

EVOLUTION OF INTRINSIC GROWTH AND ENERGY ACQUISITION RATES. I. TRADE-OFFS WITH SWIMMING PERFORMANCE IN *MENIDIA MENIDIA*

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Abstract.—Latitudinal populations of the Atlantic silverside, *Menidia menidia*, show substantial genetic variation in rates of energy acquisition and allocation. Reared in common environments, silversides from northern latitudes consume more food, grow faster and more efficiently, store more energy, and produce greater quantities of eggs than their southern conspecifics. The persistence of seemingly inferior southern genotypes in the face of ostensibly superior northern genotypes suggest that there are hidden evolutionary trade-offs associated with these elevated acquisition and allocation rates. We tested the hypothesis that rapid growth and high levels of food consumption trade-off against locomotory performance in *M. menidia*. We compared both aerobic (prolonged and endurance) and anaerobic (burst) swimming capacities between intrinsically fast-growing fish from the north (Nova Scotia, NS) and intrinsically slow-growing fish from the south (South Carolina, SC) and between growth-manipulated phenotypes within each population. We also compared swimming speeds and endurance between fasted and recently fed fish within populations. Maximum prolonged and burst swimming speeds of NS fish were significantly lower than those of SC fish, and swimming speeds of fast-growing phenotypes were lower than those of slow-growing phenotypes within populations. Fed fish had lower burst speeds and less endurance than fasted fish from the same population. Thus, high rates of growth and the consumption of large meals clearly diminish swimming performance, which likely increases vulnerability to predation and decreases survival and relative fitness. The submaximal growth rate of southern *M. menidia* appears to be adaptive, resulting from balancing selection on rates of somatic growth.

Key words.—Countergradient variation, latitude, life-history evolution, locomotory performance, metabolism, swimming speed, fish.

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The fitness benefits of rapid somatic growth in the early life history of ectotherms are abundantly clear. Rapid growth tends to decrease age at first reproduction, thereby shortening generation time and increasing reproductive life span (Levontin 1965). Elevated growth also increases body size and therefore fecundity later in life, because the two are often positively correlated (e.g., Shine 1988; Wootton 1990; Roff 1992). For organisms suffering high juvenile mortality, rapid somatic growth enables them to minimize the time spent in vulnerable life stages, thereby increasing survivorship (Williams 1966; Lack 1968). Given the positive influences of rapid growth on fitness, natural selection is generally assumed to maximize rates of energy intake and utilization (Lotka 1922; Ware 1982) and growth (e.g., Ricklefs 1969; Stearns and Koella 1986; Perrin and Rubin 1990). Indeed, growth rate often is used as a surrogate for fitness when direct measures of reproductive success are unattainable (Stearns 1992). Thus, variation in juvenile growth commonly is viewed as the result of environmental limitations (e.g., temperature or food availability) rather than selection.

A growing body of evidence, however, suggests that variation in growth may be adaptive. Substantial genetic variation in growth rates within and among species in nature has been documented, demonstrating that organisms rarely grow at their physiological maxima (Case 1978; Calow 1982;

Arendt 1997). Additionally, rates of food intake and somatic growth often show compensation after periods of inhibition (e.g., Russell and Wootton 1992; Jobling and Koskela 1996; Nicieza and Metcalfe 1997). Organismal growth rates can also be increased by artificial selection (Gjerde 1986) and the insertion of growth-hormone genes (Farrell et al. 1997; Stevens et al. 1998). Recent life-history models (e.g., Sibily et al. 1985; Abrams et al. 1996) suggest that growth rates are likely to be optimized, not maximized, by natural selection. However, a general theory that explains the various patterns of growth variation in nature is lacking.

One pattern of growth variation that is particularly difficult to reconcile with current theory is countergradient variation. In cases of countergradient variation in growth, the genetic capacity for growth varies inversely with the ecological potential for growth across an environmental gradient, typically latitude or altitude (Levins 1968, 1969). Conover and Schultz (1995) identified evidence of countergradient variation in growth in a variety of animal taxa including molluscs, fishes, amphibians, and reptiles. More recently, countergradient variation in growth has been documented in insects (James and Partridge 1995; Arnett and Gotelli 1999) and in many species of molluscs (Palmer 1994; Parsons 1997; Dittman et al. 1998) and fishes (Schultz et al. 1996; Arendt and Wilson 1997, 1999; Conover et al. 1997; DiMichele and Westerman 1997; Power and McKinley 1997; Jonassen et al. 2000; Merila et al. 2000; Secor et al. 2000). Because the phenotypic expression of growth across environments masks the underlying distribution of genotypes, it is likely that many more examples of countergradient variation in growth remain undetected.

The evolution of submaximal growth rates, particularly in environments conducive to rapid growth, suggests the exist-

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tence of trade-offs with other fitness-related traits. Although the trade-off between growth and reproduction is perhaps the most well documented in the life-history literature (Roff 1992; Stearns 1992), trade-offs to rapid growth prior to reproduction have rarely been investigated (Case 1978; Arendt 1997). Potential trade-offs to rapid growth in the early life stages of animals include developmental stability (Leamy and Atchley 1985), competitive ability (James and Partridge 1998), resistance to pathogens (Smoker 1986; Kirpichnikov et al. 1993), longevity (Jonsson et al. 1992), energy storage (Forsman and Lindell 1991), starvation endurance (Gotthard et al. 1994), delayed skeletal ossification (Arendt and Wilson 2000), and increased risk of predation (Gotthard 2000). Adaptive variation in growth rate may also be associated with the costs of energy acquisition (Reznick et al. 2000).

In this study, we investigate the evolution of countergradient variation in growth of a small estuarine fish: the Atlantic silverside, *Menidia menidia*. Silversides exhibit countergradient variation in growth across latitudes, with northern fish exhibiting roughly twofold higher rates of food consumption and growth than southern conspecifics (Conover and Present 1990; Present and Conover 1992). Rapid growth and elevated food consumption in northern fish appear to be an adaptive response to size-dependent selection against slow-growing fish that enter winter at a small size (Conover 1992; Schultz et al. 1998). Previous work on *M. menidia* has failed to reveal a trade-off to elevated food consumption and growth. When compared over a range of common environments with southern fish, northern *M. menidia* exhibit greater food-conversion efficiency (Present and Conover 1992; Billerbeck et al. 2000), energy (lipid) storage capacity (Schultz and Conover 1997), and reproductive output and efficiency (Klahre 1998), yet show similar metabolic rates (Billerbeck et al. 2000) and starvation endurance (Conover 1992).

We hypothesize that intraspecific variation in growth among latitudinal populations of *M. menidia* arose because high levels of growth and food consumption trade off against locomotor performance. The principle of allocation (Cody 1966; Levins 1968; Sibly and Calow 1986) suggests that the allocation of energy to growth or to the metabolism of ingested food (specific dynamic action; SDA) may limit the energy available for active metabolism and thus diminish locomotor capacity. Small fish in early life stages may be particularly susceptible to conflicts in energy allocation due to their low metabolic scope, high weight-specific rates of metabolism and food consumption, and poor anaerobic capacity (Conover and Schultz 1997). Additionally, the allocation conflicts imposed on all living organisms by limitations in energy availability are likely to be compounded in aquatic environments due to the relatively low oxygen levels and high viscosity of water as compared to air.

To elucidate potential trade-offs with growth and food consumption in *M. menidia*, we employed both common-garden comparisons and phenotypic manipulations as suggested by Reznick (1985) and Sibly (1991). Given that a gradual cline in growth rates across latitudes has been documented previously for *M. menidia* (Conover and Present 1990; Present and Conover 1992), we focused our attention on populations at the extremes of the species' geographic range. We compared both aerobic and anaerobic swimming capacity be-

tween intrinsically fast-growing fish from northern populations and intrinsically slow-growing fish from southern populations over the range of temperatures likely to be encountered by fish at all latitudes during the growing season. We then experimentally manipulated growth rate (via ration restriction) and compared swimming ability within populations between fish that grew maximally and those that grew conservatively. To distinguish the effects of growth and food intake, fish in all growth trials were fasted before testing. In a series of separate experiments designed to isolate trade-offs with food consumption, we compared swimming speeds and endurance between fasted and recently food-satiated fish within populations over a range of temperatures.

MATERIALS AND METHODS

General Protocol

Potential trade-offs between growth and food consumption and three types of swimming were investigated: (1) maximum prolonged capacity; (2) swimming endurance; and (3) maximum burst capacity. Prolonged swimming and swimming endurance are generally considered measures of aerobic capacity, whereas burst swimming is largely anaerobic (Beamish 1978). Because *M. menidia* are schooling fish, all performance tests were conducted on small groups (five or six individuals) of size-matched (± 1 mm) juveniles ranging in mean size from 18 mm to 35 mm total length. Fish tested were from second and third generation laboratory-reared stocks drawn from two sites along the Atlantic coast of North America: Nova Scotia, Canada (NS), at 44°N latitude and South Carolina, USA (SC), at 33°N latitude. Stocks were raised in a common environment (light cycle, food, temperature, salinity) at the Flax Pond Marine Laboratory (Stony Brook, NY) to control environmental and maternal effects and to isolate genetic differences between populations. All fish were reared at room temperature (20–23°C) and tested at ambient salinity (26–28 ppt) under a 15:9 h L:D photoperiod. Details of stock origination, collection, and culture may be found in Billerbeck et al. (2000).

Because trade-offs may only be expressed under certain conditions, it is necessary to experiment across a range of environments (Roff 1992; Stearns 1992). In aquatic ectotherms, temperature directly affects physiological performance (Hochachka and Somero 1984). Increases in temperature also cause disproportionate decreases in oxygen concentration due to the nonlinear relationship between temperature and oxygen solubility. To account for such thermal effects, we initially evaluated swimming performance at three temperatures: 17°C, 23°C, 28°C (Conover 1992). Having established in these early experiments that differences in locomotor capacities between *M. menidia* populations were consistent across temperatures (no population \times temperature interactions), we conducted later experiments at the intermediate temperatures (23–25°C) that juvenile fish are likely to encounter most frequently across a wide range of latitudes (Conover 1992).

Theoretical models (Spouge and Larkin 1979; Brainerd and Patek 1998) and empirical tests (Swain 1992a,b; Brainerd and Patek 1998) suggest that vertebral number may affect swimming performance in fishes. Vertebral counts are known

to differ among latitudinal populations of *M. menidia* (Billerbeck et al. 1997). Therefore, when possible, fish were X-rayed and scored for vertebral number upon completion of an experiment.

Prolonged Swimming Performance

We used critical swimming speed (U_{crit}), the maximum velocity attained by a fish over a set time period (Beamish 1978), as a measure of prolonged swimming capacity. Three sets of critical swimming trials were conducted. To test the hypothesis that rapid growth evolved at the expense of swimming ability, we first compared U_{crit} between NS fish and SC fish (growing at their respective maximal growth rates) at three test temperatures: 17°C, 23°C, and 28°C. Because populations might differ in swimming performance due to influences other than growth (i.e., intraspecific variation in other aspects of their physiology or morphology), we isolated the effect of growth by comparing U_{crit} of fast- and slow-growing phenotypes within each population at 23°C in the second set of experiments. Different growth phenotypes were created by rearing fish within a stock on either low (fed *Artemia* nauplii for 0.5–1.0 h, once per day) or high (fed *Artemia* nauplii for 1.0 h, three times per day) ration levels for 14 days prior to performance tests. To estimate growth rates of the generated phenotypes, mean initial fish size prior to and mean final fish size after growth manipulation were determined via subsampling ($n = 20$ –30 fish per subsample). All fish tested in the between- and within-population swim trials were starved 20–24 h prior to testing to eliminate SDA effects, which last roughly 6–7 h after the consumption of a meal in *M. menidia* (Billerbeck et al. 2000). To test the hypothesis that food consumption diminishes swimming performance, in the third set of experiments we compared U_{crit} between fasted (unfed) and recently satiated (fed) fish within both the NS and SC stocks at 17°C, 23°C, and 28°C. One day prior to an experiment, fish were size-matched, randomly assigned to treatment group (unfed or fed), and starved for 20–24 h. Fed fish then were offered unlimited live *Artemia* nauplii for 30 min prior to testing.

Critical swimming speeds were determined by swimming fish to exhaustion via incremental (ramp) velocity swim tests conducted in a Vogel-style flume (Vogel 1981) modeled after Kelsch (1996). The recirculating propeller-driven system consisted of a 200-L reservoir, a vertical loop of 10-cm diameter flexible PVC, and an open U-shaped swimway of rigid PVC measuring 1.0 m long \times 10 cm wide \times 10 cm deep. The reservoir was used to heat/chill and oxygen-saturate the water in the flume. A variable speed motor (Grainger, Inc., Bohemia, NY), mounted over the reservoir with the propeller arm oriented vertically, propelled water up into the swimway. Water velocity was controlled and monitored using a tachometer (Grainger, Inc.). Tachometer readings (rpm) were calibrated to water velocities (cm/sec) using an electronic flywheel flow meter (Kent type 265 miniflow) and corroborated manually by timing the passage of a small drogue through the swimway. Rectilinear flow was achieved by affixing three honeycombed collimators overlaid with fine netting (2-mm mesh) in the swimway: one upstream, one midstream, and one downstream. The mid- and downstream flow

straighteners demarcated a 20-cm long swim chamber in which fish were tested. The downstream collimator served as a retaining screen to collect fish as they fatigued.

Average critical swimming speeds were determined for groups of six fish ranging in mean size from 18 mm to 26 mm total length. All fish were temperature and swim acclimated (swum continuously at 6–7 cm/sec, except during feeding) for 10–14 days prior to performance trials. One day prior to testing, fish were size-matched (± 1.0 mm) and fasted for 20–24 h. To begin a trial, a group was transferred to the flume and acclimated at low water velocity (5–10 cm/sec) for 15 min. After acclimation, flow was raised to the initial test velocity: 11.25 cm/sec at 17°C, 13.50 cm/sec at 23°C, and 15.75 cm/sec at 28°C. Water velocity then was raised in stepwise increments of roughly one body length (2.25 cm/sec) at set time intervals (15 min for between- and within-population contrasts; 5 min for feeding contrasts) until fish fatigued (fell back upon the retaining screen). The shorter time interval was chosen for the feeding trials in an effort to exhaust fish during the height of their feeding metabolism (SDA), which occurs roughly 30–60 min after feeding in *M. menidia* (Billerbeck et al. 2000).

As each fish in a group fatigued, the time of exhaustion was recorded, it was removed from the flume, sacrificed, and measured for total length under a dissection scope (to ± 0.1 mm) using digital calipers. Although the quantity of food consumed by fed fish was not directly measured, maximum body depths (distension of the stomachs) of fasted and satiated fish were recorded as a rough indicator of consumption. Exhaustion times of fish were converted to critical velocities using the equation: U_{crit} (cm/sec) = $V + (T/t \times v)$, where V = highest speed maintained for a full time interval, v = velocity increment, T = time at fatigue velocity, and t = time increment (Brett 1964).

Mean critical swimming speeds of groups were compared among treatments (NS vs. SC, fast vs. slow in each population, and fed vs. unfed in each population) via ANCOVA, with mean fish length as the covariate. U_{crit} for any fish that failed to exhaust during a trial was scored as the maximum velocity of the flume, 40.5 cm/sec. The effect of vertebral number on U_{crit} within populations was also tested via ANCOVA, using fish length as the covariate.

Burst Swimming Performance

Simulated predator attacks were used to elicit burst-swimming responses in schools of five, size-matched (± 0.5 mm) fish ranging from 30 mm to 35 mm total length. The ‘‘predator’’ consisted of a 10-cm plasticized bluefish (*Pomatomus saltatrix*) attached to the end of a dowel rod. Burst swimming tests were conducted at 24–25°C in a shallow test arena (1 m long \times 1 m wide \times 7.5 cm deep). When a group of fish occupied a central location in the arena, they were attacked by manually thrusting the predator toward the school. Preliminary experiments revealed that these simulated predator attacks were much more successful at eliciting a burst response in silversides than other methods (i.e., electric shock, sound, physical disturbance). Two attacks per group were recorded at 125 frames/sec using a high-speed video camera (Redlake MASI, Inc., San Diego, CA) mounted above the

tank. The high-speed images were transferred onto VHS videotape, and these analog images were then digitally recorded onto a personal computer using a frame grabber (Coreco Imaging, Bedford, MA) capable of digitizing video images at 640×480 pixels with 8-bit accuracy. Spatially-calibrated Cartesian coordinates were obtained by digitizing the head of each fish in each frame (x, y at time t) using Optimas image-analysis software (Media Cybernetics, Des Moines, IA). The burst speed (linear displacement/time) for each time interval (0.008 sec) was calculated for each fish. These velocities were smoothed by calculating three-point running averages to avoid overestimation of burst speed due to yaw of the fish's head (Fuiman 1986). The single highest swimming velocity was determined for each fish and then averaged over all fish in a test group. Because attack speed of the predator was not controlled, it was measured as for the prey above and statistically analyzed to determine its influence on prey burst speeds.

Three sets of comparisons of burst capacity were made: (1) NS versus SC fish, both growing maximally; (2) fast-versus slow-growing fish within the NS population; and (3) fasted (unfed) versus satiated (fed) fish within both the NS and SC populations. All fish were starved for 20–24 h prior to testing, with the exception of fed fish, which were offered live *Artemia* nauplii for 30 min immediately prior to each experiment. Growth-manipulated NS fish were reared on live *Artemia* nauplii for 13–17 days prior to testing: Fast-growth fish were provided high food ration levels (fed nauplii to excess twice per day), whereas slow-growth fish received low rations (fed nauplii once per day = 50% fish wet body weight). To begin growth manipulation, 200–300 fish were size-matched (± 1 mm) for each treatment group and divided into two replicate tanks. Fish in the fast-growth and slow-growth treatments were spawned by the same parental stocks, reared under identical conditions prior to selection, and drawn from the middle of the size distributions in their respective tanks. However, fast-growth fish were chosen at a smaller initial size (younger age) and their growth was manipulated over a slightly shorter time period (see Fig. 4) to size-match them with slow-growth fish at the end of the growth manipulation period. During growth manipulation, 15 fish were sampled from each tank every fourth day to estimate growth and to adjust ration levels. Attacks were conducted on groups of growth-manipulated fish once they reached 33–34 mm. The average growth rate of fish in each trial was estimated by subtracting mean initial fish size prior to growth manipulation from mean final fish size after growth manipulation. Differences in burst speed due to the fixed effects of population and feeding status were tested via two-way ANOVA. Burst speeds between fast- and slow-growing phenotypes within populations were tested via single-classification ANOVA.

Swimming Endurance

Mean swimming endurance (time to exhaustion) was contrasted between groups of fasted and satiated fish within both the NS and SC populations via paired, fixed-velocity flume experiments (Hammer 1995) conducted at 23°C. As above, fish were swim-acclimated 10–14 days prior to testing. One

day prior to an experiment, 12 fish from a population were size-matched (± 0.5 mm), split randomly into two treatment groups (unfed or fed), and starved for 20–24 h. Fed fish were offered unlimited live *Artemia* for 30 min immediately prior to transfer into the flume. To begin a trial, water velocity was increased from 0 cm/sec to the test velocity over a 15-min period (increased by one-fifth test velocity every 3 min). Test velocities for NS fish were 24 cm/sec for small fish (20–23 mm) and 28 cm/sec for larger fish (24–26 mm). Test velocities for SC fish were 27 cm/sec for small fish (20–22 mm), 32 cm/sec for medium-sized fish (23–24 mm), and 34 cm/sec for the largest fish (25–27 mm). Velocities were chosen such that all fish in a trial would fatigue within one hour (during peak SDA) based on results of preliminary experiments. The total time to exhaustion was recorded for each fish in a trial and then averaged across all fish in a test group. Average endurance between fasted and satiated schools within populations was analyzed via paired t -tests.

Statistical Analyses

Statistical analyses tested the null hypothesis that treatments (population, growth manipulation, and food consumption) had no effect on the various forms of swimming performance tested. Normality of data was tested using a Shapiro-Wilk W -test, and heterogeneity of variances was tested using both Bartlett's and Levene's tests. Prior to conducting analysis of covariance, the assumption of heterogeneity of slopes (interactions) was tested. Unless otherwise indicated in the results of a given test, slopes did not differ (interactions were not statistically significant) between treatment groups. ANOVAs were conducted only when covariates (e.g., fish length, predator attack speed) were nonsignificant. All statistical analyses were performed using JMP (SAS Institute, Inc., Cary, NC).

RESULTS

Effect of Population Origin

Critical swimming speed (U_{crit}) differed significantly between populations (ANCOVA, population effect: $F_{1,59} = 8.86$, $P = 0.004$) after accounting for the effects of temperature ($F_{1,59} = 9.37$, $P = 0.003$), fish length ($F_{1,59} = 4.84$, $P = 0.032$), and length \times temperature interaction ($F_{1,59} = 12.82$, $P = 0.001$). Thus, overall, SC fish swam faster than NS fish (Fig. 1). The difference in U_{crit} between populations at 28°C was actually greater than it appears in Figure 1 because 12% (seven of 60) of SC fish but only 3% (two of 60) NS fish failed to exhaust, resulting in a greater underestimation of critical swimming speeds of SC fish. Although vertebral counts ranged four to five centra within populations, ANCOVA using mean fish length as the covariate revealed no effect of mean vertebral number on mean U_{crit} in any of the prolonged swimming trials (NS: 17°C, $F_{1,7} = 4.26$, $P = 0.078$; 23°C, $F_{1,7} = 0.44$, $P = 0.528$; 28°C, $F_{1,9} = 2.74$, $P = 0.132$; and SC: 17°C, $F_{1,7} = 0.02$, $P = 0.894$; 23°C, $F_{1,7} = 2.54$, $P = 0.155$; 28°C, $F_{1,9} = 0.62$, $P = 0.451$).

Burst speeds of fish from the NS population were also considerably slower than those of fish from the SC population at 24–25°C (two-way ANOVA, population effect: $F_{1,53} =$

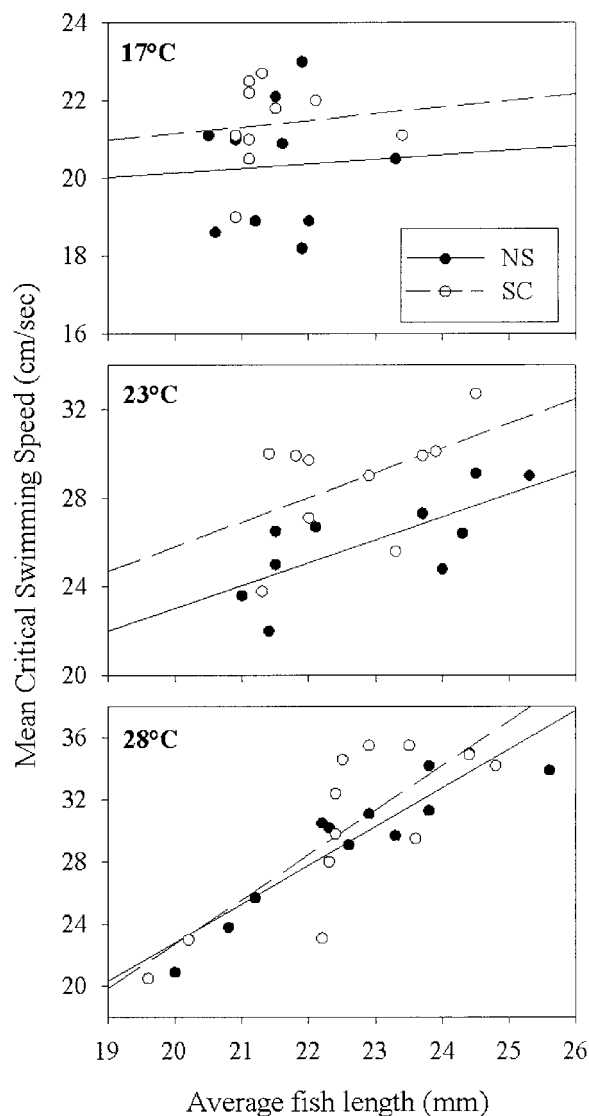


FIG. 1. Average critical swimming speeds of schools (six individuals) of NS and SC fish measured over a range of sizes at three test temperatures in a Vogel-style flume. ANCOVA revealed a significant difference in U_{crit} between populations ($F_{1,59} = 8.86$, $P = 0.004$), after accounting for fish length ($F_{1,59} = 4.84$, $P = 0.032$), temperature ($F_{1,59} = 9.37$, $P = 0.003$), and length \times temperature interaction ($F_{1,59} = 12.82$, $P = 0.001$).

37.45, $P < 0.001$). On average, burst speeds of SC fish were 22.8 cm/sec (16%) faster than those of NS fish (Fig. 2, open boxes). Neither fish size (ANOVA: $F_{1,54} = 0.02$, $P = 0.898$) nor speed of predator attack (ANOVA: $F_{1,54} = 1.76$, $P = 0.190$) significantly influenced voluntary burst speeds, thus they were not used as covariates.

Effect of Growth Manipulation

Fast-growing (1.0 mm/day) NS fish showed diminished U_{crit} -values compared to slow-growing (0.60 mm/day) NS fish (ANOVA: $F_{1,9} = 7.95$, $P = 0.020$) at 23°C (Fig. 3). Critical swimming speeds of slow-growing fish were 2.4 cm/sec (8%) greater on average than those of fast-growing fish. Differences in U_{crit} between growth-manipulated SC fish

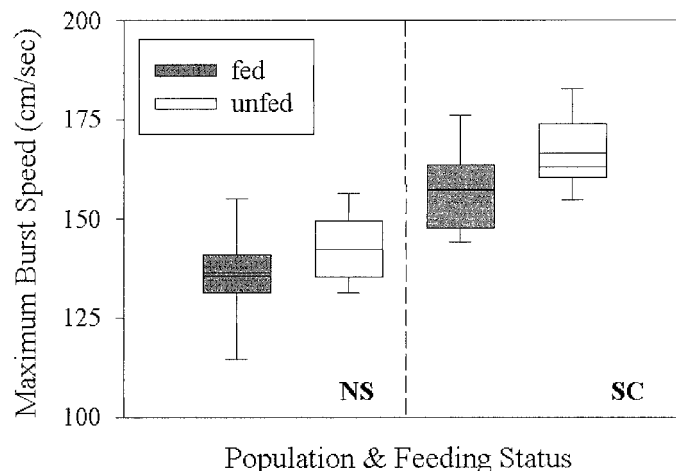


FIG. 2. Mean voluntary burst speeds of schools (five individuals) of fed and unfed fish from both NS and SC in response to simulated-predator attack at 24–25°C. Boxes include 25th through 75th percentiles; whiskers represent fifth and 95th percentiles. Two-way ANOVA revealed significant population ($F_{1,53} = 37.45$, $P < 0.001$) and feeding ($F_{1,53} = 4.52$, $P = 0.038$) effects, with SC fish swimming faster than NS fish and unfed fish swimming faster than fed fish.

growing at 0.39 mm/day and 0.27 mm/day were in the same direction (fast-growers $<$ slow-growers) and of similar magnitude (2.1 cm/sec difference), but were not significant (ANCOVA: $F_{1,7} = 1.30$, $P = 0.290$; Fig. 3).

NS fish that grew rapidly (1.2–1.3 mm/day) also showed substantially diminished burst capacity at 24–25°C compared to fish from the same population that grew more conservatively (0.50–0.64 mm/day; Fig. 4; ANOVA: $F_{1,14} = 12.03$, $P = 0.004$). The difference in maximum burst speeds between growth phenotypes was 21.3 cm/sec (15%).

Effect of Food Consumption

The consumption of a meal immediately prior to prolonged swimming trials marginally diminished the U_{crit} of NS fish at 28°C (ANCOVA: $F_{1,12} = 3.66$, $P = 0.082$), yet had little effect on U_{crit} at 23°C (ANCOVA: $F_{1,16} = 0.01$, $P = 0.944$) or 17°C (ANCOVA: $F_{1,18} = 0.72$, $P = 0.260$; Fig. 5). Differences in U_{crit} between pre- and postprandial SC fish also were nonsignificant (ANCOVA 28°C: $F_{1,17} = 0.04$, $P = 0.852$; 23°C: $F_{1,12} = 2.22$, $P = 0.164$; 17°C: $F_{1,18} = 0.24$, $P = 0.629$). Food consumption prior to these experiments, however, did cause a significant distension of fish stomachs. Maximum body depths of fed NS fish were significantly greater than those of unfed NS fish at all test temperatures (ANCOVA, 17°C: $F_{1,18} = 10.03$, $P = 0.003$; 23°C: $F_{1,16} = 7.34$, $P = 0.008$; 28°C: $F_{1,12} = 8.29$, $P = 0.008$), although they differed significantly only at high temperature for SC fish (ANCOVA, 17°C: $F_{1,18} = 0.58$, $P = 0.228$; 23°C: $F_{1,12} = 2.35$, $P = 0.077$; 28°C: $F_{1,16} = 36.81$, $P < 0.0001$).

Swimming endurance of fed NS fish was substantially lower than that of unfed NS fish of similar size at 23°C (paired t -test: $df = 10$, $P = 0.012$), but was not significant between fed and unfed SC fish (paired t -test: $df = 10$, $P = 0.394$; Fig. 6). Maximum body depths of fed and unfed NS fish in the swimming endurance trials differed significantly (paired

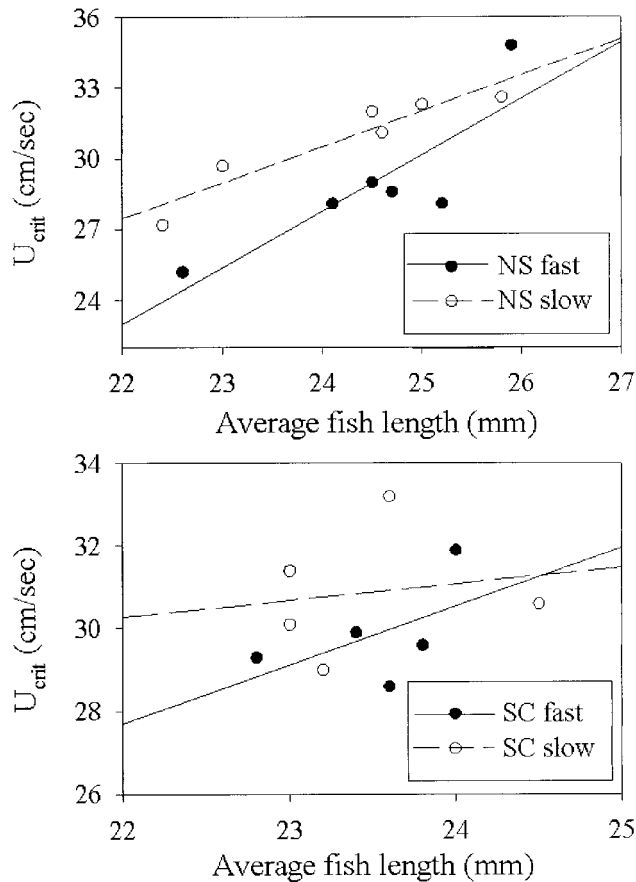


FIG. 3. Mean critical swimming speeds (U_{crit}) of fast- and slow-growing phenotypes from NS (top panel) and SC (bottom panel) measured at 23°C. Fast-growing (~ 1.0 mm/day) NS fish exhibited lower U_{crit} than slow-growing (~ 0.6 mm/day) NS fish (ANCOVA: $F_{1,9} = 7.95$, $P = 0.020$). Phenotypic variation in growth rates of SC fish (0.39 mm/day vs. 0.27 mm/day) did not affect critical swimming speed (ANCOVA: $F_{1,7} = 1.30$, $P = 0.290$).

t -test: $df = 10$, $P = 0.002$), but those of SC fish did not ($df = 10$, $P = 0.631$).

Burst swimming speeds decreased significantly in both populations due to food consumption (two-way ANOVA, feeding effect: $F_{1,53} = 4.52$, $P = 0.038$; Fig. 2). On average, bursts of unfed fish were 8 cm/sec (5%) faster than those of fed fish.

DISCUSSION

These experiments clearly demonstrate that intrinsic growth rate and food consumption trade off with swimming performance in the Atlantic silverside, *M. menidia*. Across a range of temperatures, intrinsic growth rate and locomotory performance were negatively correlated: fast-growing NS fish exhibited slower burst and prolonged swimming speeds than slow-growing SC fish. The genetic basis of these physiological trade-offs is evident because performance trials were conducted on fish stocks reared for multiple generations under common-garden conditions that controlled for environmental effects on growth. Correlations between growth and swimming within populations mirrored those found between populations: Fish that grew rapidly were poorer burst and

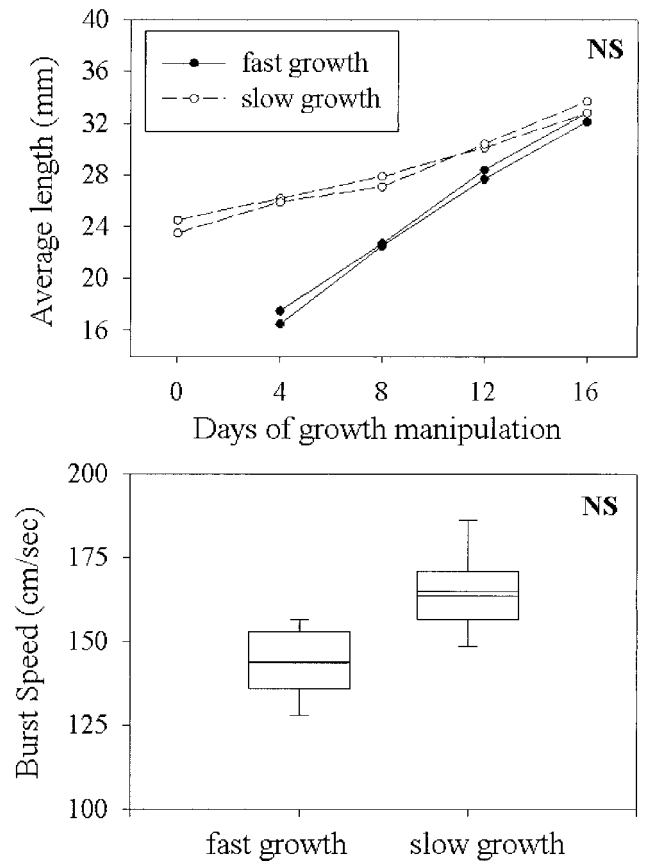


FIG. 4. Growth trajectories of NS fish generated via ration manipulation. Fish grew rapidly (1.2–1.3 mm/day) on ad libitum rations and moderately (0.5–0.6 mm/day) on restricted rations (top panel). Mean burst capacities of schools (five individuals) of NS fish growing at these different rates, both under simulated-predator attack at 24–25°C (bottom panel). Boxes are drawn as in Figure 2. Fish with rapid growth rates swam significantly slower than those with moderate growth rates (ANOVA: $F_{1,14} = 12.03$, $P = 0.004$).

prolonged swimmers than those from the same population that grew more conservatively. Food consumption also was negatively correlated with locomotor capacity: High levels of food consumption diminished swimming endurance and burst swimming speeds (although not prolonged swimming). It appears that the rapid somatic growth rates and the high levels of food consumption required to fuel the rapid growth of fish from northern latitudes have evolved at the expense of locomotor capacity. To our knowledge, these data provide the first evidence of genetically based trade-offs between food consumption and growth and locomotory performance in any organism.

The agreement in sign of within- and between-population correlations of swimming performance and growth in this study strongly suggests intrinsic growth rate as the causal factor in locomotor differences between populations. Although differential swimming ability of NS and SC fish might reflect intraspecific variation in aspects of morphology or physiology unrelated to growth, swimming differences between fast- and slow-growing fish within populations clearly result from growth, because fish are alike in all other respects. Variation in vertebral number can be rejected as the cause

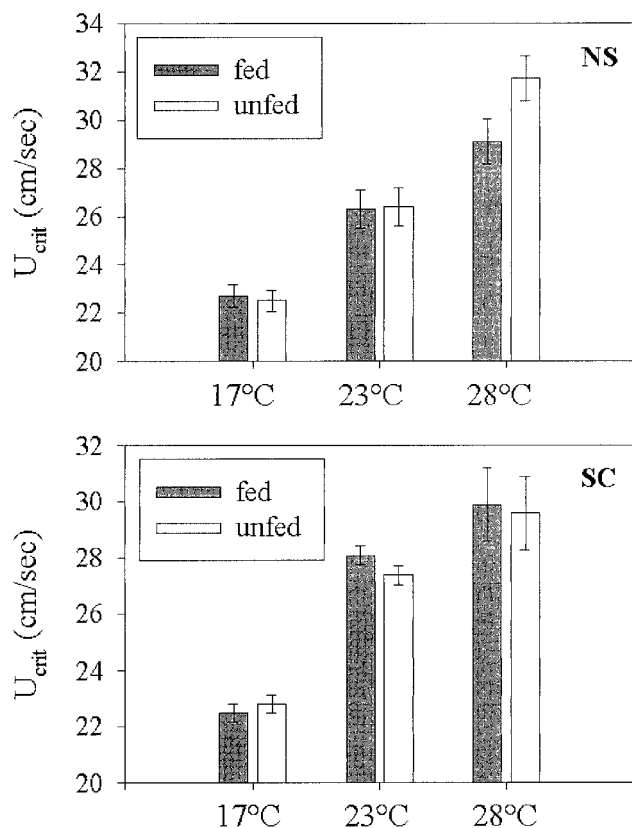


FIG. 5. Least-square mean critical swimming speeds (U_{crit}) from ANCOVA of schools (six individuals) of fed versus unfed fish from NS (top panel) and SC (bottom panel) measured via incremental-velocity flume experiments at three test temperatures. Vertical lines represent ± 1 SE. The consumption of a meal marginally reduced swimming speeds of NS fish at 28°C (ANCOVA: $F_{1,12} = 3.66$, $P = 0.082$) and had no effect on locomotor capacity at lower temperatures or in SC fish.

of differential swimming performance in *M. menidia* because vertebral counts were not correlated with swimming speeds in either population. Moreover, although fast- versus slow-growing fish within populations differed in swimming ability, their vertebral counts were similar. Additionally, theoretical models generally predict that low vertebral counts reduce flexibility and resultant swimming ability. In direct contrast to these predictions, we found that fish with fewer vertebrae (SC) consistently swam faster than fish with more vertebrae (NS).

Recent studies of ectotherm exercise physiology have uncovered negative effects of rapid growth and food consumption on locomotion that are consistent with our findings. Phenotypically fast-growing fathead minnows (Kolok and Oris 1995) and rainbow trout (Gregory and Wood 1998, 1999) exhibited lower critical swimming speeds than slow-growing conspecifics when exercised to exhaustion. Farrell et al. (1997) showed that growth hormone enhanced transgenic coho salmon swam slower than nontransgenic controls; and Klukowski et al. (1998) discovered that the injection of testosterone in fence lizards diminished growth, yet increased both sprint speed and stamina. Critical swimming speeds of satiated rainbow trout were also significantly lower than those

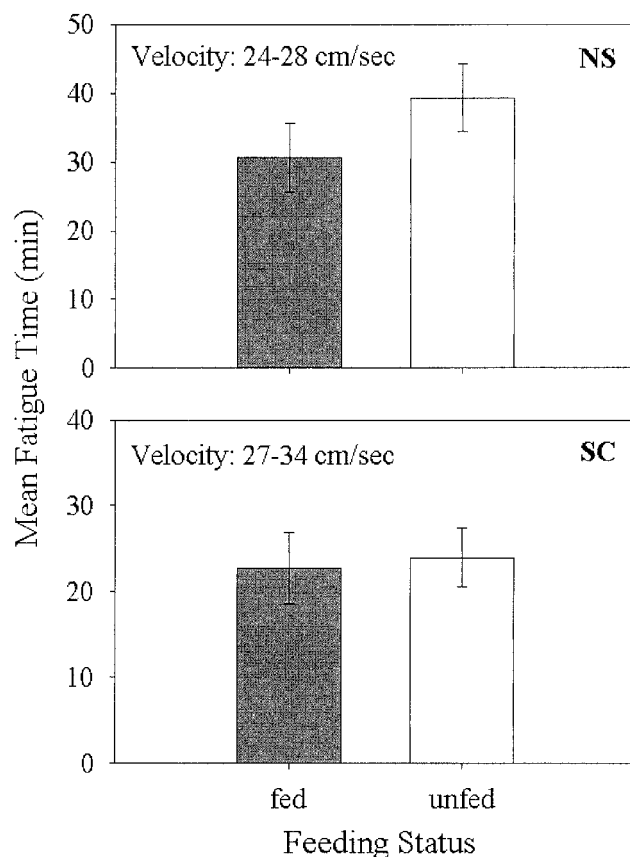


FIG. 6. Mean swimming endurance of schools (six individuals) of fed and unfed NS (top panel) and SC (bottom panel) fish. Swimming endurance of unfed NS fish was significantly greater than that of fed NS fish (paired t -test: $df = 10$, $P = 0.012$). Vertical lines represent ± 1 SE. Differences between fed versus unfed SC fish were not significant.

of fasted individuals (Alsop and Wood 1997). Our studies show that trade-offs between consumption and growth and locomotory performance have a genetic basis and therefore not only affect phenotypes, but may also influence the evolution of animal growth rates.

Trade-offs between food consumption and growth and aerobic swimming capacity likely result from conflicts in energy allocation between feeding metabolism (specific dynamic action; SDA), growth, and activity. Energy expended metabolizing a meal or synthesizing new somatic tissue may be unavailable for swimming, thus diminishing an organism's scope for activity (Fry 1971). SDA clearly represents a significant energy drain in *M. menidia*: Peak metabolic rates immediately (30–60 min) after feeding may be more than triple routine rates (Billerbeck et al. 2000). Metabolism then slowly returns to routine levels over a period of roughly 6–7 h, depending on temperature and meal size. Respirometry experiments also have revealed slightly higher routine metabolic rates of fasted *M. menidia* from NS compared to those from SC; thus, rapid growth may elevate maintenance costs (Billerbeck et al. 2000). Although the energetics of swimming have not been assessed in *M. menidia*, swimming has been shown to entail a substantial energy cost in other fishes, increasing metabolic rates as much as 15-fold at top speeds

(Brett 1964; Beamish 1978). If fish that are metabolizing a large meal or growing rapidly are unable to switch their allocation of energy away from SDA or growth, their energetic demands may exceed energy availability when they are forced to swim, resulting in failure. Although energy limitations may underlie the physiological trade-offs demonstrated herein, such a conclusion must remain tentative until maximum metabolic rates of *M. menidia* have been quantified.

Trade-offs with locomotor performance were apparent only with substantial differences in intrinsic growth rates and food consumption. Although not measured in these experiments, maximal growth rates of larval and juvenile *M. menidia* from NS are 1.5 to 3.0 times greater than those from SC, depending on temperature (Present and Conover 1992; Billerbeck et al. 2000). Ration restriction of NS fish resulted in roughly a 50% reduction in growth rate (~ 0.5 mm/day) and significantly enhanced burst and endurance swimming performances. However, ration manipulation of SC fish generated only a 30% reduction in growth rates (~ 0.1 mm/day) and did not measurably affect swimming performance. The effect of food consumption on locomotor ability was apparent only in fish from the NS population that consistently have been shown to consume larger meals than SC fish (Present and Conover 1992; Billerbeck et al. 2000). Although we did not quantify food consumption directly in these experiments, measures of maximum body depth differed significantly between fasted and satiated NS fish in all experiments, but were generally nonsignificant in SC fish. Consequently, feeding effects on locomotor performance were more pronounced in the northern population.

In addition to the potential bioenergetic conflicts described above, differences in morphology and physiology resulting from variation in food consumption and rates of growth and development may affect both aerobic and anaerobic swimming performance. In our experiments, fish that had recently consumed a meal had greater maximum body depths than fasted fish of equal length. An increase in body depth increases the cross-sectional area of a fish, which may result in greater frictional drag. Developmental (age-related) differences in morphology and physiology may arise because at any given size a fast-growing fish will always be younger than a slow-growing fish, perhaps leading to reduced size-specific neuromuscular coordination. In some species, fast-growing fish have been shown to have higher percentages of small-diameter white muscle fibers (Weatherley et al. 1988; Meyer-Rochow and Ingram 1993; Valente et al. 1999) and greater numbers of similar-diameter red muscle fibers (Valente et al. 1999) than slow-growing fish, resulting from differences in the timing of muscle fiber recruitment during development. If muscle fiber attributes influence fish swimming ability, these studies suggest a potential mechanism for the trade-offs documented here. However, the relationship between muscle fiber characteristics and swimming has not been assessed. Nevertheless, it is possible that aspects of rapid growth other than metabolism may be acting to diminish both aerobic and anaerobic swimming abilities.

Diminished locomotor performance likely increases the mortality rate of juvenile fishes. Survival in fish early life history is thought to be determined primarily by encounter rates with food (Laurence 1972) and the ability to escape

predators (Webb 1981), both of which are strongly influenced by swimming ability. Thus, a reduction in swimming performance may translate directly into diminished fitness (Weihs 1980; Webb and Corolla 1981). This is especially true for small, schooling fish, such as *M. menidia*, whose primary means of evading predation is swimming; they lack any specialized defensive structures or strategies such as spines, toxins, armor plates, disruptive coloration, or inflatable found in some fish taxa. Although often assumed, the direct effect of swimming capacity on survivorship of fishes has rarely been tested. Recent experiments by Lankford et al. (2001) clearly demonstrate that the decrease in swimming performance resulting from either food consumption or rapid growth shown here increases mortality risk in juvenile *M. menidia* exposed to a variety of natural predators.

Despite arguments to the contrary, much of prevailing ecological and evolutionary theory assumes that organisms should grow maximally prior to reproduction. Our experiments revealed negative correlations between food consumption and growth and locomotor performance both within and between populations of ectotherms, suggesting a substantial fitness cost to rapid growth. These physiological trade-offs may explain the persistence of submaximal intrinsic growth rates in southern *M. menidia*, and thus the evolution of countergradient variation in growth. Although the costs of growth demonstrated here are limited to organisms that use locomotion (and more specifically speed) as a means of predator escape, they may be viewed in the larger context of trade-offs between growth and defense. Plant ecologists have commonly seen diminished growth as a cost of resistance to herbivores and pathogens (Fritz and Simms 1992), yet trade-offs between growth and defense in animals have rarely been considered. Our study suggests that trade-offs with defense may be important in the evolution of animal growth rates.

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