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Intrastream variation in growth rates and time of first otolith increment formation for young of the year *Etheostoma simoterum* (Cope) (Perciformes: Percidae)

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Growth rates and otolith-estimated hatching dates of young of the year *Etheostoma simoterum* were studied at four localities along an elevational gradient in the Little River, Tennessee, U.S.A. during the summer of 1983. Changes in otolith increment width and mean daily air temperature corresponded well with each other, suggesting that increments were laid down daily. Growth rate increased nearly threefold from the highest elevation site to the lowest. Median otolith-estimated hatching dates differed by about 2 weeks between sites, and the pattern was not directly related to elevation. These data indicate that within-stream, life-history variation of a broadly distributed species should be taken into consideration when studying factors regulating stream fish populations along elevational gradients.

Key words: elevational gradients; streams; otolith; growth; hatching; *Etheostoma simoterum*.

I. INTRODUCTION

The characteristics of populations, such as growth and population size, vary in time and space. For fishes, early life-history studies are important for understanding the causes of this variation (Rothschild *et al.*, 1982). Most studies of early life-histories of fishes have been directed at commercially important or sport fishes, whereas relatively few have been directed at other species.

In streams, biotic and abiotic factors change along a stream course. Several studies have suggested that upstream areas are characterized by stochastic effects of climatic variation and abiotic limitation, whereas downstream areas are more stable and biotic interactions are more important (Horwitz, 1978; Schlosser, 1982, 1987). Few studies, however, exist that have examined how fish populations change along a stream's course (but see Matthews & Styron 1981; Anderson, 1985). As a first step in examining this problem, we asked, ' How much variation do we see in the growth and time of hatching (approximated as time of first increment formation) in a single species that has a broad longitudinal distribution? ' This question was addressed by enumeration of otolith increments, which are known to be daily in a number of fish species (Pannella, 1971; Brothers *et al.*, 1976; Gjosaeter *et al.*, 1984; Campana & Neilson, 1985). The study species was *Etheostoma simoterum* (Cope), the snubnose darter (Family: Percidae), a species reaching adult sizes of 40–70 mm S.L. and found in the Cumberland and Tennessee River systems of Tennessee, Virginia and Kentucky, U.S.A. (Lee *et al.*, 1980). Only the young of the year were studied.

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II. MATERIALS AND METHODS

Young of the year *E. simoterum* were collected in the Little River, located in eastern Tennessee, U.S.A. The Little River originates as three tributaries, which join just inside the boundary of the Great Smoky Mountain National Park. The river then flows in a westerly direction towards Maryville before swinging north towards Knoxville. The most upstream site, site 1 (elevation 378 m; 35°38′02″N, 84°40′62″W), was located in the Middle Prong, one of the Little River's tributaries, near the Tremont Ranger Station about 1·6 km upstream of its confluence with the Western Prong. Site 2 (elevation 337 m; 35°39′55″N, 84°42′49″W) was located just inside of the boundary of the park, about 0·5 km downstream of the confluence of the Western and Eastern Prong. It was 2·5 km downstream from site 1. Site 3 (elevation 308 m; 35°41′01″N, 84°47′42″W) was located in Townsend, just north of Kinzel Springs, about 10 km downstream of site 2. Site 4 (elevation 275 m; 35°45′02″N, 84°50′19″W) was located at the mill dam in Melrose, about 12 km downstream of site 3. Stream widths at sites 1 to 4 were approximately 7–14, 21–31, 22–30 and 18–40 m respectively.

Eight to 19 fish (mean = 14·2, S.D. = 3·0) were collected from each site on 4 or 6 July, 31 July or 3 August and 21 August 1983. All fish were collected with handnets while snorkelling and immediately preserved in 95% ethanol. In the laboratory, the length of the fish (S.L.) was measured. No correction was made for shrinkage; instead, we assumed that shrinkage was a constant proportion for all fish. The otoliths (sagittae, lapilli and asterisci) were removed from the fish with dissecting needles and placed in a drop of immersion oil on a microscope slide. Although increments were wider in the sagittae, rings were counted from the lapilli owing to their round shape, which facilitated counting. The lapilli from the smaller fish were examined without additional preparation. The lapilli from the larger fish were ground by hand on a glass plate with Carborundum 600 grit. This procedure thinned the otolith and allowed us to view more easily all of the increments, from the core to the margin. A final polish with 3 μm diamond compound minimized surface irregularities and roughness. Lapilli were viewed at a magnification of 1000 to 2700 ×, using a compound light microscope adapted for video viewing. Increment counts and measurements were made off the video monitor.

To determine whether the rings that we counted were daily, a validation study was conducted in 1988. Fish were collected from the river, subjected to a sharp temperature rise in aquaria, put in an enclosure in the stream, and then recaptured and subjected to the same temperature rise. We planned to count the number of rings between two temperature induced otolith marks (Brothers, 1990). Unfortunately, a heavy rainstorm, producing high water occurred after several days, nearly destroying the enclosure. Only two fish were recovered, and the rings after the first temperature shock were not countable. We also collected five fish from the river on 16 July, the day the fish from the enclosure were sacrificed, and all seven fish were preserved in 95% ethanol. For three of the five fish, all otolith increments were measured to the nearest μm. The width of each increment was divided by the otolith's radius (relative otolith increment width), and then plotted against mean daily air temperature obtained from National Oceanic and Atmospheric Administration's weather station, Knoxville WSO AP, located about 25 km NE of the area where the validation study was conducted.

III. RESULTS

VALIDATION STUDY

Examination of the otoliths of all seven fish revealed a distinct mark consisting of two optically dense increments that, based on counting back from the margin, should have been laid down around 11–12 June (Fig. 1). Temperature and rainfall data for June and July showed that the only substantial amount of precipitation occurred on 9–11 July, and air temperature at this time decreased rapidly (Fig. 2). We also compared daily changes in air temperature with daily changes in relative

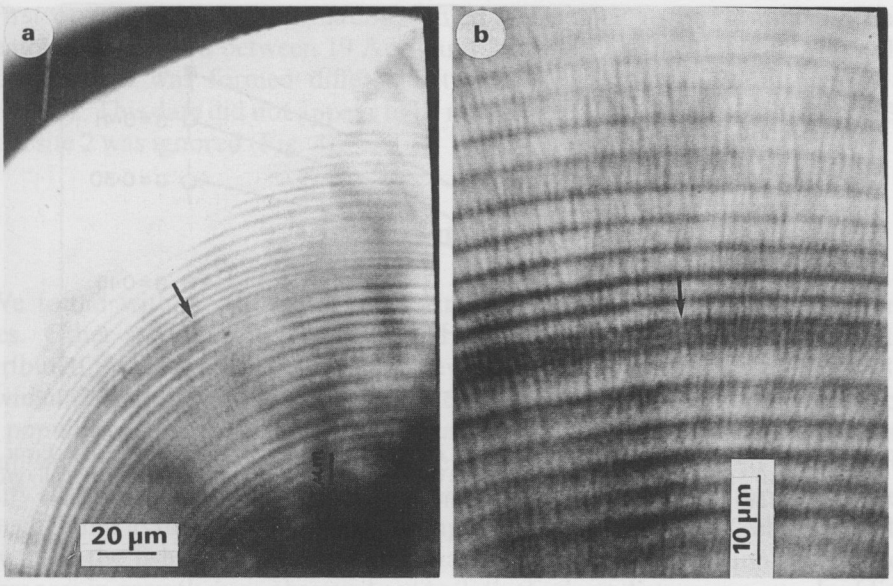

FIG. 1. Photographs of video image showing distinct mark (indicated by arrow) formed in otoliths (lapilli) of two fish around 11–12 June 1988. Photographs are of (a) a 29 mm and (b) a 31 mm S.L. fish. Scale bar is 20 µm for (a) and 10 µm for (b).

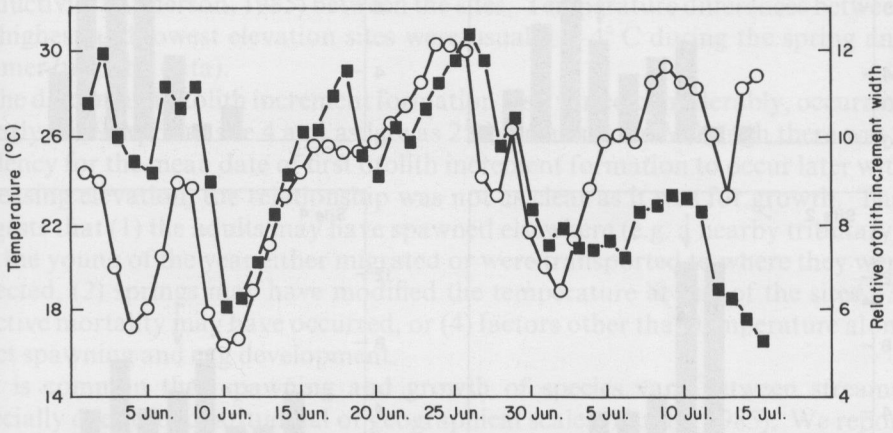

FIG. 2. Relationship between relative otolith increment width (10 × otolith increment width/otolith radius) averaged for three fish and mean daily air temperature (° C) in June and July 1988. ○, temperature, ■, relative otolith increment width.

otolith increments (Fig. 2) and found good correspondence ($r = 0{\cdot}62$, $n = 44$, $P < 0{\cdot}01$), further suggesting that the increments were daily.

GROWTH AND DATE OF FIRST OTOLITH INCREMENT FORMATION

The mean size of the fish differed between the four sites at each of the samplings (ANOVA, $P < 0{\cdot}004$ in all cases). Moreover, the differences between sites increased with time (difference was 3·6 mm in early July, 13·0 mm in early August and

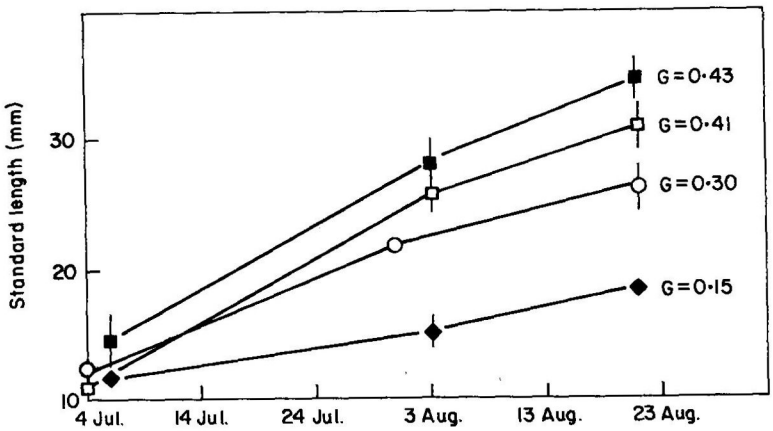

FIG. 3. Mean size (mm S.L.) of fish at three points in time during summer 1983 at sites 1–4. Error bars represent 0·5 S.D.; where not visible, the errors were smaller than the symbols. 'G' is the daily growth rate (mm day^{-1}) over the entire period at each site. ◆, Site 1; ○, site 2; □, site 3; ■, site 4.

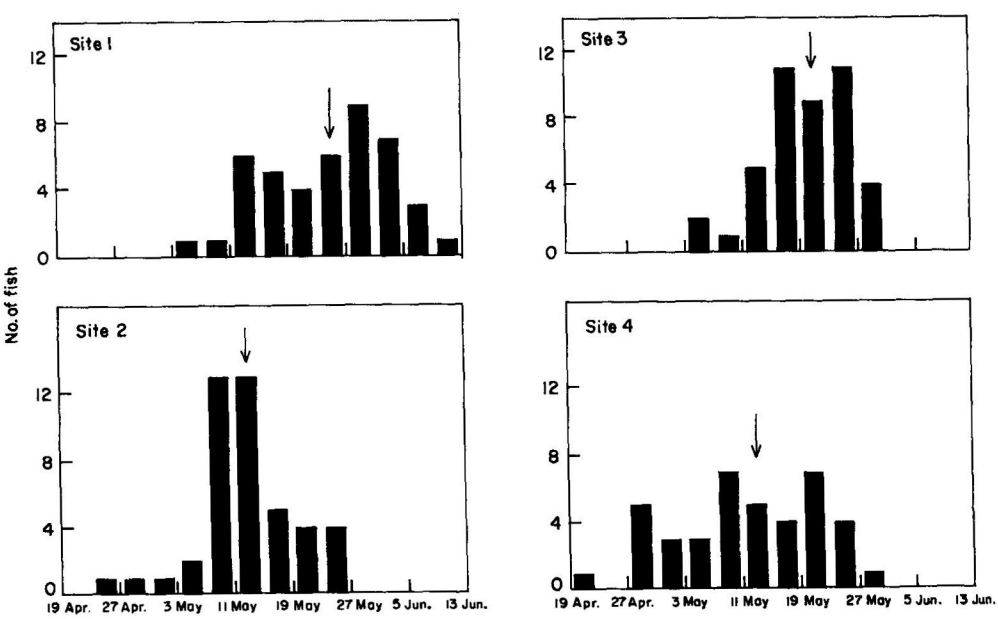

FIG. 4. The number of fish *v.* the dates when the first otolith increment was formed during summer 1983. Arrows indicate median date.

16·0 mm in late August; Fig. 3). Examination of the daily growth rate (mm day^{-1}) of the fish showed that growth decreased with increasing elevation (Regression, $F_{1,2}=23{\cdot}4$, $P=0{\cdot}04$). Furthermore, at site 1, the growth rate was higher in August than in July, whereas at the other three sites the growth rate was higher in July than in August (Fig. 3).

First otolith increment formation, which is assumed to be around the time of hatching, occurred between 19 April and 25 June. The median date when the first increment was formed differed between sites (Kruskal–Wallis, $H = 53{\cdot}4$, $P < 0{\cdot}005$). This date did not appear to be related to elevation (regression, $P > 0{\cdot}3$), unless site 2 was ignored (Fig. 4).

IV. DISCUSSION

We found within-stream differences in growth rate and estimated hatching dates. Other studies have also reported within-stream differences for broadly distributed fishes (Allen, 1951; Matthews & Styron, 1981; Anderson, 1985; Newman & Waters, 1989). Such differences can have profound consequences on fish populations. Growth is a fundamental property of individuals that affects an organism's reproductive potential, susceptibility to predators and competitive ability (Werner & Gilliam, 1984; Luecke *et al.*, 1990). Growth, in turn, is affected by such things as food availability and temperature (Weatherley & Gill, 1987). The growth of the fish in this study was negatively related to elevation, and major differences in growth were observed over relatively short distances, e.g. a doubling of growth occurred between sites 1 and 2, a distance of only 2·5 km and a difference of 41 m in elevation. On the other hand, sites 3 and 4 were 12 km apart and differed by 33 m in elevation, but growth rate only increased 5%. These differences in growth are probably related to elevational differences in temperature and stream productivity (Anderson, 1985) between the sites. Temperature differences between the highest and lowest elevation sites were usually 3–4° C during the spring and summer (unpubl. data).

The date of first otolith increment formation also varied considerably, occurring as early as 19 April at site 4 and as late as 25 June at site 1. Although there was a tendency for the mean date of first otolith increment formation to occur later with increasing elevation, the relationship was not as clear as it was for growth. This suggests that (1) the adults may have spawned elsewhere (e.g. a nearby tributary), and the young of the year either migrated or were transported to where they were collected, (2) springs may have modified the temperature at one of the sites, (3) selective mortality may have occurred, or (4) factors other than temperature alone affect spawning and egg development.

It is common that spawning and growth of species vary between streams, especially over broad latitudinal or geographical scales (Hubbs, 1985). We report rather large differences in growth and ' hatching ' over extremely short distances. The consequences of such differences need to be integrated into our current ideas of species interactions and the forces that shape stream fish communities along elevational gradients.

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