

Age and growth of the fallfish *Semotilus corporalis* with daily otolith increments as a method of annulus verification

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Daily increments were found in the otoliths of the fallfish *Semotilus corporalis* from three stream populations in central New York. By counting these increments one can verify annual marks and validate other less precise methods of aging. Results suggested that a false first annulus was observed in the only previous study of fallfish age and growth. Annual growth in length is shown to be linear. All three populations' growth rates were significantly different. Furthermore, the difference among these local populations can account for much of the variability in the rate of growth exhibited throughout the species' range. It is therefore proposed that the nature of the local habitat, in particular the size of the stream and the density of conspecifics, may be the major determinant of the rate of growth in the fallfish.

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Des augmentations journalières ont été observées sur les otolithes de ouitouches, *Semotilus corporalis*, de trois populations de ruisseaux du centre de l'état de New-York. Le dénombrement de ces additions peut servir à vérifier les marques annuelles et l'âge tel que déterminé par des méthodes moins précises. Les résultats semblent indiquer qu'un faux premier annulus a été observé dans la seule autre étude antérieure sur l'âge et la croissance des ouitouches. La croissance annuelle en longueur est linéaire. Les taux de croissance différent significativement chez les trois populations. De plus, la différence entre ces populations locales explique en grande partie la variabilité du taux de croissance qui existe dans toute la répartition de l'espèce. Ces résultats indiquent que la nature de l'habitat, en particulier la taille du ruisseau et la densité au sein de la population, est probablement le principal facteur déterminant du taux de croissance chez les ouitouches.

[Traduit par le journal]

Introduction

Determining the age of fishes depends primarily on periodicity in the growth history of the fish. This periodicity is detectable in the fish's hard parts, such as scales, otoliths, bones, and spines. Before the past decade all methods of aging were limited in their resolution to annual or seasonal periods. There are two major problems associated with this level of resolution. The first is that the fish must undergo distinct annual or seasonal cycles of growth for recognizable marks to be formed on their hard parts. Tropical, larval, and 1st-year fishes are all difficult to age because of this problem.

The second problem is not one of feasibility but one of accuracy and precision. Estimating the age of a fish in years by use of a method which, at its finest resolution, consists of counting annual marks, subjects the estimate obtained to a wide degree of error; in short, one unit miscounted results in the age estimate being an entire year astray. Furthermore, there is a general lack of verification of age determinations for all age classes in the stock. Lately, a series of papers concerning errors in

the aging of fishes have underscored the problem. The causes usually cited are false annuli, hidden or missing annuli, and misinterpreted spawning or metamorphic marks (e.g., Beamish 1979; Carlander 1974; Linfield 1974; Williams and Bedford 1974).

Recently, however, the situation has improved with the discovery of daily incremental marks on the otolith by Panella (1971). Otoliths are calcium carbonate accretions situated in the semicircular canals of bony fishes which assist in balance and sound perception. These marks can help to verify the ages of young individuals (Brothers et al. 1976; Brothers 1980; Brothers and McFarland 1980; Struhsaker and Uchiyama 1976; Taubert and Coble 1977), and, in some fishes, are the only way of routinely aging populations (e.g. the tropical wrasse, *Thalassoma bifasciatum*, B. C. Victor, in preparation). Furthermore, by counting the number of daily increments between successive annual marks one can verify both the number and position of these annuli. In this way the technique allows for a remarkably fine level of resolution both for validating age determina-

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tions by other methods and, in some species, for routine aging using this method alone.

In this study we used daily otolith increments to age three local populations of the fallfish *Semotilus corporalis*. The fallfish is the largest native Eastern cyprinid and ranges from Ontario south to Virginia (Scott and Crossman 1973). The life history of the fallfish has been previously documented by Reed (1971), who used scale annuli for aging. We shall, however, demonstrate that in his study a false first annulus was probably observed and, as a result, the age and growth profile of this species has been misrepresented. A revised profile shows the growth of fallfish to be remarkably linear. In addition, the variation in growth rates between populations appears to be accounted for by local habitat differences unrelated to latitude.

Materials and methods

Approximately 100 fallfish were collected from each of three streams in the vicinity of Ithaca, New York. The three streams were Willseyville Creek in the town of Willseyville, Catatonk Creek in the town of Candor, both in Tioga County, and Fall Creek in the town of Ithaca in Tompkins County. All three sampling sites are within a radius of 20 km around Willseyville in southern central New York State. The two former streams are in the Susquehanna River drainage while Fall Creek is part of the Finger Lakes - Great Lakes drainage.

Fish were captured by a combination of seining, angling, and electrofishing and were weighed, measured (TL), and sexed while fresh or after being frozen. The collections were all made during the late fall of 1978 and early spring of 1979. Our aim was to collect the fish while the otolith was no longer growing, i.e. during the formation of the annual winter mark. Preliminary observations of the dates of cessation of otolith growth in fall and its resumption in spring showed that most of the collections were made within the period of winter mark formation, while a few fell at most 1 or 2 weeks beyond the limits. Both fall and spring collections were made at each of the collection sites.

We obtained the utricular otoliths, or lapilli, from each fish by cutting horizontally through the cranium which exposed the brain. The pair of lapilli, lying just lateral to the optic lobes, were removed with fine forceps, cleaned, and placed in a drop of immersion oil on a glass slide. A sample of scales was also taken. Preparation of the otolith followed the procedure outlined in Brothers et al. (1976). The fallfish lapillus, being somewhat ovoid, was ground on both of the flatter sides until a section roughly 1 mm thick remained. Grinding was done by hand on a glass plate with Carborundum 600 grit in oil. The section thus obtained included the nucleus and was sufficiently translucent to allow examination with transmitted light. The otolith was then returned to the immersion oil and viewed under a compound microscope at magnifications ranging from 400 to 1000 \times . All measurements of length on the otolith were from the nucleus out along the longest radius of the section. The shape of the otolith and the position of the longest radius were notably constant for all individuals examined.

The number of fine increments visible on each otolith was counted. The count was begun at the nucleus and progressed

outwards in the direction of the longest radius. The number of increments was recorded on a Clay Adams multiple register hand counter, and as each prospective annual mark was encountered the tally was continued on a new register. On completion of the count, the age in years was recorded (the number of annuli encountered plus the one at the edge of the otolith).

In order to verify that the increments we observed were actually daily ones, we raised a cohort of fallfish in the lab. Eggs were collected from newly built fallfish nests in Willseyville Creek during May 1979. The eggs and young fish were maintained in a temperature-controlled flow-through tank with a temperature cycle corresponding to that in the stream. Otoliths first appeared around the time of hatching, about 5 days after fertilization, and for 2 weeks thereafter individuals were killed each day and their otoliths were examined. We also captured young-of-the-year from the same stream during June and July and counted the number of increments on their otoliths. Lastly, we captured older fish at different times throughout the growing season and counted the number of increments between the last winter mark on the otolith and the edge.

Results and discussion

Age determination

It is generally accepted in the literature that the term otolith is synonymous with sagitta, or the saccular otolith, primarily because all past work on aging by otoliths has been done with the sagitta (Taubert and Coble 1977; Panella 1980). However, in the fallfish and probably in all cyprinids, the sagitta is not useful for age determination because it shows no clear marks. The lapillus, or utricular otolith, should be used instead. Consequently, in this discussion, we shall use the term otolith to refer to the lapillus.

It has been known for a long time that the otoliths of some fishes have annuli. An annulus viewed without high magnification consists merely of the transition from a translucent band to one that is opaque. With increased magnification, however, these bands resolve into a multitude of fine lines. On the otolith of the fallfish they are particularly apparent. At this magnification, the annulus is visible as an interruption in the usual sequence of increments just before the start of the opaque band. It can be recognized as a discontinuity preceded by increasingly fine, light increments and followed, further out along the radius, by progressively larger and darker ones (Fig. 1). The area of fine increments corresponds to the "hyaline" (or translucent) zone, and the larger, darker increments correspond to the "opaque" zone of classical otolith reading under low magnification. The general interpretation is that the translucent band is formed during the slow or no growth period in the fall and winter and the opaque one during spring and summer (Blacker 1974). The annulus, or winter mark, was found at the edge of otoliths from fallfish captured in early spring and had not yet formed at the edge of otoliths from those captured in the early fall.

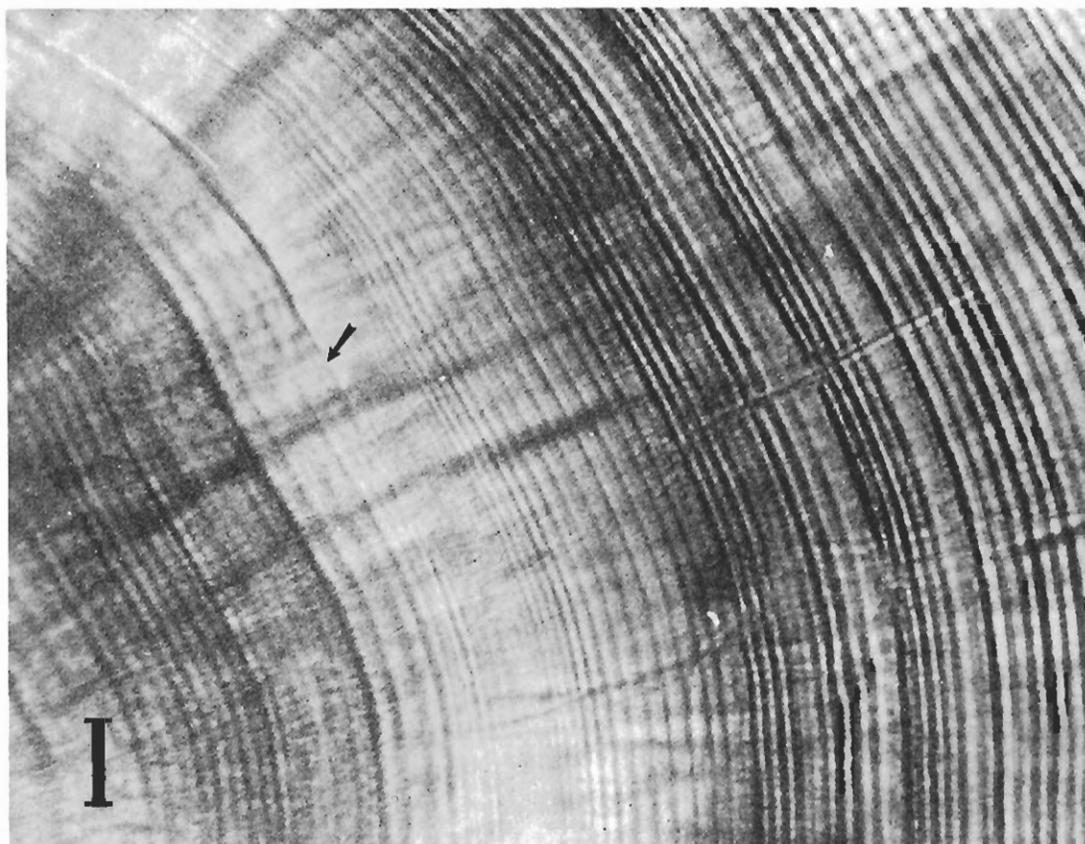


FIG. 1. A portion of an otolith from a 2-year-old fallfish showing daily increments and an annulus (arrow). The scale bar represents 20 μm .

Increments such as these on other species' otoliths have been shown to be daily. Panella (1971) counted the rings on hake (*Merluccius productus*) otoliths and found an average of 360 per year. Brothers et al. (1976), Struhsaker and Uchiyama (1976), and Taubert and Coble (1977) demonstrated experimentally that the number of increments on otoliths of laboratory-raised fish corresponded with their age in days. In our laboratory-raised fallfish we found that otoliths first formed around the time of hatching and for the next 2 weeks a new increment was laid down each day.

Young-of-the-year fallfish captured during their first summer showed an increasing number of increments as the season progressed and this number corresponded with the number of days since the hatching period for the population. In Willseyville Creek in 1979 I first observed nests at the beginning of May. Juvenile fallfish captured there on June 26 had an average of 58 increments on their otoliths ($n = 25$), while juveniles captured on July 18 had an average of 74 increments on their otoliths ($n = 25$) (corresponding overall to a hatching date of May 1).

Older fish showed a similar pattern of increasing numbers of increments between the last annulus and the edge of the otolith as the season progressed. In fact, by counting back from the date of capture, one can calculate when the first increments after the annulus were laid down. In a series of older fish captured late in the season from Willseyville Creek in 1978 ($n = 8$), the count revealed that the first increment was laid down in early May. After the 1st week of October of that year all of the fish captured from the three streams had the annulus forming on the very edge of their otoliths. Total increment counts between successive annuli for all ages generally matched this 5-month season. These counts ranged from 110 to 154 and showed no significant tendency to diminish with age: the mean total count per year for successive age-classes were 131 ($n = 13$), 133 ($n = 20$), 129 ($n = 5$), 129 ($n = 5$), 122 ($n = 5$), 125 ($n = 3$), 122 ($n = 3$), 126 ($n = 1$), 129 ($n = 1$).

On the majority of otoliths annuli were relatively easy to identify at low magnification, in contrast to fallfish scales which are often hard to read (Fig. 2). In some older fish, however, the difference in opacity between

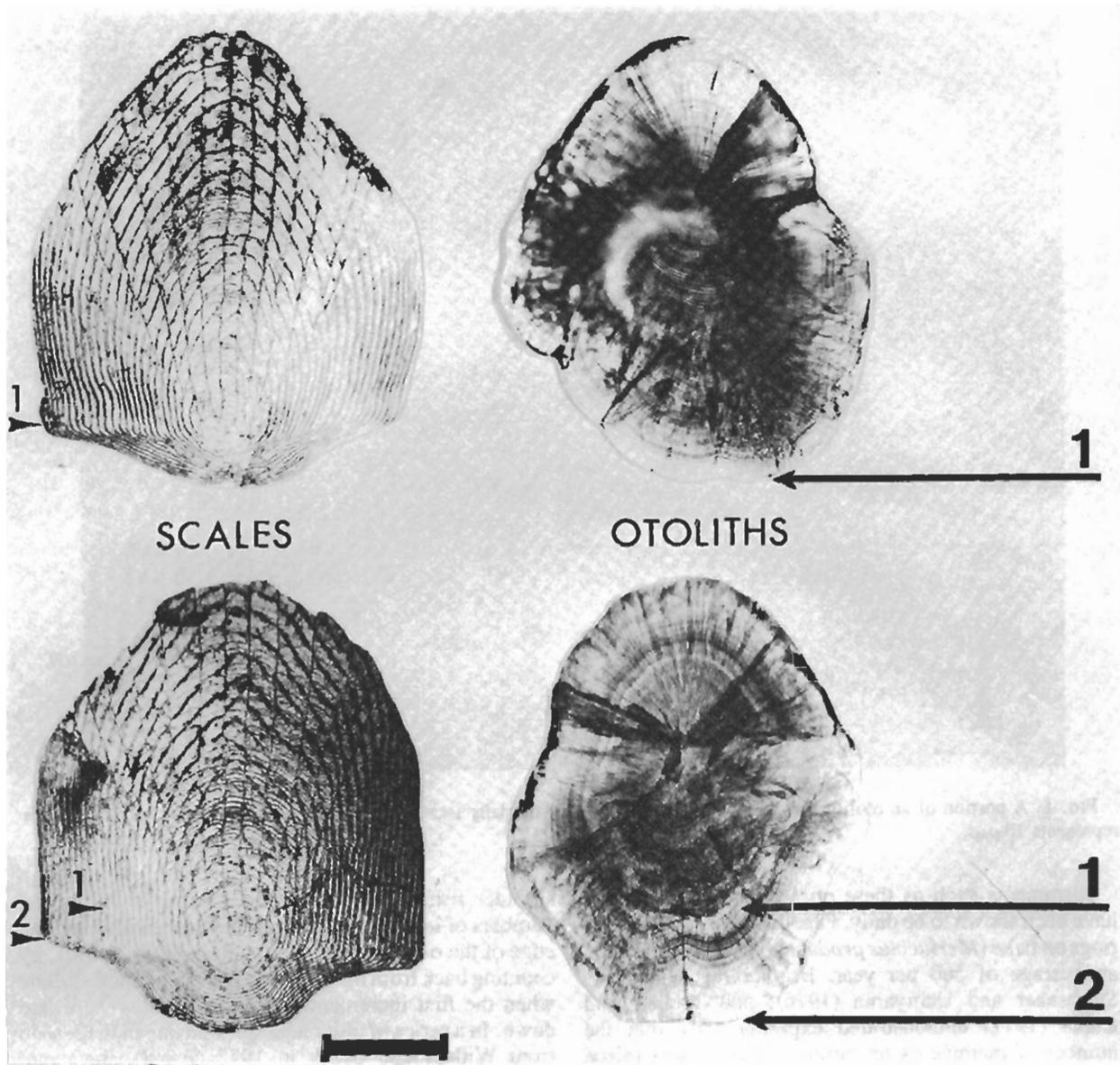


FIG. 2. Scales and otolith sections from fallfish with annuli indicated. (A) Scale and otolith section from an 80.9-mm TL 1-year-old from Fall Creek. (B) Scale and otolith section from a 158.8-mm TL 2-year-old from Fall Creek. The scale bar represents 0.3 mm for the top pair and 0.55 mm for the lower pair.

the translucent and opaque zones was diminished (Fig. 3) and decisions whether an annulus existed or not became more subjective. Also, because the core of the otolith (laid down during the first season of growth) is relatively more opaque, decisions on where the first annulus was were difficult. These problems were a product of the criterion used for annulus identification at low magnification, i.e. a transition from a translucent zone to one that is opaque. At high magnification, when the criterion for an annulus is a discontinuity preceded

by increasingly narrow increments and followed by increasingly wide ones, no such problems were present. We found no aberrant counts of increments between successive annuli, which had they existed, would have implied false annuli and required independent methods of validation. The daily otolith increment method of aging is sufficient for aging all age-classes of fallfish; however, its most useful application is for verifying more easily used techniques.

The technique is especially valuable for validating the

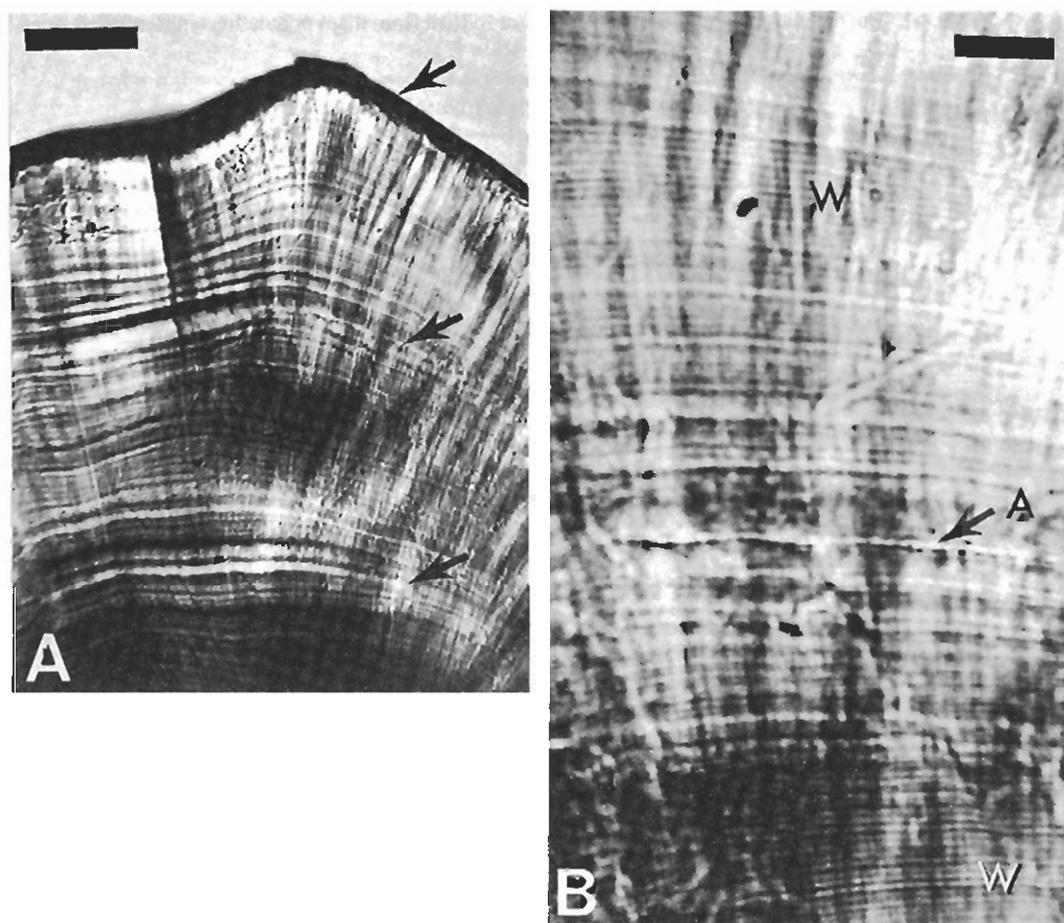


FIG. 3. Otolith section and detail from a 365.5-mm TL 9-year-old from Willseyville Creek. (A) A section of the otolith showing the last three annuli. The scale bar represents 50 μm . (B) A magnification of the eighth annulus. Relatively wide increments (W) can be seen before and after the annulus (A). The scale bar represents 10 μm .

position of the first annulus. The unusually large size of the juvenile fallfish captured by Reed (up to 69 mm TL) led him to search for a hidden first annulus on fallfish scales, which he subsequently found (R. J. Reed, personal communication). However, our examination of the otoliths of all the large juvenile fallfish that we captured (up to 82 mm TL) showed that they were indeed young-of-the-year. None had more than 143 daily increments, and these were regular and uninterrupted. No sign of any unusual increment pattern corresponding to Reed's supposed first annulus was found. Furthermore, in his study the increase in length in the "2nd" year was about half that of any other year of the fish's life, leading to an implausibly dented growth curve. Individuals in their "1st" year were found in only two of the eight streams examined (Reed 1971). Based on these facts, we believe Reed's first annulus was a false annulus, and the groups of fish he designated as 1st

and 2nd year fish do not constitute different age-classes but were, in fact, all 1st-year fish.

Growth

The growth curves of the three fallfish populations were linear (no significant departure from linear regression; Snedecor and Cochran 1967) (Fig. 4). Comparisons of the regression coefficients indicated that the Fall Creek population grew faster than the Catatank Creek population, which, in turn, was faster growing than the Willseyville Creek population ($p < 0.025$ and $p < 0.001$, respectively) (Table 1). After relatively fast growth the first season, additional increases in length stay somewhat constant without much leveling off characteristic of many other fish growth curves. On the Walford graph of the fallfish data a line virtually parallel to the diagonal is obtained (Fig. 5) (method described in Ricker 1975). Ricker reports a similar line is characteris-

TABLE 1. The mean total length at each annulus of fallfish from three populations in Central New York

Site	Mean total length (mm) at each annulus								
	1	2	3	4	5	6	7	8	9
Willseyville Creek	56.2 (21)*	100.5 (33)	146.6 (1)	179.3 (30)	223.2 (11)	263.1 (6)	282.6 (3)	—	359.1 (1)
Catatonk Creek	63.5 (30)	115.1 (19)	151.3 (5)	201.1 (34)	233.8 (8)	267.7 (5)	—	—	—
Fall Creek	73.2 (18)	139.6 (41)	177.7 (18)	230.0 (27)	275.9 (3)	328.0 (2)	356.3 (2)	—	—

*Sample size in parentheses.

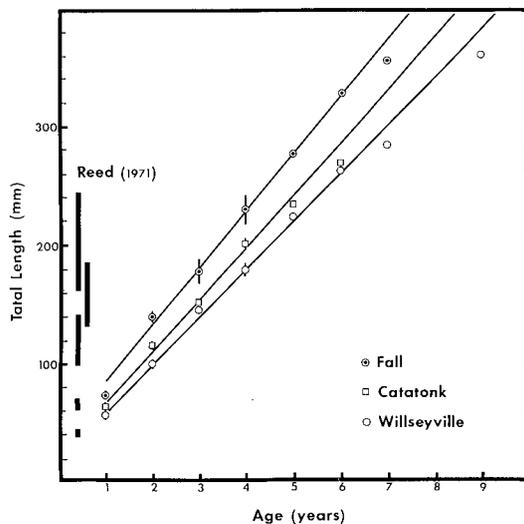


FIG. 4. Relationship of fallfish length to age for three local stream populations near Ithaca, New York. Mean and 95% confidence intervals shown for samples of over 20 individuals, mean alone for smaller samples. The bars at left represent the range of mean TL for the first 5 years reported by Reed (1971). For Fall Creek $b = 48.3$, $n = 111$, $r^2 = 0.902$; for Catatonk Creek $b = 44.3$, $n = 101$, $r^2 = 0.968$; for Willseyville Creek $b = 39.8$, $n = 106$, $r^2 = 0.972$.

tic of some long-lived cool water fish, but its occurrence in a minnow is unusual. This linearity is probably not an artifact of incomplete collections (i.e., missing the older fish who are presumably slower growing) since the two 9-year-old fish we have captured (no fallfish exceeding 9 years old has been found in any study to date) fall close to the lines in Fig. 4. It is, however, possible that if a large sample of very old individuals were obtained the growth curve would begin to level off.

Reed (1971) reports that males exceed females in size after 3 years but even at 4 years of age we found no significant differences in size in any stream: in Willsey-

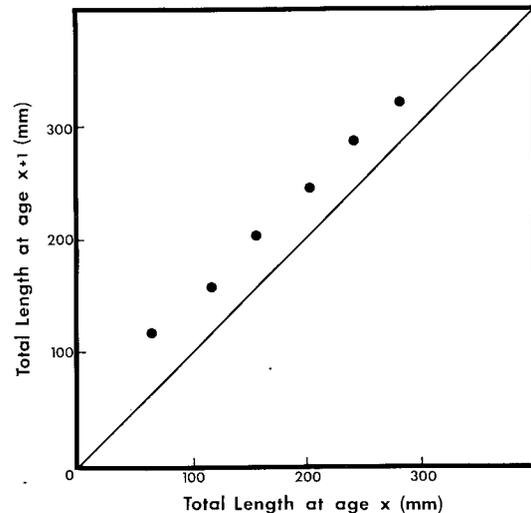


FIG. 5. Walford graph for fallfish from central New York. Points represent the mean of the mean TL at each age-class for the three populations. This graph illustrates the increase in length each year. The slope of the points shows the change in that increase with age; 45° is equivalent to no change in the rate of growth.

ville Creek, the mean TL of 4-year-old females was 179.9 mm vs. 178.1 mm for males ($n = 19$ and 11, respectively); in Catatonk Creek, females 201.6 mm vs. males 200.4 mm ($n = 20$ and 14); in Fall Creek, females 226.3 mm vs. males 231.2 mm ($n = 7$ and 20). Longevity did not seem to vary among the populations of fallfish studied. Individuals 9 years of age, the oldest yet recorded, have been captured from both fast and slow growing populations. Both 9-year-olds were females; however, there is not enough evidence to state whether longevity is different for males and females.

In this paper we have avoided using back-calculation with its usual loss of precision. This method estimates the length of an individual at a past annulus by using the

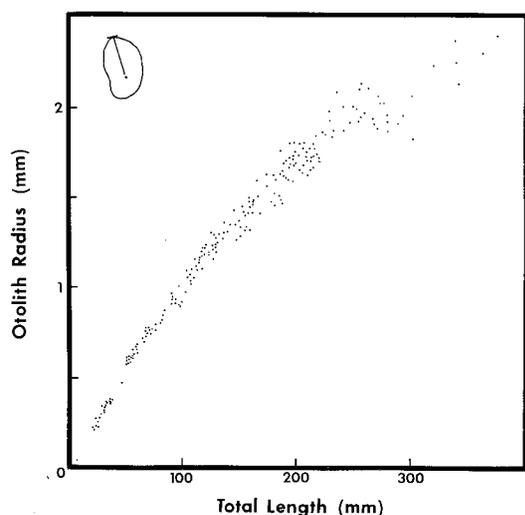


FIG. 6. Relationship of otolith radius to total length for central New York fallfish.

mean length for the population corresponding to that radius of the scale or otolith. The annuli on fallfish otoliths are, nevertheless, quite suitable for back-calculation, since the relationship between total length and otolith radius is quite consistent (Fig. 6).

The differences between the three streams in the growth rate of fallfish are clearly not a result of latitudinal differences. All three collecting sites were within 20 km of the town of Willseyville in central New York. In previous studies of growth in various *Semotilus* species, growth rates were compared over the geographical range of the species, and latitude (with its concomitant changes in the length of the growing season) was considered a particularly important determinant of growth (Powles et al. 1977; Stasiak 1978; Reed 1971). There was little emphasis on the effect of differing habitat types and Powles et al. (1977) even suggested that growth was independent of the habitat type in *Semotilus atromaculatus*.

A comparison of Reed's (1971) results with ours can clarify the relative influences of habitat type, latitude, and year to year differences on fallfish growth rates. Reed's eight collection sites ranged from New Brunswick to Pennsylvania and included a reservoir in Massachusetts. His collections also date back as far as 1953. Nevertheless, in the first two age-classes, the range of mean size of our local populations overlaps the entire range of mean size for those ages reported by Reed (Fig. 4). Furthermore, in subsequent age-classes, the differences in mean size of our local populations encompass much of the range found in Reed's study. The fact that so much of the variability in growth rate evident among Reed's disparate populations can be matched by three local stream populations in the center

of the species' range suggests that local habitat differences are the primary determinant of the rate of growth in fallfish.

The most apparent difference between the three sites was the size of the stream. The Willseyville Creek collections (exhibiting the slowest growth) were made along a 100-m stretch of the stream with an average width of about 3 m and a greatest depth of less than 1 m. The fish from Catatunk Creek were taken from a 500-m section of the stream where the mean width was about 10 m and the maximum depth about 1.5 m. The Fall Creek collections required a several kilometre length of stream to obtain the desired sample size where the average width was about 12 m and the depth ranged up to several metres. Fall Creek has a drainage area of 10 412 ha, Catatunk Creek has one of 6864 ha, and Willseyville Creek has a drainage area of less than half that of Catatunk Creek (Dunn 1970). Since collecting was continued until 100 individuals were captured in each stream, the area and effort required are some indication of the density of fallfish. Both the area and the effort expended per unit area increased greatly with stream size. Despite some lessening of capture efficiency in larger streams, we believe that the density of fallfish was inversely related to the size of the stream. Apparently the combination of large stream size and low density of fallfish was a major contributor to growth, perhaps through moderated temperatures or increased food supply. Further investigation of the specific features of the local habitat that determine growth rate is necessary for a comprehensive understanding of the pattern of variability in the growth of this and other species.

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