

## EVOLUTION OF INTRINSIC GROWTH AND ENERGY ACQUISITION RATES. II. TRADE-OFFS WITH VULNERABILITY TO PREDATION IN *MENIDIA MENIDIA*

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**Abstract.**—The Atlantic silverside (*Menidia menidia*) exhibits countergradient latitudinal variation in somatic growth rate along the East Coast of North America. Larvae and juveniles from high-latitude populations display higher intrinsic rates of energy consumption and growth than genotypes from low-latitude populations. The existence of submaximal growth in some environments suggests that trade-offs must counter the oft-cited theoretical benefits of energy and growth maximization (e.g., “bigger is better,” “faster is better”) in the immature life stages. We hypothesized that energy and growth maximization trades off against investment in defense from predators. We conducted laboratory selection experiments to compare vulnerability to predation of silversides from: (1) fast-growing northern (Nova Scotia, NS) versus slow-growing southern (South Carolina, SC) source populations; (2) phenotypically manipulated fast-growing versus moderately-growing NS fish; and (3) recently fed versus unfed NS and SC fish. Tests involved fish drawn from common-garden environments and were conducted by subjecting mixed-treatment schools of size-matched silversides to natural, common piscine predators. NS silversides suffered significantly higher predation mortality than SC silversides. Parallel results were found in phenotypic manipulation of growth: NS silversides reared on a fast-growth trajectory (~1.0 mm/day) were significantly more vulnerable to predation than those growing at a moderate rate (~0.5 mm/day). Food consumption also affected vulnerability to predators: Silversides with large meals in their stomachs suffered significantly higher predation mortality than unfed silversides. Differences in predation vulnerability were likely due to swimming performance, not attractiveness to predators. Our findings demonstrate that maximization of energy intake and growth rate engenders fitness costs in the form of increased vulnerability to predation.

**Key words.**—Countergradient variation, evolutionary physiology, genotype-environment covariance, growth rate, latitude, life-history evolution, locomotory performance, optimal foraging theory.

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At what rate should immature organisms grow to maximize their fitness? Ecological theory suggests that natural selection favors genotypes that maximize net energy acquisition and growth (Lotka 1922; Ware 1982; Stearns 1992). Because rates of survival and reproductive output generally increase with size in many organisms, individuals that grow faster would reap the benefits of large size earlier in life and experience higher survival and fitness (Sauer and Slade 1987; Sogard 1997). Despite evidence and theoretical arguments to the contrary (Priede 1977; Calow 1982; Sibly et al. 1985; Abrams et al. 1996; Arendt 1997; Conover and Schultz 1997; Gotthard 2000), this faster-is-better paradigm is pervasive: Many life-history studies employ growth rate as a direct scalar of relative fitness among juveniles (e.g., Hatfield and Schluter 1999), and habitat quality is routinely evaluated based on positive associations with growth (e.g., Able et al. 1999; Meng et al. 2000).

If rapid somatic growth through the immature stages maximizes fitness, intrinsic rates of energy intake and utilization efficiency should approach the maximum allowed by phylogenetic history, genetic constraints, and physicochemical design. Few studies have identified potential trade-offs that would counter the benefits of rapid growth (Gotthard et al.

1994; Arendt 1997; Arendt and Wilson 2000; Tessier et al. 2000), yet there is ample evidence of heritability and local adaptation of growth rate in many organisms (reviewed by Arendt 1997). Recent studies have revealed that intrinsic growth capacity varies inversely with ecological opportunity for growth across environmental gradients in many species, a phenomenon termed countergradient variation (Conover and Present 1990; Arendt 1997; Conover and Schultz 1997; Arendt and Wilson 1999; Arnett and Gotelli 1999; Jonassen et al. 2000). Such clinal patterns challenge the energy/growth maximization paradigm because many populations display submaximal rates of growth that are clearly the result of selection.

Countergradient variation in growth occurs in the Atlantic silverside (*Menidia menidia*). In this estuarine fish, intrinsic growth rate increases with latitude along the Atlantic coast of North America (Conover and Present 1990). During the brief (3–4 months) growing season at high latitudes, silversides grow at twice the rate of those in the south, where the growing season is much longer (9–10 months). Common-garden experiments on multigeneration laboratory colonies of silversides have demonstrated that the cline in growth rate with length of the growing season ( $r = 0.97$ ,  $n = 6$ ) has a strong genetic basis (Conover 1998). The reason for selection of rapid growth in northern silversides is clear: winter survival is strongly size dependent and favors larger phenotypes (Conover and Present 1990; Billerbeck et al. 1997; Schultz et al. 1998). However, the fitness benefits of slow growth in the south have been paradoxical.

The intrinsic growth rate of *M. menidia* covaries positively with several other traits that should enhance fitness in all

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environments, including energy acquisition and growth efficiency (Present and Conover 1992; Billerbeck et al. 2000), lipid energy storage (Schultz and Conover 1997), and reproductive output (Klahre 1998). Additionally, large silversides evade predators more effectively (Juanes and Conover 1994) and have higher fecundities (Conover 1985) than smaller silversides. Northern fish are not more vulnerable to starvation mortality; they do not grow more slowly in food-poor environments; and their superior performance is independent of temperature, thereby ruling out either food level or temperature  $\times$  genotype interactions as potential explanations (Conover and Present 1990; Conover 1992; Billerbeck et al. 2000). Thus, northern genotypes appear to be superfish, equaling or exceeding southern fish in all components of fitness. This and other examples of superorganisms appear to challenge the assumption of trade-offs in life history theory (Reznick et al. 2000), because the superior genotypes are expected to dominate in all environments.

One unexplored possibility is that energy acquisition and growth trade off against investment in defense from sources of mortality (Arendt 1997). Atlantic silversides are small, surface-dwelling fishes that rely primarily on swimming ability to avoid predators. Billerbeck et al. (2001) found that food consumption and rapid growth are associated with reduced burst and sustained swimming performance within and among silverside populations. Here we test the hypothesis that rapid growing genotypes, growth manipulated phenotypes, and individuals that consume large meals display reduced ability to escape common, natural predators.

## MATERIALS AND METHODS

### *Experimental Subjects*

Experiments were conducted on juvenile silversides from northern (Nova Scotia [NS], Canada) and southern (South Carolina [SC], USA) populations. Experimental subjects were second or third generation individuals spawned from laboratory-reared stocks that originated from wild NS ( $\sim 44^\circ\text{N}$  latitude) and SC ( $\sim 33^\circ\text{N}$  latitude) populations. Subjects were spawned and reared under common-garden conditions ( $21^\circ\text{C}$ ) at Flax Pond Marine Laboratory (FPML, SUNY Stony Brook, New York) to minimize environmental and maternal effects and to isolate genetic differences in escape performance among populations. Rearing techniques are described in Conover and Present (1990).

Laboratory selection experiments employed a variety of piscine predators as selective agents. Predators used were natural, pursuit-type predators of juvenile silversides: bluefish (*Pomatomus saltatrix*), Atlantic needlefish (*Strongylura marina*), and adult Atlantic silversides (*M. menidia*) collected from Great South Bay, New York; and striped bass (*Morone saxatilis*) collected from the upper Hudson River estuary, New York. Predators were captured with haul seines and transported to FPML where they were acclimatized to experimental tanks for 1–3 weeks prior to trials. Most trials involved *P. saltatrix* because it is the principal predator of silversides in many locations (Friedland et al. 1988; Juanes and Conover 1994, 1995; Juanes et al. 1994). All predators were maintained on a diet of live silversides drawn from NS

and SC laboratory stocks, and all prey were trained to recognize predators through constant exposure during rearing.

### *General Protocol*

Laboratory selection experiments were designed to test for effects of population of origin (NS vs. SC), phenotypic growth rate (fast vs. moderate within population), and food consumption (fed vs. unfed within population) on vulnerability to predation. A paired-contrast design was utilized: Mixed schools of silversides containing fish from two contrasting treatments (NS vs. SC, fast vs. moderate growth, or fed vs. unfed) were exposed simultaneously to predation. Selection trials were conducted in large (540-L), circular tanks to minimize confinement of prey and to permit them to express their natural flight response. Temperatures during all trials were maintained at  $22\text{--}23^\circ\text{C}$ . Trials were initiated by stocking replicate tanks with small schools ( $n = 4\text{--}5$  individuals) of size-matched ( $\pm 1$  mm) predators that were deprived of food for 18 h prior to trials. A mixed school ( $n = 16$  individuals; eight per treatment) of size-matched ( $\pm 0.5$  mm) silversides was then placed into a temporary, transparent refuge (70 L) within each tank and allowed 10 min to acclimate. Following acclimatization, refugia were removed and predators were allowed to attack until approximately 50% of prey items were captured.

Size matching of both predators and prey controlled for the ratio of prey size to predator size within and among trials. Previous studies have shown that prey : predator ( $P_y:P_r$ ) size ratio is an important determinant of silverside vulnerability to capture by predators (Juanes and Conover 1994). We therefore fixed  $P_y:P_r$  ratios at intermediate levels for each predator species to ensure that silversides would be vulnerable to predators, yet would have a moderate probability of escaping a given attack. Actual sizes of silversides used in predation trials ranged from 20 mm to 45 mm total length across trials. Predator size for each trial was adjusted based on prey size so as to maintain a constant  $P_y:P_r$  size ratio across trials.  $P_y:P_r$  size ratios for each predator were selected based on preliminary trials and were 0.5 for *P. saltatrix*, 0.4 for *M. saxatilis*, and 0.2 for *S. marina* and *M. menidia*.

### *Experimental Treatments*

#### *Population of origin*

To test whether the evolution of an aggressive growth strategy by northern silverside populations has entailed evolutionary trade-offs with escape performance, we compared the evasiveness of NS and SC genotypes when subjected simultaneously to attacks from natural piscine predators (*P. saltatrix*,  $n = 26$  trials and *M. saxatilis*,  $n = 6$  trials). NS and SC prey were grown on unlimited food at their maximal intrinsic rates prior to testing. Food was withheld from each population for 18–20 h prior to trials to minimize effects of feeding metabolism (Billerbeck et al. 2000) and to isolate effects of growth rate.

Survivors from each trial were X-rayed according to methods outlined in Billerbeck et al. (1997) and identified as NS or SC individuals based on vertebral counts made from radiographs. We characterized NS and SC populations with

respect to vertebral counts prior to predation trials by X-raying approximately 200 individuals per population. This analysis was conducted on the same tanks of fish eventually drawn upon for predation experiments. These groups showed no overlap in their vertebral counts (range in vertebral number: SC = 34–40; NS = 41–44) and survivors of predation trials fell unambiguously into either SC or NS distributions. Variation in vertebral number within populations does not influence swimming performance (Billerbeck et al. 2001) and had no influence on predation vulnerability (results not shown).

#### *Phenotypic growth rate*

In a further attempt to isolate effects of growth rate from other sources of variation (e.g., morphology or behavior) among silverside populations, we tested the relative vulnerability of different growth phenotypes within a common (NS) gene pool. Phenotypic manipulation (Preziosi et al. 1999) was used to produce NS individuals with either fast or moderate growth rates. To ensure that individuals from fast and moderate growth treatments would be the same size at the time of testing, manipulation was initiated at different starting sizes for each treatment (initial size = 16 mm for fast treatment, 24 mm for moderate treatment). Because replicate trials for this experiment used silversides from a single manipulation treatment and were therefore not independent, the experiment was repeated using a second group of phenotypically manipulated silversides.

Phenotypic manipulation of silverside growth trajectories was accomplished by manipulating food ration. Fast growth rates were elicited by providing silversides unlimited *Artemia* nauplii, whereas moderate growth rates were produced with a limited ration of *Artemia* nauplii (~50% fish wet body weight/day). Mixed schools of fast and moderate growers were then size-matched ( $\pm 0.5$  mm) and exposed to predation from *M. saxatilis* to test whether escape performance was dependent on recent growth rate within a common genetic background.

To enable identification of trial survivors as being from fast or moderate growth treatments, we marked the otoliths of silversides from the moderate treatment with alizarin complexone (ALC) prior to trials. ALC produced an internal chemical mark on otoliths that was externally invisible. Otolith marking was performed one week prior to trials by immersing fish in a solution of 50 ppm ALC for 24 h.

The effect of ALC-marking on vulnerability of silversides to predation was examined in separate experiments by subjecting mixed schools of marked and unmarked silversides to striped bass predation. Silversides used for marked and unmarked treatments were drawn from a common tank of growth-manipulated individuals with identical recent growth rates (moderate). This design was intended to control for growth rate and isolate effects of the marking procedure. The ALC-marked treatment was produced as described above and mixed silverside schools containing 12 marked and 12 unmarked individuals (size-matched) were subjected to predation from *M. saxatilis* until approximately 50% of the mixed school had been captured. Survivors were then dissected and examined for ALC marks. Summed across six

separate trials, the number of marked and unmarked survivors was 36 and 35, respectively. A replicated *G*-test indicated that vulnerability to predation was independent of ALC marking ( $P > 0.9$ ).

#### *Food consumption*

Rapid growth in silversides is accomplished primarily through the consumption of larger meals (Present and Conover 1992), which causes more than a doubling of metabolic rate (Billerbeck et al. 2000) and leads to conflicts in energy allocation to swimming (Billerbeck et al. 2001). Thus, we tested for an effect of large meals on silverside vulnerability to predation within the NS and SC populations. Schools of size-matched silversides were assigned randomly to one of two treatments (fed or unfed) and starved overnight. On the following day, the fed treatment was provided an unrestricted meal of *Artemia* nauplii and allowed to feed for 20 min, whereas the unfed treatment received no food. Fed and unfed treatments were then combined to form a mixed school and subjected to predation as described in the protocol above. To ensure that predation would occur during the period of peak feeding metabolism when bioenergetic allocation conflicts should be maximal (Billerbeck et al. 2000), trials were initiated approximately 10 min after feeding and were limited to a maximum duration of one hour. Survivors from each trial were sacrificed and identified to treatment based on the presence or absence of food in the stomach. The null hypothesis of no meal effect was tested on NS and SC silversides using *P. saltatrix* and *M. saxatilis* as predators. Additional trials were conducted on SC silversides using *S. marina* and *M. menidia* predators to further evaluate the generality of this trade-off.

To obtain estimates of voluntary meal sizes consumed by silversides in fed treatments, a separate feeding experiment was conducted in which NS and SC individuals were subjected to the feeding protocol described above and sacrificed immediately after feeding. Stomach contents were removed from each individual, dried at 60°C for 48 h, and weighed. Meal size was calculated for individual fish as a percentage of dry body weight.

#### *Statistical analyses of paired contrasts*

Relative vulnerability of silversides from contrasting treatments was estimated using frequencies of captured and uncaptured individuals that were reconstructed following the identification of trial survivors. Capture frequencies from contrasting treatments were then analyzed as  $2 \times 2$  contingency tables (model II) to test for treatment effects. Effects of population of origin, feeding status, and ALC marking were evaluated using replicated *G*-tests of independence. Effects of phenotypic growth rate were tested using Fisher's exact test. A significance level of  $\alpha = 0.05$  was used for all tests. Statistical analyses were performed using STATISTICA ver. 5.1, (StatSoft, Inc., Tulsa, OK).

#### *Differential vulnerability or predator preference?*

Selection against fish that consume large meals and/or grow rapidly may result from predator preference rather than

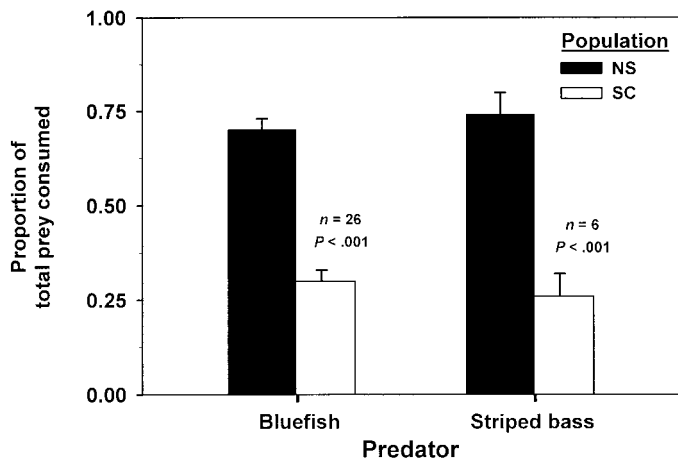


FIG. 1. Effect of genotype (population of origin) on vulnerability of silversides to natural piscine predators (bluefish, *Pomatomus saltatrix*; striped bass, *Morone saxatilis*). Replicate trials ( $n$ , number of trials) were conducted on mixed schools of silversides containing equal numbers of size-matched northern (NS) and southern (SC) individuals. Vertical lines represent 95% binomial confidence limits for frequencies pooled across trials.

silverside evasiveness, especially in the case of fed fish that are visibly fatter than unfed fish. To test this possibility, we measured silverside evasiveness independent of predator selectivity through no-choice predation trials in which *M. saxatilis* predators were allowed to forage exclusively on single-treatment categories of silversides. Evasiveness trials were conducted on fed and unfed silversides from each population in 540-L circular tanks. Trials ( $n = 3$  per treatment) were initiated by stocking each replicate tank with four size-matched *M. saxatilis* that were deprived of food for 18 h. A school of silversides ( $n = 12$ ) was introduced into refugia within each tank and allowed 10 min to acclimate. Refugia were then removed and *M. saxatilis* were allowed to attack silverside prey for 1 h.

Video recordings of trials were analyzed to obtain the exact failure time (time until capture) for each silverside. Because some silversides survived each trial, failure times included censored (Type I) observations. Statistical analyses therefore employed procedures appropriate for censored data (Marubini and Valsecchi 1995) using the software program SURVIVAL (Steinberg and Colla 1988). Maximum-likelihood estimates of survival probability ( $S_{km}$ ) were calculated for each treatment using the nonparametric Kaplan-Meier (K-M) product-limit method (Kaplan and Meier 1958). K-M survival probabilities were used to construct survivorship functions for each silverside treatment. Nonparametric Mantel log-rank tests were then used to test whether survivorship curves differed among silverside populations (NS vs. SC) or feeding treatments (NS fed vs. NS unfed; SC fed vs. SC unfed).

## RESULTS

### Population of Origin

Northern and southern silverside genotypes differed significantly in their ability to avoid predators, with fast-growing NS genotypes being highly vulnerable to predation relative to slower-growing SC genotypes (Fig. 1). When NS and SC

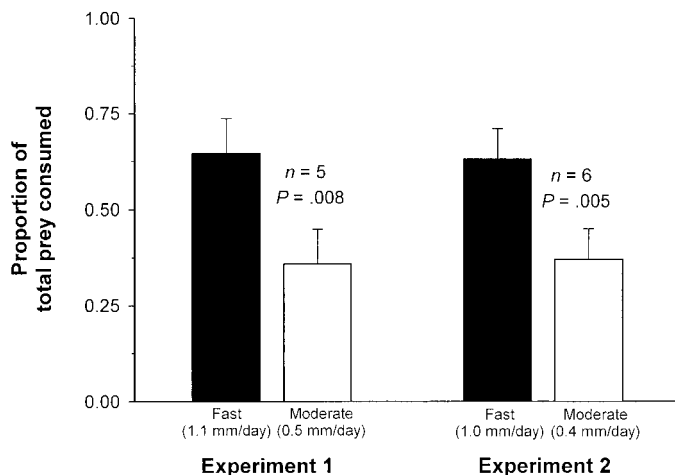


FIG. 2. Effect of growth rate within a genotype (fast vs. moderate phenotypes produced by ration manipulation) on vulnerability of NS silversides to striped bass (*Morone saxatilis*) predation. Experiments 1 and 2 were conducted using separate batches of growth-manipulated silversides. Mean linear growth rates are shown for each treatment. Vertical lines represent 95% binomial confidence limits for frequencies pooled across trials.

genotypes were attacked simultaneously by *P. saltatrix*, NS silversides accounted for an average of  $70 \pm 3\%$  of the total prey consumed per trial ( $G = 50.1$ ,  $P < 0.001$ ). Similar results occurred during predation by *M. saxatilis*, with NS silversides averaging  $74 \pm 6\%$  of total prey consumed per trial ( $G = 23.5$ ,  $P < 0.001$ ).

### Phenotypic Growth Rate

The effect of phenotypic growth rate on vulnerability of NS silversides to predation was tested in two replicated experiments. In the first experiment ( $n = 5$  trials), NS silversides reared on a fast growth trajectory (1.08 mm/day) suffered significantly higher predation mortality when attacked by *M. saxatilis* than silversides reared to identical size at moderate (0.52 mm/day) rates (Fisher exact  $P = 0.008$ ). Fast-growing silversides accounted for  $64.5 \pm 9.1\%$  of the prey captured from mixed schools (Fig. 2). Results from experiment 2 ( $n = 6$  trials) were consistent with those from experiment 1, with fast-growing silversides accounting for  $63.0 \pm 8.0\%$  of the prey captured in trials (Fisher exact  $P = 0.005$ ).

### Voluntary Meal Size

Voluntary meal sizes displayed by silversides were measured to provide estimates of the gut fullness levels achieved with the feeding protocol used to produce fed treatments for tests of selection on recent food consumption. Voluntary meal sizes consumed by NS and SC silversides subjected to this protocol were generally large, but varied among populations and across body sizes (Fig. 3). NS fish consumed considerably larger meals than SC fish over the size range examined. Average meal size for NS silversides declined from about 16% to about 9% dry body weight over the size range of 20–45 mm total body length. Over this same size range, meal sizes consumed by SC individuals declined from about 10% to about 5% dry body weight.

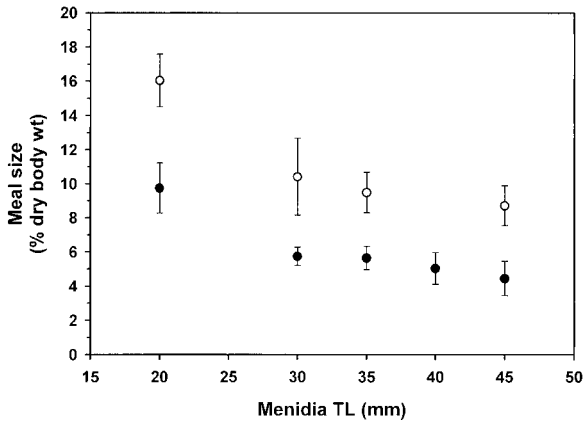


FIG. 3. Voluntary meal sizes of northern (NS) and southern (SC) Atlantic silversides (*Menidia menidia*) following an unrestricted, 20-min feeding bout.

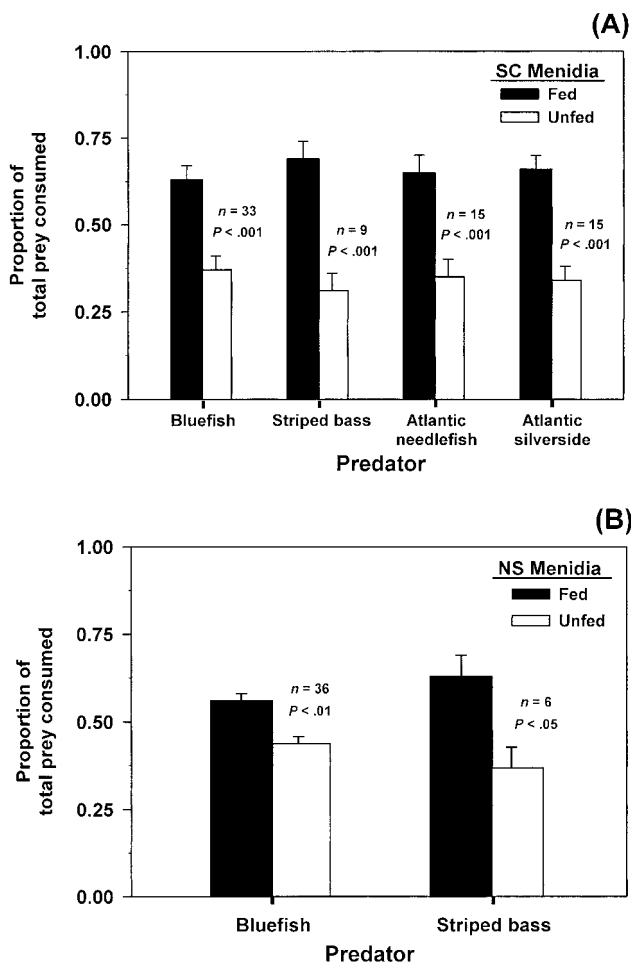


FIG. 4. Influence of recent feeding status (maximally fed vs. unfed) within a genotype on the vulnerability of (A) South Carolina (SC) and (B) Nova Scotia (NS) silversides to natural piscine predators. Vertical lines represent 95% binomial confidence limits for frequencies pooled across trials.

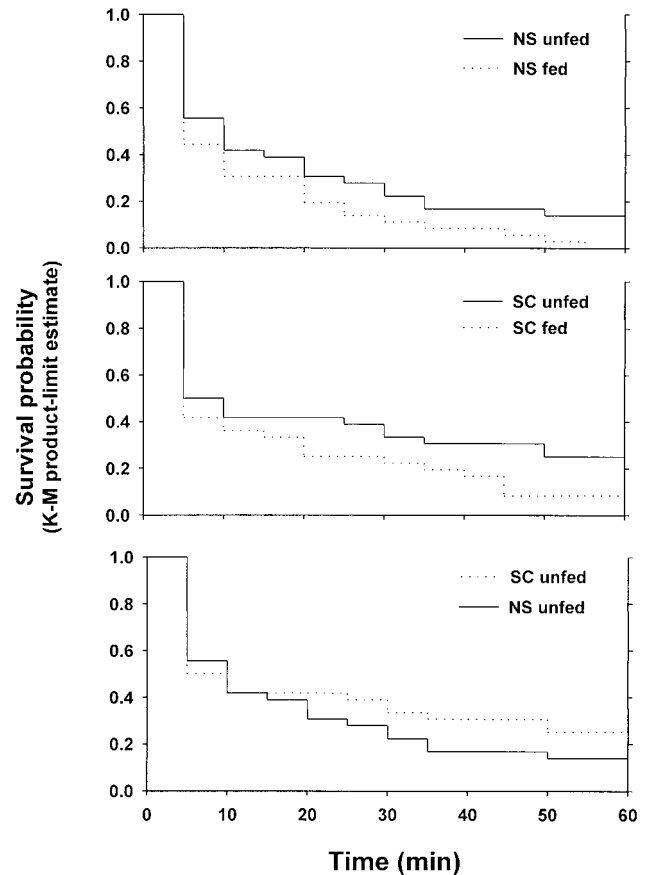


FIG. 5. Survivorship curves for silversides from no-choice predation trials.

#### Food Consumption

SC and NS silversides that consumed large meals were more likely to be captured by piscine predators than their unfed counterparts. In SC silversides, fed individuals suffered significantly higher predation mortality than unfed individuals ( $P < 0.001$  for all four predators; Fig. 4). Feeding also significantly reduced escape performance in NS silversides attacked by either *P. saltatrix* ( $P < 0.01$ ) or *M. saxatilis* ( $P < 0.05$ ; Fig. 4).

#### Differential Vulnerability or Predator Preference?

Analysis of failure times indicate that selection against silversides that display aggressive growth rates or high consumption rates can be explained at least partially by differences in evasiveness. At the population level, NS silversides were captured more rapidly by *M. saxatilis* than SC silversides ( $\chi^2 = 4.4$ ,  $df = 1$ ,  $P < 0.05$ ), suggesting they are less evasive than SC individuals (Fig. 5). Survival times of fed and unfed fish indicated that consumption of large meals reduces evasiveness in both populations. Survival times for fed SC individuals were significantly lower than those for unfed individuals ( $\chi^2 = 4.5$ ,  $df = 1$ ,  $P < 0.05$ ). Similarly, fed NS silversides were captured more rapidly than their unfed counterparts ( $\chi^2 = 4.3$ ,  $df = 1$ ,  $P < 0.05$ ; Fig. 5).

## DISCUSSION

Our findings provide evidence that physiological trade-offs between growth rate and locomotory performance (Billerbeck et al. 2001) translate into fitness trade-offs by affecting the escape performance of silversides under threat of predation. The superior evasiveness of low-latitude silverside populations suggests that a conservative growth strategy likely enhances fitness in certain environments by improving predator avoidance ability. Costs of rapid growth were clearly evidenced by substantially reduced escape performance in fast-growing genotypes, whether tested in combination with or in isolation from slow-growing genotypes. The results of the phenotypic manipulation trials suggest that the differences among populations are caused by genetic differences in growth rather than an indirect effect of covariance with some other trait. The fed-unfed trials suggest that large meals represent an additional postprandial cost of growth. Recent studies have shown negative phenotypic correlations between growth rate and swimming performance in fishes (Kolok and Oris 1995; Gregory and Wood 1998) and between phenotypic growth and predation vulnerability in other taxa (Gotthard 2000). Our findings provide the first demonstration of negative genetic covariance between intrinsic growth rate and vulnerability to predation.

Our results are consistent with the hypothesis that benefits of submaximal growth emerge from bioenergetic trade-offs between the costs of energy processing and growth versus locomotory activity (Billerbeck et al. 2001). Previous authors have argued that high rates of food consumption and growth in young fishes drive metabolism to its aerobic maximum, thereby producing a conflict with allocation of oxygen to other functions such as swimming (Priede 1985; Weiser and Medgyesy 1990; Weiser 1991). The predators we used were pursuit rather than ambush attackers, requiring prey to use a combination of sustained and repeated-burst swimming to evade capture. Such escape maneuvers are likely fueled, at least in part, by aerobic metabolism. There are, however, other nonmutually exclusive explanations for these trade-offs. For example, muscles and/or neuromuscular coordination may be less developed at a given size in fast-growing individuals (Weatherley and Gill 1987; Valente et al. 1999). The increased weight or frictional drag of a stomach filled with food may also contribute to reduced locomotion (DeBenedictis et al. 1978; Lind et al. 1999).

We do not imply that the attainment of larger size through growth is detrimental. In fishes, there are numerous well-known benefits of larger size, including enhanced resistance to starvation, lower susceptibility to predators, lower vulnerability to environmental extremes, and higher reproductive success (Shine 1988; Sogard 1997). There is also ample evidence for *M. menidia* that large size enhances fitness and reproductive success (Conover 1985; Juanes and Conover 1994; Schultz et al. 1998). However, the rate at which large size is achieved entails a cost in terms of mortality. If fitness increases with body size, theory suggests that growth rates should be maximized when the cost per unit growth decreases with or is independent of growth rate (Sibly et al. 1985). Submaximal growth rates are optimal only when the cost per unit growth increases with growth rate. Additional experi-

ments are needed to evaluate the functional relationship between growth rate and mortality in *M. menidia*.

Our findings have broad implications for behavioral ecology and foraging theory. Behavioral ecologists have long recognized that predation risk influences foraging decisions by animals and that individuals can often balance the conflicting demands of finding food and avoiding predators (Stephens and Krebs 1986). Most investigations of foraging risks, however, have addressed preconsumptive trade-offs between foraging and vigilance (Lima and Dill 1990). For example, behavioral ecologists have recognized the trade-off between growth rate and predation risk associated with the dangers of foraging (Stephens and Krebs 1986; Lima and Dill 1990). Here, the mechanism linking higher mortality risks to increased growth rate is the increased probability of encountering or being detected by predators when fast-growing animals increase their activity levels to locate and harvest additional resources (Werner and Anholt 1993; Bernays 1997; Anholt and Werner 1998). In response to this trade-off, foraging animals may balance the growth benefits of feeding against the costs of increased mortality risk in threat-sensitive (Gilliam and Fraser 1987; Anholt and Werner 1998) and state-dependent (Milinski and Heller 1978; Werner and Gilliam 1984) manners. Few studies have considered foraging trade-offs from a postconsumptive, physiological perspective. Our results indicate that foraging costs extend beyond the decision stage, and that successful feeders may reduce their escape performance by consuming a large meal. Foraging patterns that alternate between active periods of feeding under risk of predation and resting in shelter may be viewed, in part, as strategies to avoid postprandial bioenergetic conflicts in the allocation of metabolic scope to food digestion and tissue synthesis versus locomotory activity.

One of the criticisms of optimal foraging theory has been that it requires animals to make decisions based on an assessment of competing risks that occur on different time scales, that is, the immediate risk of predation versus the longer-term risk of energy deprivation and reduced growth. How do animals assess such competing risks? Although we have not yet quantified differences among genotypes in their willingness to forage in the presence of predators, we suggest that genetically based differences in energy consumption and growth such as those found in silversides provide the basis for establishment of risk-taking behavior. Northern fish should be intrinsically more willing to take foraging risks because the penalty for slow growth is greater in environments with seasonal time constraints and size-dependent winter mortality (Rowe and Ludwig 1991; Schindler 1999). We interpret the evolution of countergradient variation in growth of *M. menidia* as follows.

High-latitude populations have evolved an aggressive energy consumption and growth strategy, despite the cost of increased vulnerability to predation, because the short growing season and strong, size-dependent winter mortality at high latitudes provide no other alternative. In northern populations of silversides, directional selection for large overwintering body size is intense: Winter mortality rates approximate 99% and only the largest members of a year class survive (Conover 1992; Billerbeck et al. 1997). At low latitudes, where winter mortality is minimal, the greater relative mortality risk is

predation, and a conservative growth strategy increases fitness by reserving a larger proportion of metabolic scope for evasive swimming.

It is often argued that predation pressure on plants and animals increases at lower latitudes (e.g., Wilson 1991; Leighton 1999). Whether this is true for *M. menidia* is unknown. Predation is a major source of mortality for silversides during the growing season (Juanes and Conover 1995). The main predators of silversides (*P. saltatrix*, *M. saxatilis*, and weakfish, *Cynoscion regalis*) are all more abundant south of Cape Cod than to the north (Bigelow and Schroeder 1953; Murdy et al. 1997). However, it is not the absolute but the relative intensity of predation versus other sources of mortality that matters to our argument. The latitudinal gradient in severity of size-selective winter mortality found in *M. menidia* and other species (Conover and Present 1990; Fullerton et al. 2000) generates an increase in the proportion of total mortality that is due to predation at lower latitudes. Thus, predation risk-averse strategies of growth prevail in environments with low levels of winter mortality.

It is becoming increasingly apparent that countergradient variation and other forms of adaptive variation in juvenile growth rate are common in various taxonomic groups, including reptiles, amphibians, gastropods, insects, and plants (Niecieza et al. 1994; Conover and Schultz 1995; James and Partridge 1995; Schultz et al. 1996; Arendt and Wilson 1999; Conover et al. 1997; DiMichele and Westerman 1997; Parsons 1997; Dittman et al. 1998; Arnett and Gotelli 1997; Jonassen et al. 2000). These emerging patterns suggest that trade-offs countering the benefits of rapid juvenile growth are widespread in nature. Most life-history theorists and empiricists have generally assumed that intrinsic growth rate should be maximized, and thereby limited only by the environment, whenever an organism is not reproducing. This premise is deeply engrained, judging from the widespread view that relative fitness of juveniles or habitat quality of the environment can be routinely assessed as a positive function of growth rate. This view persists because, with few exceptions (Gotthard et al. 1994; Arendt and Wilson 2000; Gotthard 2000; Tessier et al. 2000), trade-offs to energy consumption and growth rate have rarely been identified. The results of this study and those reported by Billerbeck et al. (2001), falsify this assumption: Rapid growth engenders trade-offs that reflect the short-term physiological costs of both energy acquisition and tissue synthesis, indicating that more energy and faster growth is not always better.

The trade-off between resource acquisition and predator vulnerability also has more general implications for life-history evolution. The universality of trade-offs in life-history evolution has been questioned by the frequent observation that components of fitness, such as growth and reproduction, are positively rather than negatively correlated (Reznick et al. 2000). High levels of genetic variation in resource acquisition have been proposed as an explanation for such observations (Van Noordwijk and de Jong 1986; Houle 1991; Reznick et al. 2000). If certain genotypes consistently acquire more energy, then it is not surprising that growth and reproduction are positively correlated, as they are in *M. menidia* from different latitudes. But why don't the genotypes with higher rates of energy acquisition overwhelm all environ-

ments? The geographical patterns of physiological adaptation in *M. menidia* provide an answer. Energy consumption and processing and tissue synthesis are costly (Hammond and Diamond 1997; Billerbeck et al. 2000). They require increases in metabolism that may lead to conflicts, perhaps for oxygen, with other components of the energy budget. For silversides, and we suspect for many other species that use flight to evade predators, the trade-off is reflected in reduced locomotive ability and ultimately survival. If so, then energy maximization is not always beneficial and energy limitation does not necessarily set the stage for allocation conflicts as traditionally assumed. Rather the rate of energy acquisition is itself a trait with genetic variation, subject to varying selection pressures, displaying positive or negative covariances with environmental factors, and constrained by genetic covariation with other traits that also influence fitness.

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