REVIEW ARTICLE

Life-time growth patterns of pumpkinseed *Lepomis gibbosus* introduced to Europe, relative to native North American populations

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A b s t r a c t . The pumpkinseed *Lepomis gibbosus*, an omnivorous, nest guarding North American sunfish, was introduced into European waters about 100 years ago. To assess growth performance following introduction, we reviewed the available data for North American and European populations of pumpkinseed and compared the back-calculated age-specific growth for juveniles (standard length, SL, at age two) and adults (age two to five increment) as well as adult body size (SL at age five), von Bertalanffy growth model parameters and the index of growth (in length) performance (ϕ'). For continental comparisons of growth trajectory, mean growth curves for North American and Europe were calculated with the von Bertalanffy model using pooled data sets for each continent. Juvenile growth rate did not differ between European and North American pumpkinseed, but mean adult body size and adult growth rate were both significantly greater in North American than European populations. Adult body size decreased with increasing latitude (ANOVA) in North American populations, but this was not observed with adult growth rate. In contrast, adult body size tended to increase with latitude in European populations. Adult body size correlated significantly with ϕ'. The von Bertalanffy model described the overall growth patterns of North American and European populations reasonably well, but on the individual population level, length asymptotes were unrealistic (estimates that were > 20 % of the mean back-calculated size for the oldest age class) for a third of European populations and 80% of the North American populations. In contrast to North American pumpkinseed populations, somatic growth in European populations appears to be compromised by limited, but adequate, food resources, probably due to strong intraspecific interactions. This appears to be especially acute in adults, having potential ramifications for life span and reproductive allocation.

Key words: age-specific growth, growth increments, von Bertalanffy model, asymptotic length, introductions, acclimatisation, adaptation, growth performance index

Introduction

Among-population comparisons of growth in fish are a common and useful means to assess the adaptation of a species to different environmental conditions (e.g. Ž i v k o v et al. 1999) as well as the impact of human activities on fish populations (e.g. C r i s p & M a n n 1991). An animal species' potential to colonise new, or re-colonise previously occupied, ecosystems is

influenced by its ability to modify its allocation of energetic resources to somatic and gonadal growth in response to different environments. Probably the most extreme of adaptations in the animal kingdom is that of a species introduced to continents outside its native range. Amongst the most successful of such introductions has been that of the common carp *Cyprinus carpio* L. (W e l c o m m e 1988). Less successful on a global scale, but nonetheless widely distributed in Europe, is the pumpkinseed sunfish *Lepomis gibbosus* (L.). The native distribution of the pumpkinseed was originally restricted to eastern North America, where sunfishes are known to have existed since the Miocene (S c o t t & C r o s s m a n 1973). In the late 19th century, the pumpkinseed was introduced into European waters as a potential sport fish and/or as a garden pond fish (K ü n s t l e r 1908, R o u l e 1931, B a l o n & M i š í k 1956, d e G r o o t 1985).

The pumpkinseed received relatively little ecological investigation in Europe, with studies of growth limited in number (P a p a d o p o l & I g n a t 1967, T a n d o n 1977a, 1977b) until recently (C r i v e l l i & M e s t r e 1988, B r a b r a n d & S a l t v e i t 1989, F o x & C r i v e l l i 2001). Studies of northern European populations of pumpkinseed are particularly scarce (C o p p et al. 2002, K l a a r et al. 2004) despite a relatively wide distribution (L e v e r 1996; see also: www.fishbase.org). In southern Europe, the pumpkinseed is attracting increased scientific study (e.g. Z a p a t a & G r a n a d o - L o r e n c i o 1993, G o d i n h o & F e r r e i r a 1996, V i l a - G i s p e r t & M o r e n o - A m i c h 1998, G a r c í a - B e r t h o u & M o r e n o - A m i c h 2000a) as its range in the Iberian Peninsula expands rapidly, apparently to the detriment of indigenous fish species, mostly cyprinids (G o d i n h o & F e r r e i r a 1998, G a r c í a - B e r t h o u & M o r e n o - A m i c h 2000b).

In the present study, we review the available information on pumpkinseed growth in its native North American and introduced European ranges. The aim of this review is to compare somatic growth in the native and introduced ranges, and identify gaps in our knowledge of the pumpkinseed's growth adaptations to environmental conditions. Given the geographic patterns in growth trajectories of other fish species (e.g. M c C a u l e y & K i l g o u r 1990) and the tendency of adult body size to be largest in ectotherms living in colder climates (reviewed in A t k i n s o n 1994), we hypothesized that there would be latitudinal clines in somatic growth rates and body sizes of pumpkinseeds on both continents. Of particular relevance to our comparison are the potential intercontinental differences in the pumpkinseed's somatic growth characteristics, which could result from differences in the fish and invertebrate communities between the eastern North American region where native pumpkinseeds reside and the European continent where the species has been introduced.

Material and Methods

Data on back-calculated growth and annual growth increments, derived from scale analysis, of pumpkinseed from European and North American locations were extracted from published sources as well as from previously unpublished sources for populations in Europe for which data were less readily available. Aging and validation was carried out on populations we studied ourselves; all other data sources were assumed to have used followed these same standard procedures. We included data compiled by C a r l a n d e r (1977) for populations within the native North American range (i.e. within eastern and central N.A.). Some of these compiled data consisted of length-at-age means for a number of water bodies sampled from a U.S. state. Such data points were treated as single populations in all statistical analyses

except those of latitudinal clines from which they were excluded. We included data for populations only if length at annulus formation was given or could be estimated by length at capture at the beginning or end of the growing season, and if at least 5 age classes were observed, so as to avoid the inclusion of misleading growth parameters (due to short life span) and to permit calculation of an adult growth indicator (described below).

Comparisons between North American and European populations were made using back-calculated estimates of standard length (SL). Data given in total length (TL) or in fork length (FL) were converted to SL (nearest mm) using conversion factors given in the respective publications (or received from the authors). In all other cases, conversion factors from C a r l a n d e r (1977) were used: specifically $SL = TL/1.25$ and $SL = 1.04$ $FL/1.25$. We used length-at-age and mean annual increments taken from the difference in mean lengths at age for intraspecific comparisons of body size and growth (Ž i v k o v et al. 1999). To permit wider comparisons with existing literature, we also calculated the von Bertalanffy model (R i c k e r 1975) and the index of growth (in length) performance ϕ' (M u n r o & P a u l y 1983), which is derived using von Bertalanffy parameters ($\phi' = \log_{10}[k] + 2*\log_{10}[L_\infty]$, where k is the rate at which ultimate length, L_∞, is approached). ϕ' was reported by Ž i v k o v et al. (1999) to be one of few reliable growth indices for common bream *Abramis brama* L. All these parameters (and their standard errors) were calculated using the programme FiSAT (G a y a n i l o et al. 1994). However, a number of the pumpkinseed populations do not have asymptotic growth trajectories, and therefore, L_∞ and k parameters calculated with this equation can be unrealistic (see F o x 1994, Ž i v k o v et al. 1999). To ensure that our comparisons were not skewed by such data, we excluded populations with L_∞ greater than 20 % larger than the mean length of the oldest age-class in our Europe – North American comparisons of von Bertalanffy model parameters.

For continental comparisons of growth trajectory, mean growth curves for North American and European populations were calculated with the von Bertalanffy model using pooled data sets for each continent. The influence of environmental conditions on fish life history traits involves a complex of factors, and these influences can be masked because age explains the majority of annual growth rate variation (M a c e i n a 1992). Therefore, to compare somatic growth of European and North American populations, the SL at age two was used as an indicator of 'juvenile growth rate'. In the absence of age-at-maturity information for the some of populations available for comparison, and acknowledging that age-at-maturity is variable in both the native (F o x 1994) and introduced range (C o p p et al. 2002), this indicator was chosen because the majority of pumpkinseeds in both native and introduced populations (F o x 1994, F o x & C r i v e l l i 2001) have been found to achieve maturity during their third year of life (age 2 to age 3 increment), and would thus be considered adults. The increment between ages two and five was used as an indicator of 'adult growth rate', as this is the period in which 100% maturation would be achieved in most pumpkinseed populations (F o x 1994). SL at age 5 was used as an indicator of 'adult body size', as older fish were unavailable for comparison in many of the populations.

These growth indicators were compared between European and North American populations with Student's t-tests. Pearson correlation analysis was used to: 1) test our hypothesis that there are latitudinal clines in somatic growth rates and body sizes on both continents, and 2) test for intercontinental differences in the ontogenetic patterns of growth, based on growth increments (i.e. in size-structured populations juvenile and adult growth rates would not be correlated, as growth determinants are not the same). These relationships, using least-squares regression lines for graphical presentation, were examined separately

Table 1. Latitude and back-calculated standard lengths (SL) at age (A) of pumpkinseed populations from various sources in Europe(upper half) and North America (lower half). Data for populations of maximum reported age <5 are excluded.

Location	Lat (°N)	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	Source
Europe												
Tapada Pequena Reservoir (Portugal)	38	31	45	60	67	71	74					Godinho & Ferreira (1996)
Tapada Grande Reservoir (Portugal)	38	37	50	59	64	75						Godinho (2004)
Monte Novo Reservoir (Portugal)	39	43	65	81	88	92	96	99				Godinho (2004)
Divor Reservoir (Portugal)	39	45	60	70	80	85	85	85	90			Brabrand & Saltveit (1989)
Kerkini Reservoir (Greece)	41	61	73	84	93	101	109					Neophitou & Giapis (1994)
Lake Banyoles (Spain)	42	40	78	103	116	122	124	130				Fox & Vila-Giapert (unpublished)
Fumemorte Canal (France)	43	32	58	71	84	93	101	102				Fox & Crivelli (2001)
Sollac Marsh (France)	43	31	58	84	100	109	114	122				Fox & Crivelli (2001)
Dabas Pond (Hungary)	47	32	50	66	76	80						Tandon (1977a)
Danube (Slovakia)	47	39	67	87	103	117	128					Krupka (1973)
Cottesmore Pond (England)	51	27	37	49	56	63						Copp et al. (2002)
Odra River (Poland) (unpublished)	53	65	87	109	124	138	142	145				Heese & Przybylski
European means:		*40*	*61*	*77*	*88*	*96*	*108*	*114*	*90*			
North America												
Unspecified lake (North Carolina, USA)	36	29	53	82	106	136	154	187				Carlander (1977)
Multiple water bodies (Delaware, USA)	39	55	104	124	138	148						Carlander (1977)
26 ponds (Rhode Island, USA)	41	33	63	90	112	126	136	144				Carlander (1977)
Unnamed pond (Michigan, USA)	41	46	65	77	91	98						Bailey & Lagler (1938)
Lower Loch Alpine L. (Michigan, USA)	42	33	57	69	78	87	98	108				Carlander (1977)
Deep Lake (Michigan, USA)	43		32	45	75	93	108	120	134	136		Carbine & Applegate (1948)
Lower Dowsley Pond (Ontario, CAN)	44	31	61	87	104	120						Fox & Keast (1990)
Lake Opinicon (Ontario, CAN)	44	41	55	70	86	101	112	123				Fox & Keast (1990)
Upper Poole Pond (Ontario, CAN)	44	34	52	70	87	97						Fox & Keast (1990)
Houghton Lake (Michigan, USA)	44	30	60	95	133	158	172	180				Creaser (1926)
Flora Lake (Wisconsin, USA)	44	44	43	63	85	102	120	137				Parker (1958)

Table 1. continued.

Location	Lat (°N)	Mean back calculated SL at age (mm)										Source
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	
55 lakes (NW Wisconsin, USA)	45	45	64	84	104	119	123	137	147			Snow & Sand (1992)
Plastic Lake (Ontario, CAN)		45	25	48	66	82	99	120				Sun & Harvey (1986)
Crosson Lake (Ontario, CAN)	45	25	46	61	77	95	112					Sun & Harvey (1986)
Upper Beverly Lake (Ontario, CAN)	45	31	46	65	85	106	122	131	139	146		Deacon & Keast (1987)
Lower Beverly Lake (Ontario, CAN)	45	35	52	68	82	96	103	109	111	110		Deacon & Keast (1987)
Lac Vert (Québec, CAN)		46	27	42	57	71	84	102				Beaulieu (1979)
Multiple streams (North Carolina, USA)	N/A	27	61	86	104	122	158					Carlander (1977)
Multiple water bodies (Illinois, USA)	N/A	71	90	108	114	130						Carlander (1977)
Multiple water bodies Ohio, USA)	N/A	30	61	90	112	126						Carlander (1977)
14 water bodies (Pennsylvania, USA)	N/A	20	49	75	98	108	112	116	130	148	144	Carlander (1977)
Unspecified pond (New York, USA)	N/A	26	51	81	102	117						Carlander (1977)
Multiple water bodies (Minnesota, USA)	N/A	34	63	87	112	130	146	157	165	173		Carlander (1977)
Multiple water bodies (Minnesota, USA)	N/A	37	83	104	132	157	195					Carlander (1977)
North American means:		*35*	*60*	*82*	*100*	*116*	*130*	*137*	*136*	*144*	*144*	

Table 2. For pumpkinseed populations in Europe and North America, the location, latitude (Lat) and estimates of von Bertalanffy parameters (asymptotic lengths, L_∞ in mm; growth coefficients, k, t_0, maximum lifespan = maxL), the index of length growth performance (ϕ'), and the coefficient of determination (r^2) are given, where appropriate, with the standard error (SE). Underlined L_∞ values are not > 20% of the mean back-calculated SL of the oldest age class (i.e. potentially realistic asymptotic lengths), * indicate means derived using 'realistic' estimates only.

Location	Lat(°)	L_∞	SE	k	SE	t_0	SE	ϕ'	SE	r^2	maxL
Europe											
Tapada Pequena Reservoir (Portugal)	38	_81.3_	4.0	0.41	0.07	-0.151	0.195	3.43	0.45	0.995	5
Tapada Grande Reservoir (Portugal)	38	112.5	47.3	0.16	0.14	-1.482	0.983	3.32	0.91	0.897	5
Monte Novo Reservoir (Portugal)	39	_101.1_	1.3	0.50	0.03	-0.108	0.082	3.70	0.37	0.998	7
Divor Reservoir (Portugal)*	39	_91.1_	2.2	0.43	0.06	-0.550	0.241	3.56	0.42	0.989	8
Kerkini Reservoir (Greece)	41	163.5	7.1	0.13	0.01	-2.729	0.160	3.53	0.54	1.000	6
Lake Banyoles (Spain)*	42	_131.8_	1.7	0.57	0.04	0.367	0.054	3.99	0.36	0.998	7
Fumemorte Canal (France)*	43	_113.6_	3.9	0.34	0.04	0.013	0.120	3.65	0.59	0.997	7
Sollac Marsh (France)*	43	_133.5_	4.6	0.36	0.04	0.029	0.096	3.80	0.54	0.997	7
Dabas Pond (Hungary)	47	_94.9_	7.1	0.38	0.08	-0.059	0.186	3.54	0.45	0.996	5
Danube (Slovakia)	49	168.3	5.3	0.23	0.02	-0.158	0.059	3.82	0.54	1.000	6
Cottesmore Pond (England)	51	94.5	18.8	0.19	0.08	-0.721	0.343	3.23	0.39	0.996	5
Odra River (Poland)	53	_162.7_	7.2	0.31	0.05	-0.584	0.228	3.92	0.52	0.994	7
European means:		110.5*	9.3	0.40*	0.02	-0.194*	0.085	3.67	0.06	—	7*
North America											
Unspecified lake (North Carolina, USA, D167)	36	280.5	97.2	0.15	0.08	0.472	0.313	4.07	0.44	0.981	7
Multiple water bodies (Delaware, USA, H158)	39	_154.0_	4.9	0.63	0.08	0.287	0.097	4.17	0.32	0.997	5
26 ponds (Rhode Island, USA, S188)	41	_172.6_	5.7	0.27	0.02	0.247	0.071	3.91	0.58	0.999	7
Unnamed pond (Michigan, USA)	41	130.4	14.6	0.24	0.07	-0.802	0.289	3.62	0.57	0.997	5
Lower Loch Alpine Lake (Michigan, USA, K82)	42	142.8	23.5	0.18	0.06	-0.612	0.396	3.56	0.71	0.989	7
Deep Lake (Michigan, USA)	43	190.7	27.2	0.17	0.05	0.048	0.257	3.78	0.66	0.990	8
Lower Dowsley Pond (Ontario, CAN)	44	174.2	10.7	0.24	0.03	0.195	0.065	3.87	0.62	1.000	5
Lake Opinicon (Ontario, CAN)	44	184.5	33.9	0.14	0.05	-0.647	0.330	3.67	0.33	0.994	7
Upper Poole Pond (Ontario, CAN)	44	145.5	28.5	0.21	0.08	-0.212	0.254	3.65	0.28	0.996	5
Houghton Lake (Michigan, USA)	44	256.1	41.2	0.20	0.06	0.473	0.199	4.11	0.71	0.990	7
Flora Lake (Wisconsin, USA)	44	205.5	47.1	0.16	0.07	-0.327	0.388	3.84	0.39	0.993	6

Table 2. continued.

| Location	Lat(°)	L_∞	SE	k	SE	t_0	SE	ϕ'	SE	r^2	maxL
Welsh Lake (New Brunswick, CAN)	45	<u>123.3</u>	2.9	0.56	0.06	0.565	0.089	3.93	0.36	0.992	8
55 lakes (NW Wisconsin, USA)	45	195.7	19.1	0.16	0.03	-0.588	0.250	3.79	0.73	0.995	8
Plastic Lake (Ontario, CAN)	45	180.0	95.1	0.16	0.14	0.124	0.516	3.74	0.43	0.970	6
Crosson Lake (Ontario, CAN)	45	168.0	55.3	0.17	0.10	0.152	0.336	3.68	0.42	0.986	6
Upper Beverly Lake (Ontario, CAN)	45	219.0	31.3	0.13	0.03	-0.026	0.245	3.78	0.44	0.992	9
Lower Beverly Lake (Ontario, CAN)	45	<u>125.3</u>	5.8	0.26	0.04	-0.147	0.208	3.62	0.63	0.991	9
Lac Vert (Québec, CAN)	46	153.0	60.5	0.16	0.11	-0.054	0.447	3.58	0.50	0.982	6
Multiple streams (North Carolina, USA, D68)	N/A	237.0	104.1	0.17	0.12	0.312	0.385	3.98	0.56	0.978	6
Multiple water bodies (Illinois, USA, L129)	N/A	175.8	50.4	0.20	0.14	-1.639	0.972	3.79	0.73	0.988	5
Multiple water bodies Ohio, USA, R101)	N/A	189.0	19.8	0.24	0.05	0.289	0.097	3.93	0.35	0.999	5
14 water bodies (Pennsylvania, USA, M342)	N/A	<u>160.1</u>	11.5	0.23	0.05	0.393	0.229	3.78	0.64	0.982	10
Unspecified pond (New York, USA, S372)	N/A	175.5	37.8	0.24	0.09	0.386	0.179	3.86	0.32	0.995	5
Multiple water bodies (Minnesota, USA, M258)	N/A	213.4	6.3	0.19	0.01	0.014	0.074	3.94	0.70	0.999	9
Multiple water bodies (Minnesota, USA, S62)	N/A	292.5	117.4	0.17	0.12	0.211	0.385	4.16	0.54	0.981	6
North American means :		147.1*	9.8	0.39*	0.09	0.269*	0.118	3.28	0.60	—	8*

for European and North American populations. A post-hoc Analysis of Covariance with adult body size as the dependent variable, continent as the independent variable and latitude as the covariate was used to test whether intercontinental differences in latitudinal trend were significant. Differences in the parameters, L_∞ and k were assessed with Student's t-tests (unpaired). Other comparisons were undertaken with Student's t-test or its non-parametric equivalent (Mann-Whitney U-test). Differences are reported as significant when $\alpha = 0.05$, but probabilities of $0.05 < P \leq 0.10$ are also reported to increase the heuristic value of the analyses.

Results

Juvenile growth rate (SL at age 2) was highly variable in pumpkinseed populations from both continents, with the lowest value observed in Cottesmore Pond (England) and highest in water bodies of Delaware, USA (Table 1). Cottesmore Pond also had the smallest adult body size (SL at age 5) of any pumpkinseed population, whereas the Houghton Lake (USA) population had the largest adults. Juvenile growth rate did not differ between populations from the two continents ($t = 0.07$, df = 35, $P = 0.95$). However, both the adult growth rate and adult body size (Table 1) were significantly larger in North American populations ($t = 2.78$, $P = 0.0086$; $t = 4.13$, $P = 0.0002$, respectively).

Judging from the coefficients of determination (r^2), the von Bertalanffy growth model describes the overall growth patterns reasonably well (Table 2), but at the individual population level it overestimated L_∞ for populations from both continents, with 66% of estimates being realistic (our '20%' criterion) for Europe, but only 20% realistic for North America (Table 2). Further differences in the growth patterns of native and introduced pumpkinseed populations were revealed by their respective growth trajectories (Fig. 1). The lowest length asymptotes were in European populations, with the greatest European L_∞ value (Table 2) being less than half the mean value for North American populations (Table 3). Mean L_∞ was smaller for European than North American populations, but at 90% significance only, and other parameters of the von Bertalanffy growth model (all data included) did not show a significant difference (Table 3). However, based purely on realistic von Bertalanffy estimates (our 20% criterion), L_∞ was also significantly smaller ($t = -2.3$, df = 11, $P < 0.05$) for European (mean $L_\infty = 113.8$, SE = 9.6) than North American populations (mean $L_\infty = 147.1$, SE = 9.8). The growth performance index (ϕ'), which is derived using von Bertalanffy parameters, and adult body size were significantly correlated (Fig. 2) in Europe ($r = 0.923$, df = 10, $P = 0.0001$) and in North America ($r = 0.938$, df = 23, $P = 0.0001$), with mean ϕ' significantly lower (Mann-Whitney U-test, $P = 0.02$) in Europe (mean $\phi' = 3.624$, SE = 0.07) than in North America (mean $\phi' = 3.832$, SE = 0.04). Correlations between annual length increments revealed a major difference between continents in the relationship between growth in early and subsequent years. No correlation was observed between juvenile growth rate (SL at age 2) and that of adults (length increment from age 2–5) in North American pumpkinseed populations ($r = -0.119$, df = 23, $P = 0.571$), whereas these factors were significantly correlated in European pumpkinseed populations ($r = 0.60$, df = 10, $P = 0.04$). Closer examination, on an age increment basis, revealed that the trend in European pumpkinseed populations was due to a significant positive correlation between the older juvenile (age 1 to age 2) and young adult increments (Table 4). A change in growth rates of North American pumpkinseed populations is suggested by the significant negative correlation
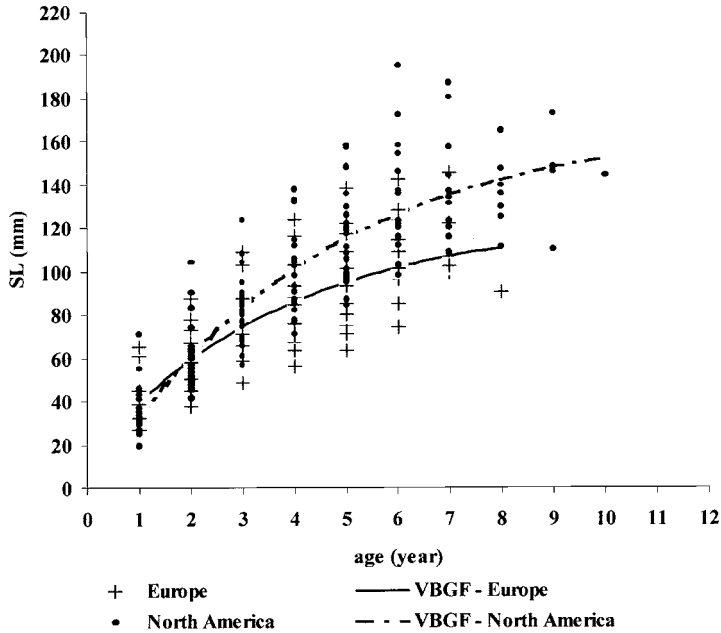
Fig. 1. Composite growth curves generated from pooled lengths at age, fitted with the von Bertalanffy growth model, for populations of North American and European pumpkinseed *Lepomis gibbosus*.

between young juvenile and adult (age 3 to age 4 increment) pumpkinseed (Table 4), which is followed by significant positive correlations between all adult age increments.

Latitudinal clines in juvenile pumpkinseed growth and body size parameters were not strongly evident in populations on either continent. Juvenile growth rate was not significantly correlated with latitude on either continent, although in North America, the negative relationship between these variables was nearly significant (r = -0.42, P = 0.087). In the case of adult growth and body size parameters, only the relationship between adult body size and latitude was significant, and in North America only (r = -0.48, P = 0.044). In

Table 3. Given for European and North American pumpkinseed populations (pooled data) from bibliographic sources (Table 1) are the total number of SL-at-age values included for each continent (n), the mean parameters and their standard errors for the von Bertalanffy growth model (asymptotic lengths, L_∞; growth coefficient, k; maximum lifespan, maxL), the coefficient of determination (r^2) for the von Bertalanffy growth models, and the index of length growth performance (ϕ').

	Europe	SE	N. America	SE	t	P
n	76		167			
L_∞ (mm SL)	128.1	19.8	168.6	12.8	1.7140	0.087
k	0.265	0.114	0.232	0.042	0.2116	0.786
ϕ'	3.640	0.712	3.819	0.639	0.1892	0.850
r^2	0.620		0.788			
maxL (years)	8		10			

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European populations, adult growth rate tended to increase with latitude, but the relationship was weak ($r = 0.49$, $P = 0.102$). However, what was more interesting was the tendency for adult body size to decrease with latitude in North America, but increase with latitude in Europe (Fig. 3). This intercontinental difference in latitudinal trend (continent by latitude interaction) was significant (ANCOVA: $F_{1,26} = 5.73$, $P = 0.024$). Further inspection of the European data showed that if the two pond populations are removed from the analysis, there is a strong positive relationship between latitude and adult body size ($r = 0.87$, $P < 0.0001$); the opposite of what is shown in North America.
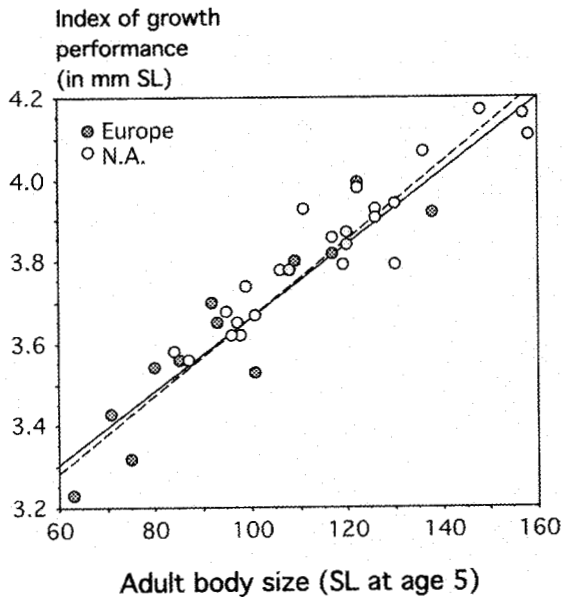
Fig. 2. Correlation between adult body size (SL at age 5) and ϕ', the index of growth performance (M u n r o & P a u l y 1983) for native North American (dashed line, open circles) and introduced European pumpkinseed (solid line, solid circles).

Table 4. Pearson correlations ($P \leq 0.05$, in bold and underlined) between mean annual length increments for European and North American pumpkinseed populations.

	A1–A2	A2–A3	A3–A4	A4–A5
Europe				
A0-A1	-0.03	0.07	0.13	0.40
A1-A2	—	**0.81**	**0.74**	0.19
A2-A3		—	**0.76**	0.23
A3-A4			—	0.50
North America				
A0-A1	-0.06	-0.27	**-0.42**	0.10
A1-A2	—	0.17	0.27	-0.05
A2-A3		—	**0.71**	**0.50**
A3-A4			—	**0.58**

Discussion

In eastern North America, pumpkinseed populations are often size-structured in association with predation and competition, with larvae of different developmental phases representing 'ecological species' (K e a s t 1978), and juveniles presenting a distinct ecological niche from that of adults (e.g. O s e n b e r g et al. 1992). The main difference relates to a diet transition from soft-bodied macroinvertebrates to Gastropoda, which adult pumpkinseed are more able to handle and crush with a specialised pharyngeal apparatus. According to O s e n b e r g et al. (1988), pumpkinseed juvenile growth rates were related to *Lepomis* spp. abundance (strong competitive effect) whereas those of adults depended on Gastropoda abundance. In contrast, such size-structured populations have never been observed in Europe (C o p p et al. 2002; also Table 1). Moreover, in eastern North America, fish assemblages are characterized by shorter-lived, low-fecundity, reproductively specialized species, whereas in Europe, the species are generally longer-lived, highly fecund, and reproductively un-specialized (for a review comparison, see M a h o n 1984). In both its native and introduced range, the pumpkinseed is an omnivore and tends to feed on the most abundant prey types (e.g. Z a p a t a & G r a n a d o - L o r e n c i o 1993, G o d i n h o et al. 1997a, W o l f r a m - W a i s et al. 1999).

A high degree of variation in growth trajectories, often attributed to the influence of environmental conditions, is common in freshwater fish species (M a n n 1991). This phenomenon is apparent in both native American and introduced European populations of pumpkinseed (Table 1), although the native and introduced populations appear to differ in adult growth but not juvenile. In animals with indeterminate growth, such as pumpkinseed, average population growth trajectories (Fig. 1), approximated using by the
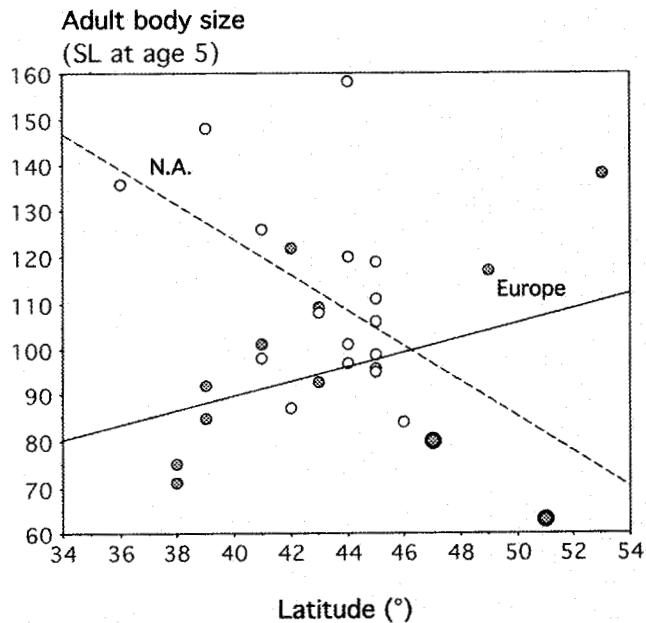
Fig. 3. The relationships (least-squares regression lines) between adult body size (mean SL at age 5) and latitude (°N) are presented for North American (N.A.) and European pumpkinseed populations. This relationship is significant for N.A. (solid line, open circles), but not for European populations (dashed line, solid circles) unless the two pond (thick shaded circles) are removed from the analysis. See text for further explanation.

von Bertalanffy equation, may reflect the optimization of resource allocation between growth and reproduction (K o z l o w s k i 1992, 1996), although not in all populations. Lower adult growth rates and lower ultimate lengths (L_∞) of introduced European populations, relative to native North American populations, may be the result of higher reproductive effort associated with the colonization of new ecosystems (the '*r*-selection' of M a c A r t h u r & W i l s o n 1967), if growth can be demonstrated to be density independent. Higher reproductive effort is also expected to be associated with survival in harsh systems, such as Iberian reservoirs and temporary streams, which are subjected to extended periods of elevated temperature, habitat restriction due to anoxia, and limited food resources. The timing of allocation to gonadal and somatic growth may also be a factor, as this appears to differ between the native and introduced populations of pumpkinseed (C o p p et al. 2002). In centrarchids, juvenile growth was expected to be faster in warmer waters (M c C a u l e y & K i l g o u r 1990, F o x & C r i v e l l i 2001), but this was not evident in European pumpkinseed populations. However, growth data currently available in Northern Europe is limited to two populations, so further study is required to verify this lack of correlation in juvenile growth rates as well as the tendency in adult growth rates to increase with increasing latitude.

The aforementioned explanations for the smaller size of acclimatised European pumpkinseed populations seems more plausible than that proposed by C r i v e l l i & M e s t r e (1988) – that small size of European pumpkinseed resulted from the selective importation of small-bodied specimens for the aquarium trade. As mentioned earlier, the bibliographic evidence suggests pumpkinseed were introduced for angling (K ü n s t l e r 1908) or use as an ornamental (garden pond) fish (B a l o n & M i š í k 1956, C o p p et al. 2002). In France, pumpkinseed were apparently perceived (at least, initially, in some areas) as an interesting game fish (K ü n s t l e r 1908), as persistent introductions followed the initial failed attempts to establish the species (R o u l e 1931). However, the initial large sizes observed at local French markets soon disappeared (K ü n s t l e r 1908), and the pumpkinseed was quickly considered a pest due to its small size, large appetite, and great localised abundance (R o u l e 1931).

In Iberia, the pumpkinseed was inadvertently introduced when largemouth bass *Micropterus salmoides* were introduced as a sport fish. Such unintentional introductions of pumpkinseed appear to be common in Europe. For example, young pumpkinseed were reported in the Czech literature to have been imported into the former Czechoslovakia inadvertently with young carp (T a n d o n 1976), and similar inadvertent translocations are thought to have been responsible for the species' spread amongst still waters of Southern England (R. H o r s f i e l d, personal communication). The impact of pumpkinseed in central Europe remains largely un-assessed, whereas in Iberia, the most obvious potential impacts of pumpkinseed introduction involve predation on fish eggs (G a r c í a d e J a l ó n et al. 1993, G a r c í a - B e r t h o u & M o r e n o - A m i c h 2000b) and on endemic mollusc subspecies (G a r c í a - B e r t h o u & M o r e n o - A m i c h 2000a). The pumpkinseed has been found to contribute to the decline of some indigenous fish species (G o d i n h o & F e r r e i r a 1998), possibly through competition for food and piscivory (F.N. G o d i n h o, unpublished data). According to several authors, *Lepomis* spp. populations are very susceptible to food competition, even when dietary overlap is limited (O l s o n et al. 1995). The perception in Europe of the pumpkinseed as a pest probably explains the limited scientific attention it has received until recently; however its present and future impact on European fish assemblages warrants attention, particularly in the extreme latitudes of its European range.

Available evidence for pumpkinseed in northern Europe (C o p p et al. 2002) suggests that strong intra-specific interactions, combined with little or no predation pressure, may explain the small size and low fecundity of some pumpkinseed populations in Europe (C r i v e l l i & M e s t r e 1988, C o p p et al. 2002), a phenomenon also reported in some North American pumpkinseed populations (data in D e a c o n & K e a s t 1987, F o x 1994). In Portuguese reservoirs, competition also seems to occur, potentially stimulated by metabolically-demanding high temperatures and low food availability — benthic invertebrates in general and gastropods in particular (F.N. G o d i n h o , unpublished data). Predation pressure has been demonstrated to have a strong influence on body size in some fish species (e.g. H o l o p a i n e n et al. 1991). In its native range, the pumpkinseed may be pushed to greater body sizes to outgrow predation pressure by piscivorous fishes such as the bass (*Micropterus* spp.).

Largemouth bass *Micropterus salmoides* has been introduced into Europe, but has very restricted distribution in much of Europe, and is absent in many water bodies (outside of Iberia) where the pumpkinseed is now found (e.g. W h e e l e r 1969, d e G r o o t 1985, K e i t h & A l l a r d i 2001). In Northern Europe, the pumpkinseed appears to have few natural fish predators other than pike-perch *Sander lucioperca*, where present, and the most common piscivorous fish in Europe, northern pike *Esox lucius* (W h e e l e r 1969). Pike have been thought indifferent to pumpkinseed unless no other prey item is available. However, G u t i et al. (1991) reported pumpkinseed to be the second most abundant fish prey in pike from a series of moorland water bodies in Hungary. In Southern Europe, particularly in Spain and Portugal (which have no native piscivorous fish species), pike, pumpkinseed, and largemouth bass were introduced in the first half of the 20th century, with catastrophic impacts on the native fauna (G o d i n h o et al. 1997b, G a r c í a - B e r t h o u & M o r e n o - A m i c h 2000b). Initial growth (ages 0–4) of pumpkinseed is relatively fast in those Portuguese waters and in Lake Banyoles (Spain) where largemouth bass is established (Table 1), suggesting that slow-growing European populations are those with elevated intraspecific competition due to few or no predators, such as the Cottesmore Pond population in England (C o p p et al. 2002) and probably Dabas Pond in Hungary as well (Table 1).

A switch to small size and reduced fecundity (C o p p et al. 2002) reflects an ontogenetic shift from the precocial, specialist, dispersive phenotype (sensu B a l o n 1999) to the altricial, 'dwarf', generalist, maintenance phenotype. A 'maintenance' phenotype seems plausible for the slowest growing populations, such as those of Cottesmore Pond (C o p p et al. 2002) and the Tapada Pequena Reservoir of southern Portugal (G o d i n h o & F e r r e i r a 1996) in which dietary overlap was extensive, benthic prey availability was low and gastropods were absent. The inability for larger pumpkinseed to segregate by trophic resources as they grow (due to the absence or low density of Gastropoda), may also be a factor influencing the overall slow growth of larger pumpkinseeds in Portugal as compared to North America, as they are forced to compete with juveniles for the same food sources. Limited food supplies may also explain slow growth in many other European pumpkinseed populations (B ă n ă r e s c u 1964, S p ă t a r u 1967, B r a b r a n d & S a l t v e i t 1989) for which strong dietary overlap between year classes is often reported (e.g. Z a p a t a & G r a n a d o - L o r e n c i o 1993, G o d i n h o et al. 1997a, C o p p et al. 2002, D e c l e r k et al. 2002). Our review of ontogenetic patterns in pumpkinseed growth rates suggests that in European populations the factors determining juvenile growth are the same as those determining adult growth, whereas in North American populations, different factors

appear to drive juvenile and adult growth rates — this is emphasized by the significant inverse correlation between age increment 1–2 and that of 3–4 (Table 4).

Elevated adult growth rates in North American pumpkinseed have been linked to a shift to molluscivory (e.g. O s e n b e r g et al. 1988, 1992), a shift that occurs rarely in European populations. Although Mollusca and Bivalvia can represent considerable proportions in the diet of European pumpkinseed (Mollusca 33%, S p ă t a r u 1967; Gastropoda 12.8%, G u t i et al. 1991), G a r c í a - B e r t h o u & M o r e n o - A m i c h (2000a), they are generally not a common feature in the diet (e.g. B r a b r a n d & S a l t v e i t 1989, Z a p a t a & G r a n a d o - L o r e n c i o 1993, C o p p et al. 2002, D e c l e r c k et al. 2002). Indeed, the only evidence in Europe of an ontogenetic shift in pumpkinseed (>90 mm SL) towards Mollusca (representing over 30% of the diet) was in Lake Banyoles (G a r c í a - B e r t h o u & M o r e n o - A m i c h (2000a), which also has the fastest growing pumpkinseed population in Iberia (Table 1).

Dietary competition with Eurasian perch *Perca fluviatilis* was proposed early on (R o u l e 1930), with pumpkinseed perceived as the culprit of supposed decreases in perch abundance. However, despite a similar ontogenetic shift to benthivory in the two species, pumpkinseed and perch generally exploit different habitats (e.g. C o p p 1993, C o p p et al. 1994, R o s s i e r 1995, G o z l a n et al. 1998), so a causal impact of pumpkinseed (predation, competition) on perch remains unsubstantiated. Not all European populations demonstrate slow growth rates. The upper Odra River population (Table 2) exhibits a growth trajectory similar to that of many native North American populations. But unlike many North American populations, adult growth rate in the Odra population declines at age 5, achieving a similar ultimate length as the Greek population (Table 1); this is probably a result of the prevailing thermal conditions, being that the Odra study site is influenced by a continuous supply of warm water from a nearby electric power plant (H e e s e & P r z y b y s z e w s k i 1985).

In both North America and Europe, the correlation between adult body size and latitude was weak in spite of being significant for North American populations, for which the linear model only explains 23% of the variance among populations. This low value indicates that a small part of the variance is due to factors varying with latitude (e.g. temperature, photoperiod), but the major proportion of variance is due to other (local) factors, such as strong intra-specific interactions, little or no predation pressure, and limited resources are particularly acute in small ponds (e.g. C o p p et al. 2002). Indeed, when the two pond populations were removed from the analysis of correlation between adult body size and latitude in European populations, a very significant correlation was revealed. This suggests that the latitudinal effect is masked by local conditions, and growth patterns in European pumpkinseed reflect a combination of latitudinal and local influences.

An inverse relationship between L_∞ and k (the rate at which the growth curve approaches the asymptote), which is normally an inherent property of von Bertalanffy growth function (M o r e a u et al. 1985), was not observed in the pumpkinseed populations on either continent. Estimates of maximum body size potential derived with the von Bertalanffy growth model appear to be more realistic for introduced than native pumpkinseed populations — we were able to include 66% of European L_∞ estimates in contrast to only 20% of North American estimates. This could suggest that stunted 'maintenance' growth patterns in pumpkinseed are better suited to the mathematical (asymptotic) basis of von Bertalanffy growth models than those of the precocial native populations. Nonetheless, our results support previous recommendations (F o x 1994, Ž i v k o v et al. 1999) that size at age, in particular those associated with juvenile and adult growth, are better parameters for

inter-population comparisons of somatic growth than von Bertalanffy growth parameters. Similar to Ž i v k o v et al. (1999), we found the index of growth performance (M u n r o & P a u l y 1983) to correlate with adult body size (Fig. 2), which for its simplicity is probably the more reliable indicator of growth performance.

In conclusion, our hypothesis, that there are latitudinal clines in somatic growth rates and body sizes, was rejected for juvenile but not adult growth. Adult body size decreased with increasing latitude in North America, but increased with increasing latitude in Europe (Fig. 3). Similarly, our intercontinental comparison of ontogenetic growth patterns revealed a major difference between continents in the relationship between growth in early and subsequent years: similar juvenile growth performance in native and introduced populations, but faster adult growth in North American than European populations. This suggests that growth patterns in introduced European pumpkinseed reflect a combination of latitudinal and local influences, which require clarification through further study. Given that the data used here are derived from bibliographic sources, with inherent between-operator variation in the interpretation of age and growth, future research on pumpkinseed needs to concentrate on truly comparable estimates of age, growth, reproduction (age and size at maturity) and diet, combined with field assessments of biotic conditions (e.g. predation pressure, food availability, water character) to identify the reason for the generally smaller body size of introduced relative to native pumpkinseed populations. Of particular interest for future studies, particularly from an energetic point of view, is the potential for habitat-based dimorphism (pelagic vs. littoral, riverine vs. lacustrine) in pumpkinseed (R o b i n s o n et al. 1993, B r i n s m e a d & F o x 2002, V i l a - G i s p e r t & F o x , unpublished data), and the role of zooplanktivory, especially of Cladocerans, which are a preferred prey in many European pumpkinseed populations (C o p p et al. 2002; G o d i n h o , unpublished data), especially in the pelagic zone (B r a b r a n d & S a l t v e i t 1989).

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