Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes

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Summary. How do organisms adapt to the differences in temperature and length of the growing season that occur with latitude? Among Atlantic silversides (*Menidia menidia*) along the east coast of North America, the length of the first growing season declines by a factor of about 2.5 with increasing latitude. Yet body size at the end of the first growing season does not decline. High-latitude fish must, therefore, grow faster within the growing season than do low-latitude fish. This geographical pattern has a genetic basis. Laboratory experiments on fish from six different locations revealed a latitudinal gradient in the capacity for growth (i.e., maximum growth potential). In two subsequent experiments using fish from Nova Scotia (NS), New York (NY) and South Carolina (SC) that had been separately reared in a common environment for several generations, differences in growth rate among populations were highly significant. The rank order was NS > NY > SC, but the difference among populations depended on temperature. High-latitude fish outperformed those from low latitudes primarily at the high temperatures that low-latitude fish would be expected to experience most often in nature. These results suggest that instead of being adapted for growth at low temperatures, fish from high latitudes are adapted for rapid elevation of growth rate during the brief interval of the year when high temperatures occur. Selection on growth rate results from size-dependent winter mortality: the importance to winter survival of being large increases with latitude but the length of the growing season simultaneously decreases. The end result is countergradient variation in growth rate, a phenomenon that may be much more widespread than currently recognized.

Key words: Life history – Countergradient variation – Growth rate – Seasonality – Latitudinal variation

Ray (1960) and Lindsey (1966) documented that Bergmann's Rule of increasing body size with latitude in ho-

meotherms is also characteristic of poikilotherm species. Although this geographical pattern in poikilotherms could simply be a consequence of variation in age at maturity, the generality of Bergmann's Rule across a variety of taxa has led to the suggestion that the increase in body size with latitude is adaptive (Mayr 1963). But if large body size at high latitudes enhances fitness, then poikilotherms are faced with a dilemma. All else being equal, the lower temperature and/or shorter growing season of high-latitude environments slows the rate of growth and thereby limits size attained per year. This dilemma may be particularly acute during the first winter of life when individuals of relatively small size must cope with a prolonged period of low temperature. In teleosts, for example, numerous cases of size-selective overwintering mortality (large surviving more readily than small) among young-of-the-year (YOY) fish have been reported (Hunt 1969; Oliver et al. 1979; Toneys and Coble 1979; Shuter et al. 1980; Adams et al. 1982; Conover and Ross 1982; Henderson et al. 1988).

What adaptations might arise to counteract the negative effect on growth of lower temperatures and shorter growing seasons with increasing latitude? Numerous studies have illustrated "latitudinal compensation" in various metabolic rate processes both within and among a wide variety of poikilotherm species (see reviews by Bullock 1955; Cossins and Bowler 1987). The usual observation is that high latitude populations or species have a higher metabolic rate at a given temperature than those at low latitudes. In this way, the metabolic rate and activity of organisms at different latitudes is similar, despite differences in mean environmental temperature. Whether the same is true of growth rate, however, is not so clear. The conventional wisdom appears to be that high latitude forms grow more slowly (Bullock 1955; Clarke 1987), but this phenotypic pattern does not necessarily mean that genetic variation in growth rate is nil or has a parallel trend. The capacity for growth (i.e., maximum growth potential) could, for example, evolve in a direction opposite to that of the phenotypic pattern so as to at least partially counteract the negative influence of the physical environment on growth, a phe-
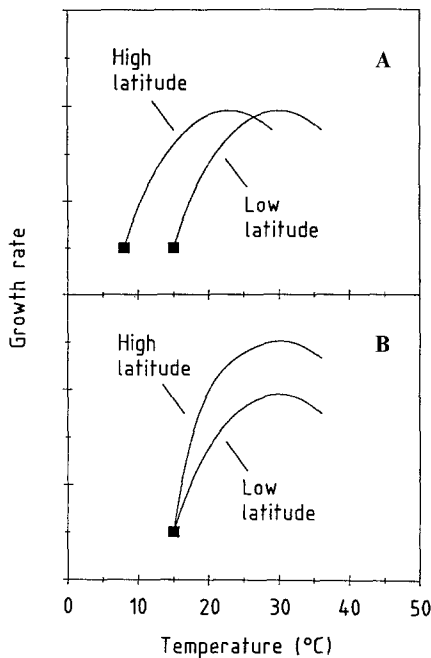
Fig. 1A, B. Two hypothetical compensatory adjustments to the expected temperature differences across latitudes. In each graph, the solid box represents the temperature at the onset of spawning. **A** The high-latitude population spawns at a lower temperature, and the growth rate vs. temperature curve is shifted to the left. The high-latitude population therefore grows faster at low temperatures than does the low-latitude population, but not at higher temperatures. Maximum growth rate is the same but occurs at a different temperature. **B** Both populations spawn at the same temperature and growth occurs over the same range of temperatures, but the high-latitude population has a higher capacity for growth

nomenon termed "countergradient variation" by Levins (1969). Under this scenario, individuals from high-latitude environments would grow faster than those from low latitudes when compared at the same temperature (e.g., Ament 1979; Dehnel 1955).

Alternatively, Levinton (1983) has proposed that genetic variation in growth rate with respect to latitude represents adaptation to the temperatures most frequently encountered in nature. He argues that the temperature-growth rate response curves of high-latitude forms may simply be shifted to a lower range of temperatures (as in Fig. 1A). The capacity to grow rapidly at low temperatures imposes physiological constraints that preclude rapid growth at high temperatures such that high-latitude forms grow faster than those from low latitudes at low temperatures but conversely at high temperatures. Data for several marine invertebrates support these assertions (Levinton 1983; Levinton and Monahan 1983; Lonsdale and Levinton 1985).

An assumption of the Levinton (1983) model, however, is that organisms from different latitudes do in fact reproduce and grow at different temperatures. This need not be the case. Individuals of a given species could reproduce and grow at essentially the same temperatures independent of latitude simply by restricting these physiological activities to the appropriate portion of the annual temperature cycle. If so, it would be the length

of the growing season (rather than the temperatures at which growth occurs) that declines with increasing latitude. In species with such life histories, compensation for length of the growing season could be said to occur if growth rates of organisms from short growing season environments generally exceeded those from long growing season environments across all temperatures that permit growth (as in Fig. 1B).

In this paper, we consider the evidence for genetic variation in growth rate and its adaptive significance across a latitudinal gradient in a fish, the Atlantic silverside (*Menidia menidia*). More specifically, we ask the question "if growth rate variation occurs, does it represent adaptation to temperature or length of the growing season?" Our approach in evaluating these alternatives is as follows. First, data from the literature is used to assess latitudinal variation in spawning temperatures, length of the first growing season, size attained at the end of the first growing season, and growth rate. Then, experiments on laboratory-reared stocks of fish that originated from different latitudes are used to test for genetic variation in the response of growth rate to temperature.

Materials and methods

Study species

The Atlantic silverside inhabits salt marshes, bays, and estuaries along the east coast of North America from northern Florida, USA ($\sim 30°$ N Lat.) to the Gulf of St. Lawrence ($\sim 46°$ N Lat.) (Johnson 1975), and is generally one of the most abundant fishes of the shore zone (Bayliff 1950; Conover and Ross 1982). The entire life cycle is completed in one year: all fish are mature at age one and proportionately very few reach a second breeding season (Conover and Ross 1982). The Atlantic silverside is a multiple or batch spawner (Conover 1985), with breeding events occurring on a semilunar cycle over a protracted period encompassing the spring and early summer (Middaugh 1981; Conover and Kynard 1984). In northern populations, an offshore winter migration to the continental shelf occurs in autumn (Conover and Murawski 1982) followed by a return to the shore zone in spring.

Preliminary growth experiments

Recent work described in Conover and Heins (1987) involved the rearing at five different temperatures of fish collected as embryos (several thousand) from each of six different locations along the east coast: South Carolina (SC), North Carolina (NC), Virginia (VA), and New York (NY), USA, and Nova Scotia (NS) and Prince Edward Island (PEI), Canada. Although these experiments were not designed to measure growth rate per se, temperature, food levels, and fish density were controlled in the same manner for all populations. Growth rate for each group of fish at each temperature (sexes pooled) was therefore estimated as the difference between the mean TL at termination (usually 25-30 mm) minus TL at assignment to the five temperature levels (8 mm for all treatments) divided by duration in days.

Establishment of laboratory populations

The genetic component of differences in a physiological trait can be estimated by comparison of progeny from different populations

reared under identical environmental conditions. To rule out the possibility of non-genetic differences arising from maternal effects, or from environmental effects on progeny prior to their transfer to a controlled environment, such comparisons should ideally be carried out on progeny from laboratory stocks that have themselves been reared in a common environment for several generations (e.g., Lonsdale and Levinton 1985). Differences in physiological traits that persist after several generations of rearing in a common laboratory environment can be presumed to have a genetic basis.

Laboratory stocks (hereafter referred to as populations) were originated with fish from the NS, NY and SC sites. These three sources were specifically chosen because they represent the northern, middle, and southern extent of the species' range (Johnson 1975). Excess fish that had been reared at 28° C (NY and SC populations) or at 19° C (NS population, sufficient excess fish not available from 28° C) in the preliminary experiments were used to establish the three laboratory breeding populations. These juveniles were reared to an adult size (~60–100 mm TL) in 700 L circular fiberglass tanks on flow-through seawater at temperatures exceeding 20° C and induced to spawn by photoperiod manipulation (methodology provided in Conover and Fleisher 1986).

Embryos from spawning adults were collected by placing a mop of yarn in each tank. When several hundred embryos had accumulated, the yarn was transferred to larval rearing containers in temperature-controlled seawater baths (Conover and Fleisher 1986). All such offspring from each of the three populations were reared at 28° C (the temperature of maximum growth) during the embryonic and larval periods. Upon reaching the juvenile stage, they were transferred to the larger tanks, and so on for at least three generations before use in the experiments described below. The number of spawning adults in each generation ranged from 41 to 233 ($\bar{x}=98$).

Growth experiments on laboratory populations

To compare the capacity for somatic growth as a function of temperature in fish from the three laboratory populations, two independent experiments were conducted under conditions of unlimited food. In Experiment I, growth was measured for each population at 17, 21, and 28° C (± 1° C). In Experiment II, growth was measured at these temperatures and also at 32° C. Experiment I was conducted on third generation NS and NY fish and fourth generation SC fish. Fourth generation NY fish and fifth generation NS and SC fish were used in Experiment II.

The protocol for both experiments was as follows. For each temperature treatment within each population, several hundred embryos were removed from the spawning tanks within several days of fertilization and transferred to a rearing container at one of the temperatures designated for growth comparisons. Hence, embryonic and larval development took place at the same temperature where growth rate would later be measured. The embryos were hatched and larvae grown on excess food until reaching a mean size of 6–8 mm TL, whereupon 30 individuals were randomly placed in each of four containers at the same temperature. Simultaneously, a fifth group of approximately 20 fish was randomly selected and preserved in 5% formalin for estimation of the TL and body weight of fish at the start of an experiment. Three of the containers with live fish were designated as replicates and one was a replacement pool of fish. Any fish that died in the three replicates during the first few days of the experiment (5 days at 17° C, 4 days at 21° C, 3 days at 28 and 32° C) were replaced with fish from the replacement pool. This allowed us to compensate for mortality due to handling. There was no replacement for fish that died after this initial period, but these were minimal (mean = 1.6 fish per replicate).

Live 24 h-old brine shrimp nauplii (Aquarium Products, Glen Burnie, MD; lot 120) were provided to all experimental fish. Excess food was continuously maintained by adding fresh nauplii daily as necessary. The experimental containers had screened openings that allowed water to circulate between the bath and the container

but retained most of the nauplii. Each container held about 16 L of seawater.

Duration of experiments depended on the temperature at which they were conducted: 17, 21, 28, and 32° C experiments lasted 28, 19, 11, and 11 d, respectively. This was done to standardize the size range through which the fish grew at each temperature, such that the fish in each treatment would be about 15–20 mm TL at the end of the experiment.

Midway through each experiment, a subsample of eight fish was randomly removed from each replicate, preserved in 10% formalin and measured. At the end of the experiment, all remaining fish were sacrificed, preserved, and measured. The mean daily growth rate of the fish in each replicate was estimated as the difference between the mean length at the end minus that at the beginning of the experiment divided by the duration in days. Growth rates based on the midpoint vs. final measurements differed little (only 2 of the 19 comparisons from both experiments where three replicate estimates were available differed significantly in paired t-tests, and the mid-point estimate was higher in one instance but lower in the other). All data reported herein are for the full duration of each experiment.

Exceptions to the standard protocol described above were the following. In three cases, poor hatching of eggs and survival of larvae to the 6–8 mm size did not allow us to establish three standard replicates. In Experiment I, there were sufficient 6–8 mm NY fish at 17° C to start only one container, but two additional containers were started with NY fish of somewhat larger initial mean length (11.7 mm). The fish in these latter containers were also grown for 35 rather than the standard 28 days used in all other 17° C experiments because the fish were needed for purposes, beyond the growth experiments, where larger size was required. The estimates of growth rate from these three groups of fish differed little (see Fig. 4 below) and were treated as replicates in statistical analyses. In Experiment II, poor larval survival limited the experiments at 32° C to two replicate containers of SC fish and one replicate of NY fish.
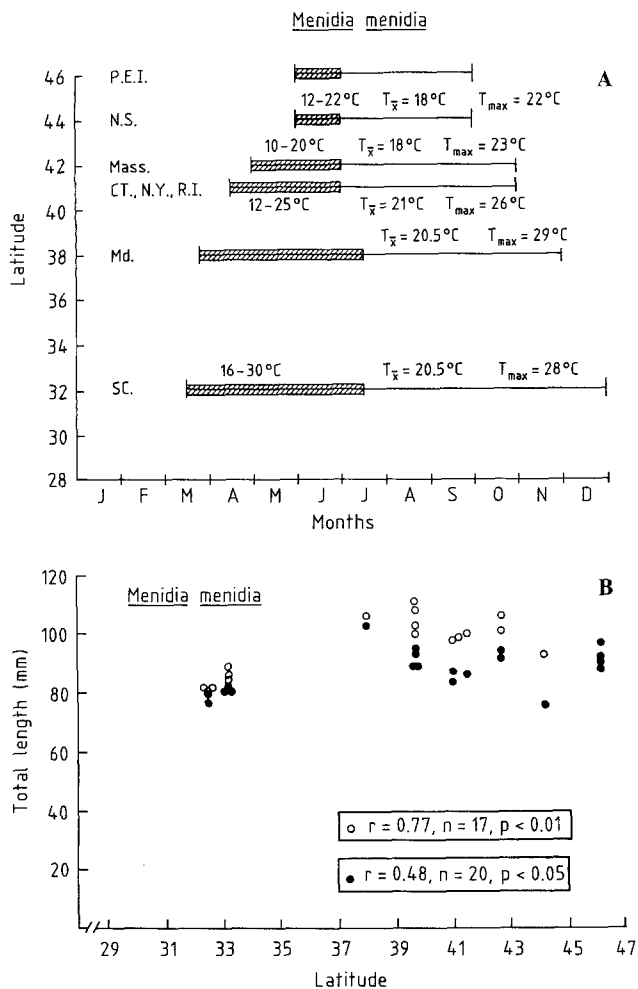
Statistical analyses

To test the null hypothesis that there were no genetically-based differences in the growth rates of *M. menidia* from different latitudes, we employed a Model I factorial analysis of variance (ANOVA). Population and temperature were considered as fixed factors. Scheffe's a posteriori multiple range tests were performed subsequent to the ANOVAs in order to determine which levels of population or temperature differed ($p < 0.05$). All analyses were run on the Statgraphics statistical package (STSC, Inc., Rockville, Md., USA). Heteroscedasticity was evaluated using Bartlett's test, and the data were found to be homoscedastic ($0.25 > p > 0.10$). The 32° C data in Experiment II were excluded from the ANOVA because there was only one replicate of NY fish at this temperature. Two-sample t-tests were used to compare growth rate at 28 and 32° C within the NS and SC populations, and between these two populations at 32° C.

Results

Spawning and growing seasons at different latitudes

The onset of the breeding season occurs much later in the year with increasing latitude beginning, for example, in March at about 32° N and in June at 44–46° N (Fig. 2A). The temperature at which the breeding season begins may decline somewhat at higher latitudes but it is difficult to determine if this is part of a latitudinal trend because temperatures at which spawning occurs have been recorded at only four sites.

Menidia menidia

46 P.E.I.   12-22°C   T$_{\bar{x}}$ = 18°C   T$_{max}$ = 22°C   A
44 N.S.
     10-20°C   T$_{\bar{x}}$ = 18°C   T$_{max}$ = 23°C
42 Mass.
    CT., N.Y., R.I.   12-25°C   T$_{\bar{x}}$ = 21°C   T$_{max}$ = 26°C
40
                         T$_{\bar{x}}$ = 20.5°C   T$_{max}$ = 29°C
38 Md.
36
34
         16-30°C   T$_{\bar{x}}$ = 20.5°C   T$_{max}$ = 28°C
32 SC.
30
28
    J F M A M J J A S O N D
                  Months

120 Menidia menidia   B
100
 80
 60
 40   [o r = 0.77, n = 17, p < 0.01]
 20   [• r = 0.48, n = 20, p < 0.05]

    29 31 33 35 37 39 41 43 45 47
                  Latitude

Fig. 2A, B. Life history of the Atlantic silverside at different latitudes along the Atlantic coast of North America. **A** The spawning season (hatched bars) is based on the reported occurrence of ripe adults. Temperatures at which spawning has been reported to occur are provided above or below the hatched bars. The length of the growing season (horizontal line) represents the period from the beginning of the spawning season to the onset of offshore winter migration (where available data permitted) or when autumn temperatures declined to 12° C (see text for additional details). Mean and maximum average monthly temperature within the growing season are given above or below the horizontal line. **B** Body size (TL) at the end of growing season vs. latitude. The closed circles are empirical sizes of YOY fish in autumn and the open circles are size of age-one fish in the spring. Mean lengths of the sexes, where reported, were averaged. Linear correlation coefficients (r), sample sizes (n), and levels of significance are also given. (Based on Anderson et al. 1977; Austin and Amish 1974; Austin et al. 1973; Barkman et al. 1981; Bayliff 1950; Bengston 1984; Cadigan and Fell 1985; Conover and Ross 1982; Conover 1984; Conover, unpubl. data; Daborn et al. 1979; Hildebrand 1922; Jessop 1983; Jessop and Morantz 1982; Kendall 1902; Middaugh 1981; D.P. Middaugh, unpubl. data[1]; Needler 1940; Ogburn et al. 1988; Vouglitois 1983; and Warkentine and Rachlin 1987)

The growing season ends much earlier at higher latitudes (Fig. 2A). In the field, growth of *M. menidia* levels off as autumn water temperatures descend to about 12° C at all latitudes (Bayliff 1950; Conover and Ross

[1] D.P. Middaugh, EPA, Gulf Breeze Laboratory, Gulf Breeze, FL, USA

1982; Ogburn et al. 1988). Laboratory studies also confirm that growth ceases at about 12° C (Conover, unpubl. data). We therefore used 12° C as an indication of the end of the growing season for locations in Fig. 2 where no growth data were available.

Further evidence that the growing season ends earlier, but at about the same temperature, with increasing latitude comes from the timing of winter migration. The habitat shift to deeper offshore waters begins as temperatures reach about 8–12° C; it occurs in late Sept. in Nova Scotia (Daborn et al. 1979; Jessop 1983), late Oct./ early Nov. in Massachusetts (Conover and Ross 1982), and late Nov./Dec. in Chesapeake Bay (Bayliff 1950). Offshore migration apparently does not occur in South Carolina as fish are found there close to shore throughout the winter (Anderson et al. 1977; Ogburn et al. 1988). The combined effect of delayed spawning in the spring and earlier cessation of growth in autumn means that the length of the growing season declines by a factor of 2.5 with increasing latitude.

Even though the temperatures bracketing the growing season (12° C) appear to change little with latitude, the mean temperature within the growing season (average of mean monthly temperatures) declines by about 3° C with increasing latitude (Fig. 2A). This occurs primarily because the maximum average monthly temperature is considerably higher at the lower latitudes.

All else being equal, silversides from the northernmost latitudes should be less than half the size of those from southern latitudes at the end of the first growing season. Instead, data from the literature suggest that body size at the end of the growing season is positively correlated with latitude, whether based on the mean lengths of YOY fish in autumn or on one-year-old adults in the spring (Fig. 2B). It is difficult to judge whether the increasing trend in body size with latitude is linear. It appears that body size increases up to about 39° N and then levels off, or perhaps declines slightly, at higher latitudes. In any event, it is evident that fish from the northern-most latitudes are at least as large as those from the south. Clearly, all else isn't equal: YOY fish from high-latitude populations must grow at least twice as fast within the growing season as do those from low-latitude populations.

Preliminary growth experiments

Mean daily growth rate at five temperatures for fish from six latitudes is presented in Fig. 3. Three observations about these data can be made. First, it is clear that growth rate increased with latitude across all temperatures. Fish from the two high latitude sources (NS and PEI) grew faster than did those from a middle latitude (NY), which grew faster than those from lower latitudes (VA, NC, SC). Second, the growth rates were most similar at the lower temperatures: it is at high temperatures where the northern fish most out-performed their southern counterparts. Third, the differences in growth rate at the higher temperatures were very large, differing by a factor of about two when measured in terms of length.
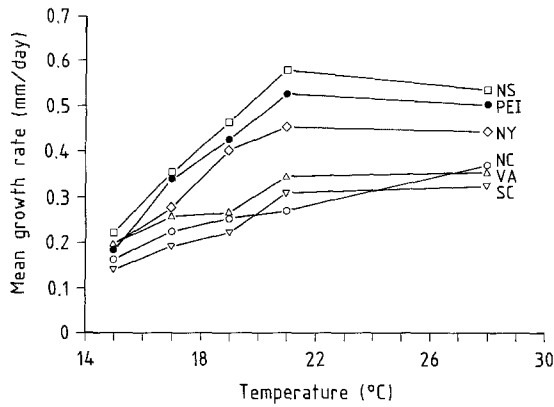
Fig. 3. Average growth rate of *M. menidia* collected as embryos from six different latitudes and reared in the laboratory at five different temperatures. Lines connect points representing mean growth rate of fish averaged across 1–7 different aquaria (mean = 2.1) at each population × temperature combination (*NS* = Nova Scotia; *PEI* = Prince Edward Island; *NY* = New York; *NC* = North Carolina; *VA* = Virginia; *SC* = South Carolina)

These data (Fig. 3) have several weaknesses when used to compare the genetic capacity for growth. First, stocking densities were high and variable (5–8 fish/L) so that the absolute values of the growth rates and the leveling off of growth rate between 21 and 28° C may have been affected by crowding. Second, non-genetic factors such as environmental or maternal effects on the embryos prior to their transfer to the lab could be partially responsible for the observed differences in growth among populations. For these reasons, we do not believe that more thorough statistical treatment or interpretation of these data is warranted. These potential flaws have, however, been corrected in the experiments described below.

Growth rate of the laboratory populations

In Experiment I, mean daily growth rate increased with temperature up to 28° C in all three populations (Fig. 4). The growth rates of NY and NS fish were higher than those from SC at all temperatures. NY and NS fish grew at similar rates at the low temperatures, but NS fish grew much faster than those from NY at high temperature.

In Experiment II, we extended the thermal range to 32° C in order to determine the temperature of maximum growth in each population. Growth rate at 32° C did not differ significantly from that at 28° C in either the SC or NS fish ($P > 0.10$). The NY fish could not be statistically compared because enough fish for only one replicate were available. The growth rate of this one replicate of NY fish was, however, slightly lower than those at 28° C. Hence, in all three populations, growth rate does not appear to increase further with temperature above 28° C.

The results of the analysis of variance show that in both Experiment I and II, the effects of population, temperature, and population × temperature interaction were
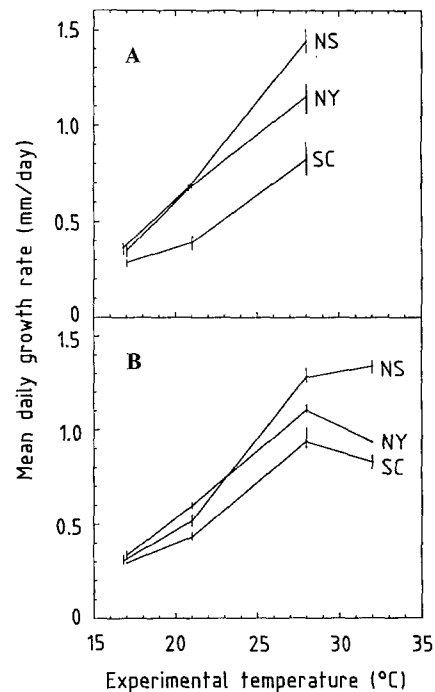
Fig. 4A, B. Mean daily growth rate vs. temperature in laboratory-reared populations of *Menidia menidia* that were orginally established from three different latitudinal sources (Nova Scotia – NS, New York – NY, South Carolina – SC). Experiments I and II are shown in **A** and **B**, respectively. Plotted are the means and ranges of replicate estimates of mean daily growth rate [three in all cases except NY at 32° C (1 replicate) and SC at 32° C (2 replicates)]

Table 1. results of Model I analysis of variance of the effects of population and experimental temperature on mean daily growth rate in *Menidia menidia*. (32° C data not included.)

Source of Variation	d.f.	Mean Square	F	p
Experiment I:				
Population	2	0.2573	111.87	<0.0001
Temperature	2	1.5300	665.22	<0.0001
Population × Temperature	4	0.0621	27.00	<0.0001
Error	18	0.0023		
Experiment II:				
Population	2	0.0558	62.00	<0.0001
Temperature	2	1.5372	1708.00	<0.0001
Population × Temperature	4	0.0267	29.67	<0.0001
Error	18	0.0009		

each highly significant (Table 1). Hence, population significantly affected growth rate, as did temperature. A posteriori analyses demonstrated that in Experiment I, the growth rates of each population averaged across all temperatures differed significantly from one another. In Experiment II, the growth rates of SC fish were significantly lower than those of NY and NS, but among the latter two populations, growth did not significantly differ.

Table 2. Mean wet weights (mg) and total growth (mg wet weight per individual = Final-Initial Weight) of three laboratory stocks of *Menidia menidia* averaged across Experiments I and II

Experimental Temperature (° C)		South Carolina	New York	Nova Scotia
32	Initial Weight	0.8	2.6	1.5
	Final Weight	19.6	40.0	59.4
	Total Growth	18.8	37.4	57.9
28	Initial Weight	2.0	1.5	1.1
	Final Weight	32.6	42.1	58.1
	Total Growth	30.6	40.6	57.0
21	Initial Weight	1.8	1.1	1.3
	Final Weight	21.0	35.5	37.4
	Total Growth	19.2	34.4	36.1
17	Initial Weight	1.4	1.7	1.8
	Final Weight	16.5	25.1	28.9
	Total Growth	15.1	23.4	27.1

The significant population vs. temperature interaction term demonstrates that the effect of temperature on growth differed among the populations. At 17° C, the growth rates of all three populations differed little, but at 28° C they differed greatly. Hence, while NS fish grew 1.04–1.28 times faster in length than SC fish at 17° C, they grew 1.36–1.76 times faster at 28° C. At 32° C, the mean daily growth rates of NS fish were significantly greater ($P < 0.001$) than those of the SC fish, and the magnitude of the difference (NS fish grew 1.5 × faster) was similar to that at 28° C.

The differences in growth among populations based on weight are, of course, much more dramatic (Table 2). To illustrate, in the 11 days over which 28° C experiments ran, the NS fish gained an average of 57 mg per individual, NY fish gained 41 mg, and SC fish gained 31 mg (mean of Exps. I and II). At the end of the 28° C experiment, mean weights of the SC, NY, and NS fish were 15, 27, and 52 times their initial weight, respectively.

Discussion

Spawning in the Atlantic silverside begins at about the same temperature but later in the year with increasing latitude (Fig. 2A). Coupled with the earlier onset of winter at higher latitudes, the growing season declines by a factor of about 2.5 with increasing latitude. Average temperature within the growing season also declines somewhat. Paradoxically, body size at the end of the first growing season does not decline with increasing latitude (Fig. 2B). These data clearly suggest the existence of latitudinal compensation in growth. The compensation appears to be achieved, however, not by extending the spawning and growing season into lower temperatures at higher latitudes, but by growing faster within the brief period of the year when high temperatures occur.

The results of our experimental studies confirm these findings by illustrating two main points. First, the capacity for growth increases with latitude and the persistence

of this pattern after several generations of rearing in a common environment indicates a genetic basis. (Subsequent observations continue to show similar growth differences after 7–8 laboratory generations.) Moreover, the magnitude of the difference in growth capacity is substantial. Much of the difference in growth rate with latitude in the Atlantic silverside can therefore be attributed to genotype.

Second, the difference in performance of northern fish relative to more southern ones is greatest at the higher rather than lower temperatures that permit growth. In other words, the phenotypic plasticity of growth with respect to temperature increases with latitude and the increase in plasticity is genetically based. This pattern is evident in both the preliminary experiments and those conducted on laboratory populations.

These results are not those expected if, as Levinton (1983) proposed, the capacity for growth was adapted to the temperatures most frequently encountered in nature. He predicted that high latitude populations should grow faster than low latitude populations at low temperatures but the reverse should be true at high temperatures (as in Fig. 1A). Instead, our results show that northern fish grow faster than southern fish primarily at the temperatures (28–32° C) southern fish would be expected to encounter most frequently. Temperatures as high as 28° C are rarely reached in Nova Scotian estuaries (see daily temperature records in Jessop 1983), but temperatures of about 28° C occur over a three month period in SC (Ogburn et al. 1988). Moreover, there is no evidence that the ability of Atlantic silversides from northern climates to grow fast at low temperatures has evolved at the expense of growth at higher temperatures. Even at 32° C, a temperature where egg and early larval survival was very poor, the fish from NS grew much faster than those from SC.

The results of our analysis are consistent with adaptation to length of the growing season. Because spawning begins at roughly the same temperatures across latitudes, there is no reason for young fish to evolve the capacity to grow at lower temperatures. It is the length of the growing season that differs with latitude. Our experiments suggest that northern fish compensate for their shorter growing season by increasing growth rate more rapidly with temperature than do southern fish, rather than by having a higher capacity for low-temperature growth (as in Fig. 1 B). Hence, northern fish have the capacity to grow very rapidly during the brief period of the year when high temperautes occur.

Adaptation to temperature vs. length of the growing season are not mutually exclusive. Many organisms probably adopt a mixed strategy by adapting to differences in both temperature and length of the growing season. When making latitudinal comparisons, however, the effects of temperature and seasonality need to be considered separately. Recent studies of largemouth bass (*Micropterus salmoides*) illustrate this point. The occurrence of latitudinal growth compensation in largemouth bass is suggested by the studies of Williamson (1986) and Isely et al. (1987): both showed that, in a common environment, the northern subspecies grows significantly
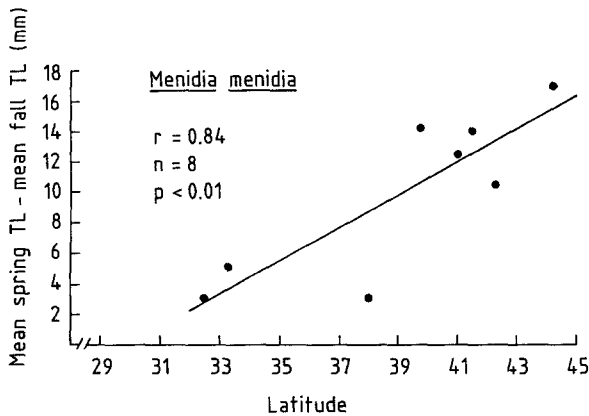
Fig. 5. Size-selective winter mortality vs. latitude among populations of *Menidia menidia* as estimated by the difference in mean length of fish captured just before (mean fall TL), and just after (mean spring TL), the winter from eight different locations along the coast. Based on references listed in Fig. 2

faster than the southern form. When experimentally stocked in the same pond, the northern subspecies also spawns an average of 11 d earlier in the spring than does the southern subspecies (Isely et al. 1987). This suggests that northern fish have an innate tendency to spawn at a slightly lower temperature/shorter daylength than do those from the south, but the difference is so slight that it does not counteract the decline in length of the growing season that occurs with increasing latitude among natural populations (Modde and Scalet 1985). Nonetheless, there is evidence of adaptation to both temperature and length of the growing season.

A major problem in all latitudinal comparisons, including ours, is that temperature and length of the growing season covary across the same environmental gradient. Hence, it is difficult to separate unambiguously their unique effects. Our hypothesis that growth rate evolves in response to length of the growing season could be independently tested by studies in other geographic regions. Growth rates could be compared among populations where variation in length of the growing season is generated, for example, by some factor other than temperature such as duration of wet vs. dry seasons.

The results of this study provide an example of countergradient variation in which the genetic influence on phenotypic expression of a character has a directional trend opposite to that of an environmental influence (Levins 1969). Countergradient variation minimizes the range of phenotypes (in this case, body size) produced along an environmental gradient. To the extent that they are genetically-based, many of the previously documented examples of latitudinal compensation in metabolism (Bullock 1955) and growth rate (e.g., Dehnel 1955; Schneider 1967; Ament 1979) also represent countergradient variation. Berven et al. (1979) clearly demonstrated the phenomenon among populations of the green frog (*Rana clamitans*) from different altitudes. Few other examples are known, but this may simply reflect the cryptic nature of countergradient variation. Genetic differences that have a countergradient pattern remain perfectly hid-

den until comparisons under controlled conditions are performed.

Selection on growth rate

Our results do not by themselves show that countergradient variation in growth is adaptive. Why should high-latitude fish compensate rather than simply growing slower? One answer may be size-selective winter mortality. Previous studies comparing the abundance and size distributions of *M. menidia* before and after the offshore winter migration in a Massachusetts estuary (Conover and Ross 1982; Conover 1984), showed that mortality was high (90–99%) and biased toward smaller fish. Very few fish less than 80 mm in length survived the winter and the mean lengths of fish shifted upward by as much as 14%, but maximum length was unchanged (see Fig. 2 in Conover 1984). Moreover, experiments confirmed that small fish were more susceptible than larger fish to mortality from chronic exposure to low temperature (Conover 1984).

As an index of the level of size-dependent winter mortality, we computed the difference between the average empirical mean length of Atlantic silversides in the early spring vs. the late fall for the eight locations along the coast where data were available. The magnitude of this index is positively correlated with latitude (Fig. 5). In low-latitude populations, mean length over the winter increases by only 2–4 mm but the winter increase in mean length at high latitudes is 10–17 mm. This pattern is the reverse of that expected if growth was responsible for the winter increase in mean length because growth in winter is most likely to occur, if anywhere, at the lower latitudes where winter temperatures are milder.

Henderson et al. (1988) clearly demonstrated that starvation is one cause of size-selective winter mortality. In an atherinid from the coast of England (*Atherina boyeri*), larger fish are able to store more fat prior to winter. Because feeding does not occur, fat reserves are the only source of energy during a 100 d period in mid-winter. Smaller fish (< 59 mm S.L.) have insufficient reserves and starve to death. Predation could also cause size-selective mortality, particularly in conjunction with the effects of starvation, but specific evidence is lacking.

In summary, high-latitude fish are faced with a dilemma. The importance of large size to winter survival increases with latitude, but the time available to grow large (i.e., the length of the growing season) simultaneously decreases. The end result is a latitudinal gradient in selection for rapid growth. Boyce (1979) and Lindstedt and Boyce (1985) reached similar conclusions for homeotherms.

Life history trade-offs?

Even if sufficient to explain rapid growth at high latitudes, size-selective winter mortality can provide only a partial explanation for the latitudinal gradient in growth rate and body size. Although large size may not

be required to survive the winter at low latitudes, wouldn't it still be beneficial to be large for other reasons? Numerous studies of the early life history of fishes demonstrate the benefits of increasing size to feeding success, avoidance of predators, swimming success, and overall survival (reviewed by Lasker 1981). Large body size may also translate into increased reproductive success later in life. The suggestion from this literature is that a fish should grow as fast as possible during the early life history so as to reap the benefits of large size. Our results suggest that there are no genetic constraints preventing southern fish from evolving a higher capacity for growth if there were selection pressure to do so. All else being equal, if NS genotypes were placed in a southern environment they would, at the end of the growing season, reach a size many times larger than do SC fish. If the genotypic variation for higher growth capacity exists within the species why don't southern fish evolve it?

One possibility is that there are life history trade-offs associated with having a high genetic capacity for growth. There may, for example, be a negative correlation between growth capacity and survivorship under certain environmental conditions. Individuals with a high capacity for growth may have higher maintenance energy requirements that could negatively influence growth and survival in environments where temperatures are high and food levels are low, especially during the larval period when fish are especially susceptible to starvation (Lasker 1981). Moreover, the temporal pattern of food availability is not the same at different latitudes. At high latitudes, the growing season for *M. menidia* coincides with a brief pulse of generally high productivity (i.e., the spring plankton bloom: Sverdrup et al. 1942; Cushing 1975). Having a high genetic capacity for growth would enable such fish to exploit maximally this pattern of resource availablility. At low latitudes, however, the production cycle has a lower amplitude and productivity is spread out more evenly over the year. If at low latitudes, high environmental temperatures occasionally coincide with periods of low resource availability (e.g., mid-summer?), then the survival of individuals with high growth capacity (and possibly higher basal metabolism) might be compromised. A more conservative response of growth rate to temperature might provide a better match between food requirements and the pattern of resource availability at low latitudes. Studies on growth and survival under restricted rations and on the temporal pattern of food availability in the field are needed to evaluate this issue.

Alternatively, there may be different constraints on body size at different latitudes. Large size may be beneficial to winter survival at high latitudes, but at low latitudes other factors that favor smaller body size may exist.

Our study is the first to demonstrate countergradient variation in the genetic capacity for growth in fishes. Conover (in press) presented evidence that it may be widespread and discusses the implications for resource management and aquaculture. Further testing of other species may prove valuable, both for understanding the evolution of somatic growth rate and its life history consequences, as well as for identifying native stocks of resource species with high growth capacity.

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