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Energetic Adaptations along a Broad Latitudinal Gradient: Implications for Widely Distributed Assemblages

JAMES E. GARVEY, DENNIS R. DEVRIES, RUSSELL A. WRIGHT, AND JEFFREY G. MINER

Most community-based models in ecology assume that all individuals within a species respond similarly to environmental conditions and thereby exert identical effects as consumers or prey. Rather, individuals differ among systems, with important implications for population demographics and community interactions. For widely distributed assemblages made up of poikilotherms with high first-year mortality, species-specific differences in growth reaction norms as affected by both temperature and genotype will influence biotic interactions. For a broadly distributed fish assemblage, first-year growth does not vary with latitude for a planktivorous prey species, but declines with increasing latitude for a terminal piscivore. Size-based competitive interactions between these species are likely to be more intense at high latitudes, as they spend an extended time sharing resources during early life. Such patterns probably are pervasive and must be considered when seeking to understand species interactions. Improving our knowledge of how temperature and local adaptations affect size-based interactions should enhance our ability to manage and conserve widespread assemblages.

Keywords: latitude, community growth, ectotherm, biotic interaction

Ecologists have long directed their research efforts toward understanding mechanisms governing community composition. This work has largely been conducted at local or regional scales, with the intent of identifying important physical and biological mechanisms. A number of general models have arisen to explain the relative importance of reproduction and colonization by species (Menge and Sutherland 1987) and the productivity (Oksanen et al. 1981), size (Rosenzweig 1995), and permanence (Wellborn et al. 1996) of ecosystems. Nutrients, disturbance, competition, and predation all have been accepted as important forces affecting community composition within the context of these models. Within aquatic ecosystems, researchers have debated the relative roles of top-down consumer regulation and bottom-up resource control of communities and ecosystems (Carpenter and Kitchell 1992). Both are important structuring forces, with their relative effect depending on a host of factors, including the presence of omnivory (Diehl 1995), strength of interactions among species (Peacor and Werner 2001), and resource exchange between adjacent ecosystems (Polis et al. 1996).

Although these general models illuminate patterns of species diversity and ecosystem structure and function, food web models typically assume that all individuals within a species respond similarly to environmental conditions and thereby exert identical effects as consumers or prey (Chase 1999). In reality, responses and effects vary among individ-

uals within and among populations as a function of several factors, including life stage (Bystrom et al. 1998), body size (Stein et al. 1988), and reaction norms (Schlichting and Pigliucci 1998). Thus, understanding how food web effects vary among individuals and populations as a function of their unique characteristics may lend insight into why different ecosystems contain unique species assemblages.

Interactions driven by phenotypic differences among individuals (e.g., growth rate, body size) typically occur during early life in poikilotherms (i.e., organisms whose body temperature varies with the environment) such as insects, plants, reptiles, amphibians, gastropods, and fish. In this article, we explore how phenotypic differences during early ontogeny affect the relative abundance and thereby the effect of these species within communities. Many phenotypic characteris-

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tics of these organisms are determined largely by the influence of the environment (e.g., temperature) on traits such as physiological performance (e.g., growth). Compelling evidence continues to emerge that local adaptations involving trade-offs between growth and other physical or behavioral traits lead to different distributions of reaction norms among populations, with important consequences for patterns of community composition across broad environmental gradients.

We are specifically interested in how the gradient in seasonal temperature across latitudes and latitude-specific, genetic effects on growth plasticity affect body size, primarily because seasonal growth affects the composition of widespread, poikilotherm-dominated communities. We provide one example with two widely distributed fish species in North America and explore general patterns that may arise in other broadly distributed assemblages.

Variation in early interactions

The numerical influence of many poikilothermic species on community interactions is determined during early life stages, because high mortality occurs during this time (i.e., Type III survivorship; figure 1a). Species often compensate for poor survival of offspring with high fecundity or frequent reproduction (Winemiller and Rose 1992). Slight differences in the survival of these initially abundant offspring strongly affect the relative size of a cohort within a population (figure 1b; Cowan et al. 2000). Hence, the influence of these species on communities and ecosystems is determined by subtle differences in the success of a relatively small percentage of individuals produced during a short period in life. As the surviving individuals within an abundant cohort grow, they exert consumer effects that linger for a generation (Mittelbach et al. 1995, Ludsin et al. 2001). Conversely, if relatively small cohorts are produced consistently across several years, the impact of the consumer species will be considerably reduced.

Many terrestrial and aquatic assemblages consist of poikilothermic species with variable early survival. Several amphibian species breed in ephemeral ponds during spring. Eggs hatch and larvae metamorphose in these systems, emerging as juveniles with features similar to those of adults. Variable conditions within these ponds effectively cause these communities to reform or coalesce each year (see Thompson et al. 2001), with outcomes depending greatly on factors such as temperature, drying rate, and timing of appearance (Skelly 1996). Similarly, densities of crustacean zooplankton in tem-

perate lakes typically peak during spring, with relative species composition determined by factors such as phytoplankton composition, temperature, and the bank of dormant eggs in the sediment (Caceres 1997). Population densities of insects can fluctuate widely among years as a function of variable control by their predators and the environment (Jones et al. 1998). In freshwater lakes, the structure of fish assemblages is often determined during spring as fish spawn in succession,

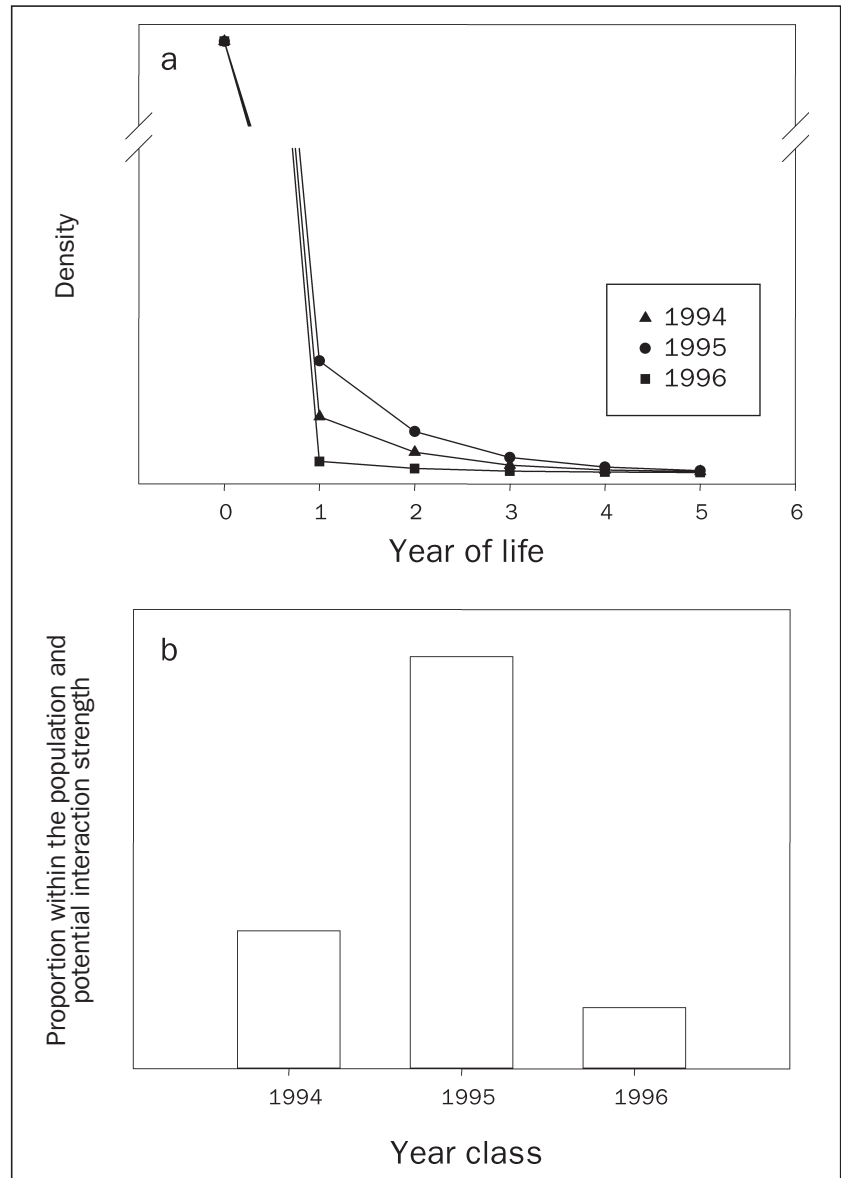


Figure 1. Hypothetical survivorship curves (a) and relative cohort size (b) within a population comprising three year-classes (1994, triangle; 1995, circle; 1996, square). The overlapping symbols in the upper left corner show that the same number of offspring are produced during each year (a). However, first-year mortality is very high relative to other years, as signified by the break in the y-axis. Differences in first-year mortality lead to proportionally different densities of each year class contributing to the population (b). Events affecting survival during the first year of life strongly affect the relative contribution of cohorts to population size and their subsequent effect on other co-occurring species.

with piscivorous species appearing early in the season and prey fish hatching later in the year (Mittelbach and Persson 1998). Factors influencing the relative success of interacting species within these systems early in life clearly shape future community composition.

All of these systems are sensitive to factors that affect schedules of reproduction and growth, because interactions are driven largely by the time that individuals remain in each life stage or size range. Several factors can affect the intensity of early ontogenetic interactions, including temperature, productivity, and the relative timing of adult breeding and offspring hatching. For example, relative timing of appearance among early life stages of amphibians in small ponds can dramatically affect community structure by determining the outcome of competitive interactions (Lawler and Morin 1993). These relative timing effects also are important for larval fishes, affecting interspecific competition and thus the relative growth, survival, and abundance of species within a community (Garvey and Stein 1998a). With respect to predator-prey interactions during early life, reproduction of predators and their prey is often timed such that young predators can effectively consume prey of increasing energetic value during the first year of life. If such a switch to prey that are more energy rich is successful, rapid growth occurs (Mittelbach and Persson 1998). Again, the relative timing of offspring appearance determines the time at which prey become vulnerable, because the size range of prey that predators can consume is limited and prey can grow beyond vulnerable sizes in a relatively short time (DeVries et al. 1998).

Although adult life stages within many communities are often specialized (e.g., predator or herbivore), early life stages are typically restricted to the same limited habitat and food resources because all individuals must pass through the same range of initial sizes (Werner and Gilliam 1984). If the growth of early larval and juvenile stages of top consumer species (e.g., keystone; Power et al. 1996) is compromised, either through environmental effects (e.g., low temperature) or competition with numerically dominant species that are often prey during later life, then the dominance of the top consumer within the community may be reduced. This phenomenon is widespread in both amphibian (Wilbur 1997) and fish (Olson et al. 1995) assemblages and is most likely influenced by factors that also influence phenotypic characteristics of the interacting species. These interactions are pervasive in assemblages dominated by indeterminately growing poikilotherms, with temperature, length of growing season, and perhaps genotype being important underlying factors. The challenge for ecologists is to tease apart the contribution of these environmental effects relative to biotic ones. In our view, a future thrust of community ecology will revolve around understanding how energetic tradeoffs between growth and other plastic traits translate to the relative strength of interactions such as predation or competition between species. Ultimately, this approach should lend insight into how communities consisting of widely distributed poikilotherms vary along gradients of

latitude and altitude, which vary predictably in temperature and growing season duration.

Energetic adaptations and early interactions

Growth of poikilotherms is affected by the environment (e.g., seasonal temperature) and genotype (Roff 1992) as well as interactions between these two factors (Conover and Schultz 1995). Although this is well accepted, models of population, community, or ecosystem structure often assume that growth responses and other reaction norms are similar among individuals and driven primarily by the environment (Chase 1999). Further, these models tend to assume that maximal growth rate is an important measure of success within the community because rapid growth should expedite time to reproductive maturity and, in many systems, reduce competitive interactions and predation risk.

It is well known, however, that most organisms within communities do not grow at their physiological maximum rate (Abrams et al. 1996). Of course, food limitation may play a role. But maximizing growth may not increase fitness if increased growth rates incur some cost (Billerbeck et al. 2001). In a community context, foraging in young organisms typically is risky, and habitats must be chosen that minimize the ratio of predatory mortality to growth (Werner and Gilliam 1984). Although this is associated with the interplay between behavior and habitat use (Lima and Dill 1990), other tradeoffs between growth and physiological performance may occur as well (Billerbeck et al. 2001). Within species, differences in growth among populations have often been attributed to environmental effects (figure 2a; Peacor and Werner 2001). Conversely, differences in growth performance between species under similar circumstances are attributed to genetic differences (Skelly 1996). For widely distributed species, identifying how environmental and genetic factors contribute in both an additive and a multiplicative fashion to shape patterns of growth and community performance becomes imperative for predicting community interactions.

In some species with broad distributions, genetic and environmental factors covary along ecological gradients to affect phenotypic variation (figure 2; Conover and Schultz 1995). Genotypes might vary along environmental gradients in ways that intensify environmental effects on phenotypes, a process known as cogradients variation (CoGV; figure 2b). In contrast, genotypes might counterbalance environmental effects, particularly those that otherwise reduce fitness (figure 2c). The latter scenario, termed countergradient variation (CnGV; Levins 1969), most likely is common in many widely distributed species and may affect species interactions across geographic-scale (i.e., latitudinal) gradients. Only recently have investigators explored how covariance between genotypes and environments (e.g., CnGV) affects population dynamics along environmental gradients (Conover and Schultz 1995). Differences among species in CoGV or CnGV have important implications for species interactions during early ontogeny.

Because an extensive thermal gradient exists across latitudes, growth of early life stages of poikilothermic species should vary as well. In fact, fall size (size reached by the first fall of life) in many species often declines with increasing latitude, potentially compromising first-year survival and persistence of individuals in northern populations relative to southern ones (Jensen et al. 2000). However, genetically driven CnGV in growth rates has been revealed within a growing number of

species, including fish, reptiles, gastropods, insects, and amphibians, such that the absolute body size of individuals across latitudes does not differ after one growing season (Conover and Schultz 1995). And in one species, the ant lion *Myrmeleon immaculatus*, CnGV in growth has been shown to be responsible for Bergmann's phenomenon, by which northern individuals are larger than southern conspecifics (Arnett and Gotelli 1999). These species should persist in assemblages along broad geographic gradients.

For a marine fish (Atlantic silversides, or *Menidia menidia*) that persists over a 17-degree range in latitude (29 to 46 degrees north [$^{\circ}$ N]), the growing season is 2.5 times shorter at the northern extreme of the range compared with the southern limit (Billerbeck et al. 2001). However, body size at the end of the first growing season in the north is not correspondingly smaller than that in the south. Thus, individuals must grow faster in the north to reach a similar body size by fall. Common garden and reciprocal transplant experiments have demonstrated a strong genetic component to these patterns in silversides as well as other organisms (Conover and Schultz 1995).

Clearly, tradeoffs between growth and other phenotypic characteristics must occur. Otherwise, average fall size would be greater in the south than in the north. Individuals must balance the relative benefits and costs of growing; if expected future fitness declines with increasing growth rate, first-year size will decline. In many organisms, first-winter survival depends on the interplay among winter duration, body size, metabolic rate, and energy reserves. Large individuals have lower mass-specific metabolic costs, higher mass-specific fat reserves, and a lower probability of winter starvation (Garvey et al. 1998; see Wikelski et al. 1997 for exceptions). The benefit of maximizing first-summer growth and fat deposition to successfully navigate winter should increase dramatically with increasing latitude, leading to strong selection for CnGV in growth (Billerbeck et al. 2001). In the south, extended growing seasons should facilitate growth. However, maximum growth typically does not occur, most likely as a function of associated costs. In addition to the reduction in foraging activity of prey by predators, other costs of foraging and rapid growth in young organisms have recently been revealed. In silversides, increased foraging, typified by northern individuals, reduces swimming performance (Billerbeck et al. 2001), thereby increasing predatory mortality (Lankford et al. 2001). Costs of foraging activity, assimilation, and tissue synthesis are high,

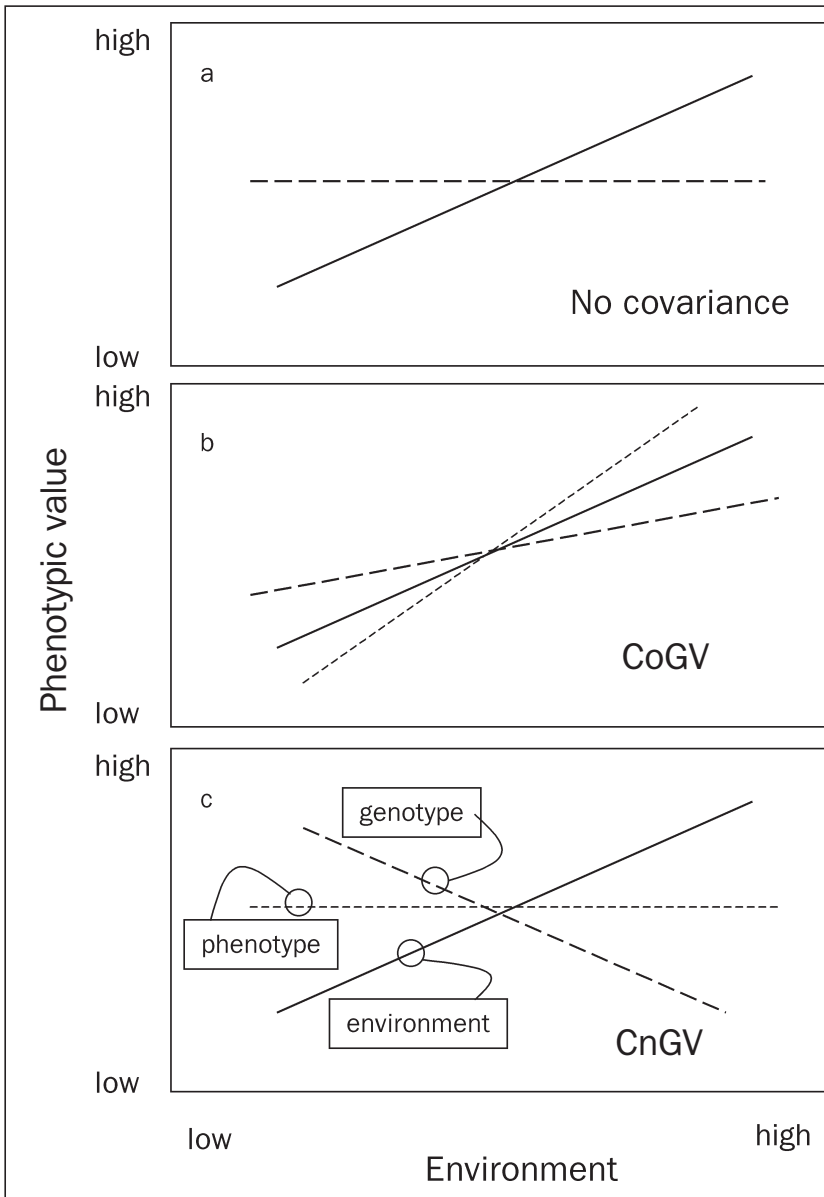


Figure 2. If the environment (solid line) influences a phenotype, three possible patterns of phenotypic variation (dotted line) arise depending on the genotypic influence (dashed line). (a) No covariance; genetic variation is random with respect to the environment. Phenotype depends entirely on the environment. Here the solid line represents both the environmental influence and the phenotypic pattern. (b) Cogradients variation (CoGV); the genetic influence is in the same direction as the environmental influence. (c) Countergradient variation (CnGV); the genetic influence opposes the environmental influence along the gradient. (Adapted from Conover and Schultz 1995.)

potentially competing with other energetically demanding functions such as flight (Lankford et al. 2001). Other developmental, morphological constraints also may be associated with fast growth (Arendt and Wilson 1999).

Because growth variation among individuals within species often is not a simple function of latitudinal variation in temperature, community ecologists need to consider how CnGV or CoGV in growth of component populations modifies interactions. An emerging hypothesis revolves around the relative effect of winter starvation and predation on first-year survival in organisms. It has long been thought that cumulative predation mortality increases with declining latitude in many aquatic and terrestrial systems (Wilson 1991). Indeed, a classic pattern is that the toxicity of holothurians and sponges increases with declining latitude, presumably covarying with increased predation pressure (Bakus and Green 1974). Because a similar latitudinal predation gradient has been suggested for silversides (Lankford et al. 2001), gastropods (Trussell 2000), largemouth bass (Garvey et al. 1998), and Eurasian perch (Bystrom et al. 1998), the relative effect of winter and predation on growth rates and associated tradeoffs should vary along a latitudinal gradient in many widely distributed assemblages. In the following section, we explore the potential impact of energetic tradeoffs that affect community interactions among early life stages along a latitudinal gradient.

Widely distributed assemblages

Early life history interactions within communities dominated by poikilotherms will most likely vary with adaptations affecting plasticity in growth of component species. Because CnGV in growth has been documented in many diverse taxa, individual- and population-specific energetic adaptations must be strongly considered when teasing apart community interactions. This is a challenging but necessary task, given the complexity of interactions within even apparently simple species assemblages. We first highlight the potential importance of these adaptations for a widely distributed assemblage of freshwater fish in North America and then explore general patterns that may arise in other assemblages with similar characteristics.

Largemouth–bluegill assemblages. Largemouth bass (*Micropterus salmoides*) and its primary prey, bluegill (*Lepomis macrochirus*), are mem-



Figure 3. Overlapping distribution (shaded area) of largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) in North America. Largemouth bass–bluegill assemblages span about 24 degrees north latitude (24°N to 48°N).



Figure 4. An age 0 largemouth bass (*Micropterus salmoides*) during midsummer at a mid-temperate latitude. Although *M. salmoides* is an important piscivore and familiar sport fish during the adult life stage, it is during early life at small sizes that seasonal temperature and biotic interactions influence growth rates, survival, and ultimately the impact of this species on aquatic ecosystems.

bers of a widely studied fish assemblage that is pervasive throughout North America (figure 3). Small differences in the relative timing of spawning of these species can dramatically affect their interactions. Largemouth bass (figure 4) spawn in the littoral zone during spring. After spending a brief time on nests, age 0 largemouth bass disperse but remain in the littoral zone. As they grow larger, they consume first zooplankton, then macroinvertebrates, and finally fish (Garvey and Stein 1998b). The switch to piscivory is largely driven by the density and relative size of prey fish (Garvey et al. 2000). Bluegill adults spawn in littoral nests about a month later than largemouth bass. Zooplanktivorous larval bluegill hatch and then move to the limnetic zone. After a brief time, they return to the littoral zone, consuming macroinvertebrates and potentially competing with prepiscivorous largemouth bass (Olson et al. 1995). Although largemouth bass spawning generally lasts only 1 month, bluegill spawning can occur for more than 3 months (Garvey et al. 2002). Because of the disparity in spawning duration, and because the hatch dates and growth rates of both species are temperature dependent, the relative overlap between age 0 largemouth bass and age 0 bluegill can vary substantially on both temporal and spatial scales, driving patterns of largemouth bass growth and predatory influence.

Patterns of first-year growth differ for bluegill and largemouth bass along a latitudinal gradient in North America. Recall that fall size of all poikilotherms should decline with increasing latitude because of a shortened growing season.

However, species-specific differences in CnGV in growth may alter these expectations. In a review of the literature, we found that mean size by fall did not vary with latitude for age 0 bluegill (figure 5a). By contrast, mean size by fall of age 0 largemouth bass declined with increasing latitude (figure 5b). To quantify how length of the growing season and seasonal temperature at each latitude contributed to these patterns, we used a bioenergetics model for each species to estimate the average proportion of maximum daily ration that must be consumed to achieve the observed growth (Hanson et al. 1997). Temperatures in simulations mimicked those found at each latitude (Fullerton et al. 2000); simulations began at hatching (20 degrees Celsius [$^{\circ}$ C] for bluegill; 15 $^{\circ}$ C for largemouth bass) and ended when fall temperatures reached 10 $^{\circ}$ C, below which foraging activity declines (Fullerton et al. 2000). With increasing latitude, average daily ration increased for age 0 bluegill and declined for age 0 largemouth bass (figure 5c, 5d). Dynamic mechanisms underlying these patterns have important implications both for populations (e.g., influence of environment versus genotype) and for communities (e.g., size-structured interactions).

Several factors may contribute to the observed patterns of growth and consumption of bluegill and largemouth bass along the North American latitudinal gradient. For age 0 bluegill, northern individuals reached the same fall sizes as southern counterparts, even though the northern growing season was shorter and summer temperatures were cooler. Most

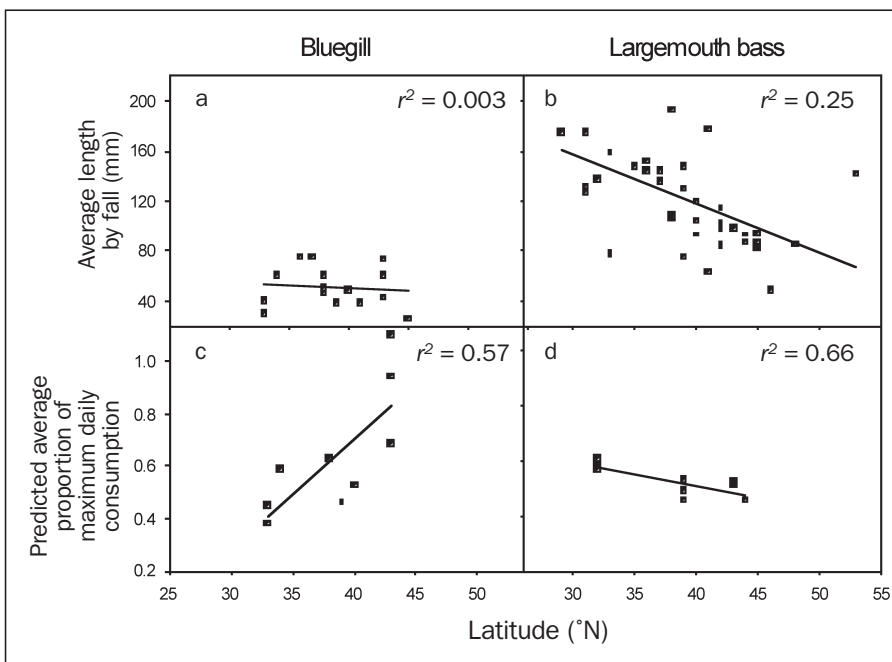


Figure 5. Latitudinal patterns of mean fall size for populations of age 0 bluegill (a) and age 0 largemouth bass (b) in North American lakes, and predicted average proportion of daily maximum consumption for bluegill (c) and largemouth bass (d) in selected populations. (Data are derived from Beamesderfer and North [1995] and Carlander [1977].) Consumption was predicted using observed growth and assumed latitude-specific summer–fall temperatures in a mass-balance bioenergetics model (Hanson et al. 1997).

likely, northern fish grew more rapidly, leading to this invariant pattern of fall size. It is unlikely that greater productivity in northern systems led to increased growth of northern relative to southern counterparts. Perhaps prolonged spawning in the south contributed to a greater proportion of small, late-hatched individuals, reducing mean sizes. However, spawning of bluegill in the north may continue late in the season as well, also reducing mean sizes (Garvey et al. 2002). An intriguing possibility is that CnGV is responsible, whereby northern bluegills have inherently faster growth rates and potentially greater consumption rates than southern conspecifics. CnGV in growth has been documented to occur in sunfish as a function of competitive interactions with congeners (Arendt and Wilson 1999). We hypothesize that CnGV is an important mechanism influencing growth of age 0 bluegill across a latitudinal gradient in North America.

In contrast to bluegill growth, the growth of age 0 largemouth bass varied as might be expected if it depended largely on both the low seasonal tem-

perature and perhaps the low seasonal productivity of northern systems. Although we might conclude that growth varies strongly with the environment and is under little genetic control (unless CoGV is contributing), experimental evidence and the literature suggest otherwise. We conducted an experiment in controlled-environment rooms to determine how both local and latitudinally driven factors influence overwinter growth and survival of age 0 largemouth bass (Fullerton et al. 2000). Age 0 largemouth bass were collected from lentic systems at three points along a latitudinal gradient within this species range (south, 33°N, Alabama; middle, 40°N, Ohio; north, 45°N, Wisconsin). Individuals were fed a maintenance ration of fish prey (calculated with a bioenergetics model; Wright et al. 1999) for 15 weeks at temperatures ranging from 8°C to 15°C. Northern largemouth bass grew more than their southern counterparts; growth of individuals from the middle latitude was intermediate. Similarly, offspring of the northern subspecies of largemouth bass grew more rapidly than those of the Florida subspecies when reared in ponds in Illinois (Isely et al. 1987). Controlled experiments suggest a pattern of growth consistent with CnGV for age 0 largemouth bass. A lack of congruence between field results (figure 5) and experimental results (see above) suggests that environmental constraints such as reduced intake of energy-dense prey may counter positive growth effects of CnGV for largemouth bass with increasing latitude.

To generate testable predictions about how energy allocation tradeoffs influence fitness, we used dynamic optimization modeling (Mangel and Clark 1988). This powerful modeling approach has been used in many organisms to determine optimal solutions that maximize expected future fitness of individuals. Models begin by setting the final conditions necessary to maximize fitness (i.e., a future fitness function). They then work in reverse, iterative time steps, determining what behavioral or physiological decisions maximize expected future fitness. We have developed a model for largemouth bass, asking what energy allocation decisions are necessary to maximize the expected number of eggs produced during 6 years. In each model time step, fish of a given state (i.e., body size, level of maturation, and amount of fat reserves) consume a ration, and must trade off how much con-

sumed energy is allocated to growth in length, fat reserves, or gonads to maximize their future reproductive output (i.e., expected future fitness). Temperature regimes quantified in southern, mid-temperate, and north-temperate lakes were used to simulate latitudinal conditions. Regardless of initial internal state or ration, expected future fitness of largemouth bass declined with increasing latitude, albeit in a nonlinear fashion: Fitness declined dramatically as seasonal temperatures approached those near the northernmost extent of the species' range. In one simulation, a 50% increase in caloric intake increased expected fitness far more for northern largemouth bass than for middle or southern latitude counterparts. However, absolute expected future fitness in the north was still only about 50% of that in the south. Hence, selection for caloric

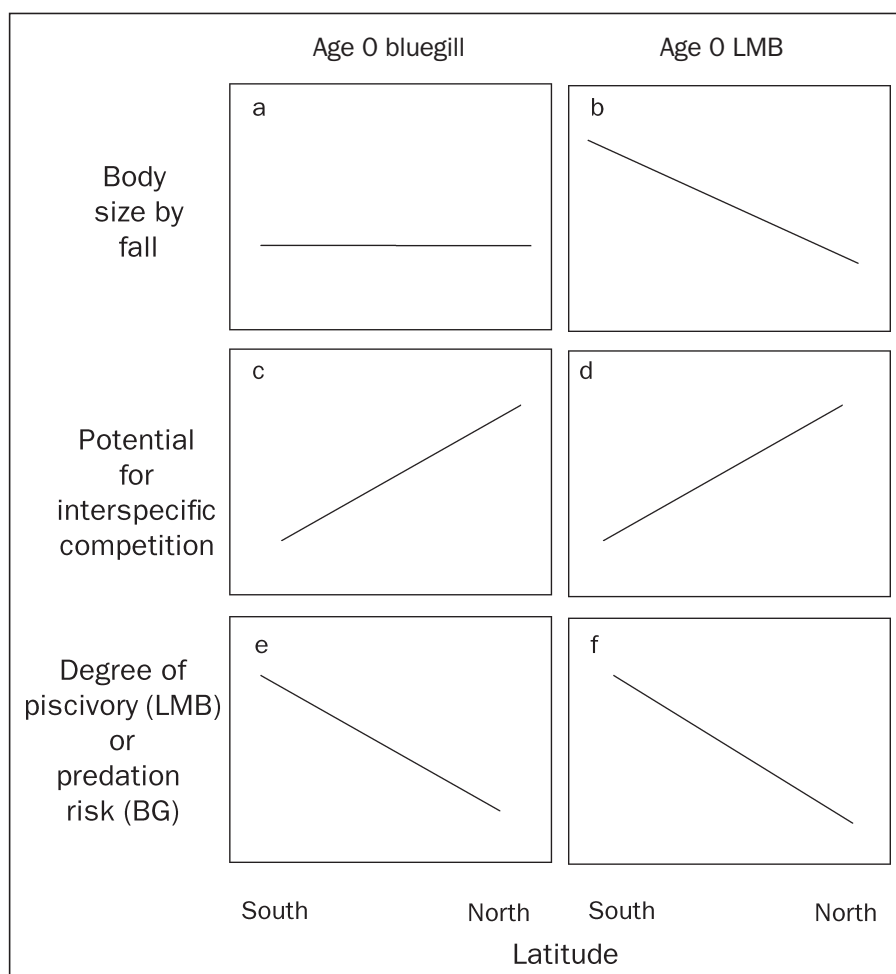


Figure 6. Predicted size and size-dependent interactions for age 0 bluegill (BG) and age 0 largemouth bass (LMB) as a function of latitude, given the literature-derived field pattern in which bluegill size by fall does not change with increasing latitude (a), whereas that of largemouth bass declines (b). Potential for interspecific competition between age 0 bluegill (c) and largemouth bass (d) increases with latitude, because largemouth bass spend a greater time at sizes in which diets overlap between the species. Predation risk to age 0 largemouth bass declines with increasing latitude for age 0 bluegill, because largemouth bass remain at relatively small sizes during the summer (e). Consequently, largemouth bass are less likely to become piscivorous during their first year of life with increasing latitude (f).

increase through increased consumption or greater assimilation should be more advantageous in the north.

Because the dynamic model predicts that southern largemouth bass should invest most energy in growth to enhance reproductive success, genotypes with rapid growth should be found in southern systems. However, common garden experiments (see above) suggest that northern counterparts grow more rapidly. As discussed earlier, rapid growth may be selected against because it incurs some cost, which may be associated with foraging activity. Although increased activity may lead to increased growth, Wright and colleagues (1999) suggest that northern individuals forage with an increased cost in terms of encounters with predators. Indeed, in laboratory feeding trials, we have found that young, northern-origin largemouth bass move 225% to 350% more through vegetated habitat than do southern largemouth bass.

We hypothesize that CnGV operating within populations may dampen latitudinal environmental effects on species interactions. Differences in growth rates will determine the relative length of time that both species remain at respective sizes and thus in each ontogenetic stage. Growth of age 0 largemouth bass may be reduced and stage duration increased if exploitative competition with bluegill occurs (Olson et al. 1995). Because fall size of age 0 bluegill and age 0 largemouth bass varies differentially with latitude (figure 6a, 6b), these differences may dramatically affect biotic interactions. The response of piscivory by age 0 largemouth bass may have particularly robust effects on observed variation in largemouth bass growth. The dietary transition to piscivory is an important factor driving growth of age 0 largemouth bass (Olson 1996) and other age 0 piscivores (Mittelbach and Persson 1998), largely because of the increased energetic intake contributed by fish prey relative to macroinvertebrates and zooplankton.

Although CnGV may be an important determinant of potential maximum growth rates of both age 0 bluegill and largemouth bass in northern systems, differences in species interactions appear to translate into very different observed patterns of growth along a latitudinal gradient. With increasing latitude, competition should increase between bluegill and age 0 largemouth bass, because relatively slow-growing age 0 largemouth bass at high latitudes spend a longer time at sizes at which diets overlap with those of age 0 bluegill (figure 6c, 6d). This may explain why patterns of early interspecific competition have been detected in northern systems (e.g., Michigan lakes; Olson et al. 1995), but little evidence has arisen for this phenomenon in southern lakes (Walters and Kitchell 2001). The relative degree of piscivory of age 0 largemouth bass, and thereby predation risk for age 0 bluegill, also should vary along a latitudinal gradient (figure 6e, 6f). In southern systems, age 0 largemouth bass grow sufficiently rapidly to switch to piscivory on age 0 bluegill as they appear. At middle latitudes, relative timing of appearance between largemouth bass and bluegill, in addition to interspecific competition, may only allow largemouth bass to switch to piscivory late in the season (Garvey and Stein 1998b). Bimodal

body size distributions may occur, because only the earliest hatched largemouth bass may successfully become piscivores. At northern latitudes, largemouth bass typically do not become piscivorous until the second year of life.

Other assemblages. The tradeoffs between achieving sizes that ensure survival during winter and avoiding behavioral or physiological tactics that increase predation should underlie many interactions in widely distributed assemblages. The Atlantic silversides is an important prey fish for several predators in the Atlantic Ocean, including the bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis*; Lankford et al. 2001). The early growth and survival of these piscivorous fish depend to a large degree on the size structure and abundance of Atlantic silversides (Conover et al. 1997). Differences in predators' seasonal schedules of growth (e.g., striped bass also display CnGV in growth; Conover et al. 1997) and prey as affected by CnGV in growth rates may greatly affect their interactions along a latitudinal gradient. The underlying implications of CnGV in growth on these interactions have not been explored.

As demonstrated with the bluegill–largemouth bass assemblage, other biotic interactions such as competition may interact with predation to affect energetic tradeoffs. The Eurasian perch (*Perca fluviatilis*) is piscivorous (and often cannibalistic) during the adult stage but consumes zooplankton and benthos during early life (Bergman and Greenberg 1994). This species often must compete with the zooplanktivorous roach (*Rutilus rutilus*) and benthivorous ruffe (*Gymnocephalus cernuus*) during early ontogeny. Competition reduces the body size of perch, potentially increasing the susceptibility of this species to predation and first-winter mortality. Bystrom and colleagues (1998) suggest that the importance of these mortality mechanisms varies with latitude. Growth adaptations among these widely distributed assemblages should modify interactions and thereby merit exploration.

The potential tradeoffs between energetic adaptations to environmental conditions and biotic interactions within widely distributed communities are not restricted to fish assemblages. Myriad size-structured interactions occur in both terrestrial and aquatic systems dominated by poikilotherms. Many species of widely distributed frogs must contend with predation when snakes, particularly the geographically cosmopolitan garter snake (*Thamnophis* spp.), prey on individuals transforming from the larval to the terrestrial life stage (Wassersug and Sperry 1977). If development time and growth decline with increasing latitude, frogs within northern assemblages should be more susceptible to predation. However, it is not unfeasible that these northern individuals may adjust growth rates and developmental schedules to increase the probability of winter survival while simultaneously reducing predation risk, although the relevant tradeoffs remain unexplored. Competitive interactions among amphibian larvae and cannibalism within salamander species (Wilbur 1997) are also quite likely to be affected by growth

adaptations along broad environmental gradients. Hence, any community affected by interactions that depend on size and life stage should be quite sensitive to the relative adaptations of component species to environmental and biotic constraints that covary with latitude.

Conclusions

Variation among populations in average reaction norms, particularly those that affect plasticity in growth rates during the first year of life, should have broad implications for assemblages dominated by widely distributed poikilotherms. Other models of community assembly generally provide insight at local or regional scales and may consider phenotypic plasticity in responses and effects (Peacor and Werner 2001). To understand variation in species interactions throughout their overlapping ranges, researchers must focus on variation in individual growth responses as affected both by plasticity and by broad selective patterns. An understanding of energetic adaptations is necessary for predicting how community structure varies among years and among broadly distributed systems. Only by explicitly quantifying the genetic and environmental components of growth of species within communities through carefully designed common-garden and reciprocal transplant experiments can we understand how species interactions vary along a latitudinal gradient (Fauth 1998). Approaches such as dynamic programming and individual-based modeling also can lend insight into the optimal behavioral and physiological decisions underlying patterns of growth and assemblage structure.

The relative importance of biotic interactions and first-winter survival along a latitudinal gradient is a useful initial organizing principle for future research exploring variation among communities. At southern latitudes, biotic interactions may constrain growth rates of young poikilotherms. Selection for growth rates that reflect the tradeoffs between growth and other phenotypic characteristics should be quite important. At northern latitudes, rapid first-year growth is necessary to ensure that body sizes are sufficiently large to survive winter. Hence, selection for rapid growth even at the cost of relatively greater predation risk may occur. Because the growth of predators or competitors is compromised relatively more by the truncated growing season and reduction in temperature, we should expect relatively stronger selection for rapid growth rates in northern systems. Conversely, if predation intensity declines with increasing latitude, as has been suggested for many systems, then again we would see an increased benefit of rapid growth with increasing latitude.

The conservation or management of species often focuses on how contemporary processes affect populations or communities. An understanding of unique, species-specific energetic adaptations during early life is also necessary for predicting responses to human activities. For example, the applied field of fisheries management is characterized by uncertainty (Rice 1999), largely because of the strong effect of unpredictable early life history interactions on cohort size, population dynamics, and community structure. An improved

grasp of how energetic adaptations affect population and community responses will allow resource managers to develop specific actions depending on geographic location. A manager may find that resource issues in low-latitude systems require a very different suite of remedies than those at high latitudes. Because species interactions are tightly linked to environmental temperature, regional changes in seasonal temperature, such as those that will most likely occur with increased atmospheric carbon dioxide concentrations, may affect species in different ways, greatly altering community structure. As we improve our knowledge of temperature effects and local adaptations, options for widely distributed populations or communities may become more flexible, improving our ability to manage and conserve them.

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