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Optimal resource allocation explains changes in the zebra mussel growth pattern through time

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ABSTRACT

Questions: Do optimal adjustments of resource allocation to selection pressure shape lifetime growth patterns? How rapid are the changes of growth trajectories through time?

Data: Phenotypic data on age and size of the invasive mussel *Dreissena polymorpha* collected twice at intervals of 5 to 39 years (approximately 1.7–3.3 to 13–26 generations) from 12 European populations. Calculated shifts of mortality and production conditions through time (selection factors), changes to Bertalanffy's growth curves, phenotypic rates of growth curve change (haldanes and darwins for Bertalanffy's parameters).

Methods: We compared the empirical relationships between the shifts of Bertalanffy's parameters and mortality and production indices through time with the relationships predicted by a published model of optimal resource allocation in zebra mussels.

Conclusions: Shifts of mortality and production conditions over time in the populations appeared to generate rapid optimal-like changes of *Dreissena* resource allocation. In line with the model predictions, changes in the mortality and production rates across time correlated positively with the shift of Bertalanffy's growth rate parameter and negatively with the shift of asymptotic size. Across populations, the minimum phenotypic rate of change of asymptotic size and Bertalanffy's growth coefficient ranged from 0.003 to 0.256 and from 0.038 to 0.658 haldanes (1870–86,668 and 17,773–18,7354 darwins), respectively. The phenotypic rates, controlled for the time intervals over which they were measured, were on average higher than the mean phenotypic rates derived from published data.

Keywords: Bertalanffy's growth curve, bivalves, body size, *Dreissena polymorpha*, exotic species, invasions, life-history strategy, mortality, phenotypic plasticity, phenotypic rate of evolution,

INTRODUCTION

Human-mediated disturbances of the environment, including the worldwide spread of species, attract the attention of evolutionists, ecologists and conservation biologists, as they

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help explain community-level processes, multi-trophic relationships, and the nature and rates of microevolution (Nalepa and Schloesser, 1993; Hendry and Kinnison, 1999; Sakai *et al.*, 2001; Ashley *et al.*, 2003; Simon and Townsend, 2003; Stockwell *et al.*, 2003). Traditionally, evolutionary and ecological processes have been seen in two different time perspectives, which has blurred the picture of anthropogenic changes of the environment (Thompson, 1998; Ashley *et al.*, 2003; Stockwell *et al.*, 2003). Emerging work, however, reveals much overlap between the ecological and evolutionary time scales: adaptive microevolution occurs over the observable time interval of decades or several generations, the time horizon of ecological and conservation concern (Reznick *et al.*, 1997; Thompson, 1998; Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Ashley *et al.*, 2003; Stockwell *et al.*, 2003; Yoshida *et al.*, 2003). Rapid contemporary microevolution alters interspecific interactions and generates co-evolutionary responses at different trophic levels, and thereby significantly affects community dynamics and ecosystem energy fluxes in complex and often untraceable ways (Thompson, 1998; Bohannan and Lenski, 2000; Bolker *et al.*, 2003; Turchin, 2003; Yoshida *et al.*, 2003; Werner and Peacor, 2003). From this perspective, identifying the selective forces that drive adaptive changes of exotic species and assessing the rates of such changes will enable broader ecological inferences to be drawn.

Recent work on the Ponto-Caspian invader *Dreissena polymorpha* Pallas suggests that the differences in zebra mussel life histories across Europe can be explained by optimization of resource allocation between growth and reproduction in response to predation, trophic conditions and overgrowth in habitats (Czarnołęski *et al.*, 2003). Modelling of zebra mussel allocation by Czarnołęski and colleagues demonstrated that higher predation and improved food conditions favour earlier maturation and the shifting of resources from growth to reproduction, leading to a negative dependence of asymptotic size on mortality and production rates in mussel populations, and to a positive relationship between Bertalanffy's growth coefficient and the two environmental factors (see Methods for parameter definitions). Empirical data showed that the predicted life-history patterns do exist across populations of zebra mussels (Czarnołęski *et al.*, 2003). This indicates that shifts in mortality and production conditions have fuelled adaptive changes of zebra mussels, through plastic and/or genetic response, since the establishment of mussels in Central Europe almost two centuries ago, and that the dynamics of such changes must have differed between populations. However, inferring the adaptive nature, directions and rates of phenotypic changes from the evidence on cross-population differences might lead to imprecise conclusions (Hendry and Kinnison, 1999). Our study attempts to shed light on this important issue. To assess changes of mortality and production conditions and shifts of life-history traits over time, we use data on 12 European populations of zebra mussels studied twice at different intervals. Using the predictions of a model of optimal resource allocation in *Dreissena polymorpha* (Czarnołęski *et al.*, 2003), we examine whether the life-history shifts in populations can be explained on the basis of optimization theory (Roff, 1992; Stearns, 1992; Kozłowski, 1992; Perrin and Sibly, 1993). If so, changes of mortality and production rates over time in populations should correlate positively with shifts of the mussel body size asymptote and negatively with changes of Bertalanffy's growth coefficient. Finally, we derive phenotypic rates of growth curve change through time, comparing them with published evidence on phenotypic and genetic rates of evolution. We stress that shifts of growth patterns are likely to reflect phenotypic plasticity; therefore, our estimates of phenotypic rates in zebra mussels integrate plastic and genetic components with unknown relative proportions.

MATERIALS AND METHODS

We use zebra mussel data on European populations collected by A. Stańczykowska, K. Lewandowski and colleagues between 1960 and 1999 (Table 1). Originally, the data were collected for purposes other than this analysis, for example to evaluate population dynamics and their ecosystem-level effects (Stańczykowska, 1977; Stańczykowska and Lewandowski, 1993). Recently, the data set most complete and comparable in terms of sample size, mussel age assessment and age distribution in samples was used to test for optimality of cross-population life-history polymorphism (Czarnołęski *et al.*, 2003). Here we use a subset of data on 12 populations studied twice at intervals from 5 to 39 years. The age of mussels was estimated from annual growth increments according to the method of Lewandowski (1982); shell length, width and height were measured with a Vernier caliper to the nearest 0.1 mm. Following Czarnołęski *et al.* (2003), we used the geometric mean from three dimensions of each mussel to express body size, l (mm).

Significance of growth pattern changes

The growth curve of an average mussel in a population in a certain time period was expressed by Bertalanffy's formula (Bertalanffy, 1957), $l = L(1 - \exp(-kt))$, fitted to data on age t and body size index l using the least squares method with the Simplex procedure. The coefficient k (year^{-1}) defines the rate at which the asymptotic size L (mm) is approached.

The significance of growth curve change between study periods was checked with the approximate randomization test (Noreen, 1989), developed in Visual Basic language according to Weinberg and Helser's (1996) method. After fitting Bertalanffy's curves to two data sets (time series) from each population, we obtained two curves and two residual sums of squares (SS_1 and SS_2). If the curves are identical, the total residual sum of squares does not change after fitting a single curve to pooled data, but it rises if the curves are different. The difference in the total residual sums of squares between the fit based on the pooled data (SS_{12}) and the fit based on two separate data sets was used as a test statistic, $Diff = SS_{12} - (SS_1 + SS_2)$, which measures the difference between two curves (Weinberg and Helser, 1996). To assess the significance of the test statistic, we generated its probability distribution under the assumption that the null hypothesis is true. After pooling the data from two periods, we assigned them randomly and without replacement to two groups, keeping the number of observations per group the same as in the original data. Then the curves were fitted to the new groups, and residual sums of squares from each new group, SS_1* and SS_2*, were used to calculate the randomly obtained statistic $Diff* = SS_{12} - (SS_1* + SS_2*)$. The procedure was repeated 10,000 times to obtain the probability density function. The significance level of a single test was the probability that the randomly generated $Diff*$ is as large as or larger than the observed $Diff$ (Weinberg and Helser, 1996). We accounted for multiple comparisons with the sequential Bonferoni correction (Rice, 1989).

Relation of shifts in growth pattern to changes in selection factors

We evaluate selection factors (mortality and biomass production rates) according to the methods applied earlier to evaluate the optimality of cross-population patterns in *Dreissena polymorpha* (Czarnołęski *et al.*, 2003). Our historical data were collected from lake bottoms. This usually resulted in under-representation of individuals from the first two age-classes, because planktonic juveniles settle not only on lake bottoms but also on plants, from which they then migrate to bottom colonies (Stańczykowska, 1977; Stańczykowska and Lewandowski, 1993). It would be difficult to reconstruct proper age distributions from our data and to estimate mortality curves. Therefore, the average mortality rate in a population in a given time period was approximated by the reciprocal of the age of the oldest individual in the sample (M, year^{-1}), following Beverton's (1963) method for fish, modified by Czarnołęski *et al.* (2003) for zebra mussels. To reduce the confounding effect of different sample sizes in the data, 50 specimens were randomly chosen from each data set, and from these the oldest age-class was recorded. The procedure was repeated 100 times with replacement, and the recorded maximum age was averaged across the repetitions and used to calculate M. Information on the environmental factors that influenced zebra mussel biomass production in the periods from which the data originate was unavailable, so we used the average value of the body size index of survivors of the first winter (L_1, mm) to express the juvenile production rate in populations in each study period. Because juveniles do not allocate resources to reproduction, Czarnołęski *et al.* (2003) argued that the size of young-of-the-year zebra mussels from Eastern Europe could be a convenient proxy of the environmental conditions directly affecting the growth rate.

For each population, we calculated the changes of the mortality and biomass production indices and shifts of Bertalanffy's curve parameters over time: ΔM, ΔL_1, Δk and ΔL (parameter value from the later sample minus the value from the earlier sample). We examined the relations of the shifts in growth curves to the changes in mortality and production rates over time, using multiple regression analysis (Statistica 6.1, StatSoft).

Rates of growth pattern change

We assess the phenotypic rates of change of growth curve shape across time in the populations by calculating darwins and haldanes for Bertalanffy's parameters. Darwins specify the rates of proportional change of traits in units of e per million years (Haldane, 1949; Gingerich, 1993, 2001; Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). We calculated darwins by dividing the change of natural logarithms of k and L in each population by the corresponding time interval in millions of years. Haldanes account for the within-population variability of traits, expressing the rates of change in standard deviation units per generation (Gingerich, 1993, 2001; Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). Unfortunately, our data lack information on the variability of Bertalanffy's parameters in the populations, preventing us from calculating the actual value of the pooled standard deviation of the parameters across time, the statistics required for haldanes. To overcome this statistical problem, we used other zebra mussel material (M. Mikołajczyk, unpublished results), from which we extracted information on the variability of growth curves in the studied populations. The material, samples of shells of dead zebra mussels, was collected from lake bottoms in 1998 and 1999 from six of the studied populations. The length, width and height of approximately 1000 left valves from each population were measured; from 50 valves subsampled from each population data set, annual growth increments were identified with Lewandowski's (1982) age-assessment method, and the lengths attained by each mussel in consecutive years of life were measured to the nearest 0.1 mm. We used the lengths to reconstruct the corresponding mussel heights and widths based on the regressions of mussel width and height on length derived from the population data sets ($N = \sim 1000$). From the estimated dimensions, we calculated indices of body size attained by the subsampled mussels in consecutive years of life. We fitted

Bertalanffy's equations to the age–body size data of each mussel (Statistica 6.0, StatSoft), obtaining 50 individual growth curves per population. We excluded from further analysis outliers with Bertalanffy's asymptote $L > 100$ mm, the cases beyond the reported parameter range (Czarnołęski *et al.*, 2003). From the 44–50 curves left per population, we calculated standard deviations of Bertalanffy's parameters in each population, our proxy of pooled standard deviations of the parameters k and L.

To calculate haldanes of the change of Bertalanffy's parameters in the studied populations, we standardized the values of k and L from each study period (Table 1) by our proxies of standard deviations of the parameters. We divided these standardized changes by the number of generations that passed in populations between the study periods. Typically, there is considerable uncertainty regarding generation lengths used for calculating haldanes (Hendry and Kinnison, 1999). To estimate the number of generations in the studied populations, we assumed that the mussels matured within 1–2 years, the range typical for European *Dreissena polymorpha* (reviewed in Czarnołęski *et al.*, 2003). Given that generation time generally does not exceed 1.5 times the maturation age (Stearns, 1992), we estimated the generation length at approximately 1.5–3 years. For each population, we estimated the minimum and maximum haldane values from the upper and lower limits of the generation length range, respectively.

We evaluate how rapid the phenotypic rates of growth pattern change in zebra mussels are in relation to published evidence on evolutionary rates. We used a database on haldanes and darwins calculated for different traits and organisms, kindly provided for our analysis by M. Kinnison and A. Hendry and published in Kinnison and Hendry (2001). To control our comparison for the common link between evolutionary rates and the time interval over which they are measured (Gingerich, 1983, 1993, 2001; Kinnison and Hendry, 2001; Stockwell *et al.*, 2003), we fitted regressions to logged absolute values of the published rates and time intervals (Statistica 6.1, StatSoft). Following the suggestions of Gingerich (1993), Kinnison and Hendry (2001) and M. Kinnison (personal communication), we used the robust regression method of least absolute deviations, reducing the effects of outliers (Quinn and Keough, 2002). Note that such reference regressions were fitted only to the phenotypic rates derived from allochronic studies, the subset of Kinnison and Hendry's database most comparable with the kind of data we have for zebra mussels. To compare our phenotypic rates with published rates, we calculated deviations of our darwins and haldanes from the reference regressions. We used Student's t-test to determine whether the mean deviations were significantly different from zero. In the analysis for haldanes, we used only our minimum estimates of haldanes (assuming a 1.5 year generation length), which made our analysis more conservative in terms of detecting high rates of change. For the purpose of comparison, we additionally derived time-scaling regressions for combined data of Kinnison and Hendry on phenotypic and genetic rates from allochronic as well as from synchronic studies.

RESULTS

On average, mussel mortality rate decreased in the intervals of 5 to 39 years in the 12 populations (mean $\Delta M = -0.031$, $t_{11} = -2.231$, $P < 0.05$); the negative direction of change of the biomass production index was non-significant (mean $\Delta L_1 = -0.895$, $t_{11} = -1.249$, $P = 0.24$). The changes of the mortality and production indices were not correlated ($b = 0.02$, $P = 0.95$; Fig. 1). The mortality and production rate indices changed by 2–39% and 1–68%, respectively.

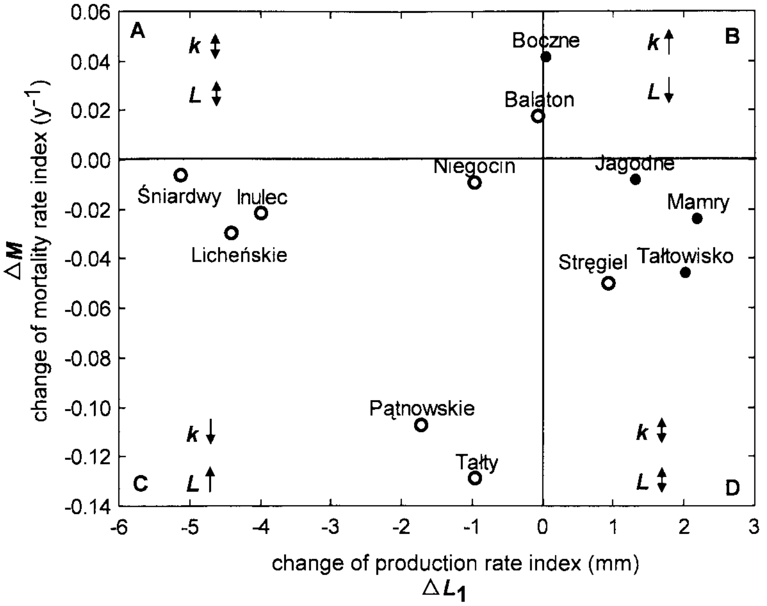

Fig. 1. Changes of selection factors M and L_1 across time in 12 populations of *Dreissena polymorpha*. Mortality rate index M is the reciprocal of the age of the oldest mussel in a given population sample; production rate index L_1 is the average size of young-of-the-year. Sectors A, B, C and D define selection regimes based on the directions of change of the selection factors. Arrows indicate the directions of change of Bertalanffy's growth curve parameters [coefficient of growth rate k (year^{-1}) and asymptotic size L (mm)] predicted for each selection context from the model of optimal resource allocation in *Dreissena polymorpha* (Czarnołęski *et al.*, 2003). The model predicts that a rise of either the mortality M or production rate L_1 index generates a decrease of the mussel asymptote L and an increase in coefficient k. Therefore, under the selection conditions in Sectors B and C, where the factors M and L_1 act in the same directions, growth responses are predictable: Sector B – growth coefficient k should increase and asymptotic size L should decrease; Sector C – coefficient k should decrease and asymptote L should increase. Under selection conditions in Sectors A and D, where the factors M and L_1 act in opposite directions, the final direction of growth pattern changes will depend on the relative strength of the two forces (indicated by double-headed arrows). Empirical data, in accord with model predictions, show that in all studied populations the changes of Bertalanffy's parameters k and L were negatively related. Open circles denote the populations in which coefficient k decreased while asymptote L increased; solid circles denote the cases in which coefficient k increased and asymptote L decreased. In all populations in Sectors B and C (predictable response direction), the growth pattern changed in the predicted manner; in Sectors A and D (unclear response direction), the direction of growth shifts differed across populations.

The randomization test results indicate that the shape of Bertalanffy's growth curves changed significantly across time in 10 of the 12 populations (Table 1). Bertalanffy's growth coefficient k and asymptote L shifted their values in the populations by 18–257% and 3–131%. Figure 2 illustrates the largest and smallest changes of growth patterns found in our data. Analysis of the partial regressions indicates that the change of production rate index ΔL_1 was negatively associated with the change of body size asymptote ΔL and positively with the change of Bertalanffy's growth coefficient Δk (Fig. 3A,C). The change of mortality rate index ΔM was negatively correlated with ΔL and positively with Δk

Table 1. Data on European populations of *Dreissena polymorpha* collected at two points in time (Sample 1 and Sample 2), studied here to examine changes of Bertalanffy's growth curves (Sample 1 vs. Sample 2)

	Sample 1			Sample 2			Sample 1 vs. Sample 2		Phenotypic rate of change			
									Darwins ($\times 10^3$)		Haldanes	
Lake	Date	k	L	Date	k	L	*Diff*	P	k	L	k	L
Balaton	1974	0.68	13.4	1984	0.56	14.3	0.01	N.S.	19.416	6.500	—	—
Boczne	1960	0.11	31.0	1967	0.38	16.9	1.57	<0.002	177.099	86.668	0.230–0.459	0.256–0.512
Inulec	1994	0.74	16.5	1999	0.29	20.7	1.90	<0.002	187.354	45.355	0.658–1.316	0.166–0.333
Jagodne	1962	0.76	11.3	1972	1.33	11.0	0.16	<0.05	55.962	2.691	—	—
Licheńskie	1973	0.97	12.7	1999	0.14	29.4	0.95	<0.002	74.449	32.284	0.164–0.328	0.099–0.198
Mamry	1960	0.17	19.9	1999	0.34	18.5	1.52	<0.002	17.773	1.870	0.038–0.077	0.003–0.006
Niegocin	1962	0.63	12.7	1999	0.26	21.0	0.46	<0.002	23.610	13.541	—	—
Pątnowskie	1973	0.88	11.0	1999	0.22	22.6	0.26	<0.002	53.319	27.694	0.128–0.255	0.069–0.137
Stręgiel	1960	0.30	19.4	1972	0.17	27.0	0.07	N.S.	47.332	27.547	—	—
Śniardwy	1993*	0.99	15.4	1999	0.38	17.7	2.91	<0.002	159.421	22.659	0.589–1.179	0.027–0.054
Tałtowisko	1960	0.14	30.0	1970	0.50	17.4	1.99	<0.002	127.297	54.473	—	—
Tałty	1961	0.74	11.3	1972	0.18	23.3	0.56	<0.002	128.518	65.786	—	—

Note: k (year^{-1}) is Bertalanffy's coefficient of the growth rate at which asymptotic size L (mm) is approached. Statistic *Diff* compares the shape of Bertalanffy's curve in a population between two study periods (see Methods); its significance (P) was assessed with the approximate randomization test and corrected with the sequential Bonferroni procedure. The reported *Diff* values were standardized to account for different sample sizes by dividing *Diff* by the total number of data items used to calculate it. Darwins and haldanes (absolute values) of Bertalanffy's parameters reflect the phenotypic rate of growth pattern shifts through time. Haldanes were estimable only for cases with known within-population variability of Bertalanffy's growth curves. Lower and upper estimates of haldanes in the reported ranges refer to different assumed maturation times (1 and 2 years).

* Corrected date; given in Czarnołęski *et al.* (2003) as 1995.

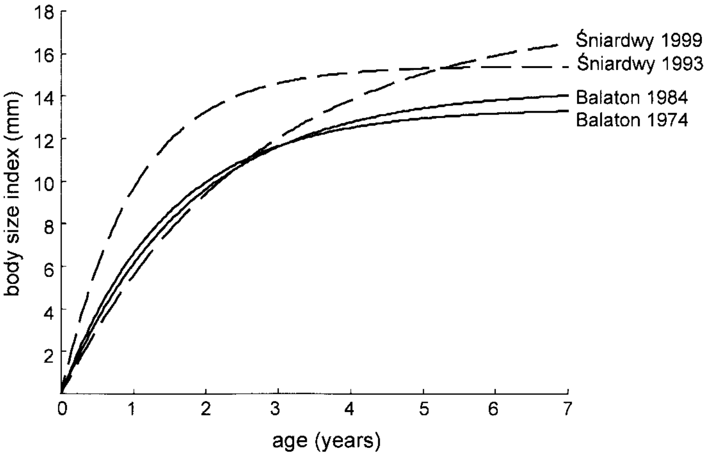

Fig. 2. An example of the smallest and largest changes of Bertalanffy's growth curves through time in the studied populations of zebra mussels (identified by comparing values of the *Diff* statistic of our randomization test comparing curves; see Table 1). Body size index is the geometric mean calculated from three dimensions of mussels.

(Fig. 3B,D). The shifts of Bertalanffy's parameters Δk and ΔL were negatively correlated ($b = -0.80$, $P < 0.002$).

The estimated number of generations ranged from approximately 1.7–3.3 (5 years) at Lake Inulec to about 13–26 (39 years) at Lake Mamry. Table 1 summarizes our estimates of the phenotypic rates of change of Bertalanffy's parameters in the studied populations; Table 2 summarizes the parameters of regressions fitted to our different sets of data. The estimates of darwins for parameters k and L were right-skewed (skewness coefficients = 0.4 and 0.8). Figure 4 and Table 2 indicate that the darwins and haldanes of Bertalanffy's growth curve parameters tended to scale inversely with the time intervals over which they were measured. As shown in Fig. 4, the darwins of Bertalanffy's parameters were consistently higher than the mean rates predicted by the reference time-scaling regression (for deviations of darwins of k: $t_{11} = 17.437$, $P < 0.0001$; for deviations of darwins of L: $t_{11} = 5.944$, $P < 0.0001$); the same was true for the minimum haldanes of Bertalanffy's growth coefficient k (for deviations of haldanes of k: $t_5 = 7.616$, $P < 0.0007$). The mean deviation of haldanes of Bertalanffy's asymptote L from the reference regression did not differ from zero ($t_5 = 0.098$, $P = 0.93$).

DISCUSSION

Our results provide insight into the magnitude of changes of selection factors and individual growth patterns across time in European zebra mussel populations. The mortality and biomass production rate indices shifted by 2–39% and 1–68% over the intervals of 5 to 39 years in the 12 populations. Bertalanffy's growth curve coefficient k and asymptotic body size L changed by 18–257% and 3–131% respectively, and in 10 of the populations the growth changes were significant (Table 1, Fig. 2). The alterations of growth curves indicate changes of the *Dreissena* lifetime pattern of resource allocation to growth and reproduction. According to the principles of life-history evolution (Roff, 1983, 1992;

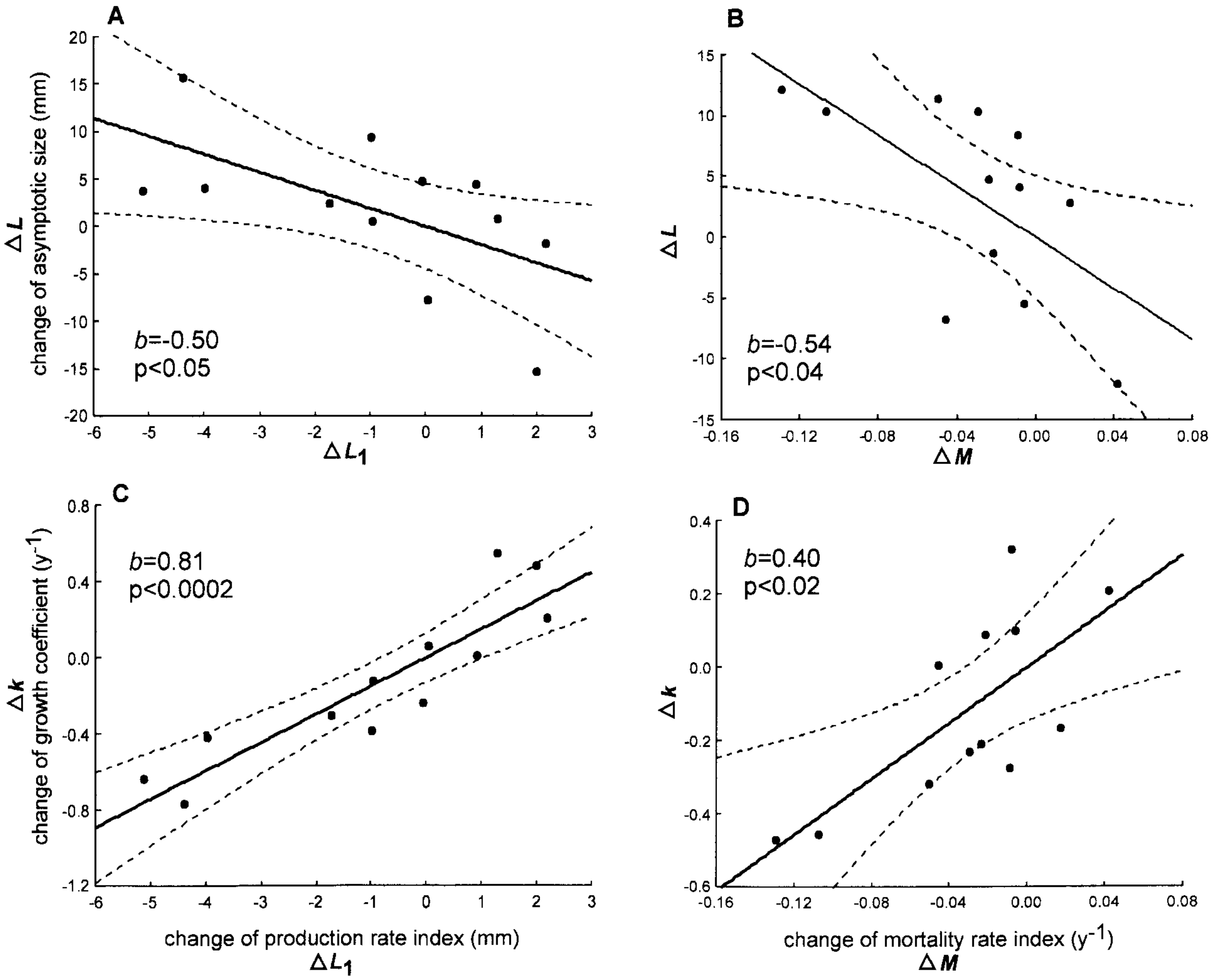

Fig. 3. Results of two multiple regression analyses (A, B and C, D) exploring the link between changes of Bertalanffy's growth curve parameters (*k* and *L*) and changes of the mortality and production rate indices across time in 12 European populations of *Dreissena polymorpha*. Dashed line indicates 95% confidence bounds; *b* is the standard partial regression coefficient.

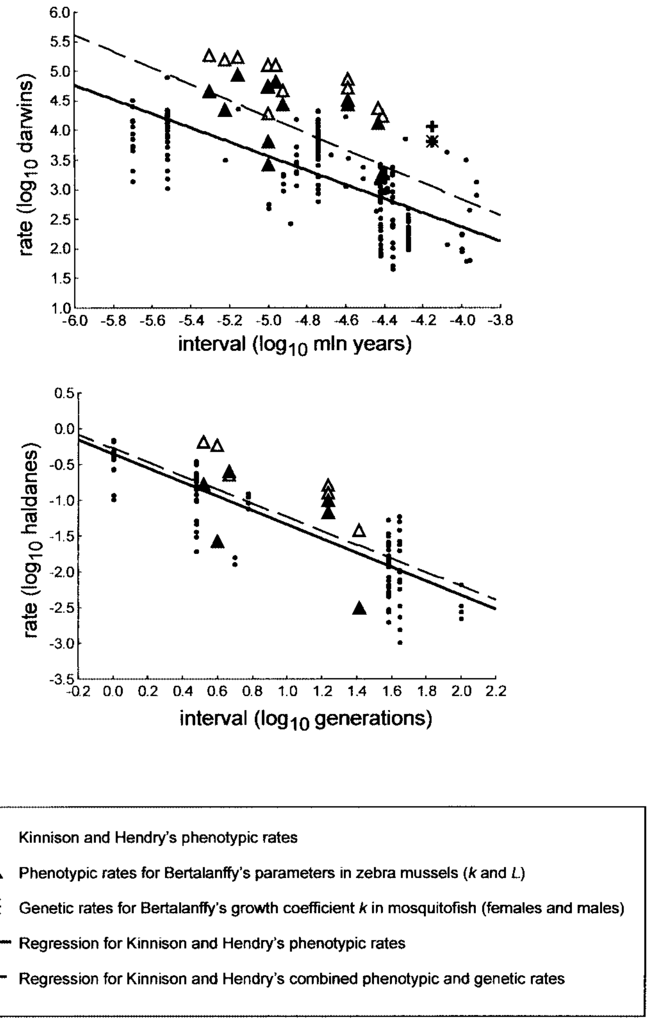

Fig. 4. Scaling of evolutionary rates (darwins and haldanes) with the time intervals over which they were calculated. Circles denote the absolute values of phenotypic rates derived from allochronic data on different traits and organisms, kindly provided for our analysis by M. Kinnison and A. Hendry and published in Kinnison and Hendry (2001). Triangles denote phenotypic rates of change of Bertalanffy's curves through time in different populations of zebra mussels (our allochronic data from Table 1). Note that we use here only our minimum estimates of haldanes. Crosses mark the genetic rates of divergence of Bertalanffy's growth coefficient *k* in Hawaiian populations of mosquitofish, estimated from Stearns's (1983) synchronic data. Solid lines represent regressions fitted to Kinnison and Hendry's phenotypic rates from allochronic data (circles), which we use as a reference for comparison of the rates of growth pattern change in zebra mussels with published rates. For the purpose of comparison, we provide additional regressions (hatched lines) fitted to the combined data of Kinnison and Hendry on phenotypic and genetic rates derived from allochronic as well as from synchronic studies (data points for genetic rates and synchronic data are not presented). Regression parameters are summarized in Table 2.

Table 2. Parameters of regressions fitted to data on evolutionary rates (darwins and haldanes) and the time intervals over which they were measured

Type of data		Rate	Intercept	Slope	Number of cases
Kinnison and Hendry's phenotypic rates from allochronic data		darwins	−2.436	−1.200	229
		haldanes	−0.356	−0.987	92
Kinnison and Hendry's combined phenotypic and genetic rates from allochronic and synchronic data		darwins	−2.725	−1.390	2582
		haldanes	−0.274	−0.962	2104
Phenotypic rates for change of Bertalanffy's parameters through time in zebra mussel populations	k	darwins	−0.280	−1.050	12
		haldanes	0.338	−0.994	6
	L	darwins	1.520	−0.5917	12
		haldanes	−0.497	−0.538	6

Note: The rates and intervals were transformed by decimal logarithms before the analysis; regressions were fitted with the least absolute deviations method. M. Kinnison and A. Hendry kindly provided us with their database on darwins and haldanes derived from allochronic and synchronic studies of different traits and organisms; the data are published in Kinnison and Hendry (2001). The regression derived from the published phenotypic rates from allochronic studies is used here as the time-scaling reference for comparing phenotypic rates of growth pattern change in zebra mussels (see Fig. 4). Darwins and haldanes calculated for zebra mussel data are phenotypic rates of growth pattern change through time in different populations. Note that the regressions for zebra mussel haldanes were based on our minimum estimates of haldanes.

Stearns, 1992; Kozłowski, 1992; Perrin and Sibly, 1993; Heino and Kaitala, 1997; Czarnołęski and Kozłowski, 1998; Kozłowski *et al.*, 2004), changes in mortality level and production conditions exert strong selective pressure on the allocation strategy of organisms, influencing their growth pattern. To maximize fitness in a given selection context, organisms are pushed to optimize lifetime resource expenditure on growth and reproduction. This should lead to predictable responses of the growth pattern to changes of the mortality and production rates in habitats (Kozłowski, 1996; Kozłowski and Teriokhin, 1999). A model of optimal resource allocation in *Dreissena polymorpha* (Czarnołęski *et al.*, 2003) demonstrated that an increased mortality rate should shorten the juvenile period and intensify resource channelling from growth to reproduction, increasing Bertalanffy's growth coefficient k and decreasing asymptotic size L. An improvement in food conditions accelerates the growth rate, typically leading to larger final size (Kozłowski, 1996; Kozłowski and Teriokhin, 1999). In sessile overgrowers such as zebra mussels, however, better food conditions usually intensify overgrowth by conspecifics (reviewed in Czarnołęski *et al.*, 2003). The model predicted that the conditions enhancing overgrowth select for earlier maturation and intense allocation of resources to reproduction at the expense of growth, by increasing age-specific mortality and reducing the body-size allometries of assimilation and respiration rates (Czarnołęski *et al.*, 2003). Consequently, though improvement of production conditions leads to an increase of juvenile size, it is expected to decrease asymptotic size L and increase Bertalanffy's growth coefficient k. If the impact of overgrowth on the mortality rate is high relative to other sources of external mortality, shifts of the mortality and production rates in populations should be positively linked; that was observed across *Dreissena* populations (Czarnołęski *et al.*, 2003) but is undetectable in our data (Fig. 1). This suggests that in addition to self-overgrowing, predators, parasites or other mortality agents unrelated to overgrowth have substantially influenced changes of *Dreissena* survival in the studied populations.

Figure 1 shows the interplay between the changes of mortality and production rate indices in the studied *Dreissena* populations, and the qualitative response of Bertalanffy's growth curve predicted for each population from the optimization model (Czarnołęski *et al.*, 2003). *Dreissena* mortality decreased across time in most populations, but the changes of production conditions were not so consistent, indicating that the strength and direction of selection differed between populations. In such a case, the adaptive response in populations with antagonistic selection (Fig. 1A,D) relies on the relative strength of the two counteracting selection forces, whereas in the remaining populations a concerted response to changes of both factors is predicted (Fig. 1B,C). Accordingly, our empirical data show that in all zebra mussel populations with a predictable direction of optimal responses (Fig. 1B,C), the growth pattern changed over time in the expected way; in the remaining populations, where mixed responses might be expected (Fig. 1A,D), the directions of growth shifts differed across populations. Further analysis of the growth curve shifts in relation to changes of the mortality and production rates in the populations indicated that an independent increase of any rate across time was associated with a proportional decrease of the *Dreissena* size asymptote L (Fig. 3A,B) and an increase in Bertalanffy's growth rate coefficient k (Fig. 3C,D). These relationships accord with the optimization model predictions and match the cross-population trends found in zebra mussels (Czarnołęski *et al.*, 2003). The relation of zebra mussel growth curves to production conditions agrees with observations of retarded growth rate in fouled organisms (Okamura, 1986). The link between *Dreissena* growth patterns and mortality rates resembles the effects of predator or parasite pressures detected in molluscs (Minchella, 1985; Reimer, 1999; Irie and Iwasa, 2003), crustaceans (Stibor and Lüning, 1994) and fish (Reznick *et al.*, 1990, 1997); it also matches the interspecific growth–mortality patterns in fish and reptiles (Charnov, 1993), explained by optimal allocation modelling (Kozłowski, 1996).

The detected changes of growth patterns with mortality and production rates, and their accordance with the model predictions, reinforce the earlier view that the phenotypic differences across European zebra mussels have arisen through adaptive processes (Czarnołęski *et al.*, 2003). The time-frame of approximately 1.7–3.3 to 13–26 generations over which we observed the optimal-like alterations elucidates the dynamics that must have fuelled the origin of the phenotypic variability of zebra mussels since their arrival in the waters of nineteenth-century Europe. However, our phenotypic data do not allow us to determine to what extent the growth shifts might be plastically and genetically based. This awaits clarification. The growth pattern appears to be highly plastic (e.g. Stibor and Lüning, 1994), but it was also found to change genetically at relatively high speed over observable periods (Stearns, 1983). Although we acknowledge that the optimal-like shifts of growth that we observed are likely to represent adaptive phenotypic plasticity, we believe it might still be informative to compare our phenotypic rates with the evidence on the phenotypic and genetic rates of change of other traits. Emerging work suggests that evolution driven by anthropogenic or non-anthropogenic agents might occur commonly along observable time scales shorter than 100 years or 150 generations (Stearns, 1983; Grant and Grant, 1995; Reznick *et al.*, 1997; Thompson, 1998; Hendry and Kinnison, 1999; Stockwell and Weeks, 1999; Kinnison and Hendry, 2001; Ashley *et al.*, 2003; Stockwell *et al.*, 2003). The vast majority of these contemporary shifts proceed relatively slowly, and only a few are very fast (Kinnison and Hendry, 2001), which can reflect the exponential distribution of directional selection in nature (Endler, 1986; Kingsolver *et al.*, 2001). Interestingly, our phenotypic rates in darwins for Bertalanffy's parameters had right-skewed distributions. Our haldanes and darwins of growth curve parameters k and L scaled inversely with the length of time over which they were measured (Fig. 4, Table 2), in accord with the classic findings of other authors (Gingerich, 1983, 1993, 2001; Kinnison and Hendry, 2001). Though the relationship appears problematic from a statistical point of view, it can be expected to arise if the effects of periods of stasis and evolutionary reversals accumulate with time (Gingerich, 1983, 1993, 2001; Hendry and Kinnison, 1999; Sheets and Mitchell, 2001). We used such time-scaling to compare our data with published evidence on the pace of evolution. As shown in Fig. 4, the rates of growth pattern change in zebra mussels lie within the range reported by Kinnison and Hendry (2001) for the phenotypic rates of change derived from allochronic studies on other traits. Our time-adjusted estimates of darwins for Bertalanffy's parameters k and L, and the haldanes for growth coefficient k, resulted on average in higher values than the mean phenotypic rates predicted by the reference time-scaling trend in published data (Fig. 4). This suggests that generally the schedule of resource allocation of the studied mussels has tended to change through time relatively quickly. Fragmentary evidence indicates that such a tempo of change might not be unusual for this complex trait even at the genetic level. Stearns (1983) found that growth pattern was the most rapidly evolving life-history trait in Hawaiian mosquitofish. Based on his data, we calculated that Bertalanffy's growth coefficient k of mosquitofish diverged genetically between populations at rates of up to 6457 (males) and 11,585 (females) darwins. After time-controlling, these genetic rates appear not to differ from the phenotypic rates for k found in zebra mussels (Fig. 4).

Altogether, our evidence revealed a relatively high pace of growth pattern change in *Dreissena polymorpha* from Europe. Regardless of whether the phenotypic changes were purely plastic or integrated plastic and genetic components, our confrontation of data with the predictions of optimization theory suggests that they reflect adaptive responses of resource allocation to changing mortality, production and overgrowth conditions in populations through time. We hope that our evidence on these rapid optimal-like alterations in long-lasting European populations spurs research on this invader's adaptive changes during its recent expansion across North America in the last two decades.

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