

Effect of initial size on daily growth and survival in freshwater *Chondrostoma nasus* larvae: a field survey

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Effects of initial size on the growth and survival of a freshwater fish, *Chondrostoma nasus*, were tested in a field survey, where individually tagged larvae were introduced into a potential nursery habitat. Characteristics of individual daily growth trajectories were utilized as a basis to explain growth, as well as survival patterns, in relation to ontogeny. Initial size only affected growth rates during the larval phase. Survival patterns could not be explained solely based on size-selective mortality processes because prey–predator interactions played a major role as well. This is confirmed by the Lande–Arnold selection model because directional, as well as stabilizing gradients, showed significant values. Thus, for the 0+ year freshwater fish, inherited size-specific effects were a significant advantage for growth performance and survival in early ontogeny. As fish grew older, however, other effects such as compensatory growth and prey–predator interactions apparently gained in importance.

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Key words: growth trajectories; initial size; Lande–Arnold selection model; ontogeny; otolith; 0+ year fish.

INTRODUCTION

Growth processes in fishes reflect numerous internal and external effects (Brett, 1979) and are therefore a good lifelong indicator for fitness of individuals or populations. Regarding internal effects, many studies focus on the physiological (Kamler, 1992; Wootton, 1998) and ontogenetic component including heritability (Fuiman & Higgs, 1997). Furthermore, external forces, such as intraspecific or interspecific interactions (*e.g.* competition and predation) (Litvak & Leggett, 1992; Pepin *et al.*, 2003) and environmental factors (*e.g.* temperature and food supply) (Elliott, 1976; Keckeis & Schiemer, 1992; Jones, 2002) have a significant impact. Especially for young-of-the-year (0+ year) fishes, growth is crucial and can determine the individual's survival.

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Egg size is a well-documented factor related to female traits such as maturity, body mass and nutrition during ovarian recrudescence (Brooks *et al.*, 1997; Trippel *et al.*, 1997; Shimada *et al.*, 2007). It has been demonstrated that fitter females produce larger eggs (Brooks *et al.*, 1997; Solemdal, 1997). These maternal effects (genetic and non-genetic) are reflected in the progeny's attributes (Kamler, 1992; Chambers, 1997). Brooks *et al.* (1997) demonstrated that larvae from larger eggs are larger at time of hatching, due to greater yolk reserves and show faster growth rates. Bertram *et al.* (1993) reported that in marine fishes, fast-growing larvae are larger-at-age, develop more quickly, spend less time in periods or sizes of high vulnerability to predation and generally suffer lower mortality (Chambers & Leggett, 1987; Houde, 1987).

Few studies, however, have investigated for how long these maternal effects have an effect on ontogenetic processes. For example, Blanc (2002) found no effects of egg size on juvenile growth performance in rainbow trout *Oncorhynchus mykiss* (Walbaum). According to Gisbert *et al.* (2000), an influence of egg size on growth is evident until 20 days post hatch (dph) in Siberian sturgeon *Acipenser baerii* Brandt, being a larger egg, however, did not provide any survival advantage. Chambers *et al.* (1988) argued that size advantages gained by fast growth during the larval period were extended to the early juvenile period in winter flounder *Pseudopleuronectes americanus* (Walbaum). In a subsequent study, Bertram *et al.* (1993) showed that larval size advantages were lost in the early juvenile period. All these studies underline the importance of initial size because size-dependent and growth-dependent processes are known to directly affect survival and reproduction (Bertram *et al.*, 1993). This is well documented for marine systems and aquaculture, but it is poorly investigated in freshwater systems.

The species under investigation in the present study was *Chondrostoma nasus* (L.), a characteristic endangered riverine fish species for the lower rhithral ('grayling zone') and the upper potamal ('the barbel zone'), especially in the Austrian Danube and its tributaries. This species has been the focus of recent research and applied studies in investigations of the river ecology and functional integrity of European river systems (Lusk & Peñáz, 1995; Keckeis & Schiemer, 2001). Schiemer & Waidbacher (1992) found that this 'rheophilic A' species performs spawning migrations in spring. Upon hatch, the offspring inhabit tributaries and shallow inshore areas of large rivers, where they feed mainly on zooplankton and detritus (Reckendorfer *et al.*, 2001), whereas juveniles and adults feed on benthic epilithic algae (Kottelat, 1997). River engineering measures have negatively affected *C. nasus* reproduction success and recruitment, severely reducing the populations (Lusk & Halačka, 1995; Keckeis *et al.*, 1996a; Kirchhofer, 1996) in many European rivers. Its physiology is well documented during ontogeny. Several studies have investigated characteristics of eggs (Lusk & Halačka, 1995; Kamler *et al.*, 1996) and of the early larval phase (Keckeis *et al.*, 1996b, 2001; Kamler *et al.*, 1998). The relationship between maternal characteristics and egg size, and egg size and larval size, respectively, has also been described for *C. nasus* (Keckeis *et al.*, 2000; Kamler & Keckeis, 2001); a significant positive relation between female age and size and egg size was observed (Keckeis *et al.*, 2000). These findings served as a basis for the present study to define maternal effects in terms of initial size. Individual data

of the offspring of large as well as small-sized females have been used to analyse any advantages of these maternal effects concerning fitness factors. If advantages for certain initial size classes occurred, the endurance of this bonus as well as the governing selection mechanisms were evaluated.

The aims of the present study were determining the effect of maternal attributes on growth rates and survival, describing how growth rate and survival change with ontogeny, and determining how long maternal effects last and assessing the implications for selection. For this purpose, the close linkage between maternal and larval traits in early ontogeny was used as a basis. Effects of larval attributes, expressed as initial size, on growth and survival patterns were monitored under natural conditions. Individual daily growth rates have been calculated by means of daily otolith-increment formation at various ontogenetic stages. On the basis of this data set, growth patterns for small and large-sized fish at different ontogenetic stages have been analysed. Characteristics of these daily growth trajectories (intercepts and slopes) have been used in a selection model (Lande & Arnold, 1983) to describe the observed survival patterns regarding initial size.

MATERIALS AND METHODS

SAMPLING DESIGN

Parental fish

Nine females and 13 males were obtained from a natural spawning population of the Fischa River (south-east of Vienna) by electrofishing. The age of the 22 fish ranged from 6+ to 13+ years. Mean \pm s.d. total length (L_T) of females was 471 ± 33 mm and of males 443 ± 45 mm. The mean \pm s.d. mass was 1253.1 ± 298.2 g for females and 942.9 ± 284.7 g for males. Mean \pm s.d. calculated number of eggs per female was $12\,220 \pm 12\,158$ resulting from a mean \pm s.d. gonad mass of 121 ± 113 g. Females were separated into small and large individuals. As *C. nasus* show promiscuity, each female was fertilized with sperm of three males to balance out paternal effects. The applied procedure also resembled the best natural spawning conditions (Peñáz, 1996).

Rearing of larvae

The eggs were fertilized artificially and reared under a 14L:10D regime, and a temperature gradient from 13 to 17°C (mean \pm s.d. = 15.7 ± 1.1 °C) resembling the natural temperature regime. Time of hatching ($\tau = 0$) was on day 13 post fertilization (hatching success was 90%). Afterwards, larvae were fed with *Artemia salina* nauplii *ad libitum*. Fish (c. 50 000) in the second larval stage (Peñáz, 1974) were released at 21 dph. The mean \pm s.d. larval size was 13.00 ± 1.33 mm L_T and 0.009 ± 0.001 g in fresh body mass.

Otolith marking

Otolith marking was necessary to distinguish the period spent in the laboratory from that in the field and the different female classes. The offspring of small females were marked once and those of larger females were marked twice. Marking was applied by short-term mass-marking using Alizarin Red Sigma® (ARS; Sigma-Aldrich Inc.; www.sigmaaldrich.com) (Beckman & Schultz, 1996). This marking dye was incorporated in the otolith structure due to osmotic shock and showed a red light emission at a wavelength from 510 to 560 nm.

Field sampling

The study was conducted in the artificially modified wetlands of the Wien River, an urban tributary of the River Danube (Vienna, Austria). After restoration, this area represents a potential nursery habitat for *C. nasus* (Bartl & Keckeis, 2004). The fish were released near the surface in the system. A randomized sampling design was applied to get 134 sampling points for microhabitat studies near the shore, as 0+ year fish prefer these warm, shallow, richly structured areas (Schiemer *et al.*, 1991). After 2 days, the first point-abundance-sampling (Persat & Copp, 1990) was carried out, with subsequent samplings at 1–2 week intervals (see Table I). At each sampling point, marked by buoys, different habitat variables, fish community composition and fish densities by the means of electrofishing were recorded (Bartl & Keckeis, 2004). For data of the seasonal growth period (a year time span) the removal method (DeLury, 1947) was applied (representing seasonal growth data in Table I). *Chondrostoma nasus* were killed by an overdose of anaesthetic (MS-222) and then preserved frozen by a freezer immediately after collection. In the laboratory, L_T and body mass of 0+ year fish were recorded shortly after capture. All recaptured fish were used for otolith analysis. Water temperature was recorded at hourly intervals using Diligence[®] data loggers (Comark Ltd; www.comarkltd.com)

OTOLITH PREPARATION

Otoliths are often used to reflect daily growth patterns in larval fishes (Stevenson & Campana, 1992). Due to the linear relationship between otolith size and L_T , length at a certain point in time can be backcalculated, and growth rates over a longer period can be determined for each individual fish (Ricker, 1979). Lapilli were used because they are the only otoliths to show a concentric daily increment formation in cyprinids and are deposited from the very beginning of otolith formation. The lapilli were put in Epon[®] (Agar Scientific Ltd; www.agarscientific.com), an Araldite mixture, and analysed using an epifluorescence light microscope Nikon Eclipse[®] E800 (www.nikon.com) with Optimas[®] 6.2, software for image analysis. Three different lengths of the otolith were measured twice: (1) diameter 1, along the anterior–posterior axis, the longest measurable distance of the otolith; (2) diameter 2, the distance at an angle of 90° to diameter 1 passing the centre of the otolith and (3) the radius, defined as the distance from the centre to the edge of the otolith, lying in the largest of the four created quadrants in an angle of 45° (Fig. 1).

TABLE I. Number of recaptured and analysed *Chondrostoma nasus* during the 1 year study period. Daily growth analysis was conducted until 63 days post hatch (dph) [daily growth (DG) period], the seasonal analysis for the whole period [seasonal growth (SG) period]

Age at recapture (dph)	Recaptured fish	DG period	SG period
23	9		9
29	38	26	33
36	26	21	24
44	28	15	19
50	33	21	29
63	9	8	9
156	44		44
226	33		33
365	11		11

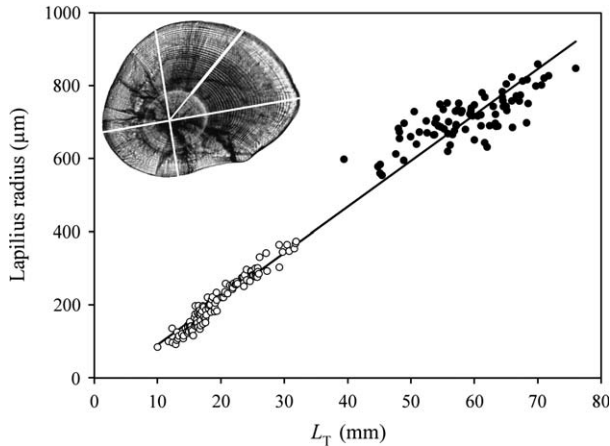


FIG. 1. The relationship between total length (L_T) and lapillus radius: the curve used for backcalculation was fitted by $y = 12.573 - 33.847x$ ($n = 202$, $r^2 = 0.98$, $P < 0.001$). Values are for the daily (○) and seasonal (●) growth periods. Otolith insert shows the measured distances; thick white line represents growth in the field, mark shows time at release. Only the daily growth periods were used for further investigation.

DATA ANALYSIS

Increase in L_T was backcalculated using a simple remodelled regression (Ricker, 1979) (Fig. 1). The regression formula is based on the whole data set [investigation period: May 2000 to April 2001, a seasonal growth period (SG) in Table I] of recaptured individuals, whereas only daily increments up to an age of 70 dph [daily growth period (DG) in Table I] were obtained for further analysis. Afterwards, the otolith becomes too thick for single increment determination. Therefore, only otoliths of *C. nasus* recaptured before the end of June (63 dph) were analysed for daily increment formation (Table I and Fig. 1). In this study, results of seasonal growth period were used to strengthen the findings of the daily period and discuss the observed patterns at a broader time scale.

Different size groups in females and larvae, respectively, were distinguished by means of a *t*-test design following the approach of a general linear model (GLM) (Bortz, 2005). The median L_T was used to separate these groups. *Chondrostoma nasus* smaller than the median were treated as 'small', ones larger than the median as 'large' fish. Larval initial size (L_T at time of release) was determined for each individual fish using a regression formula (Fig. 1).

Changes in growth patterns were analysed with respect to time (dph) and ontogeny (larval and juvenile phase) in early development. After determination of stages (Peñáz, 1974), larvae and juveniles were compared. For all comparisons based on a normal distribution *t*-tests were performed between the two groups, otherwise a non-parametric test, the Mann–Whitney *U*-test, was applied.

Specific growth rates (*g*) as a function of L_T were calculated after Wootton (1998) for each individual fish for each day as well as an average over the whole daily period. Growth patterns and seasonal abundance were described by linear or polynomial regressions, respectively.

Dependencies between abiotic factors (*e.g.* temperature) or biotic variables (*e.g.* age and L_T) and *g* were described with Pearson-*r* correlations. Single error probability was corrected after Bonferroni (Sachs, 1996).

An orthogonal quadratic regression as a selection model (Lande & Arnold, 1983) was applied to calculate selection patterns. This model represents a procedure to measure directional, stabilizing and disruptive natural selection. The following assumptions have

been met: (1) normality of the predictors (intercept and slope of individual growth trajectories) and (2) a longitudinal study design at time scale. The general formula is as follows: $\hat{W} = a_0 + a_1x_0 + a_2x_1 + 0.5a_3x_0^2 + 0.5a_4x_1^2 + a_5x_0x_1$, where \hat{W} is the fitness parameter, a_0 – a_5 are constants and selection indices and x_0 and x_1 represent the variables. Based on the partial regression coefficients and their significance the gradients are derived, i.e. a_1 and a_2 for the ‘directional selection gradient’; a_3 , a_4 and a_5 for the ‘stabilizing selection gradient’ representing the stabilizing, the disruptive and the correlative selection effects depending on the sign. A negative sign of the gradients indicates stabilizing effects, whereas a positive sign stands for the disruptive selection effects.

In order to construct the variables for the selection analysis, the following procedure was applied: in a first step, backcalculated individual L_T was transformed into a natural logarithm. Individual linear regressions were calculated for age (abscissa) and $\ln L_T$ (ordinate) (Fig. 2). After z -transformation (Z_i) intercepts (zb_0) and slopes (zb_1) of these regressions were used as variables for the model. The applied type of the model is as: $\hat{W} = a_0 + a_1zb_0 + a_2zb_1 + 0.5a_3(zb_0)^2 + 0.5a_4(zb_1)^2 + a_5(zb_0zb_1)$. Standardized age post-hatch ($\tau_1\tau_x^{-1}$) was used as the fitness component (\hat{W}), where τ_i represented age at certain

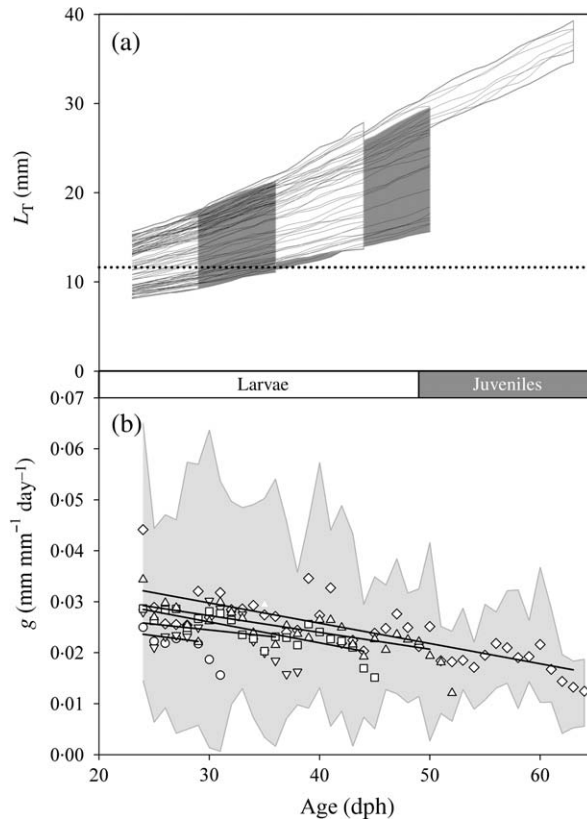


FIG. 2. (a) Daily increase in total length (L_T) of individual *Chondrostoma nasus* gained from back-calculation of lapilli radii; at different sampling dates [· · ·, the median of all initial sizes (11.6 mm); below this line, individuals are categorized as small, above as large-sized fish based on a t -test following a GLM approach]. (b) Daily specific growth rates (g) of individual *C. nasus*: daily means at different sampling dates [29 (○), 36 (▽), 44 (□), 50 (△) and 63 (◇) days post hatch, dph]. The range in g is given (▭). The curves were fitted by: 29 dph $y = 0.0304 - 0.0002x$, 36 dph $y = 0.0313 - 0.0002x$, 44 dph $y = 0.0383 - 0.0004x$, 50 dph $y = 0.0372 - 0.0003x$ and 63 dph $y = 0.0417 - 0.0004x$.

time and τ_x the mean age for the whole time period ($\tau_x = 40$). The significance of the model parameters was also tested by randomization (Edgington, 1987; Manly, 1997) with the package 'Computer Intensive Statistics' (Nemeschkal, 1999).

The differences of initial size groups in survival patterns were tested with a binominal test. All data analysis and statistical calculations were done with SYSTAT SPSS 12.0[®] and Sigma Plot 9.0[®] (SPSS Inc; www.spss.com).

RESULTS

The offspring of small (<435 mm) and large (≥ 435 mm) females (mean $L_T = 435$ mm; $P < 0.05$) showed no significant differences for either initial or final size, respectively, or growth patterns mean \pm s.d. initial: 11.86 ± 1.07 mm v. 11.57 ± 0.96 mm (t -test, d.f. = 205, $P > 0.05$); mean \pm s.d. final: 39.12 ± 18.86 mm v. 34.47 ± 20.58 mm (Mann-Whitney U -test, d.f. = 205, $P > 0.05$). So these two groups were pooled for subsequent analysis.

AGE-RELATED GROWTH

Fish showed a linear increase in L_T during the analysed daily growth period [Table I and Fig. 2(a)]. The range of final L_T declined from sampling date to sampling date. On 44 dph, a distinct 'incision' was found in the growth trajectories of the largest larvae. An increase in mean initial L_T of the recaptured fish was observed during the sampling period [Fig. 2(a) and Table II].

Individual g showed a sinusoidal pattern in terms of age [Fig. 2(b)]. The broad range reflected the highly adaptive and variable nature of these patterns. Trend lines of these growth rates clearly declined with age for each sampling date. For the whole daily period, mean g were negatively correlated with age ($r^2 = 0.60$, $n = 41$, $P < 0.001$), but positively correlated with water temperature ($r^2 = 0.44$, $n = 41$, $P < 0.01$). Temperature was characterized by a slight

TABLE II. Descriptive statistics (range and mean \pm s.d.) for initial and final total length (L_T) of *Chondrostoma nasus* during the daily growth period

Age at recapture (dph)	Range	Mean \pm s.d.	c.v.	n
Initial L_T (mm) at age 23 dph				
29	6.9	10.9 ± 2.2	20.1	26
36	7.0	11.9 ± 2.4	20.2	21
44	6.1	12.2 ± 2.2	17.8	15
50	6.5	11.4 ± 2.2	18.9	21
63	4.7	13.8 ± 0.9	6.4	8
Final L_T (mm) at given age				
29	8.3	12.6 ± 2.6	20.9	26
36	10.0	16.4 ± 3.7	22.7	21
44	14.1	20.5 ± 4.4	21.6	15
50	13.9	22.5 ± 4.7	20.7	21
63	11.8	34.7 ± 1.5	4.1	8

dph, days post hatch; n , number of individuals analysed.

seasonal increase over the daily period, with high daily fluctuations (mean \pm s.d. = $16.8 \pm 3.0^\circ$ C).

SIZE-RELATED GROWTH

Initial and final L_T showed a strong positive relationship at each sampling date (Fig. 3). During the first four sampling dates, the correlation between the two variables was highly significant ($r^2 = 0.99, 0.99, 0.91$ and 0.98 , respectively, $P < 0.001$), however, at the last sampling date, initial L_T no longer influenced final L_T ($r^2 = 0.19$; $P > 0.05$).

The two different size groups (small and large fish in terms of initial L_T) were distinguished by means of a t -test design following the approach of GLM. The median was used as a benchmark for group codes (mean = 11.60 mm; $P < 0.001$). Individuals less than the median represented small and those greater than the median represented large fish classes. This approach was needed to analyse size-specific effects on g in more detail.

For each individual, g rate for the first week after release was calculated regardless of the final age; this was then related to the individual's initial L_T . This relationship was highly significant ($r^2 = 0.16$, $n = 91$, $P < 0.001$) but explained only a small percentage of the variation (Fig. 4). Larger individuals in terms of initial L_T not only had a larger final L_T (Fig. 3), they also showed higher g (Fig. 4). Frequency distributions of g reflected that effect, as the two size groups clearly separated. Whereas large-sized fish had higher abundances and a maximum in upper growth rate classes (18.0% at 0.026 mm mm day $^{-1}$), smaller-sized fish showed peak abundance in the lower half (22.5% at 0.023 mm mm day $^{-1}$) (Fig. 4). These rates were also significant different between the two groups (t -test, d.f. = 89 , $P < 0.001$).

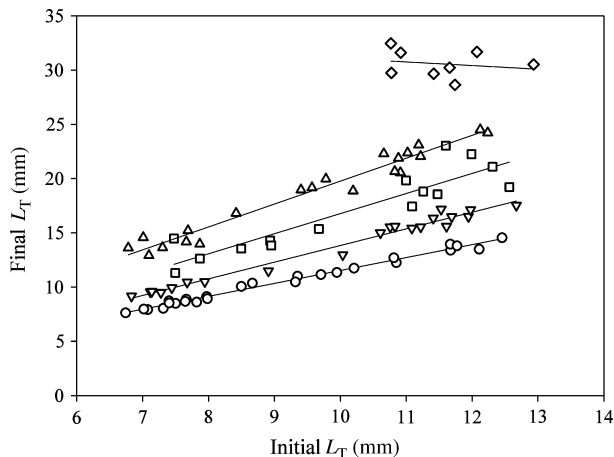


FIG. 3. The relationship between initial total length (L_T) and final L_T from individual *Chondrostoma nasus* caught on different sampling dates [29 (○), 36 (▽), 44 (□), 50 (△) and 63 (◇) days post hatch (dph), representing the juvenile stage]. The curves were fitted by: 29 dph $y = -0.375 + 1.191x$, 36 dph $y = -1.500 + 1.534x$, 44 dph $y = -1.745 + 1.853x$, 50 dph $y = -1.353 + 2.113x$ and 63 dph $y = -34.421 - 0.333x$.

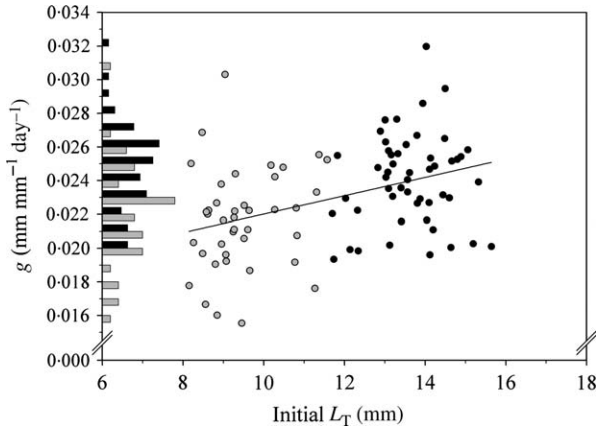


FIG. 4. Specific growth rates (g) in relation to initial total length (L_T) of small (○) and large (●) *Chondrostoma nasus* (L_T median = 11.6 mm) calculated over the whole daily period regardless of their final age. The curve was fitted by $y = 0.0005 + 0.017x$ ($r^2 = 0.15$, $n = 91$, $P < 0.001$). The frequency distributions of g of small (□) and large (■) fish are also given.

As initial L_T was closely related to final L_T (Fig. 3), the relationship between final L_T and g was also analysed. Growth rates over the whole DG period were plotted against final L_T . A dome-shaped relationship was found, which can be described by a quadratic function ($r^2 = 0.42$, $n = 91$, $P < 0.001$) (Fig. 5). Its maximum was at 26.78 mm, the transition from larvae to juveniles for *C. nasus* (Peñáz, 1974). No differences between the two initial L_T groups were found because fish had been analysed regardless of their age at time of recapture; accordingly, fish with large initial L_T caught earlier had a smaller final L_T than fish with smaller initial L_T caught on later sampling dates.

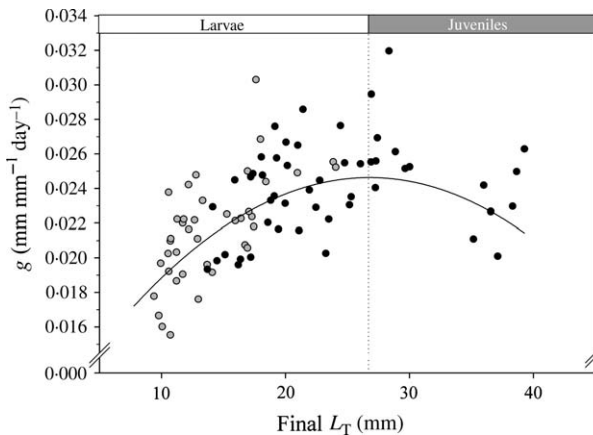


FIG. 5. Specific growth rates (g) in final total length of (L_T): small (○) and large (●) *Chondrostoma nasus* based on a t -test following a GLM approach. The curve was fitted by: $y = 0.00002x^2 + 0.001x + 0.010$ ($r^2 = 0.41$, $n = 91$, $P < 0.001$). (.) the maximum (first ablation) of this function ($x = 26.7$ mm).

For each sampling date, Pearson correlations were calculated between g and initial and final L_T , respectively (Table III). During the early larval phase, initial L_T had a positive significant effect on g . Larger larvae grew faster. Later larval stages were not significantly influenced by initial L_T , whereas juveniles showed a significant negative correlation with initial L_T . This was affirmed by the evaluation of the year-span data. Final L_T was always positively correlated with g during early ontogeny (Table III).

Overall, larvae had significantly higher g (mean \pm s.d. = 0.032 ± 0.010 mm mm⁻¹ day⁻¹; $n = 80$) compared to juveniles (mean \pm s.d. = 0.025 ± 0.003 mm mm⁻¹ day⁻¹; $n = 127$) (Mann–Whitney U -test, $n = 207$, $P < 0.001$). No significant differences between the two ontogenetic stages were seen in terms of initial L_T (larvae: mean \pm s.d. = 11.66 ± 0.97 mm, $n = 80$ v. juveniles: mean \pm s.d. = 11.38 ± 0.73 mm, $n = 127$; Mann–Whitney U -test, $n = 207$, $P > 0.05$).

SURVIVAL

To illustrate which initial L_T class would have a positive effect on survival, the percentage of large-sized fish was plotted against time (Fig. 6). The beginning of the study was characterized by a clear shift to large-sized fish; this increase was followed by a decrease by the end of the period.

Selection patterns, calculated after Lande & Arnold (1983) showed significant values for directional and stabilizing selection gradients (Table IV). A positive value in the directional selection gradient (a_1 and a_2) indicates an advantage for individuals starting growth from larger sizes. A negative sign in the stabilizing selection gradient (a_3 – a_5) indicating an influence of stabilizing effects, however, implies an advantage for individuals with average growing speeds.

ANALYSIS OF THE SG PERIOD

The observed patterns in growth and survival for the DG period were placed in the context of the patterns seen over a year's time span. In this way, an indication of the endurance of maternal attributes could be derived. G and initial L_T were highly negatively correlated for 156 dph ($r = -0.60$, $n = 40$, $P < 0.001$)

TABLE III. Correlations calculated between specific growth rate (g) of *Chondrostoma nasus* and initial and final total lengths (L_T), based on the daily growth analysis. Values present the significance, the sign the direction of the correlation. The significance level of $P = 0.05$ was corrected after Bonferroni to $P = 0.025$ for the single observations

Age (dph)	Developmental period		Initial L_T		Final L_T	n
29	Larvae	+	0.013	+	0.004	26
35	Larvae	+	0.001	+	0.000	21
42	Larvae	+	NS	+	0.023	14
49	Larvae–juveniles	+	NS	+	0.018	22
63	Juveniles	–	0.005	+	NS	8

dph, days post hatch; NS, non-significant.

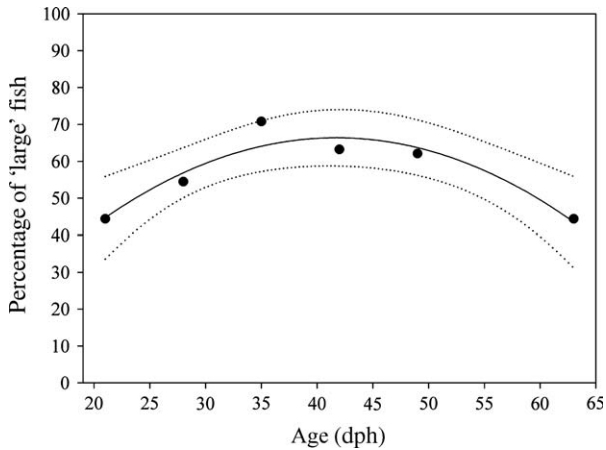


FIG. 6. Percentage of 'large' *Chondrostoma nasus* of the total catch in relation to age (days post hatch, dph) at different sampling dates. The curve was fitted by $y = -0.050x^2 + 4.207x - 21.372$ ($r^2 = 0.81$, $n = 6$, $P < 0.05$). The CL of the curve (···) are given.

as well as for 226 dph ($r = -0.70$, $n = 33$, $P < 0.001$) and 365 dph ($r = -0.63$, $n = 11$, $P < 0.01$), respectively.

In relation to survival patterns, the different percentage of initial L_T groups at 24 dph were compared to those at 365 dph. No significant differences could be observed (binominal test, $P > 0.05$; 24 dph: mean = 41.8%, $n = 9$; 365 dph: mean = 42.4%, $n = 11$).

DISCUSSION

A linear increase in L_T is often described during the larval phase in fishes (Ottera, 1993; Limburg, 1996). In the present study, individuals with larger initial L_T gained a greater final L_T during the larval phase. As significant correlations could not be observed in the early juvenile phase, no patterns of L_T

TABLE IV. Values and significance of the selection model after Lande & Arnold (1983), a_0 – a_5 are the model coefficients: a_0 , the model constant; a_1 and a_2 , the directional selection gradient and a_3 – a_5 , the disruptive to stabilizing selection gradient. The sign indicates the form of selection. Bonferroni corrections have not been made as the significant values (bold) do not exceed 0.05. The significance of the orthogonal quadratic function is 0.001, $r^2 = 0.16$

	Coefficient	Significance
a_0	1.003	0.000
a_1	0.083	0.005
a_2	0.053	0.060
a_3	0.026	0.125
a_4	-0.025	0.019
a_5	0.017	0.632

selectivity in terms of initial L_T were perceived from 156 to 365 dph. Initial L_T therefore only had an effect on final L_T during the larval phase.

Do large *C. nasus* merely remain larger during the early phase or do they actually grow faster? Based on the fact that larger larvae (in terms of initial L_T) have their maximum frequency in the upper growth rate categories, they not only stay larger, but they also grow faster. This demonstrates a clear effect of initial L_T on g . The general advantages of fast-growing larvae are that they are larger for a given age, resulting in quicker development (e.g. swimming ability and feeding mode), and being less vulnerable to predation, therefore suffering lower mortality (Chambers & Leggett, 1987; Houde, 1987; Litvak & Leggett, 1992; Bertram *et al.*, 1993; Pepin, 1993). This holds true for the early larval period. The relationship is reversed during the juvenile period. This reversed relationship in the late ontogenetic phase of 0+ year *C. nasus* suggests the occurrence of compensatory growth. The dome-shaped g in relation to final L_T strengthens this finding, as its maximum lies in the transition phase from larva to juvenile. According to Houde (1997), such patterns reflect ontogenetic shifts, which alter g until the transition phase, e.g. morphological transformations, due to changes in feeding mode or swimming behaviour. The transition L_T of *C. nasus* from larvae to juveniles is similar to that of other cyprinid species, e.g. 20–25 mm standard length (L_S) after 20–30 dph for common carp *Cyprinus carpio* L. (Vilizzi & Walker, 1999) and 19 mm L_T for roach *Rutilus rutilus* (L.) (Tong, 1985).

Many fish species exhibit phenomena of allometric growth (smaller fishes have higher size-specific growth rates) (Ali *et al.*, 2003) and compensatory growth (Wootton, 1998). These species facing severe shifts in their life-history patterns (e.g. settlement) or overwintering periods tend to exhibit flexible, compensatory growth patterns. In wild Ambon damsel *Pomacentrus amboinensis* Bleeker, an Australian pomacentrid, for example, small individuals show compensatory growth performance, which reduces the risk of size-selective mortality (Gagliano & McCormick, 2007). Furthermore, larger-sized fishes at settlement survive better than smaller-sized ones (Vigliola & Meekan, 2002; McCormick & Hoey, 2004). In *P. americanus*, Bertram *et al.* (1993) reported that larvae with high growth rates grew more slowly as juveniles and *vice versa*. Otherwise their overwinter survival would be impaired due to being below or exceeding of the favourable size. Survival advantages (e.g. vulnerability to predation) and favourable overwinter survival size are potential explanations for the observed compensatory growth patterns in *C. nasus*.

As initial size influences larval growth, the question arises whether survival is affected as well. Many studies illuminate the double-edged aspect of this issue (Pepin, 1991, 1993; Litvak & Leggett, 1992; Leggett & Deblois, 1994; Vigliola & Meekan, 2002; Kestemont *et al.*, 2003; Pepin *et al.*, 2003; Magnhagen & Heibo, 2004). On the one hand, larger larvae suffer lower mortality because they grow faster and attain experience (e.g. swimming and feeding mode) earlier than slower growing larvae (Litvak & Leggett, 1992; Pepin, 1993; Gaudin, 2001). On the other hand, they are more easily detected by (visual) predators because their encounter probability is much higher (Litvak & Leggett, 1992). The survival pattern of large-sized 0+ year *C. nasus* shows these two effects and is also confirmed by the calculated selection patterns. The shift to larger-sized *C. nasus*

early in the study period is consistent with the pattern of decreasing mortality with increasing body size (Kamler, 1992; Houde, 1997; Kristiansen *et al.*, 2000) which is also seen in the positive significance of the directional selection gradient. Accordingly, intraspecific competition declines and fishes are able to grow faster. As stated above, the larger they become, however, the greater the predation risk (Litvak & Leggett, 1992; Pepin *et al.*, 2003). Finally, higher predation pressure from piscivorous fishes [in the investigated system: brown trout *Salmo trutta* L., pike *Esox lucius* L. and pikeperch *Sander lucioperca* (L.)] and waterfowl (heron) as well as crows on larger larvae, causes habitat shifts in fish populations (Harvey, 1991; Urho, 1996; Gaudin, 2001; Magnhagen & Heibo, 2004). In this study, the significant values for the stabilizing selection gradient underline these findings for *C. nasus*. Thus, these two effects seem to compensate each other because no significant differences were observed in the percentage of large-sized individuals early *v.* later in the study period. This is confirmed by the analysis of the full year's data, where no significant differences could be shown between the two groups.

Compared to other freshwater species, *C. nasus* show many physiological traits in early ontogeny, which can be regarded as positively associated with survival, *e.g.* Kamler & Keckeis (2001) consider *C. nasus* to be a highly reproductive species characterized by relatively large eggs with thick capsules that prevent mechanical damage related to the shear stress in the bed sediments. The size at transition from yolk to exogenous feeding represents the second largest in cyprinids (Kamler & Keckeis, 2001). Specific growth rates in terms of energy of the early stages are twice as high as in salmonid species. This reflects on one hand the characteristics of their spawning mode, *C. nasus* are strictly lithophilic migratory species (Peñáz, 1996; Huber & Kirchhofer, 2001), and on the other those of their natural habitat (rheophilic, riverine species). Therefore, fast growth performance is necessary to maintain a high survival on the population level. The pattern revealed in this study, that maternal attributes have a significant effect on size-specific growth patterns as well as survival in the early ontogenetic phase, mirrors the above-mentioned characteristics of *C. nasus* in their early life history. Large larvae, in terms of initial size, had an advantage, as they did not only show higher final sizes but also they grew faster. This is based on the well-known size-specific effects of body size on consumption and growth rates (Keckeis & Schiemer, 1992; Kamler & Keckeis, 2001). The ability of food detection (Wanzenböck & Schiemer, 1989), the intake of larger food sizes (Flore *et al.*, 2000), higher swimming speeds (Wanzenböck, 1992; Flore & Keckeis, 1998) and prey capture success lead to faster growth. This is compensated for, however, as the fish grows older. Then, other effects such as compensatory growth and prey–predator interactions seem to gain importance.

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