

# Variation in intrinsic individual growth rate among populations of leatherside chub (*Snyderichthys copei* Jordan & Gilbert): adaptation to temperature or length of growing season?

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**Abstract** – Leatherside chub (*Snyderichthys copei* Jordan & Gilbert) comprises two lineages (northern and southern) whose centres of geographical range differ by about 3° latitude corresponding to about 30% shorter growing season and about 2 °C lower mean temperature during the growing season. We document patterns of variation in size-at-age among populations of leatherside chub in nature, and we test for variation in intrinsic growth rate of juvenile chub in a common-environment experiment to determine if lineages exhibit different intrinsic growth rates. Northern leatherside chubs at ages 1–3 were about 15% shorter in length compared with southern populations. Variation in hatching date or age at maturity could not account for differences in growth and body size, suggesting that temperature-specific intrinsic growth rates differed among populations. Based on a common environment experiment, we found that reaction norms for temperature-specific growth in length and mass were crossed. At the lower temperature, individuals from the north exhibited higher intrinsic growth in length, and at the higher temperature individuals from the south exhibited higher intrinsic growth in mass. Crossing reaction norms for temperature-specific intrinsic growth rates support a model of local adaptation to thermal regime.

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**Key words:** body size variation; ectotherm; indeterminate growth; temperature-specific growth

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**Un resumen en español se incluye detrás del texto principal de este artículo.**

## Introduction

The study of variation in individual growth rates within and among populations has received remarkably little attention compared with other life-history traits (Conover & Schultz 1995; Arendt 1997). One reason for this lack of study is the perception that variation in intrinsic individual growth rates (i.e., genetically based variation) is negligible in ectotherms. The argument is that, given the well-docu-

mented benefits of large body size for ectotherms (e.g., greater fecundity, higher reproductive success and lower risk of mortality; Wootton 1985; Miller et al. 1988), selection should always favour rapid growth resulting in uniformly high intrinsic individual growth rates among populations within a species (see arguments in Schultz et al. 1996). Accordingly, variation in body size among populations is usually assumed to result almost completely from variation in environmental factors that decrease potential growth rates,

such as, temperature or resource availability (Arendt 1997). However, recent work has documented widespread variation in intrinsic growth rate in some ectothermic species (Conover & Present 1990; Gotthard et al. 1994; Arendt & Wilson 1997).

Latitudinal gradients in temperature and length of growing season produce one of the most consistent and pervasive environmental patterns affecting growth of ectotherms (Belk & Houston 2002). Two competing models exist to explain the evolution of variation in intrinsic growth rates across a latitudinal gradient. The first model, referred to as thermal adaptation, predicts that intrinsic growth rates will be adapted to the local thermal regime (Levinton 1983). For example, organisms found at higher latitudes and consequently experiencing lower mean temperatures would exhibit higher intrinsic growth rates at lower temperatures relative to organisms from lower latitudes, and vice versa. Organisms would exhibit the highest growth rates at temperatures similar to those in their native environment. This model predicts crossing reaction norms for temperature-specific growth rates among populations experiencing higher or lower average temperatures.

The second model predicts adaptation to shorter growing seasons at higher latitudes (rather than lower temperatures) and is characterized by counter-gradient variation for growth (Conover & Present 1990). Counter-gradient variation (Conover & Schultz 1995) is characterized by evolution of relatively high intrinsic growth rates in environments that have strong negative effects on growth. For example, relatively short growing seasons at higher latitudes enhance selection for large body size, and consequently select for rapid intrinsic growth rates in northern relative to southern populations. This model predicts parallel reaction norms for temperature-specific growth rates among populations experiencing longer or shorter growing seasons (Conover & Present 1990).

To clearly understand the generation and maintenance of patterns of geographical variation in growth rates and to test the generality of the two models described above, it is important to document variation in species from varied habitats and geographical locations. Patterns of geographical variation in intrinsic growth rates across latitudes have been clearly documented in several marine fish species (e.g., *Menidia menidia* L., Atlantic silversides, Conover & Present 1990; *Fundulus heteroclitus* L., Atlantic herring, Schultz et al. 1996; and *Morone saxatilis* Walbaum, striped bass, Conover et al. 1997). One could argue that effects of latitude should be even more pronounced in continental freshwater fishes. Continental climates exhibit greater variation and reach greater extremes than maritime climates resulting in stronger selection on growth rates. In addition,

populations of freshwater fishes are typically more fragmented and isolated compared with marine species, preventing the potentially homogenizing effects of dispersal and gene flow. Thus, we expect rapid evolution of adaptive variation in intrinsic growth rates in freshwater species; however, few studies have addressed this topic.

To describe patterns of geographical variation in intrinsic growth rate in a freshwater species, we chose a fish species with a highly fragmented distribution that occurs in habitats that experience extreme seasonal variation in environment. The leatherside chub, *Snyderichthys copei* (previously *Gila copei*), is a small cyprinid fish that occurs in the Bonneville Basin and upper Snake River drainage of western North America. Previously, all populations of leatherside chub were believed to represent a cohesive species with no obvious differences among populations (Wilson & Belk 2001). However, recent phylogenetic analysis based on mtDNA gene sequences (cyt B) suggests that leatherside chub comprises two distinct lineages. Specifically, populations located in northern Utah, southern Idaho, and southern Wyoming make up one distinct lineage, and populations located in central and southern Utah make up another (Johnson & Jordan 2000; Dowling et al. 2002). Populations composing these two lineages are geographically isolated in separate drainage basins connected only by the uninhabitable Great Salt Lake. Centres of geographical range for the two lineages differ by about 3° latitude resulting in shorter growing season and lower mean temperatures for the northern lineage (Table 1).

We describe patterns of variation in size-at-age among populations of leatherside chub, and we test for variation in intrinsic growth rate of juveniles between populations. Results suggest genetically based variation for growth among lineages of leatherside chub, but patterns of temperature-specific growth contrast with those described for marine species. Our data support a thermal adaptation model of evolution of variation in intrinsic growth rate.

Table 1. Latitude, elevation, mean stream temperature (SD) during the growing season and mean cumulative degree days (SD) in the growing season (above 8 °C) at two locations where leatherside chub were collected for comparison of field growth rates.

Location	Sulfur Creek, WY (north)	East Fork Sevier River, UT (south)
Latitude	41°07'N	38°12'N
Elevation	2200 m	1850 m
Mean stream temperature during growing season	11.4 °C (5.7)	13.6 °C (4.8)
Mean cumulative degree days	1062 (380)	1595 (143)
Mean cumulative degree days (first year)	812 (266)	1094 (86)

## Materials and Methods

To determine differences in growth rate and environment between northern and southern lineages, we selected two locations representing the latitudinal extremes of the species distribution (locations 3 and 6 in Fig. 1, Table 1). We used water temperature profiles collected at United States Geological Survey gauging stations located within 1 km of the sample location for the years 1982–1991 to characterize environmental variation. From these data we calculated mean temperature during the growing season and estimated length of growing season. We did not use data from 1989 and 1990 for the northern location because they were incomplete. We used cumulative degree days above the minimum temperature for growth of leatherside chub (estimated as 8 °C from laboratory growth experiment) as a measure of growing season length. For fish in their first year, we calculated mean length of growing season starting from the mean

hatch date. For fish in their second and third years, we used data from the entire growing season.

To determine body size variation in the field, we collected 50 leatherside chub in autumn 1995 from each of the two locations identified above (Fig. 1). Fish were collected with the use of a backpack electroshocker. Leatherside chub was common, and the fish community comprised the same species at both locations (co-occurring species included mountain sucker, *Catostomus platyrhynchus* Cope, speckled dace, *Rhinichthys osculus* Girard, mottled sculpin, *Cottus bairdi* Girard, reidside shiner, *Richardsonius balteatus* Richardson, and introduced brown trout, *Salmo trutta* L.).

As body size depends on time of hatching and subsequent growth rates, fish collections made at each site were designed to estimate both hatching date and annual growth rates. To estimate hatching date, we collected 10 individuals that were <1 year old at each site. The remaining 40 individuals collected were ≥1 year old and were used to determine annual growth rates. In addition to the two primary collecting sites, we collected about 10 individuals <1 year old from three other sites (locations 1, 4 and 5 in Fig. 1), to facilitate comparison of estimated spawning date with latitude.

To estimate body size at previous ages and annual growth rates we measured standard length (mm) and mass (g), determined reproductive status, and removed otoliths (lapilli) for each fish. We estimated individual age and standard lengths at previous ages from otoliths according to validated methods described in Johnson et al. (1995). We compared estimated standard length at 1–3 years of age between locations by a nonparametric two-sample test (Wilcoxon rank sum test; SAS 1990), because sample values were not normally distributed.

We estimated hatch dates from counts of daily rings on otoliths from individuals <1 year old. We thin-sectioned otoliths, and used a Zeiss Axiophot MC100 microscope (Zeiss, Göttingen, Germany) at 1000× magnification to count daily rings according to methods described by Brothers (1987). We subtracted estimated age in days from capture date to determine hatch date. To test for a relationship between date of hatch and latitudinal location we regressed hatch date on latitudinal location (SAS 1990).

Body size may also be influenced by differences in age at maturity. To determine if differences in age at maturity influenced differences in growth rate between northern and southern populations, we determined the percent of individuals mature in each age class. If the population that exhibits smaller body size matures at younger ages, then lower growth rates could be caused by allocation of energy to reproduction rather than direct environmental effects on growth or differences in intrinsic growth rates. However, if age at maturity does not differ between populations or if maturity is delayed in the population with smaller body sizes, then

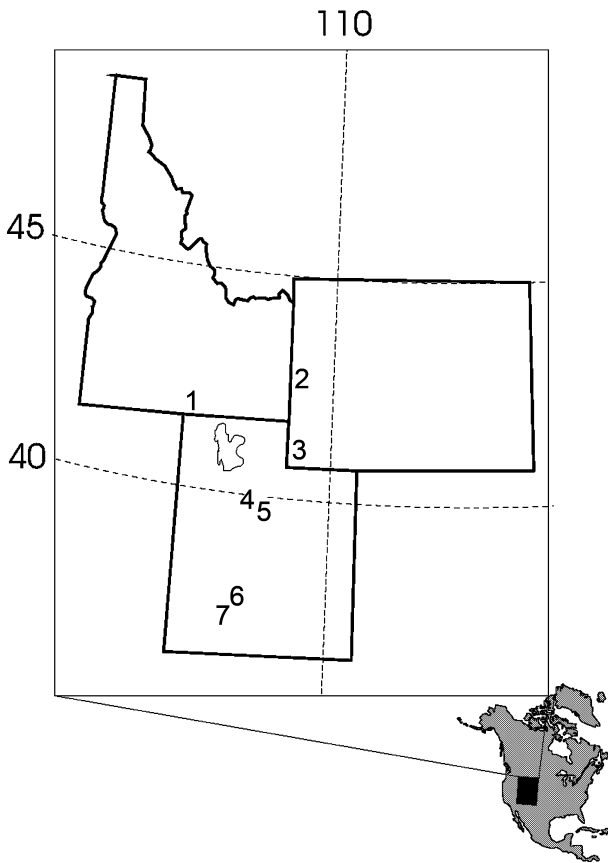


Fig. 1. Geographical locations of collections for determining field growth rates (3 and 6; Sulfur Creek, Uinta Co., Wyoming, and East Fork Sevier River, Piute Co., Utah), additional sites for determining hatch dates (1, 4 and 5; Beaverdam Creek, Cassia Co., Idaho, Diamond Fork, Utah Co., Utah, and Thistle Creek, Utah Co., Utah), and for common-environment experiments (2 and 7; Smith's Fork, Bear River, Lincoln Co., Wyoming, and Sevier River near Panguitch, Garfield Co., Utah).

allocation to reproduction cannot explain differences in body size.

To test for genetically based variation in temperature-specific growth rates, we used fish from the latitudinal extremes of the species distribution in a common-environment experiment. Leatherside chub typically mature at age 2 (Johnson et al. 1995), and some may mature at age 1+ (in the second summer, this study). To avoid confounding growth rate with energy allocated to reproduction, we used individuals in their first summer from both locations for the experiment ( $n = 80$  from each location; locations 2 and 7 in Fig. 1). We collected fish by seining or electroshocking during autumn 1998, transferred fish to 196 l aquaria in the laboratory, and acclimated fish to room temperature (19 °C) for 3 weeks.

We measured temperature-specific growth at 10 and 19 °C. These temperatures represented conditions expected to produce slow and fast rates of growth, and both temperatures are commonly experienced by leatherside chub in nature during the growing season. The experiment followed a full factorial design with fish from two locations crossed with two temperature levels resulting in four treatment combinations. Forty individuals were assigned to each treatment combination.

During the experiment, individual fish were housed in an array of 1 l plastic containers placed in a common tank. The bottom of the container was removed and we used a silicone adhesive to glue the container to a 3 mm plastic mesh. Eighty containers were attached to the mesh in this manner, and we placed the entire array into a 1200 l aerated tank. We filled the tank with water until individual containers were about three-fourths full. This design allowed subjects to be housed individually, but maximized uniformity in water temperature and chemistry among individuals within tanks because water could flow in and out of individual containers through the mesh bottom. Ambient water temperature was 19 °C, providing one of the temperature treatments, and we used a water cooler to maintain temperature at 10 °C for the other treatment.

To begin the experiment, we measured mass and standard length, and randomly assigned individuals to treatments in the following way. First, we randomly selected an individual by location of origin (north or south) and then measured wet mass to the nearest milligram in a tared Petri dish containing a small amount of water. We then placed individuals in a shallow bowl containing water (2 cm depth) and a measurement scale, for calibration, and used a Panasonic AG-EZ1 digital camcorder (Panasonic, Cypress, CA, USA) to record a video image of the dorsal view. We measured standard length from video images at a later time. Finally, we randomly assigned individuals to a temperature and placed them in an appropriate

container. For the first 2 weeks of the experiment, we replaced fish that died with new individuals.

We ran the experiment for 71 days (actual time individual fish were in the experiment varied from 57 to 71 days because of mortality and replacement of fish). During the experiment, we fed fish rations equal to about 10% of body mass daily (0.04 g) of commercial trout chow (45% protein; Sterling Silver Cup, Salt Lake City, UT, USA). Photoperiod was maintained at 12:12 L:D during the experiment.

At the end of the experiment, we measured length and mass as described above and calculated growth rates. As individuals used in the experiment were brought directly from the wild there is a possibility that prior growth experience and maternal effects (Panagiotaki & Geffen 1992; Chambers & Leggett 1996) may affect growth rates in addition to possible differences in intrinsic growth rates. Environmental effects (whether from maternal environment or other cues) typically are manifest in fish as differences in body size at a given age (Chambers & Leggett 1996; Brooks et al. 1997). To help understand the possible influence of this potentially confounding factor we used information about beginning length and mass in our analysis. Mean standard length at the beginning of the experiment did not differ between lineages ( $F_{1,138} = 0.68$ ,  $P = 0.41$ ; northern lineage  $0 = 28.8$  mm,  $SD = 3.36$ , southern lineage  $0 = 28.4$  mm,  $SD = 2.42$ ), but mean body mass did ( $F_{1,138} = 25.05$ ,  $P < 0.0001$ ; northern lineage  $0 = 0.392$  g,  $SD = 0.14$ , southern lineage  $0 = 0.298$  g,  $SD = 0.075$ ). To determine growth rates independent of the initial difference in mass, we calculated size-specific daily growth rate for length (mm gained during experiment/mm at beginning/days in experiment) and mass (g gained during experiment/g at beginning/days in experiment) as measures of growth during the experiment. We used ANOVA of these size-specific growth rates (length and mass) to compare differences in growth rates between location of origin and temperatures. Data from all four treatment combinations were normally distributed (based on Shapiro–Wilk statistic; SAS 1990), so we used raw growth rates as the response variable in the analysis. We used location of origin and temperature as main effects, and included a location by temperature interaction. We treated temperature as a random effect and location as a fixed effect. Finally, if environmental effects were important in the experiment, we would expect the lineage with the largest beginning mass (northern lineage) to exhibit higher growth rates at all temperatures relative to the other lineage. Such a pattern would provide evidence for a strong effect of prior growth experience. Other patterns of growth, such as greater growth by the lineage with the smaller beginning mass, or greater growth rates by a given lineage at only one temperature (i.e., crossing reaction

norms), would not be expected based on differences in initial mass.

## Results

The latitudinal difference between northern and southern locations produces clear differences in mean annual temperature and length of growing season. Mean monthly stream temperatures during the growing season were 1–5 °C lower (mean difference = 2.2 °C) at the northern location than at the southern location. On average, growing season was about 33% shorter (26% shorter for newly hatched fish) in the northern location than in the southern location (Table 1).

Body sizes of leatherside chub differ significantly between northern and southern locations (Wilcoxon rank sum test, year 1,  $Z = 3.32$ ,  $P = 0.0009$ ; year 2,  $Z = 3.41$ ,  $P = 0.0007$ ; year 3,  $Z = 2.90$ ,  $P = 0.0023$ ; Fig. 2). Leatherside chub from the northern location were about 15% smaller than fish from the southern location at ages 1–3. Estimated date of hatching varied widely within populations, but was not related to latitudinal location of a population ( $F_{1,33} = 0.82$ ,  $P = 0.317$ ). Mean hatch date for all populations combined was day 171 (SD = 17.8) corresponding to late June. Age at maturity is similar for both locations, with the majority of fish maturing at 2 years. in both locations (southern lineage: age 1 = 23%, age 2 = 71%, age 3 = 100%, age 4 = 100%; northern lineage: age 1 = 0%, age 2 = 78%, age 3 = 95%, age 4 = 100%).

In the common-environment experiment, mean daily gain in length varied significantly with temperature, and lineage, and there was a significant temperature by location interaction indicating a crossing reaction norm for size-specific gain in length across temperatures (Table 2). Fish from the northern loca-

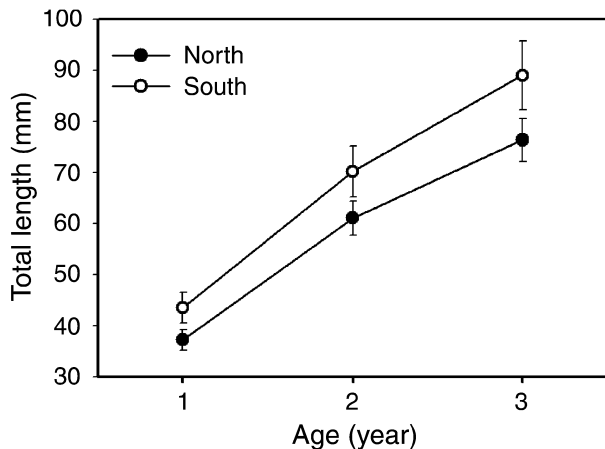


Fig. 2. Mean ( $\pm 2$  SE) total length (in mm) at ages 1–3 years for leatherside chub from northern and southern locations. Fish from both locations were collected in September to October 1995.

## Temperature-specific growth in leatherside chub

Table 2. Analysis of variance table for size-specific gain in length and mass by location of origin at two temperatures.

Source	d.f.	Mean squares	F-ratio	P-value
<b>Length</b>				
Location	1	0.0000081	6.78	0.0102
Temperature	1	0.000435	362.4	<0.0001
Location $\times$ temperature	1	0.0000048	4.03	0.047
Error	136	0.0000012		
<b>Mass</b>				
Location	1	0.000176	7.04	0.0089
Temperature	1	0.00752	300.9	<0.0001
Location $\times$ Temperature	1	0.0002	8.03	0.0053
Error	136	0.000025		

tion exhibited relatively higher size-specific gain in length at 10 °C compared with fish from the southern location. At 19 °C gain in length did not differ between lineages (Fig. 3a). Mean daily gain in mass

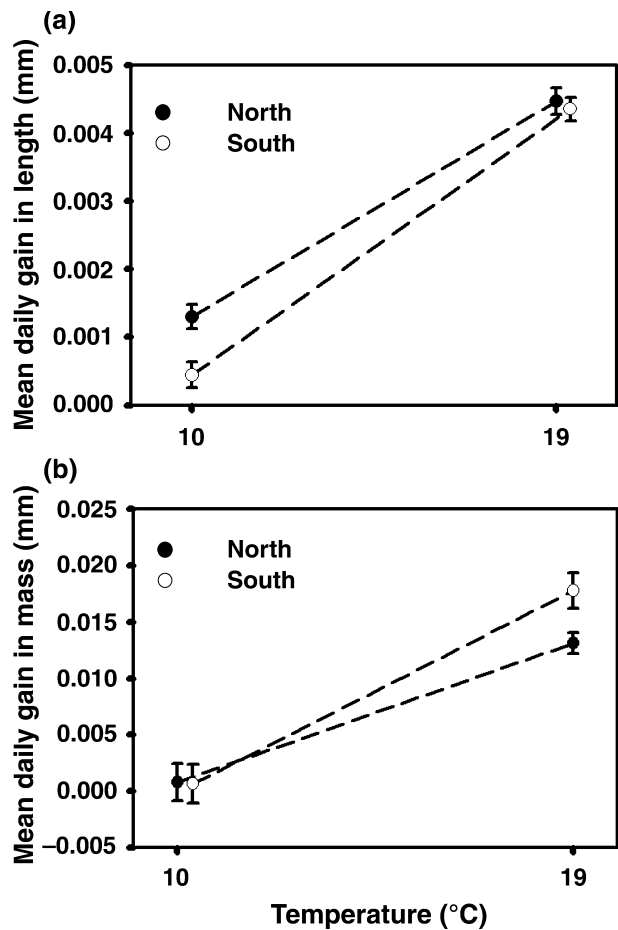


Fig. 3. (a) Mean ( $\pm 2$  SE) size-specific gain in length of individuals from northern and southern populations of leatherside chub at two temperatures in a common environment. (b) Mean ( $\pm 2$  SE) size-specific gain in mass of individuals from northern and southern populations of leatherside chub at two temperatures in a common environment. Dashed lines connecting means indicate a crossing reaction norm, but are not meant to represent actual growth rates between the two temperatures tested in the experiment.

also varied significantly with temperature and lineage, and there was a significant temperature by location interaction indicating a crossing reaction norm for size-specific growth in mass across temperatures (Table 2). Fish from the southern location exhibited relatively higher size-specific gain in mass at 19 °C compared with fish from the northern location. At 10 °C gain in mass did not differ between lineages (Fig. 3b). Patterns of growth between lineages are not consistent with an environmental effect caused by differences between locations in mass at the beginning of the experiment. Fish from the northern location had greater mass (but not length) compared with the southern location at the beginning of the experiment; however, the northern lineage exhibited higher growth in length only at the lower temperature. Similarly, fish from the southern location (lower beginning mass) exhibited higher growth in mass at the higher temperature.

## Discussion

In ectotherms with indeterminate growth, body size at a given age results from the interaction of hatch date, growth rate, age at maturity, and environmental conditions. Differences in body size between lineages of leatherside chub are not proportional to differences in growing season between the two sampling locations. Lineages do not exhibit large differences in hatch date or age at maturity. Thus, the departure in body size from that expected based on differences in growing season suggests differences in intrinsic growth rates among lineages. Common-environment experiments performed in this study confirm that lineages of leatherside chub exhibit differences in temperature-specific growth rates.

How do patterns of temperature-specific growth in leatherside chub compare with other species of fish that exhibit geographical variation in growth? In Atlantic silversides (*Menidia menidia*) and striped bass (*Morone saxatilis*) populations from higher latitudes exhibit higher intrinsic growth rates at all temperatures; i.e., parallel norms of reaction for temperature-specific growth rates among populations (Conover & Present 1990; Conover et al. 1997). In mummichog (*Fundulus heteroclitus*) populations from higher latitudes exhibit faster intrinsic growth rates at higher, but not lower temperatures (Schultz et al. 1996). Patterns of temperature-specific growth in these three species are counter-gradient, and support a model of adaptation to shorter growing seasons at higher latitudes.

In contrast, leatherside chub exhibit crossing reaction norms. Individuals from the relatively colder location have relatively higher growth rates at the colder temperature, and conversely, individuals from

the relatively warmer location have relatively higher growth rates at the warmer temperature. Crossing reaction norms support the thermal adaptation model of evolution of geographical variation in growth rate (Levinton 1983; Conover & Schultz 1995).

Adaptation to local conditions can be impeded by high rates of gene flow among populations. Currently, the Great Salt Lake provides a barrier to gene flow between the northern and southern lineages of leatherside chub. However, in recent geological time there have been several potential opportunities for mixing of the two lineages. Lake Bonneville existed prior to about 10 000 years BP (Grayson 1993). The lake provided a freshwater connection between the Bear River drainage inhabited by the northern lineage and the Utah Lake and Sevier drainages inhabited by the southern lineage. In addition, 14 500 years ago Lake Bonneville flooded catastrophically northward into the Snake River (Grayson 1993). This flood would have allowed opportunity for gene flow between lineages. Events such as these probably occurred multiple times during the Pleistocene. However, despite water exchange between basins, mtDNA data provide no evidence for gene flow between the two leatherside chub clades (Johnson & Jordan 2000). This suggests populations have had considerable time to evolve and maintain local adaptations in intrinsic growth rates.

Although there is a possibility for prior growth experience and maternal effects (Panagiotaki & Geffen 1992; Chambers & Leggett 1996) to affect growth rates in our common-environment experiment, the pattern of temperature-specific growth rates in our common-environment experiment are not consistent with a strong effect of prior environment. The expected influence of prior growth experience or maternal effect in one lineage would be increased growth rates at all temperatures relative to the other lineage. In contrast, the pattern of crossing reaction norms (in both gain in length and gain in mass), and the result that the lineage with the lower beginning mass exhibited greater growth in mass at the higher temperature is not consistent with a large effect of pre-experimental environmental conditions. Hence, our findings appear to reflect genetically based differences in growth rate between locations.

The pattern of growth rate between lineages differs depending on whether we measure growth in length or mass (Fig. 3). Although both patterns represent crossing reaction norms, and are consistent with the thermal adaptation model, it is puzzling that the pattern would differ between length and mass. These data do not provide information that would allow us to determine why growth patterns might differ between length and mass; however, they do suggest the possibility that growth in length and mass may be somewhat uncoupled, and that lineages may differ in

the propensity to increase in length or mass under favourable conditions.

Field growth data are based on two locations, and the common-environment experiment included fish from two different locations; however, these data may not represent variation among all populations of both lineages. In fact, our data suggest the possibility that each population might exhibit intrinsic growth rates that are adapted to local temperature regimes. Given that the northern lineage generally experiences cooler water temperatures compared with the southern lineage, the pattern we observed (northern lineage shows greater growth at low, but not higher temperatures) may be representative of both lineages as a whole, but further work is required to determine the generality of the pattern.

In summary, patterns of both body size in the field and growth in a common-environment suggest that the two lineages of leatherside chub exhibit genetically based differences in intrinsic growth rates. In contrast to other species of fish, the pattern of variation in temperature-specific growth rates among lineages of leatherside chub supports the thermal adaptation model of the evolution of geographical variation in growth rate. Greater isolation among populations of freshwater fishes compared with marine species may increase the likelihood of adaptation to thermal regime. However, generalizations about patterns of adaptation in marine versus freshwater systems will require studies of several species in each environment.

## Resumen

1. Gradientes latitudinales en temperatura y longitud de la estación de crecimiento producen uno de los patrones más consistentes y permeables que afectan al crecimiento de ectodermos (Belk & Houston 2002). Hay dos modelos que compiten entre sí para explicar la evolución de la variabilidad en las tasas intrínsecas de crecimiento a lo largo de gradientes latitudinales. El primer modelo se refiere a adaptaciones térmicas y predice que las tasas intrínsecas de crecimiento están adaptadas al régimen térmico local (Levinton 1983). El segundo modelo predice adaptaciones a estaciones de crecimiento más cortas en latitudes más altas (más que a temperaturas inferiores) y se caracteriza por contra-gradientes de variación en el crecimiento (Conover & Present 1990). Para entender con claridad la generación y mantenimiento de patrones de variación geográfica en las tasas de crecimiento y analizar la generalidad de ambos modelos es importante documentar variación en las especies en una variedad de hábitats y localidades geográficas.

2. Para describir patrones de variación geográfica en las tasas intrínsecas de crecimiento en peces de agua dulce, elegimos una especie de pez con una distribución muy fragmentada que ocurre en hábitats que sufren extremos estacionales de variación ambiental. *Snyderichthyes copei* (previamente *Gila copei*) es un ciprínido pequeño que ocurre en la cuenca del río Bonneville y en la zona superior de río Snake (Occidente de América del

Norte). Análisis filogenéticos recientes basados en secuencias génicas de mtDNA (cyt b) han sugerido dos linajes distintos para la especie. Los centros de los rangos geográficos para los dos linajes difieren en unos 3 grados de latitud resultando en menores estaciones de crecimiento y menores temperaturas medias para el linaje del norte (Table 1). Describimos patrones de variación en el tamaño-a-edad entre poblaciones de *Sn. copei* y analizamos variaciones en las tasas intrínsecas de crecimiento entre poblaciones basados en un experimento de jardín-común. 3. Las temperaturas medias mensuales de los ríos durante la estación de crecimiento fueron 1–5 °C menores (diferencia media = 2.2 °C) en la localidad del norte respecto de la del sur. De promedio, la estación de crecimiento fue 33% más corta (26% más corta para los peces recién emergidos) en la localidad del norte que en la del sur (Table 1). *Sn. copei* de la localidad del norte fueron sobre un 15% más pequeños que los de la localidad del sur a las edades 1–3 años (Fig. 2). En un experimento de jardín-común, las ganancias diarias medias en longitud y peso variaron significativamente con la temperatura y con el linaje y hubo una interacción temperatura × localidad significativa que indicó una norma de reacción cruzada para la temperatura-crecimiento específico en longitud y peso (Tabla 2, Fig. 3).

4. En resumen, los patrones de tamaño corporal en el río y el crecimiento en un ambiente-común sugiere que ambos linajes de *Sn. copei* muestran tasas de crecimiento intrínseca de base genética. En contraposición a otras especies de peces, los patrones de variación en las tasas de crecimiento específicas de la temperatura entre linajes de *Sn. copei* soportan el modelo de adaptación térmica en la evolución de variaciones geográficas en las tasas de crecimiento. Un mayor aislamiento entre poblaciones de peces de agua dulce comparado con especies marinas puede incrementar la probabilidad de adaptación al régimen térmico. Sin embargo, generalizaciones sobre estos patrones de adaptación en sistemas marinos versus agua dulce requerirá de estudios sobre varias especies en cada ambiente.

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