A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non-linear relationships?

JYRKI LAPPALAINEN*, ALI SERHAN TARKAN[†,1] AND CHRIS HARROD[‡,2]
*Department of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
†Istanbul University, Faculty of Fisheries, Laleli, Istanbul, Turkey
‡Department of Physiological Ecology, Max Planck Institute for Limnology, Plön, Germany

SUMMARY

1. We collated information from the literature on life history traits of the roach (a generalist freshwater fish), and analysed variation in absolute fecundity, von Bertalanffy parameters, and reproductive lifespan in relation to latitude, using both linear and non-linear regression models. We hypothesized that because most life history traits are dependent on growth rate, and growth rate is non-linearly related with temperature, it was likely that when analysed over the whole distribution range of roach, variation in key life history traits would show non-linear patterns with latitude.

2. As fecundity depends strongly on length, and the length structure of females varied among populations, latitudinal patterns in fecundity were examined based on residuals from the length–fecundity relationship. The reproductive lifespan of roach was estimated as the difference between age at maturity and maximum age of females in each population.

3. The three life history traits of roach analysed all varied among populations and were non-linearly related to latitude. Only the relationship between reproductive lifespan and latitude was a better fit to a linear that to a quadratic model, although Loess smoothing curves revealed that this relationship was actually closer to biphasic than linear in form. A latitude of 50°N formed a break point in all three life history traits.

4. The negative relationships we have described between (i) fecundity and reproductive lifespan and (ii) fecundity and egg mass suggest that lower fecundity is compensated for by longer lifespan, while lower fecundity is compensated for by an increased egg mass, when analysed independently of location.

Keywords: fecundity, growth, life history, reproductive lifespan, roach, trade-off

Correspondence: Jyrki Lappalainen, Department of Biological and Environmental Sciences, University of Helsinki, P. O. Box 65, FI-00014 Helsinki, Finland.

E-mail: jyrki.t.lappalainen@helsinki.fi

[1]Present address: Faculty of Fisheries, Muğla University, Kötekli 48000 Muğla, Turkey.

[2]Present address: School of Biological Sciences, Queen's University, Belfast BT9 7BL, UK.

Introduction

An optimal life history strategy is one that maximizes the lifetime production of offspring, determined by maximizing age-specific survival and fecundity (e.g. Roff, 1992). Life history theory predicts that high, variable or unpredictable juvenile mortality should result in decreased reproductive effort and increased lifespan, while high, variable or unpredictable adult mortality should be reflected in an increased reproductive effort early in life (Stearns, 1983). Species can

display trade-offs between the number of offspring (fecundity) and their quality (size) (Fleming & Gross, 1990) in such a way that a reduced number of offspring may be compensated for by an increased parental investment in offspring quality, e.g. increased egg size, which can result in enhanced post-hatching survival (Brown & Shine, 2005).

In ectothermic animals, such as fishes, reptiles and amphibians, growth rate is closely linked to environmental temperature, and the latter is negatively related to latitude in the northern hemisphere (New, Hulme & Jones, 1999; Vázquez & Stevens, 2004). Hence, these two relationships suggest that the growth rate of ectothermic animals should decrease with increased latitude. However, growth rate of fishes is not linearly related to temperature. Initially it increases almost linearly with temperature but, once it reaches an optimum, growth rate decreases rapidly and finally stops (Elliott, 1975). For example, the growth of European grayling (*Thymallus thymallus* L.) was reduced in a river section where water temperatures increased to the thermal tolerance limit for this species, and ultimately resulted in increased mortality (Mallet *et al.*, 1999; see also Jonassen *et al.*, 2000). Therefore, environmental temperature can be too high, and that then results in reductions in growth rate leading to non-linear and unimodal relations between latitude and growth, particularly towards the southern limits of distribution (Wilde & Muoneke, 2001). A decrease in growth rate early in life is usually associated with an increase in lifespan (Metcalfe & Monaghan, 2003), which should be especially advantageous in unstable environments. Because optimum temperatures for growth in cool and warm water fish are closer to the maximum rather than minimum tolerable temperature (Kitchell, Stewart & Weininger, 1977; Magnuson, Crowder & Medvick, 1979), the latitudinal range from optimum to maximum temperatures should be reduced relative to that from minimum to optimum temperatures. Thus, this suggests that several southern populations should be included in order to identify the possible decline in growth. Furthermore, comparisons should include populations from comparable altitudes, as Meisner (1990) demonstrated that the minimum altitude for brook trout [*Salvelinus fontinalis* (Mitchill)] in streams increased towards the southern limits of its distribution range.

Here, using information from the literature, we examine latitudinal variations in several life history traits of roach [*Rutilus rutilus* (L.)] throughout its range (36°N–71°N, 10°W–155°E) (Froese & Pauly, 2007). The roach represents a useful model species as it is an ecological generalist and is almost ubiquitous in Europe and Western Eurasia. Our principle aim was to examine variation in life history traits among populations, particularly with reference to the affect of latitude on such variation. As suggested by Reznick, Ghalambor & Nunney (2002), examinations of within-species variation across different populations are more likely to identify the actual drivers of life history strategies than those conducted on different species, even though the latter may show stronger variations. Inclusion of data from the entire distributional range should reveal the whole range of existing life history traits in roach. We predicted, first, that the life history traits should show non-linear patterns with latitude (e.g. Jonsson *et al.*, 1991) due to the postulated restrictions of growth near both the southern and northern limits of the range (Wilde & Muoneke, 2001). Second, we analysed two possible trade-offs between: (i) fecundity and egg size, and (ii) fecundity and reproductive lifespan, independently of the location of the population, and expected that, if there actually are trade-offs, then both these relationships should be negative.

Methods

Data and life history variables

We collated information on life history traits of roach from the literature, including data from a total of 27 populations in our analyses. Data on fecundity–length relationships in the literature are available either as individual length–fecundity data, length-grouped fecundity values or as simple means of fecundity and length in a population (Table 1). The smallest sample of females from a population in these studies was 14 individuals. All trade-off analyses were conducted among these 27 populations (Table 1). We incorporated two data sets in our growth analyses, one consisting of the data summarized in Table 1 and another from a review of variation in roach biology from Russia and adjacent areas (Kas'yanov, Izyumov & Kas'yanova, 1995). In

Table 1 Life history data of female roach and their literature sources. The relationship between absolute fecundity and length was based on individual data (I), grouped data (G), or mean values of fecundity and length (M). von Bertalanffy parameters (L_{as} and K) were estimated either from female lengths (fe) or from combined sex data (co). Egg size was either diameter (mm) (D) or mass (mg) (W). Reproductive lifespan of females (years) is based on difference between maximum age and age at maturity (X)

Site, country	Latitude (°N)	Altitude (m, asl)	Fecundity–length	Egg size	Von Bertalanffy	Reproductive lifespan	Source(s)
Gomishan wetland, Iran	36.90	0	M	D	fe	X	Naddafi et al. (2002b, 2005)
Anzali wetland, Iran	37.52	0	M	D	fe	X	Naddafi et al. (2002a, 2005)
Lake Sapanca, Turkey	40.00	30	G	D	fe	X	Tarkan (2006); Okgerman & Oral (2004)
Lake Volvi, Greece	40.66	37	G	–	co	X	Papageorgiou (1979)
Kakhovka Reservoir, Russia	47.50	53	G	–	fe	X	Spivak et al. (1979)
Middle Danube Delta, Slovakia	48.00	114	G	D	–	–	Bastl (1995)
Kličava Reservoir, Czech Republic	50.07	269	M	W	–	X	Pivnička & Švátora (1988)
Przecryce Reservoir, Poland	50.43	307	G	D	fe	–	Skóra (1972)
River Stour, England	50.80	<20	I	–	fe	X	Mann (1973)
River Pilica, Poland	51.00	<200	G	W	–	X	Penczak et al. (1977)
Lake Alderfen Broad, England	52.72	10	I	–	co	X	Cryer et al. (1986); Perrow et al. (1990)
Lake Tjeukemeer, Netherlands	52.83	–1	I	–	fe	X	Goldspink (1979)
Szczecin Firth, Poland	53.80	0	G	W	–	–	Peczalska (1968)
Kuybyshev Reservoir, Russia	54.00	50	G	D, W	fe	X	Kuznetsov & Khalitov (1978)
Lake Plußsee, Germany	54.17	24	I	–	co	–	Arzbach (1997)
Lake Gardno, Poland	54.65	0	G	D	fe	X	Hornatkiewicz-Żbik (2003)
Lake Lebsko, Poland	54.70	0	G	D	fe	X	Hornatkiewicz-Żbik (2003)
Lake Peipsi, Estonia	58.50	30	G	D	fe	X	Mitrofanova (1976)
Glengsholen, Norway	59.30	<25	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)
Vestvannet, Norway	59.34	25	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)
Saebyvannet, Norway	59.42	46	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)
Langnes, Norway	59.59	<100	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)
Fosterudbekken, Norway	59.64	33	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)
Vollebekken, Norway	59.69	33	I	W	fe	X	Vøllestad & L'Abée-Lund (1987, 1990)
Lake Saimaa, site 1, Finland	61.15	76	M	D	–	–	Karels et al. (2001)
Lake Saimaa, site 2, Finland	61.32	76	M	D	–	–	Karels et al. (2001)
Kyvann, Norway	63.42	183	M	W	fe	X	Vøllestad & L'Abée-Lund (1990)

Kas'yanov *et al.* (1995), age–length data (ages from 3 to 10 years) for both sexes, excluding those of semi-migratory forms, were used, and in both data sets only actual recorded lengths were analysed (i.e. back-calculated estimates of lengths were discounted). Egg size was considered as either the mean diameter or mass of mature ova. Reproductive lifespan was estimated as the difference between maximum age and the age of onset of maturity in each population (e.g. Reznick *et al.*, 2002). Additional life history data not shown in Table 1 were included in analyses dealing with latitudinal patterns in reproductive lifespan.

Statistical analyses

All roach lengths (standard and fork length) were transformed to total lengths according to Papageorgiou (1979), Backiel & Zawisza (1988) or Vila-Gispert & Moreno-Amich (2000). Fecundity–length data were analysed simultaneously over all populations as:

$$\log(\text{absolute fecundity}) = a + b \log(\text{TL}), \tag{1}$$

where TL is total length in cm, a is the intercept and b is the slope. A mean residual fecundity estimate was calculated for each population (Table 1) based on Eqn 1. In all subsequent analyses using these mean residuals, the associated degree of freedom was reduced by the two already used in the fecundity–length Eqn 1 (see García-Berthou, 2001).

Parameters from the von Bertalanffy equation (Bagenal, 1978) were based on the equation:

$$\text{TL} = L_{as}\{1 - \exp[-K(\text{age})]\}, \tag{2}$$

where TL is total length in cm, L_{as} is asymptotic length, K is a growth constant and age is years. The full von Bertalanffy equation is $L_{as} \{1 - \exp[-K(\text{age} - t_0)]\}$, where t_0 is the age at which length is theoretically zero, but was not used because the non-linear fitting usually failed or gave non-significant values for t_0. Because we used only actual recorded female lengths, and not back-calculated estimates of lengths, comparisons of K or asymptotic length with estimates from studies using the full von Bertalanffy model or back-calculated estimates of lengths at age could be misleading.

In both Eqns 1 and 2, observations were weighted by the number of individuals in each length (Eqn 1) or

age group (Eqn 2) or, when mean values were used (Eqn 1), by the total number of females. A similar weighting was used with all analyses examining variation in the three main life history traits with latitude. However, in Eqn 2 applying data from Kas'yanov *et al.* (1995), we used the number of age-groups as a weighting parameter, as the number of individuals in each age-group was not reported.

Initially we evaluated latitudinal patterns in the life history traits using linear and quadratic models. The best model was selected based on the smallest value of Akaike's information criterion (AIC), which was calculated as:

$$\text{AIC} = -2\text{res log likelihood} + 2K_{AIC}, \tag{3}$$

where K_{AIC} is the number of model parameters. In addition to these comparisons, we used the Loess smoothing procedure (SAS, 2003) to evaluate whether the relationships between life history traits and latitude, or between two life history traits in trade-off analyses, followed an alternative pattern. Loess is based on a local regression technique in which i least squares regressions are fitted for neighbourhoods centred on a predictor value x_i, where data are weighted as an increasing function of their proximity to x_i. A smoothing parameter determines the neighbourhood size used and here it was chosen objectively using an automatic selection criterion based on the unbiased selection criterion AIC_C (SAS, 2003). Here, we selected the smoothing parameter objectively between 0.5 and 1.0. We selected this range as we aimed to identify general latitudinal patterns in the life history traits rather than more local ones (parameter values <0.5).

Results

All three principal life history traits analysed, fecundity, growth and reproductive lifespan, were significantly and non-linearly related with latitude (Figs 1–3). Both asymptotic lengths and the growth coefficient K revealed non-linear relationships with latitude (Fig. 2). At southern latitudes (<45°N), growth is rapid at younger ages, but slows with increasing age (seen as a lower asymptotic length). At mid-latitudes (45–55°N), growth is steady and a large asymptotic size is reached, whereas in northern latitudes (>55°N), growth is steady but asymptotic

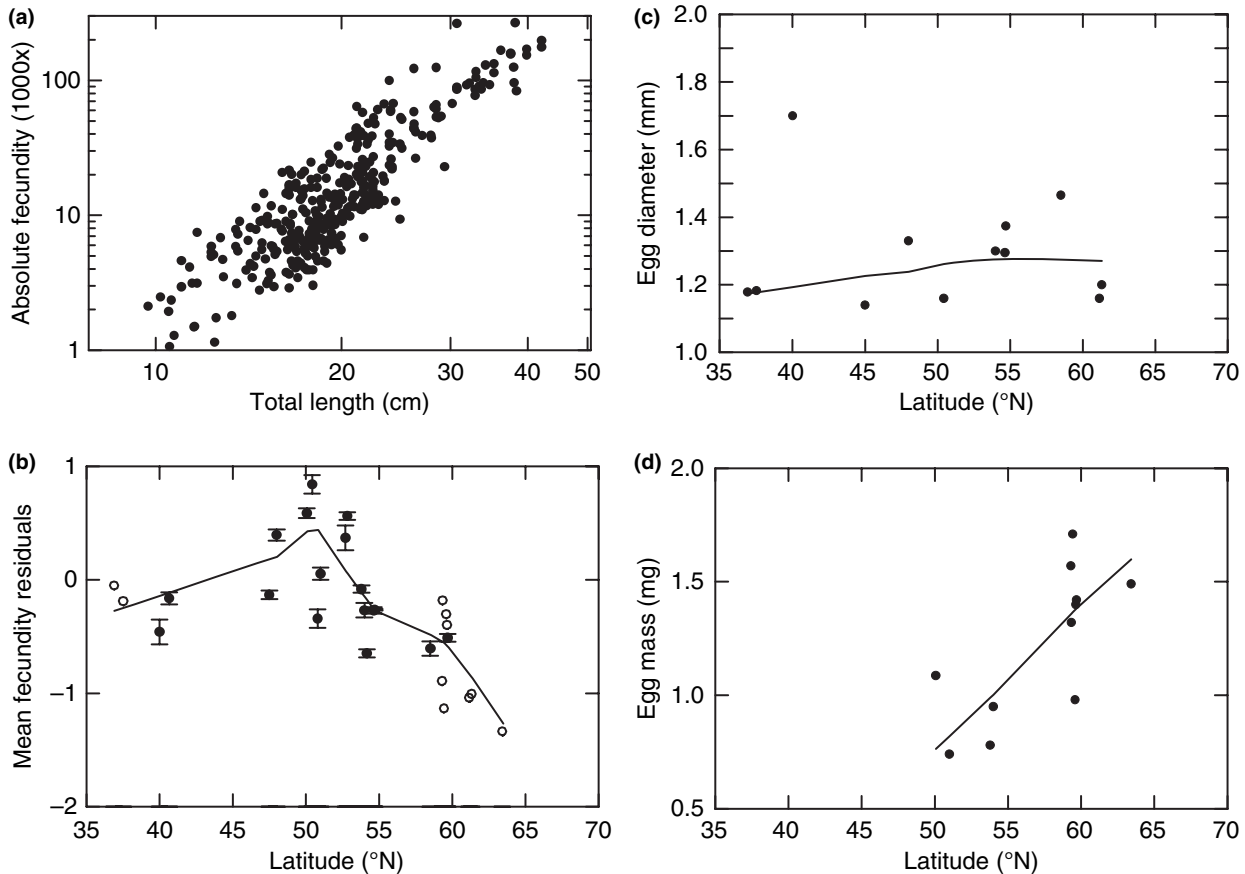**Fig. 1** Relationships between (a) total length (TL) and absolute fecundity (AF) ($r^2 = 0.80$, $P < 0.0001$, d.f. = 342; AF = −1.79 + 3.85 * TL), (b) mean fecundity residuals and latitude, (c) egg diameter and latitude, and (d) egg mass and latitude. Filled symbols with vertical bars are based on individual or grouped length data with standard errors, whilst open symbols in (b) are based on annual mean values. Solid lines are the predicted Loess function in (b), (c) and (d) (see Table 2 for Loess parameter values).

length is low and reached at an older age than in more southern latitudes (Figs 2 & 3).

Comparisons of AIC-values between linear and quadratic latitudinal equations revealed that two of the three life history traits were better described by a quadratic than by a line equation (Table 2). Based on AIC-values, only reproductive lifespan was better described by a linear equation. However, the Loess smoothed curves suggested a clear shift in all of these three life history traits at a latitude of 50°N (Figs 1–3).

The two possible trade-off mechanisms were analysed independently of population location. As hypothesized both trade-offs, between fecundity and lifespan (Spearman's rank correlation: $r_s = -0.565$, $P < 0.01$, d.f. = 19), and between fecundity and egg mass ($r_s = -0.791$, $P < 0.01$, d.f. = 9), were negatively correlated (Fig. 4).

Discussion

Our results demonstrated marked differences in the life history traits of roach among populations situated over a large latitudinal gradient. Two of the three main life history traits examined, fecundity and growth parameters, showed better fits to quadratic than linear effects of latitude. Predicted lines based on an objectively chosen Loess smoother indicated that all the life history traits examined here displayed break points close to a latitude of 50°N. Interestingly, values of fecundity and asymptotic length both became more similar towards both distributional limits. Decreases in fecundity were compensated for by a longer reproductive lifespan, whereas the observed increase in egg mass might represent a trade-off, reflecting decreased fecundity in populations located from 50°N northwards.
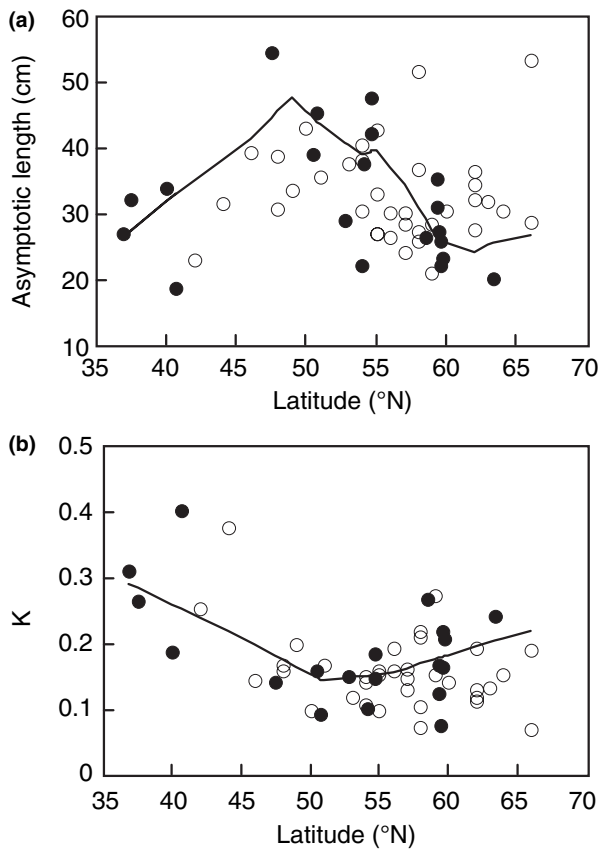
Fig. 2 Relationships between latitude and (a) female asymptotic length and (b) growth coefficient *K*. In (a) and (b) data for filled symbols are shown in Table 1, whilst open symbols relate to data from Kas'yanov *et al.* (1995). In (b) one outlier value of *K* in data from Kas'yanov *et al.* (1995) was excluded. The predicted Loess function (solid line) was fitted using an objectively selected smoothing parameter value of 0.51 (a), and 0.84 (b).

Latitudinal patterns in growth parameters

The non-linear relations shown between growth parameters and latitude is probably a consequence of the non-linear relationship between growth rate and environmental factors such as temperature (Kitchell *et al.*, 1977; Magnuson *et al.*, 1979). The decline in asymptotic length observed from 50°N northward may be linked to lower temperature, a reduced growing season and longer winters, while the decline southward might be associated with several environmental factors, including a temperature exceeding the optimal for efficient growth. Local adaptations to ambient temperature could reduce latitudinal variation in growth rate. For instance, certain species exhibit higher growth rates at high latitudes relative to those at low latitudes but at a
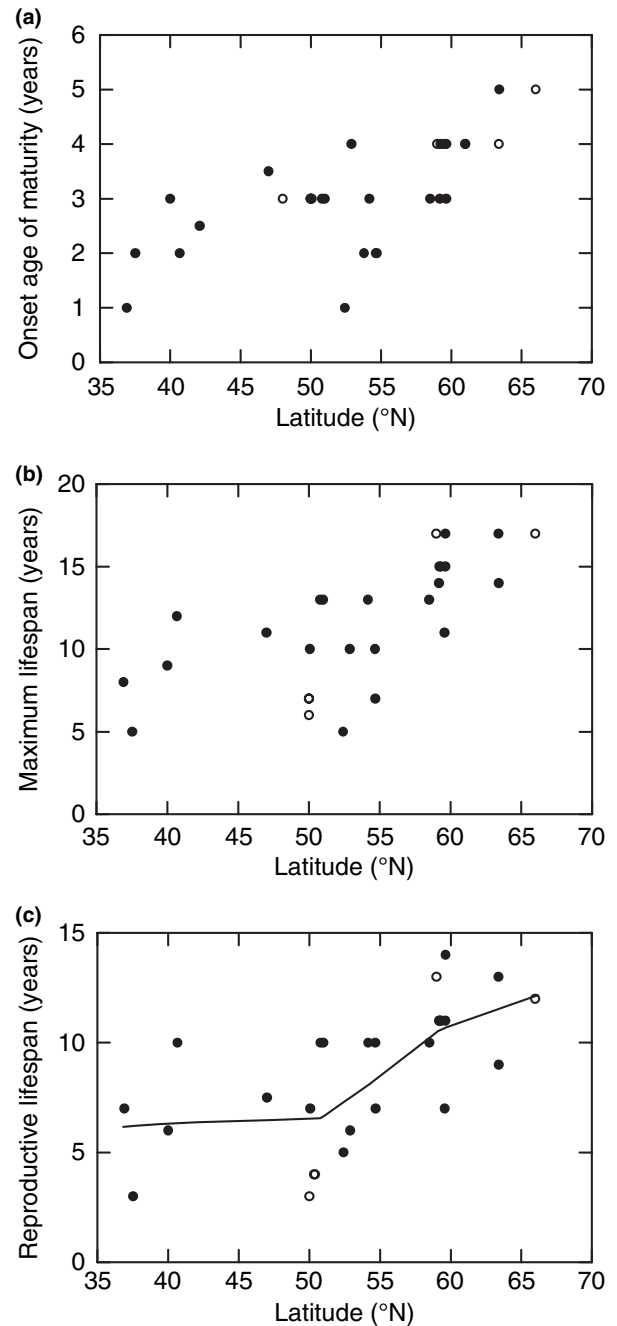

Fig. 3 Latitudinal gradients in (a) onset of maturity, (b) maximum age and (c) reproductive lifespan. The predicted Loess function (solid line) was fitted using an objectively selected smoothing parameter value of 0.83 (c). Filled symbols depict data shown in Table 1. Open symbols show additional data included from the following sources: (a) Lind & Kukko (1974); Hansen (1981); Libosvárský, Saeed & Nemcova (1985); Cowx (1990); Nyberg (1998); (b) Lind & Kukko (1974); Hansen (1981); Cowx (1990); Nyberg (1998); (c) Lind & Kukko (1974); Hansen (1981); Cowx (1990); Nyberg (1998).

Table 2 Linear and quadratic relationships between life history traits (LHT) and latitude (Lat). AIC is Akaike's information criterion value, and the best model is that showing the smallest AIC value (underlined). Loess was objectively chosen smoothing parameter between 0.5 and 1.0

Life-history trait (LHT)	Linear model (LHT = intercept + Lat)					Quadratic model (LHT = intercept + Lat + Lat^2)			
	r^2	P	d.f.	AIC	Loess	r^2	P	d.f.	AIC
Fecundity									
Mean fecundity residuals	0.13	>0.05	23	54.9	0.50	0.56	<0.001	22	<u>49.2</u>
Egg diameter	0.02	0.682	9	4.9	1.00	0.08	0.720	8	16.6
Egg mass	0.54	0.010	9	<u>9.1</u>	1.00	0.55	0.042	8	17.7
Growth									
Asymptotic length	0.02	0.291	54	490.9	0.51	0.46	<0.001	53	<u>464.5</u>
K	0.26	<0.001	52	−52.3	0.84	0.47	<0.001	51	<u>−53.7</u>
Reproductive lifespan	0.36	<0.001	25	<u>130.6</u>	0.83	0.42	<0.001	24	136.2

similar temperature (e.g. Conover & Present, 1990; Jonassen *et al.*, 2000). Conversely, some fish species may not show any thermal adaptation (Larsson *et al.*,

Fig. 4 Relationships between (a) mean fecundity residuals and reproductive lifespan of female roach and (b) mean fecundity residuals and egg mass (See Table 1 for references). The predicted Loess function (solid lines) was fitted using an objectively selected smoothing parameter value of 1 in both (a) and (b).

2005): unfortunately, thermal adaptation has not been studied in roach.

According to a review by Elliott (1981), the intake of food by roach is reduced markedly at water temperatures above 25 °C. In at least three of the four southernmost populations (Table 1), water temperatures exceeded 25 °C during summer months (Moustaka-Gouni & Tsekos, 1989; Morkoç *et al.*, 1998; Naddafi *et al.*, 2005). Elsewhere in their distribution, roach often utilize cool water refuges by descending deeper in the water column, but these lakes undergo hypolimnetic hypoxia during summer months or are so shallow that no refuge exists (Moustaka-Gouni & Tsekos, 1989; Morkoç *et al.*, 1998; Naddafi *et al.*, 2005). Such 'habitat squeeze' (e.g. Coutant, 1987; Mills *et al.*, 1990), where fish are restricted to unsuitable habitats (e.g. a warm epilimnion and an anoxic hypolimnion), may apply to other fish species and may reduce the accessibility of food, increase stress and reduce growth (Harrod & Grey, 2006).

Loess smoothers showed a break point in variation in residual fecundity, growth parameters and reproductive lifespan at latitudes close to 50°N. A theoretical explanation for such a relationship between life history traits and latitude, besides the hypothesized non-linear relationship between growth rate and temperature, could stem either from different optimum temperatures for growth or from differences between juveniles and adults in growth performance. Optimum growth temperatures are higher in juveniles than adults in some fish species (Jonassen, Imsland & Stefansson, 1999 and references therein), but not in all (Elliott, 1975). Kubecka (1994) reported that roach show a more or less linear relationship between
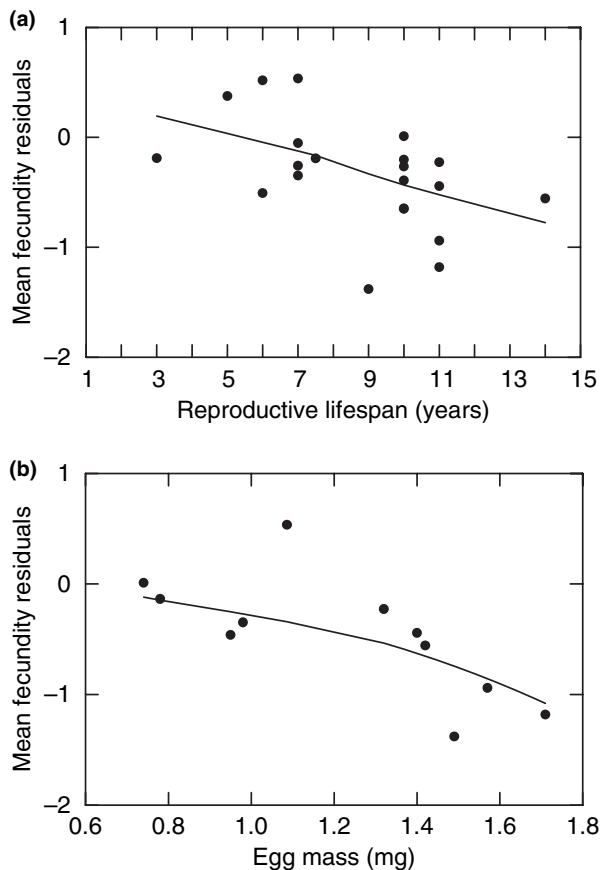
length at the end of the first growing season and latitude. Our findings are similar, as the observed patterns in growth parameters suggest that immature roach take advantage of warmer waters even at the southernmost sites (<45°N). However, this advantage may not be available to mature roach, as revealed by a reduced asymptotic length and shorter reproductive lifespan at these low latitudes.

Fecundity, egg size and trade-offs

Variation in the residual fecundity of roach followed a unimodal pattern with latitude, like that in asymptotic length. As female length is controlled for in fecundity residuals, the observed latitudinal pattern suggests that the condition of females should be highest at mid-latitudes (45–55°N), and that these individuals should be most fecund. In the literature, female fecundity is more often related to length than to mass, and therefore we could not analyse the possible effects of mass or condition on fecundity or on latitude.

Absolute fecundity and egg mass varied among the roach populations examined here. However, these traits can also vary at the population level, e.g. between years (Kuznetsov & Khalitov, 1978; Backiel & Zawisza, 1988; Pivnička & Švátora, 1988). According to Backiel & Zawisza (1988), annual differences in fecundity–length relationships increased from the intra- to the inter-population level, and were further amplified when estimated over the whole distribution range of roach. They suggested that these variations were probably connected to climatic and lake-specific factors. They were unable to relate variation in fecundity with egg size due to data limitations. However, based on the results of Kuznetsov & Khalitov (1978), both diameter and mass of eggs can display interannual variation even in similar-sized roach. Their data showed that egg mass first increased in relation to age, but subsequently decreased among the oldest females. A similar pattern of egg mass with age was reported for roach by Pivnička & Švátora (1988).

In our comparisons, reproductive lifespan displayed an inverse unimodal relationship with latitude, different to that shown for fecundity residuals. Hence, there was an apparent trade-off between fecundity and lifespan over the distribution range of roach, a relationship that was maintained when the data were analysed independently of location. When the growth coefficient was low, particularly near the northern edge of the range, the corresponding reproductive lifespan was extended. This fits closely with results presented by Britton (2007) for roach in UK. He showed a linear positive relationship between growth coefficient K and instantaneous mortality of roach, which in turn reflects the prediction of Metcalfe & Monaghan (2003) that growth rate and lifespan should be negatively correlated. The observed increase in egg mass from latitudes of 50°N and northwards could represent a trade-off for the observed reduction in fecundity. However, since no egg mass observations were available from southern populations (<50°N), the existence of a potential trade-off between egg mass and fecundity over the whole range of roach remains unclear. Nonetheless, egg mass and residuals of fecundity were negatively correlated, suggesting a trade-off between these two traits, at least in those populations where both variables were recorded. To our knowledge, the possible positive effect of increased egg mass on the subsequent survival of larvae or juveniles of roach has not been studied in roach. However, egg mass and subsequent larval survival is positively related in many species; although optimal size can vary depending on a number of factors, including the density and patchiness of prey (Sogard, 1997).

The latitudinal patterns we have shown between fecundity and growth in roach resemble those shown by Heibo, Magnhagen & Vøllestad (2005) for Eurasian perch (*Perca fluviatilis* L.). Heibo *et al.* (2005) suggested that the trade-off function for somatic and gonad growth differs along the latitudinal gradient in perch. Our data further suggest that there could be a latitudinal break-point in this trade-off function.

In conclusion, our analyses revealed that all the principal life history traits we examined showed non-linear variation with latitude. Interestingly, values for these traits converged towards both the northern and southern distributional limits. Trade-offs between fecundity and reproductive lifespan, and fecundity and egg mass were not only apparent across the latitudinal range we examined, but were also apparent when analysed independently of location. Our results show that, if a study aims to analyse intra-species patterns in life history traits, one should include multiple populations from similar latitudes in order to provide more reliable estimates of the traits, due to the large variation

typical of life history traits. The same applies also to inter-species comparisons.

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