

NONLINEAR GROWTH COST IN *MENIDIA MENIDIA*: THEORY AND EMPIRICAL EVIDENCE

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Abstract.—Juvenile growth is submaximal in many species, suggesting that a trade-off with juvenile growth must exist. In support of this, recent studies have demonstrated that rapid growth early in life results in decreased physiological performance. Theory clearly shows that for submaximal growth in juveniles to be optimal, the cost of growth must be nonlinear. However, nearly all of the empirical evidence for costs of growth comes from linear comparisons between fast- and slow-growing groups. It is consequently unclear whether any known cost can account for the evolution of submaximal juvenile growth. To test whether the cost of growth exhibits the logically necessary nonlinearity, we measured critical swimming speed (U_{crit}), the maximum speed sustained in incremental velocity trials, in Atlantic silversides, a species for which the costs and benefits of growth are well studied. To increase our ability to detect a nonlinear relationship between U_{crit} , a proxy for juvenile fitness, and growth, we manipulated ration levels to produce a broad range of growth rates (0.16 mm/day⁻¹ to 1.20 mm/day⁻¹). Controlling for size and age, we found that U_{crit} decreased precipitously as growth approached the physiological maximum. Using Akaike's information criterion, we show that swimming performance decreases with the square of growth rate, providing the first demonstration of a nonlinear cost of growth.

Key words.—Akaike's information criterion, Atlantic silversides, cost of growth, growth trade-off, *Menidia menidia*, optimal control, swimming performance.

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In an ideal Darwinian world, Law (1979 p. 82) imagined that an organism would maximize fitness if it "... starts to reproduce as soon as it is born, produces offspring in large numbers at frequent intervals, can always find a mate, is an excellent competitor, experiences no mortality, and can disperse anywhere. ...". Of course, in the real world such life histories are impossible because, as evolutionary theory has argued, trade-offs constrain the options such that exceptional performance in one trait comes at the expense of performance in another. Unfortunately, such negative correlations among life-history characters have been notoriously difficult to document, and among the most problematic have been trade-offs associated with juvenile growth (Reznick et al. 2000). We know that such trade-offs must exist because juvenile organisms in diverse taxa ranging from oysters and ant lions to fence lizards and painted turtles display intrinsic rates of growth well below their maximum (reviewed in Arendt 1997; Metcalfe and Monaghan 2001), even though fitness increases with body size.

For many years the primary trade-offs with growth were thought to be exclusively behavioral. That is, growth requires that individuals forage, and foraging entails an increased risk of predation (Lima and Dill 1990). More recently, however, physiological costs of growth have become apparent and now appear to be quite widespread. Costs of rapid growth include decreased locomotion (Gregory and Wood 1998; Billerbeck et al. 2001), increased susceptibility to predation (Gotthard 2000; Lankford et al. 2001) or disease (Lochmiller and Deerenberg 2000), increased frequency of developmental abnormalities (Leamy and Atchley 1985), and decreased longevity (e.g. penguins: Van Heezick and Davis 1990; butterflies: Gotthard et al. 1994; lizards: Olsson and Shine 2002;

nematodes: Hekimi and Guarente 2003). Evidence for costs of growth typically emerges from experiments comparing fast- and slow-growing phenotypes (e.g. Kolok and Oris 1995; Gotthard 2000; Lankford et al. 2001). While demonstrating that trade-offs exist, these observations are not sufficient to explain the evolution of submaximal juvenile growth.

Theory contends that submaximal juvenile growth is optimal only if the severity of the trade-off (i.e., the marginal cost) increases with growth rate (i.e. $\partial^2 \text{cost} / \partial \text{growth}^2 > 0$; Sibly et al. 1985; Engen and Saether 1994). Although this argument is based on results from optimal control theory, it is straightforward to show using ordinary calculus that when the cost is a linear function of growth, any trajectory from a small size to one larger would incur the same growth penalty (Appendix). Thus the optimal strategy would be composed of periods of maximal growth and periods of no growth (e.g. Kozłowski and Teriokhin 1999). Only an accelerating cost of growth would promote the evolution of an intermediate growth strategy, yet no empirical study of trade-offs associated with juvenile growth has demonstrated this necessary condition. Using the Atlantic silverside, *Menidia menidia*, as a model species we provide the first experimental evidence that the cost of growth accelerates with growth rate.

MATERIALS AND METHODS

The Atlantic silverside, *Menidia menidia* is a marine fish common to North American estuaries from Florida to Prince Edward Island, Canada (Johnson 1975). Over this latitudinal range, silverside populations exhibit threefold variation in their intrinsic capacity for growth (Conover and Present 1990). Only at their northernmost localities do juvenile silversides display maximum growth and these genotypes can be induced to grow even faster by artificially manipulating rations (Schultz et al. 2002). As in many other species, ben-

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efits of size in *Menidia* include reduced susceptibility to predation (Scharf et al. 1998) and increased fecundity (Conover 1985). The trade-off is that fast-growing juveniles are inferior swimmers at a given size (Billerbeck et al. 2001) and are thereby more vulnerable to predators (Lankford et al. 2001). Because swimming performance is relatively easily assayed and is directly tied to survival in silversides, we used swimming performance as our index of fitness.

Growth Manipulation

Our ability to detect nonlinear costs of growth depends greatly on the range of growth rates tested. Although growth rates differ substantially among silversides from different latitudes, comparisons of swimming performance among populations may be confounded by differences in traits other than growth. Phenotypic manipulations provide a means of extending the range of growth rates within a population and increase our chances of detecting nonlinear costs of growth without potentially confounding population effects (Sinervo and Huey 1990; Sinervo et al. 1992). Since plasticity in length growth ranges a priori from zero to the population's maximum growth rate, we used silversides from the population in which the intrinsic capacity for growth is the greatest (the Annapolis river, Nova Scotia, Canada) and raised them at the temperature for which their growth is maximal (27°C). By varying ration levels for several weeks prior to swimming trials, we generated the broadest possible within-population range of growth rates (0.16 mm·d⁻¹ to 1.2 mm·d⁻¹).

We established laboratory populations with individuals collected from the Annapolis River, Nova Scotia (approximately 44°N) and used second generation, laboratory-reared silversides in our experiments to control for early-environmental and maternal effects. Eggs were collected from over 300 mass spawning F2 adults and larvae were reared to 15 days postfertilization on ad libitum rations at 21°C. At 15 days postfertilization, fish were measured to the nearest 1 mm total length. From these we established growth manipulation groups of 30 size-matched fish (± 0.05 mm standard error, SE), which were transferred to new containers for growth and swim acclimation at 27°C. Mean size in these groups ranged from 6.9 mm to 14.4 mm (± 0.05 mm SE). Each group was fed a predetermined mass of live *Artemia* nauplii, chosen such that all size groups would reach a mean size of 19–22 mm at the same age. That is, different growth rates were induced but final sizes were similar. The fish in each group were swim-acclimated for at least one week prior to swim trials by providing them with continuous water movement at an average velocity of 6–7 cm·s⁻¹, suspended for one hour at the beginning and end of each day during feeding. Because fish grown in this manner converge on a common size for only a brief period of time, we were limited in the number of trials that could be performed from a single round of growth manipulation. To obtain a sufficient number of replicates, the entire growth manipulation procedure was repeated three times, resulting in a total of 11 growth manipulation groups. Growth rates of individual fish were calculated from the difference between the length at which the fish were tested and the initial group mean length divided by the time between measurements. The standard error for in-

dividual growth rates calculated in this way is ≤ 0.025 mm·d⁻¹.

Swimming Performance

Critical swimming speed is a commonly used performance measure for which individual repeatability is well established (Plaut 2001). Swimming performance was assessed by forcing fish to swim against a current in a Vogel-style flume (Vogel 1981) of sufficient diameter that no blocking effects were present (Bell and Terhune 1970; for details of flume design see Billerbeck et al. 2001). Because *M. menidia* is an obligate schooling fish, all trials were carried out on groups of three or four individuals. Water in the flume was maintained at 27°C to avoid temperature stress and all individuals were fasted for at least 15 h and a maximum of 24 h prior to swim trials to eliminate effects of digestive state on swimming performance (Alsop and Wood 1997; Billerbeck et al. 2001). All fish were tested upon attaining lengths of 19–22 mm. Prior to the start of each trial, fish were size-matched (≤ 0.2 mm SE) and transferred to the swimming flume for a 45-min acclimation period. This was sufficient time to allow the fish to recover from handling; longer acclimation periods had no apparent effect on swimming performance in preliminary trials.

Swimming performance was assessed by forcing fish to swim against a current the velocity of which was increased by 5 cm·s⁻¹ every 10 min until the fish fatigued. As each fish fatigued (fell back upon a retaining screen and failed to resume swimming) the failure time was recorded. Critical swimming speed (U_{crit} ; Brett 1964) was calculated from the time of failure as $U_{crit} = V + T(\Delta V/\Delta T)$ where V is the maximum speed successfully completed, T is the time of failure, and ΔV and ΔT are the velocity increment and time interval (5 cm·s⁻¹ and 10 min, respectively). Median critical swimming speed for each trial was used as the response variable in the statistical analysis. A total of 87 swimming trials were conducted.

Data Analysis

To determine the growth dependence of swimming performance, a series of models relating swimming to growth (G) were constructed (Table 1). In keeping with previous research on fish in general (Videler 1993) and *M. menidia* in particular (Billerbeck et al. 2001), each of these models included a linear dependence on length (L). Since we were interested in testing whether the cost of growth accelerated with and was therefore a nonlinear function of growth rate, we fitted models with no dependence on growth, and a series including linear, quadratic, and power function dependence on growth. The model that best described the cost of growth was identified using the bias-corrected Akaike information criterion (AIC_c ; Burnham and Anderson 1998). Standard significance tests and analysis of residuals were also carried out for the best model. In all models in which growth was a factor, there was a significant, negative effect of growth on swimming performance.

TABLE 1. Fitted models and model selection criteria. In each of the models L indicates total length (cm), G indicates growth rate ($\text{mm}\cdot\text{d}^{-1}$), and Greek letters denote fitted parameters. SS is the residual sum of squares, $\text{Ln}(L)$ is the log-likelihood, K is the number of parameters in the model (including one for the variance), and AIC_c is the bias corrected Akaike information criteria. The model with the smallest AIC_c is the best. Akaike weights give the proportional contribution of each model to the total likelihood (Burnham and Anderson 1998). Note that the bulk of the weight (60%) is concentrated on the models including a squared cost of growth.

Fitted model	SS	$\text{Ln}(L)$	K	AIC_c	Akaike weight
$U_{crit} = \beta_0 + \beta_1 L$	1641.42	-246.44	3	499.17	0.00
$U_{crit} = \beta_0 + \beta_1 L + \beta_2 G$	1137.47	-230.85	4	470.20	0.20
$U_{crit} = \beta_0 + \beta_1 L + \beta_2 G + \beta_2 G^2$	1114.15	-229.97	5	470.70	0.15
$U_{crit} = \beta_0 + \beta_1 L + \beta_2 G^2$	1115.24	-230.01	4	468.52	0.45
$U_{crit} = \beta_0 + \beta_1 L + \beta_2 G + \beta_3 G^2$	1112.88	-229.92	6	472.92	0.05
$U_{crit} = \beta_0 + \beta_1 L + \beta_2 G^2$	1114.69	-229.99	5	470.74	0.15

RESULTS AND DISCUSSION

Using AIC_c as our model selection criteria, we found that the best descriptor of swimming performance was $U_{crit} = \beta_0 + \beta_1 L + \beta_2 G^2$ (Table 1, Fig. 1). The parameters (± 1 SE, P) of this model were $\beta_0 = -8.19$ (± 6.87 , $P = 0.24$), $\beta_1 = 1.87$ (± 0.34 , $P < 0.001$), and $\beta_2 = -5.73$ (± 0.92 , $P < 0.001$). Moreover, this model is five times more likely than the best model without a nonlinear growth cost and 60% of the Akaike weight (Burnham and Anderson 1998) supports a squared cost of growth. Residuals from this model did not differ significantly from normality (K-S test) and showed no significant serial autocorrelation. To allay concerns regarding nonindependence of fish in each growth manipulation group, this analysis was repeated using group mean growth rates and group mean U_{crit} (corrected for variation in TL). Again, using AIC_c as our model selection criteria, we found that U_{crit} was best described by $U_{crit} = \beta_0 + \beta_2 G^2$ with $\beta_2 = -4.63$ (± 1.23). Thus, both individual and group mean swimming speeds demonstrate an accelerating cost of growth.

The differences in swimming ability we observed are clearly a physiological cost of recent growth. Because our experimental fish were the same size at the same age, they have the same lifetime average growth rate: only their growth rates

during the two to three weeks prior to testing were manipulated. These results are robust: trade-offs with swimming performance were also found in prior comparisons among size-matched fish of different ages that have had different lifetime growth rates (Billerbeck et al. 2001).

The growth phenotypes compared in this experiment are primarily the results of environmental variation, that is, ration manipulation. For selection on growth to result in evolution, genetic differences in growth must also produce a nonlinear trade-off. Although data on swimming performance for silversides with a broad range of intrinsic growth rates are lacking, comparisons among individuals from two populations with genetic differences in growth suggest that this may be the case. That is, fast-growing silversides from Nova Scotia are significantly poorer swimmers compared to slower growing conspecifics from South Carolina when both are grown on unlimited rations (Billerbeck et al. 2001).

Swimming in a school and fleeing when attacked are a silverside's principal means of defense: they do not hide when predators lurk, nor do they bear armor or spines, or harbor noxious chemicals. Although we have not measured survival directly, prior experiments confirm that differences in swimming performance are correlated directly with vulnerability to predators (Lankford et al. 2001). Hence, there is a clear accelerating cost in fitness associated with greater growth rates.

Nonlinear costs are logically necessary for the evolution of submaximal growth. Nonlinearity does not, however, guarantee that submaximal growth will evolve. Only in the context of the entire life-history is it possible to evaluate whether a particular cost is sufficient to generate submaximal growth. Although the details are too cumbersome to present in this short note, analysis of a silverside life history model indicates that the cost of growth we have found is indeed capable of explaining the evolution of submaximal growth (S.B. Munch, unpubl. ms.).

Somatic growth rates vary enormously among individuals, populations, and species (Arendt 1997). Much of our understanding of the evolutionary basis for this variation hinges on the logical necessity of nonlinear costs of growth. Although physiological costs of growth now appear to be widespread, ours is the first study to show that costs of growth in terms of fitness accelerate as maximum growth rate is approached. In other organisms, the costs of growth will likely take many forms such as less effective armor, greater sus-

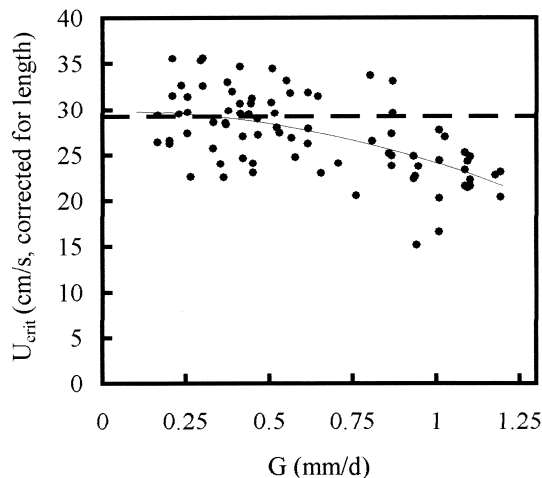


FIG. 1. U_{crit} versus growth rate. Points are trial medians after statistical removal of length effects. The dashed line indicates the mean U_{crit} for growth rates ≤ 0.6 . The solid line is the best fit model holding length constant, that is, $U_{crit} = \beta_0 + \beta_2 G^2$. Note that U_{crit} declines for growth rates greater than $0.6 \text{ mm}\cdot\text{d}^{-1}$.

ceptibility to disease, reduced longevity, and others. It remains to be seen whether nonlinear costs of growth are commensurately abundant across a broad range of organismic morphologies, physiologies, life histories, and phylogenies.

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APPENDIX

Linear costs of growth cannot result in submaximal optima. The total cost K of growing from initial size x_0 at growth rate $g \equiv g(x, t)$ to size x_T at some later time T is given by the integral $K = \int_0^T C[g] dt$, where $C[g]$ is the cost of growth. For clarity, we make a change of variables to size rather than time, noting that $dt = dx/g$, $K = \int_{x_0}^{x_T} C[g]/g dx$. If the cost is proportional to the rate growth, that is, $C(g) = ag$, then K is simply $x_T - x_0$. Thus for a given size increment (i.e. $x_T - x_0$), the total cost is independent of the growth rate and the optimal growth strategy will be to grow at either the maximal rate or not at all, assuming fitness is size dependent. Thus the submaximal growth rates exhibited by juveniles in many taxa cannot be explained by linear costs of growth.