50} , respectively. In the logistic regression analyses with the length data, we chose to first estimate L_{m50} in period 1 in the source population, and thereafter centering all fish lengths by subtracting L_{m50} before standardizing by dividing by two standard deviations. This approach ensured that the statistical test of main effects (population and period) occurred in the most

relevant size range. One of the benefits of using centered predictors is that the regression coefficients is much easier to interpret in the presence of interaction terms, i.e. the main effect can be interpreted as the effect at the mean size or age of the fish (Schielzeth 2010). Standardizing by dividing by two standard deviations has the purpose of enhancing the comparability of the effect of categorical and continuous variables (Schielzeth 2010). An equivalent procedure was used for the age data. In these logistic regressions, the slope of the logit curve describes how fast the probability of maturation changes. We have termed this slope the maturation rate. A steep logit curve indicates a high maturation rate, whereas a less steep logit curve indicates slower maturation rate. Main effects and interaction effects (differences in the maturation rate) were reported as differences to period 1 in the source population.

Somatic growth

In order to compare the somatic growth rate of vendace between localities and time periods, the growth (length at age) was modelled using the modified von Bertalanffy growth model (Roff 1984):

$$L(t) = L_{\infty}(1 - e^{-Kt}) \quad (1)$$

where $L(t)$ is the mean fish length at age t , L_{∞} is the asymptotic length when age is close to infinity, and K (Brody's growth coefficient) defines the rate at which the growth curve approaches the asymptote. L_{∞} and K were estimated by non-linear least-square regression based on the mean lengths of the different age-classes.

Significant differences were generally absent between females and males in length and age distributions, size and age at maturation and mean length at age. Consequently, we did not differentiate between the sexes in these analyses.

Mortality

Instantaneous mortality rates (Z) were estimated using standard catch curves from the fish surveys (see Ricker 1975), omitting fish ≤ 1 year from the estimations due to biased selection of the smallest fish. The age distributions were pooled for all years within each time period in order to reduce the effect of year-class

variation (Ricker 1975), which often is pronounced in vendace populations (Sandlund et al. 1991; Sarvala and Helminen 1995). The annual mortality rate (A) was calculated as $A = 1 - e^{-Z}$.

Genetics

To characterize variation in population structure between the source and colonist vendace populations, genomic DNA were extracted from gill tissue of 52 Lake Inari and 57 Lake Vaggetem individuals sampled in 2008. The individuals were genotyped at 10 microsatellite loci; BFRO018 (Susnik et al. 1999), BWF01, BWF02 (Patton et al. 1997), C2-157 (Turgeon et al. 1999), Cla-Tet06, Cla-Tet13 (Winkler and Weiss 2008), Cocl-lav06, Cocl-lav10, Cocl-lav49, and Cocl-lav52 (Rogers et al. 2004). The average number of alleles and private alleles per locus per population (normalised for differences in sample sizes) were calculated using the rarefaction procedure as implemented in HP-rare (Kalinowski 2005). Expected (H_e) and observed heterozygosity (H_o) and deviations from the Hardy–Weinberg equilibrium were calculated in GENEPOP 4.0 (Rousset 2007) to characterize genetic diversity. Genetic differentiation between the two populations was estimated by a pair-wise F_{ST} value (Weir and Cockerham 1984) and tested for statistical significance (10,000 permutations) using the program package ARLEQUIN 3.01 (Excoffier et al. 2005).

Results

Population structure

In all time periods, vendace sampled from the colonist population in Lake Vaggetem were significantly smaller than in the source population from Lake Inari with a narrower range in length distributions and smaller mean sizes (Fig. 2a; Table 2; ANOVA, $P < 0.001$). The largest specimen caught in the colonist population over the entire time-span of the study was 17 cm, whereas the source population showed fish larger than 25 cm. The mean size of fish in the colonist population decreased from 13.0 cm in period 2 to 10.1 cm in period 5, and in periods 3–5 the vast majority of the fish were less than 12 cm in length. In contrast, the mean length of fish in the source population increased slightly from 15.1 cm in

period 1 to 16.0 cm in period 4, but was only 12.3 cm in period 5.

The number of age groups and the mean age of vendace were also significantly lower in the colonist than in the source population (Fig. 2b; linear modelling assuming a Poisson error distribution, $P < 0.001$). No fish older than 6 years were observed in the colonist population, whereas vendace up to 11 years of age were observed in the catches from the source population. However, in both systems the catches were dominated by 3-year old or younger fish. Mean age varied between 1.5–2.2 and 1.2–2.7 years in the colonist and source population, respectively (Table 2).

Maturation

The size at 50% maturation differed considerably between the two vendace populations, ranging from 8.8 to 9.4 cm in the colonist population compared to 12.7–16.5 cm in the source population [Figs. 3a, S1 (Electronic Supplementary Material)]. The smallest mature individuals observed in the two lakes were 8.5 cm in the colonist population and 9.4 cm in the source population (Fig. 2a). The probability of being mature for a fish of mean size was significantly different between period 1 and the other periods ($P < 0.001$). The effect sizes (i.e., the differences in maturation probability) were small within the Inari population, as were the variation in maturation rate (Fig. S1; logit coefficients varying between -1.7 and 0 for intercepts and between -1.1 and 1.1 for slopes). On the contrary, effect size was much larger between the populations, and increased within the colonist population throughout the study periods (logit intercept difference increasing from 2.1 in period 2 to 8.8 in period 5). With fish length as the covariate, the maturation rate increased throughout the study within the colonist population (from no significant difference in period 2, then the difference increased significantly from 3.9 through 12.9 to 15.5 in period 3, 4 and 5, respectively).

In the colonist population, 90–98% of the fish were sexually mature already at age 1 year (Fig. 3b). In the source population, in contrast, 24–44% of the 1 year old fish were sexually mature (Fig. 3b), whereas >80% usually had matured at age 2 (Fig. 2b). Maturity by age was also significantly different between the populations ($P < 0.001$). Within the source population, the effect size of period was small, the logit differences

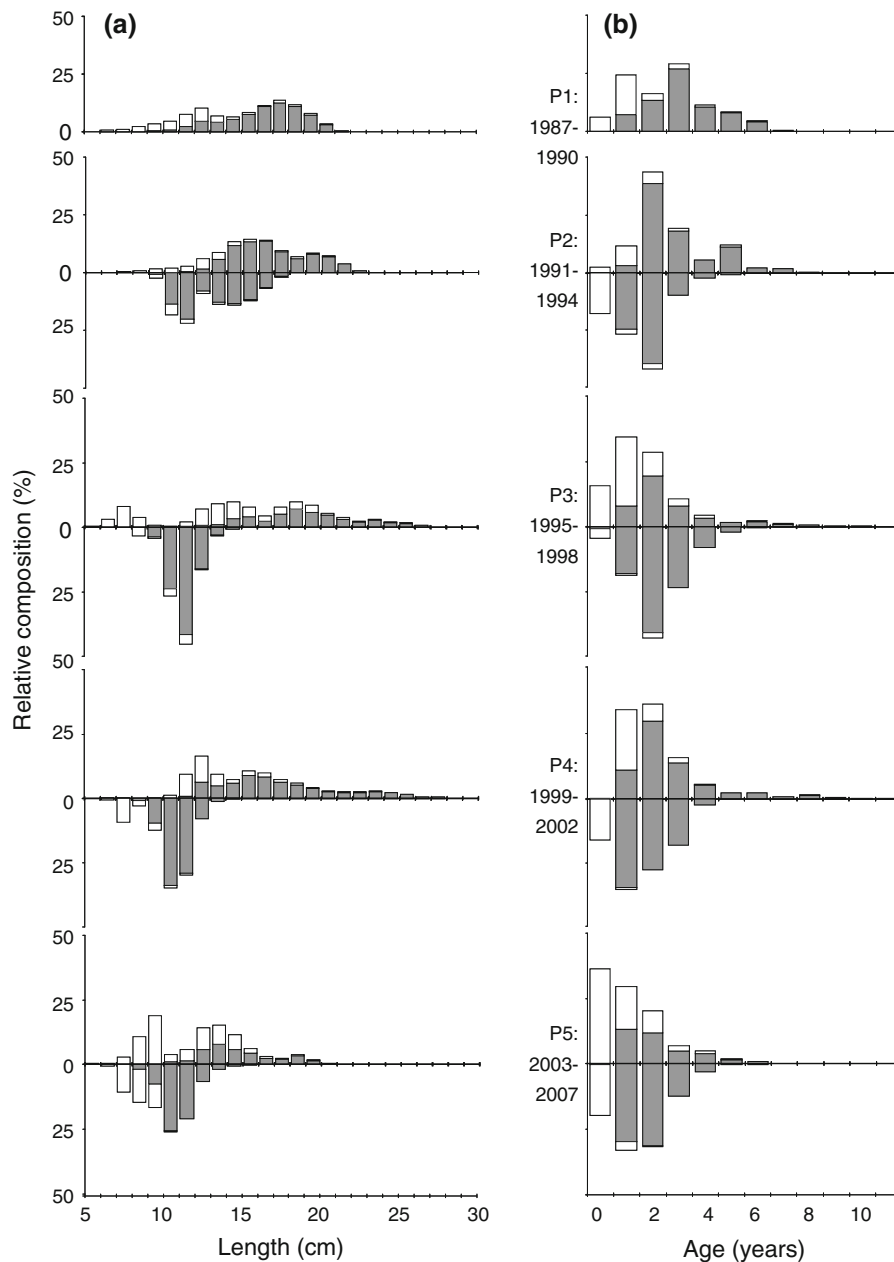


Fig. 2 Distributions of **a** size and **b** age of vendace in samples from the source Lake Inari (*upper panels*) and colonist Lake Vaggatem populations (*lower panels*) over the five time periods from 1987 to 2007. *Filled bars* = mature fish

varying non-monotonically between -0.52 and 0.53 by period. In comparison, there was a strong and increasing period effect in the colonist population, with logit differences increasing monotonically from 1.0 in period 2 to 2.9 in period 5 ($P < 0.001$ for all periods). With age as the covariate, differences in maturation rate between periods were not significant in the source population, but highly significant and increasing from

1.6 ($P = 0.003$) in period 2 to 13.4 ($P < 0.001$) in period 5 in the colonist population.

Somatic growth

The growth curves estimated from the von Bertalanffy's growth model provided a good fit to the length-at-age data, and in all time periods, vendace

Table 2 Mean length (cm) and age (years) with standard deviation (SD) and sample size (N) of vendace in the total catches from the source and colonist populations in the respective sampling periods

Population	Time period	Length	SD	N	Age	SD	N
Source (L. Inari)	1 (1987–1990)	15.12	3.34	10,066	2.61	1.56	10,022
	2 (1991–1994)	16.08	2.94	3,564	2.72	1.51	3,564
	3 (1995–1998)	15.69	4.86	1,727	1.81	1.58	1,727
	4 (1999–2002)	16.00	3.91	544	2.32	1.63	535
	5 (2003–2007)	12.33	3.00	414	1.22	1.29	395
Colonist (L. Vaggatem)	2 (1991–1994)	12.96	2.08	865	2.04	0.89	477
	3 (1995–1998)	11.28	0.96	1,173	2.22	1.04	413
	4 (1999–2002)	10.49	1.4	811	1.82	0.93	406
	5 (2003–2007)	10.14	1.6	2,101	1.48	1.07	434

All differences between populations were highly significant ($P < 0.001$, linear model, predictors population and period; a Poisson error distribution was assumed for the statistical testing of the age data)

grew slower and achieved significantly lower sizes in the colonist population than in the source population (Fig. 4). The somatic growth of vendace in the two lakes also exhibited distinct changes with time. In the colonist population the asymptotic length (L_{∞}) decreased from 15.8 cm in period 2 to 12.0 cm in period 4 and 5. In the source population the asymptotic length was much higher and increased from 19.4 cm in period 1 to 25.2 cm in period 4, followed by a decline to 18.3 cm in period 5 (Fig. 5a). Similarly, Brody's K was found to be largest in the colonist population, ranging from 1.47 to 2.36, and considerably smaller in the source population, ranging from 0.51 to 0.97 (Fig. 5b).

Mortality

The mortality rate was relatively high in both vendace populations, but consistently much higher in the colonist than in the source population (Fig. 6). In the colonist population the annual mortality (A) ranged from 0.71 to 0.75, while in the source population the mortality rate ranged from 0.43 to 0.60.

Genetics

The genetic diversity was high for both populations, but the colonist population showed a lower number of alleles (9.8 vs. 11.2) and private alleles (1.4 vs. 2.8) per locus compared to the source population. Departures from the Hardy–Weinberg equilibrium were observed in three out of 10 tests for both populations and were attributed to heterozygote deficit ($H_e = 0.726$,

$H_o = 0.622$) for the colonist vendace and heterozygote excess for the source vendace ($H_e = 0.595$, $H_o = 0.724$). The colonist and source population showed low, but highly significant genetic divergence ($F_{ST} = 0.011$, $P = 0.0023$).

Discussion

Our study demonstrates large differences in population biology and life history strategies between a source and a colonist population over the initial two decades following their separation. The differences were accompanied by a genetic divergence of the populations. The colonist population consisted of small-sized individuals that matured earlier in life and at a smaller size than the source population. The fish approached an asymptotic body size at age 3–4 years in the early phase of the invasion and at an even earlier age (1–2 years) during the later stage of invasion. In contrast, fish in the source population continued to grow for at least 5 years, reaching a much larger size than observed in the colonist population. Simultaneously, the annual mortality rates were much higher in the colonist than in the source population. Relative to the source population, the colonist population displayed typical r -selected traits (sensu MacArthur and Wilson 1967; Reznick et al. 2002) with a rapid life-history development traded off at the cost of higher mortality. Rapid life histories have been associated with pioneer-stages of invasion and succession (Sakai et al. 2001; McMahon 2002; Davis 2005; Ruesink 2005; Burton et al. 2010), and we argue

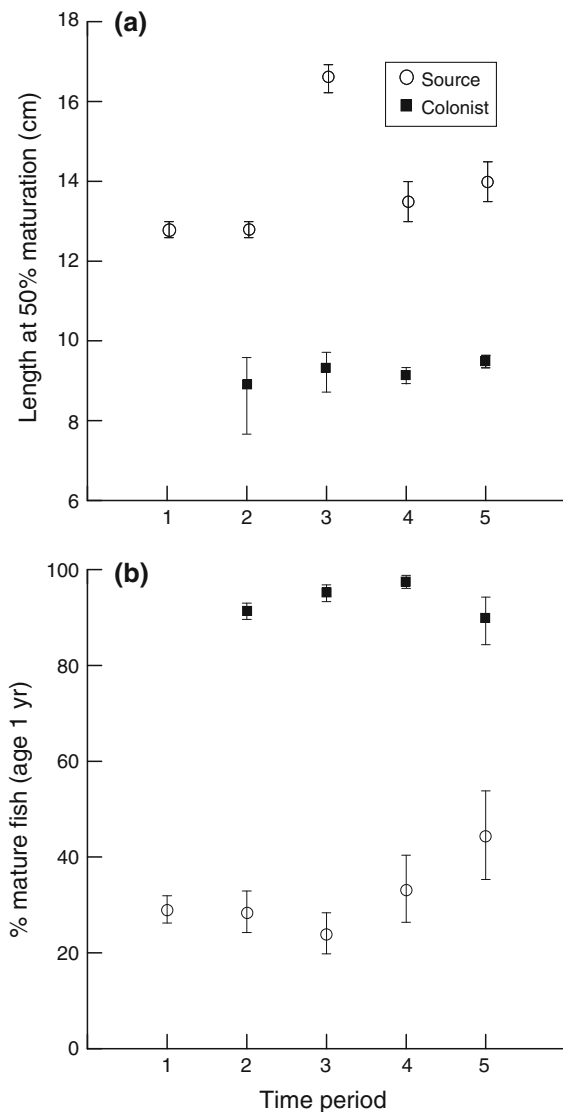


Fig. 3 **a** Mean size at first reproduction (body length with 50% mature individuals) estimated by logistic regression, and **b** percentage of sexually mature 1-year old fish from the source Lake Inari and colonist Lake Vaggatem vendace populations (period 1 = 1987–1990, 2 = 1991–1994, 3 = 1995–1998, 4 = 1999–2002, 5 = 2003–2007). Error bars show 95% confidence intervals

that the life history of the studied colonist population reflects a pioneer strategy associated with the invasion into a new environment.

During the pioneer phase of colonization and establishment of an invasive species, allocation of resources into early reproduction with high fecundity can be expected to occur in a trade-off against somatic growth and survival (Davis 2005; Burton et al. 2010).

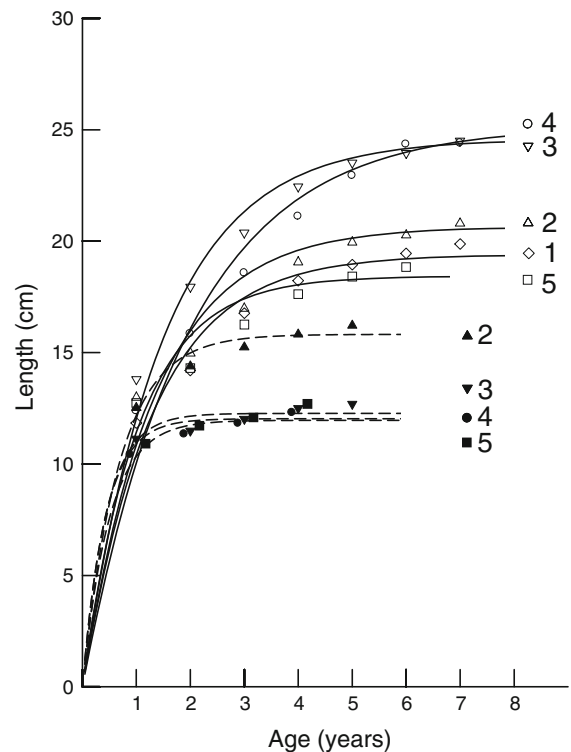


Fig. 4 Mean length at age and estimated von Bertalanffy growth curves for vendace from the source Lake Inari (open symbols solid lines) and colonist Lake Vaggatem populations (closed symbols stippled lines). Time periods as in Fig. 3

This was apparently the case in the colonist population of vendace, which has also been shown to have a much higher relative fecundity than vendace populations in the southern part of Norway (Bøhn et al. 2004). Such allocation of resources into reproduction supports the pioneer strategy hypothesis which describes species with many small offspring as more successful invaders (Rejmanek 1999; Richardson et al. 2000). In contrast, the source population displayed more characteristic *K*-selected traits such as higher age at first maturity and lower mortality rates, which typically are observed in later succession stages and in saturated communities (MacArthur and Wilson 1967; Gadgil and Solbrig 1972).

Our study provides strong empirical evidence for rapid changes in important life-history characteristics potentially enhancing the invasion of a new environment, with typical *r*-selected traits evidently playing a larger role in the life history of the colonist than of the source population. Several mechanisms may contribute to explain the observed patterns. First, the changes

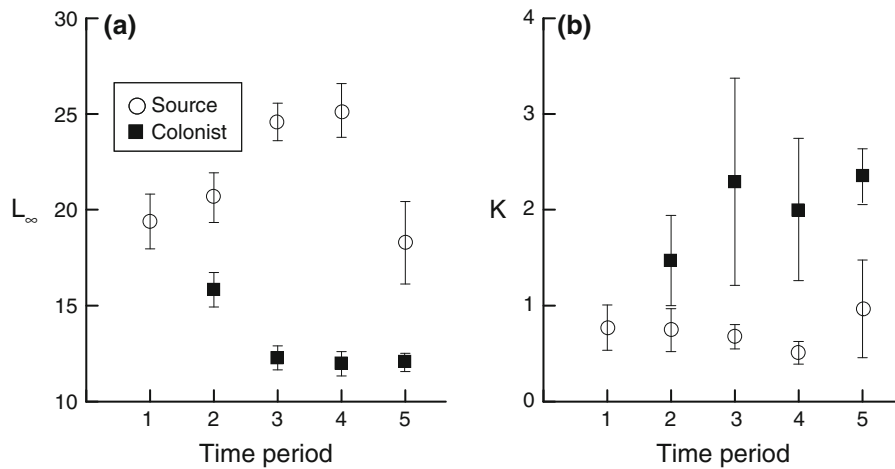


Fig. 5 Growth parameters including **a** asymptotic length (L_{∞}), and **b** growth rate to asymptote (Brody's K), estimated from the von Bertalanffy growth model for the source Lake Inari and

colonist Lake Vaggatem populations (time periods as in Fig. 3). Error bars show 95% confidence intervals

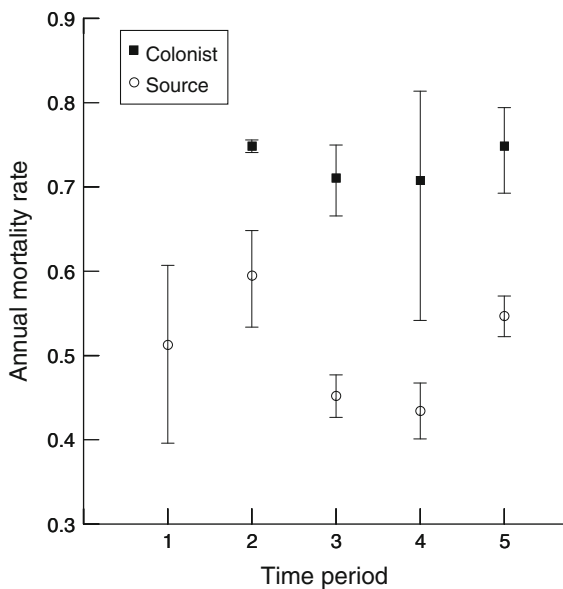


Fig. 6 Annual mortality rates for vendace older than 1 year in the different time periods in the source Lake Inari and colonist Lake Vaggatem populations (time periods as in Fig. 3). Error bars are 1 SE

in life history characteristics of the colonist population may reflect a high phenotypic plasticity. Second, the changes may be due to rapid natural selection during the colonization of the new environment. Third, founder effects during the invasion may have affected the genetic composition and performance of the colonist population. Fourth, differences in the relative

magnitude of important ecological interactions such as resource competition and predation regime may have favoured different life history strategies. Finally, potential differences in the abiotic and biotic environments between the source and colonist populations may be relevant for the observed life-history differences. We discuss each of these mechanisms in the following.

Certain life-history traits may predispose a species for rapid population expansion and thus enhance its invasiveness (McMahon 2002; Ruesink 2005; Vila-Gispert et al. 2005; Burton et al. 2010). The genetic structure of life history traits as well as high genetic diversity may in this respect provide a species with large phenotypic plasticity and/or a large potential for rapid evolutionary changes, i.e. high evolvability (Barret and Schluter 2008; Lee and Gelembiuk 2008), which both may be important during an invasion event (Sakai et al. 2001). Vendace is a flexible species in respect to changes in population ecology parameters (Sandlund 1992; Sarvala and Helminen 1995; Bøhn et al. 2004), and phenotypic plasticity is likely involved in the observed life-history differences between the source and colonist population. However, the colonist and source populations could be discriminated by a low but highly significant F_{ST} -value suggesting that founder effects as well as divergent natural selection may have influenced the colonist population, even over the short time span that has elapsed since the invasion occurred (comparable

to about 8–10 generations). Recent studies have emphasised the potential for rapid evolutionary processes in fish and other organisms (Reznick et al. 1997; Hendry et al. 2000; Hairston et al. 2005; Carroll et al. 2007), and there appears to be a strong association between rapid evolution and colonization events like species introductions and invasions (Reznick and Ghalambor 2001; Lee 2002; Whitney and Gabler 2008). Thus, given the large selective pressure that a new environment may induce (e.g. Suarez and Tsutsui 2008; Whitney and Gabler 2008) and the short generation time and fast population growth and development of the invading vendace, rapid evolution may be an important mechanism for the observed life history changes. Such a scenario of rapid evolution during the invasion may in particular be related to the observed differences in age at reproduction between the colonist and source populations. Age at sexual maturation is known from experimentally induced life-history evolution (Reznick et al. 1990) and fish farming developments (Gjedrem 2000) to have a hereditary component and may thus be subject to strong selection pressure during a colonization event. Within a founder population, young animals that reproduce will proliferate much faster than animals reproducing later, unless there is a strong trade-off in e.g. predator susceptibility or competition for resources that reduces the survival probability of the offspring of young reproducers (e.g., Reid et al. 2010). Hence, if age at first-time reproduction (i.e., 1- vs. 2-year old fish) has a genetic component in vendace, the *r*-selected, early maturation strategy is likely to become the dominant trait in the colonist population, just as observed in the present study.

Limited founder effects were detected in the colonist population as reduced number of alleles, private alleles and heterozygosity compared to the source population. Population bottlenecks are suggested to be a common feature of colonisation events, leading to reduced or modified genetic diversity compared to the source or native population (Tsutsui et al. 2000; Sakai et al. 2001; Novak 2007; Dlugosch and Parker 2008). A high propagule pressure (i.e., a large size of the founder population or a high number of consecutive founder events) will however reduce or eliminate founder effects (Lockwood et al. 2005; Novak 2007; Roman and Darling 2007). The genetic diversity in the colonist population was high and the reduction in number of alleles from the source population was only 12.5%,

suggesting that the founder population must have been a fairly large and random subset of the source population. Hence, any founder effects were likely of limited size and significance. The occurrence of private alleles and the observed genetic difference between the source and colonist population suggest that gene flow between the two systems has been limited following the initial displacement of vendace downstream from Lake Inari. Low gene flow between the two populations is to be expected as the presence of four hydropower dams between Lake Inari and Lake Vaggatem likely restricts the number and survival of downstream vendace migrants, and is an absolute barrier to upstream migration. The genetic difference between the two populations suggests that any subsequent invasions have not contributed significantly to the established colonist population, or alternatively that there is a strong selection pressure maintaining genetic difference between the populations. Moreover, vendace caught in Lake Vaggatem and other lake localities of the Pasvik watercourse have a limited size and age range relative to the Lake Inari population (Amundsen et al. 1999; Bøhn et al. 2004; this study Fig. 2), suggesting no or limited downstream displacement of vendace from Lake Inari after the initial invasion.

Large variation in vendace abundance has been observed in both the source and colonist populations, with fish densities varying more than an order of magnitude (Salonen et al. 2007; Bøhn et al. 2008). Due to different sampling methods, the fish density estimates are unfortunately not directly comparable between the source and colonist populations. However, within systems, fish density could be related to life-history traits. The highest density of vendace in the source population coincided with the lowest growth rates and the most rapid life history observed for this population. Similarly in the colonist population, the somatic growth rate declined and the life history accelerated following the rapid increase in vendace density during the 1990s (Bøhn et al. 2008, present study). Hence, within each locality the observed *trends* in life-history performance appear largely to be explained by variations in fish density and are thus probably a result of phenotypic plasticity. More remarkable, however, is that the two populations exhibited highly contrasting life-histories, which throughout the large density variations consistently were at different *levels*, with the colonist population constantly being representative of a more rapid (i.e., *r*-

selected) life-history strategy. These life-history differences suggest an evolutionary foundation with relative r - and K -selection as the dominant evolutionary forces in the colonist and source populations, respectively.

The source and colonist populations live in the same watercourse, and water chemistry, seasonal temperature development and other abiotic parameters are in general similar and likely not key explanations for the large differences in life-history strategies. There is, however, a large difference in surface-area size between the two localities (Table 1). Lake size per se has likely not induced the observed life-history differences between the populations, but contrasting lake morphometry may be a relevant factor. Lake Inari has greater mean and maximum depths than Lake Vaggatem, providing a larger deepwater predator refuge for the source population. However, a habitat shift to a deepwater refuge should expectedly induce reduced somatic growth rates of the vendace (Gjelland et al. 2009), which contrasts the present findings where the fastest growth rates were observed in the source population.

Extensive commercial fishery and more intensive stocking of large-sized salmonid predators in Lake Inari compared to Lake Vaggatem (Salonen et al. 2007) have likely induced a higher extrinsic mortality in the source than in the colonist population. This would expectedly reduce fish density and intraspecific competition and thus increase the somatic growth rates in the source population, which is in agreement with our observations. However, increased extrinsic mortality should also lead to earlier maturation and increased allocation of resources to reproduction (Reznick et al. 1996, 2004). Our data show the opposite pattern with later maturation and lower reproductive efforts in the source compared to the colonist population. This further supports our hypothesis that early reproduction in the colonist population is related to a pioneer strategy rather than representing an adaptation to certain characteristics of the new environment.

Our age estimates were obtained by scale and otolith readings in the source and invader populations, respectively. Potential bias in statistical inferences caused by differences between the two aging methods will depend on how they perform relative to each other. Comparisons of different aging methods for whitefish (*C. lavaretus*) have revealed that scale

reading underestimates age as compared to otolith reading, especially in older fish (Skurdal et al. 1985; Raitaniemi et al. 1998). In our study, the potential effect of such bias would be that the differences we have reported in growth and age at maturation between the source and colonist population are underestimated. Similarly, we may have underestimated the differences in mortality rates between the populations as potential scale-aging errors also would result in an overestimation of mortality rates in the source population (see Yule et al. 2008). However, as most of the vendace sampled in the present study were younger than 5 years, any bias related to the different aging methods should likely be of minor importance.

In conclusion, the strongly deviating life histories of the source and colonist populations demonstrate a remarkable ability of the invading species to respond to a new ecological situation within a few generations. The larger-sized individuals and lower mortality observed in the source population were replaced by small-sized individuals with early reproduction and high mortality in the colonist population, reflecting a shift towards an r -selected life-history. Our comparative study constitutes a unique in situ long-term data series, demonstrating that the invasion into a new environment can promote large and simultaneous changes in multiple life history traits. We suggest that the observed changes represent an adaptive pioneer strategy resulting in fast population increase during colonisation and establishment. This is supported by the colonist population's high number of eggs produced per gram female as compared to other Norwegian populations (Bøhn et al. 2004), and also by an extremely short generation time for a subarctic freshwater fish population, i.e. a typical "live fast and die young" strategy (Promislow and Harvey 1990). The specific mechanisms leading to the differences in life-history strategies between the source and colonist populations are difficult to discriminate, in particular because field studies rarely can fully control for differences between the compared environments. However, several causal mechanisms seem to act in concert with both phenotypic plasticity and natural selection as important contributors for the observed life-history responses of the invading species.

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