Age and growth analysis of the central mudminnow, *Umbra limi* (Kirtland, 1840)

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Summary

A rudimentary understanding of age, growth, and life-span is lacking for many non-game fishes. Growth characteristics of the central mudminnow (*Umbra limi*) have not yet been accurately described using reliable hard part analysis. The utility of scales and otoliths as ageing structures and quantified growth was examined in one lake and one stream population of central mudminnow. Scales were found to be of no utility in determining age due to inconsistent formation of yearly annuli and a high incidence of regenerated scales, while otoliths were easily extracted and considered to be an accurate ageing structure. Ages determined from scales were low compared to those from otoliths, and the difference in age interpreted from the two structures increased with fish age. A power function was fitted to describe the length-weight relationship for this species ($a = 0.0069$, $b = 3.175$). Von Bertalanffy growth parameters were estimated and compared for each population (Lake: $L_\infty = 114.20$ mm, $K = 0.30$, $t_0 = -0.93$; Stream: $L_\infty = 77.59$ mm, $K = 0.63$, $t_0 = -0.76$). The lake population showed greater size at age compared to the stream population, especially at older ages, and achieved a larger maximum size. Growth rate was also greater in the lake population (Lake: 1.74; Stream: 1.09 g year^{-1}). Females were larger at age than males in both populations, however all individuals greater than age 3 were males. This work represents the first successful account of central mudminnow growth using hard part analysis.

Introduction

Interest in managing for diverse native fish communities, including non-game fishes, is growing with the implementation of concepts such as ecosystem-based management (Slocombe, 1993; Pikitch et al., 2004). Protecting and enhancing populations of game, non-game, and commercial fishes requires knowledge of basic life history characteristics, including age and growth relationships. Even rudimentary understanding of age, growth, and life-span is lacking for many non-game fishes. In order to effectively describe fish growth, the reliability of age estimates must be considered. Otolith analysis has become the preferred method for estimating the age of game-fish and commercial fish species in North America, while age estimation on other less economically or recreationally important taxa is often performed using scale or length-frequency analysis (Bresnick and Heins, 1977; Stair et al., 1984; Knight

and Ross, 1992). Unfortunately, both of these methods have documented limitations (Devries and Frie, 1996). The general lack of otolith-derived age estimates for many non-game fishes is likely due to small body size and the inherent challenges involved in extraction and analysis of minute otoliths. In species for which this type of analysis is feasible, age and growth characteristics should be documented through reliable analysis of hard parts (e.g. otoliths).

The central mudminnow (*Umbra limi*) is a widely distributed species found in lakes, streams and wetlands in central North America west of the Appalachian Mountains (Scott and Crossman, 1973) and is usually associated with littoral habitats dominated by dense cover (Smith, 1985). The species is often abundant where it occurs, possibly due to its preference for dense cover, its ability to inhabit areas with low dissolved oxygen by respiring oxygen from both aerial and aquatic sources, and ⁄ or behavioral adaptations associated with aerial respiration limiting its exposure to predation (Gee, 1980; Ward et al., 2008). In New York, spawning takes place in mid-April when water temperatures reach 13°C (Westman, 1941). Central mudminnows feed on a wide variety of zooplankton and benthic and epiphytic macroinvertebrates (Keast, 1968; Chilton et al., 1984). Adult central mudminnows are also known to consume small littoral fishes and feed actively even during the winter (Chilton et al., 1984). The species can function as both a prey source and a competitor to other fishes in some aquatic systems (Peckham and Dineen, 1957; Tonn, 1985; Tonn and Paszkowski, 1987). Given the widespread distribution of the central mudminnow in aquatic systems throughout its range, it is somewhat surprising that age and growth characteristics have never been accurately described for this species.

Applegate (1943) used scale ages and length-frequency analysis in reporting the only published central mudminnow age estimates in the peer-reviewed literature. A Master's thesis by Westman (1941) also evaluated scales and length-frequency distributions, in addition to otoliths and opercular bones, in estimating ages for this species. Both Westman (1941) and Applegate (1943) concluded that scales were of no utility in determining age in the central mudminnow and that only the age 0 and 1 cohorts were distinguishable using length–frequency analysis. However, data were not presented to support their assertions regarding scale age. Westman (1941) also found that opercular bones were not suitable for age determination. Westman (1941) concluded that otoliths were a suitable structure for determining central mudminnow ages, but was unable to age older fish due to otolith degradation caused by formalin preservation of study specimens. Peckham and Dineen (1957) and Chilton et al. (1984) stated that they used central mudminnow otoliths for age identification, but no records of their aging analyses were provided.

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The objectives of this study were to: (i) evaluate the utility of using otoliths to determine central mudminnow age; (ii) describe and quantify the growth of this species based on length and weight at age; and (iii) determine if age and growth characteristics differed between populations and among males and females of the species. This manuscript describes the first successful account of central mudminnow growth using hard part analysis.

Materials and methods

Central mudminnows were collected from First Bisby Lake and Little Moose Lake Outlet located on a private preserve within the Adirondack Region of New York. Collections were conducted through a combination of boat and backpack electrofishing along the shoreline of First Bisby Lake on 23 September and 8 October 2008 and by backpack electrofishing in Little Moose Lake Outlet on 13 October 2008. Collections were made in habitats that were dominated by fine substrate and relatively dense cover (e.g. vegetation, woody debris). Subsamples of fish representing the size range of central mudminnow in First Bisby Lake (n = 69) and Little Moose Lake Outlet (n = 62) were euthanized and transported to the laboratory for processing. Sample sizes were small because there was no prior knowledge of the population levels in these systems. Total length, weight, and sex (based on dissection) were recorded for each individual. Scales were removed from the area just below the dorsal fin and sagittal otoliths were extracted, cleaned and dried.

An average of 14 scales from each fish was mounted between two glass microscope slides for age estimation. Scale ages were determined by viewing all scales on a slide and assigning age based on the scale with the greatest number of annuli. The number of regenerated scales on each slide was also noted. A single otolith from each fish was mounted sulcus side up on a glass microscope slide using Crystalbond™ mounting adhesive. Mounted otoliths were polished to the focus using successively finer lapping film (600, 800 and 1200 grit). Marks presumed to be annuli from scales and otoliths were counted using a dissecting microscope (9× to 37.5×) and a compound microscope (40× to 400×), respectively, using transmitted light. Two readers assigned ages independently for both scales and otoliths. Discrepancies were resolved by a third independent reader. Otoliths and scales for which discrepancies in age could not be resolved by the third reader were excluded from further analysis. Ages were assigned without prior knowledge of fish size. The amount of time that had passed since the last annulus was formed was assumed to be the same for each fish, since all fish were collected at approximately the same time of year. For the purposes of this study we assumed that rings counted as annuli were annual marks and the ages obtained using otoliths were accurate based on agreement of annuli counts by two independent readers.

Simple linear regression was used to quantify the relationship between fish size and scale regeneration. A power function

$$W = aL^b \qquad (1)m1$$

where W = weight (g), L = length (mm), and a and b are parameters, was used to describe the length weight relationship for this species (Froese, 2006). Welch Two Sample t-tests were used to compare length and weight at age between the two populations and the length and weight of mature females and

males at age 2 for both populations. The von Bertalanffy growth function

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \qquad (2)m2$$

was fitted using nonlinear least squares estimation for both populations, where L_t is the length at time t, L_∞ is the mean asymptotic length, K is the Brody growth coefficient and t_0 is the hypothetical age at which the fish would have been zero mm in length (Ricker, 1975). Analysis of residual sums of squares (ARSS) was used to compare the von Bertalanffy growth functions between the two populations (Chen et al., 1992), and likelihood ratio tests were used to compare differences in L_∞, K, and t_0 between populations (Kimura, 1980). Linear regression was used to quantify growth rate (g year^{-1}), and multiple linear regression was used to test for homogeneity of slopes between regression lines for the two populations. Y-intercepts for weight-at-age regressions were forced through the origin. An α value of 0.05 was used to determine statistical significance for all tests. Data analyses were performed using program R (The R Foundation for Statistical Computing; http://www.r-project.org). For the purposes of growth analysis, 0.5 was added to the age of each fish to account for the approx. 6 months of somatic growth that had occurred between formation of the last annulus and fish collection in the autumn.

Results

Central mudminnows from First Bisby Lake ranged from 32–100 mm in length and 0.3–12.0 g in weight. Central mudminnows from Little Moose Lake Outlet ranged from 38–83 mm in length and 0.5–5.2 g in weight. One fish from each location could not be aged using otoliths due to errors in slide preparation. Six fish from First Bisby Lake and one fish from Little Moose Lake Outlet could not be aged using scales because all scales in the sample were regenerated (Fig. 1a). There was 84% agreement between the first two readers in both First Bisby Lake and Little Moose Lake Outlet using otoliths and 71 and 80% agreement using scales, respectively. Discrepancies in otolith ages were resolved by a third reader in nine of 11 cases in First Bisby Lake and eight of 10 cases in Little Moose Lake Outlet. Discrepancies in scale ages were resolved by the third reader in 15 of 18 cases in First Bisby Lake and 12 of 12 cases in Little Moose Lake Outlet. Thus, 66 otolith and 60 scale samples were evaluated for the First Bisby Lake population and 59 otolith and 61 scale samples were evaluated for the Little Moose Lake Outlet population.

Scale analysis yielded a maximum age of 3 for central mudminnows captured from First Bisby Lake and a maximum age of 2 from Little Moose Lake Outlet. Marks presumed to be annuli were generally difficult to discern on scales because scale circuli were not continuous and 'crossing over' or obvious crowding of circuli indicating a disruption in growth were not apparent (Fig. 1b). In addition, numbers of annuli observed on different scales from the same fish were not consistent. The incidence of scale regeneration also exacerbated ageing of larger fish. The percentage of regenerated scales for individual fish increased significantly with fish length for both populations (First Bisby Lake: $F = 54.43$, $P < 0.001$; Little Moose Lake Outlet: $F = 50.51$, $P < 0.001$).

Otolith analysis yielded a maximum age of 6 in First Bisby Lake and 5 in Little Moose Lake Outlet (Table 1). Marks presumed to be annuli on otoliths were generally readily

Fig. 1. (a) A regenerated scale, (b) normal scale with two assigned annuli; and (c) sagittal otolith with four assigned annuli. All structures taken from same 89-mm fish
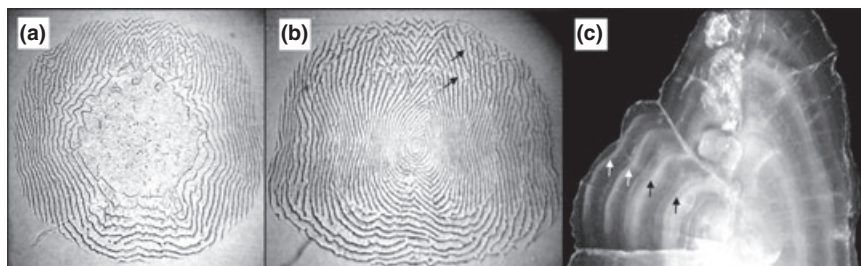
Table 1
Numbers of immature, mature female, and mature male central mudminnow in each age class in First Bisby Lake and Little Moose Lake Outlet based on ages obtained from otoliths

Water	Age	Immature	Female	Male	Total
First Bisby Lake	0	10	–	5	15
	1	1	4	9	14
	2	–	20	9	29
	3	–	2	1	3
	4	–	–	3	3
	5	–	–	1	1
	6	–	–	1	1
Little Moose Outlet	0	10	–	6	16
	1	1	–	2	3
	2	–	13	22	35
	3	–	–	2	2
	4	–	–	2	2
	5	–	–	1	1

identifiable and could be seen in all regions of the prepared otolith (Fig. 1c). Estimated ages from scales were consistently lower than those from otoliths at all ages with the exception of age 0 fish, and the median difference in age between the two structures increased with age (Fig. 2). Estimated scale- and otolith-derived ages for the same fish were in agreement for only 19 of 118 (16.1%) fish for which ages were determined using both structures. Given that scale-derived ages were consistently lower than otolith-derived ages for all age classes except age 0 – and the difficulties associated with assigning

scale-based ages described above – further evaluations of age-at-maturity, length-at-age, and weight-at-age relationships were based on otolith-derived ages only.

The majority (67% in First Bisby Lake and 63% in Little Moose Lake Outlet) of the age 0 cohort was immature in both populations, with 33 and 38% of age 0 fish mature males and no age 0 fish mature females (Table 1). Most fish (93% in First Bisby Lake, 67% in Little Moose Lake Outlet) reached maturity by age 1, and all age 2 fish were sexually mature in both populations. All individuals age 4 and older were males in First Bisby Lake (n = 5), and all individuals age 3 and older were males in Little Moose Lake Outlet (n = 5).

The pooled length–weight relationship for central mudminnow collected from First Bisby Lake and Little Moose Lake Outlet was: $W = 0.0069L^{3.175}$ ($R^2 = 0.99$; Fig. 3). Mean length and weight were greater in First Bisby Lake than in Little Moose Lake Outlet at ages 2 and 4 (Table 2). No differences were observed in length or weight at ages 0, 1, or 3. Sample sizes were too small for age 5 and 6 fish to allow for comparison. Mean length- and weight-at-age comparisons between mature males and females were possible only for age 2 fish due to low sample sizes for other age classes. Mean length and weight of females at age 2 (the only age tested) in First Bisby Lake and in Little Moose Lake Outlet were significantly greater than those of the age 2 males in First Bisby Lake and in Little Moose Lake Outlet (Table 3).

Von Bertalanffy growth function parameters were estimated for both populations (Table 4, Fig. 4a). Overall growth functions for the two populations were not coincidental. L_∞
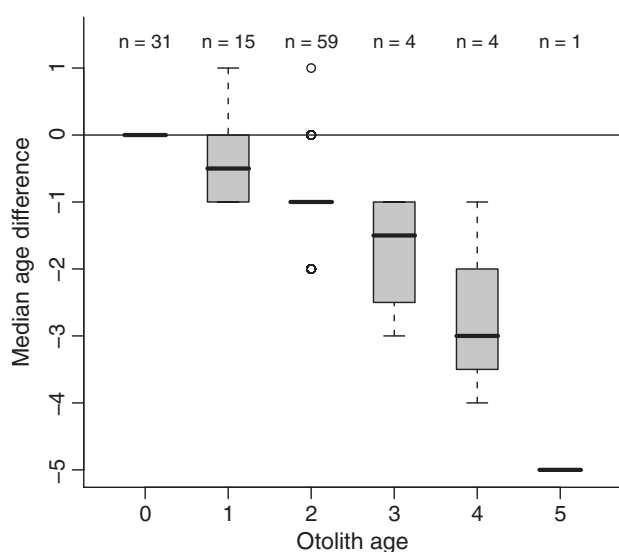

Fig. 2. Box and whisker plots of median age difference between scale and otolith age (i.e. scale age minus otolith age) at each otolith age. Note: Many older-age fish not compared as all scales in the sample were regenerated
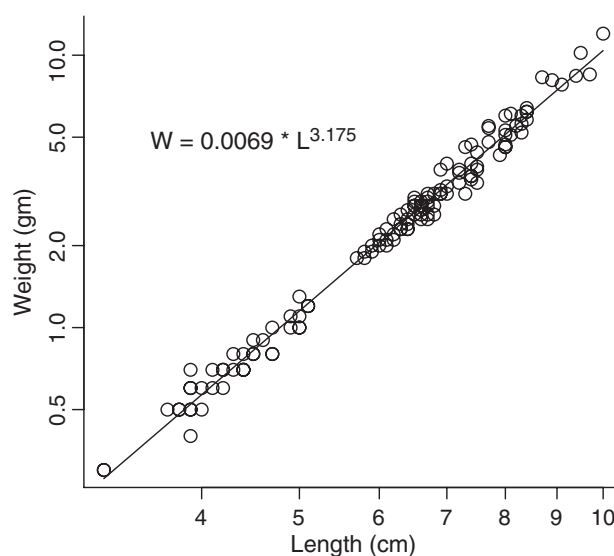

Fig. 3. Double-logarithmic plot of length and weight of combined lake and stream populations with associated power function (n = 133)

Table 2
Results of Welch two sample *t*-tests used to compare length- and weight-at-age between central mudminnow populations, First Bisby Lake and Little Moose Lake Outlet. Length and weight represent means for each age class. Ages for which no *t*-statistic or P-value is listed indicate sample sizes less than 2

	Age	First Bisby Lake	Little Moose Lake Outlet	*t*-statistic	P-value
Length (mm)	0	41.0	42.7	−0.784	0.443
	1	55.3	55.7	−0.067	0.952
	2	74.8	68.0	3.927	< 0.001
	3	85.3	68.0	2.401	0.096
	4	90.3	70.5	4.671	0.045
	5	94.0	83.0	–	–
	6	100.0	–	–	–
Weight (g)	0	42.7	0.7	−0.063	0.951
	1	55.7	1.8	−0.200	0.858
	2	68.0	3.0	5.050	< 0.001
	3	68.0	3.1	2.3648	0.099
	4	70.5	3.6	6.593	0.007
	5	83.0	5.2	–	–

Table 3
Mean length (mm), mean weight (g), test statistics, and P values from comparisons of age 2 female and male central mudminnows, First Bisby Lake (FBL) and Little Moose Lake Outlet (LMO)

	Water	Females	Males	*t*-statistic	P-value
Length (mm)	FBL	77.4	68.9	3.29	0.004
	LMO	72.0	65.7	3.40	0.004
Weight (g)	FBL	4.9	3.6	2.40	0.030
	LMO	3.4	2.7	2.63	0.020

Table 4
Von Bertalanffy growth function parameters and test statistics from comparisons of central mudminnow populations, First Bisby Lake and Little Moose Lake Outlet. Test statistics compare differences in overall growth function and individual parameters between lake and stream populations

Parameter	First Bisby Lake	Little Moose Outlet	Statistic	P-value
Overall growth function	–	–	$F_{3,\ 118} = 11.67$	< 0.001
L_∞	114.20 mm	77.59 mm	$X_1^2 = 7.79$	0.005
K	0.30	0.63	$X_1^2 = 3.56$	0.060
t_0	−0.93	−0.76	$X_1^2 = 1.74$	0.190

was significantly larger in the lake population while neither K nor t_0 differed between populations. There was a significant positive relationship between weight and age (Fig. 4b) for both populations (First Bisby Lake: $F = 784.8$, $P < 0.001$, $R^2 = 0.92$; Little Moose Lake Outlet: $F = 799.3$, $P < 0.001$, $R^2 = 0.93$). Slopes of regression lines for weight at age differed between populations ($t = -6.71$, $P < 0.001$), indicating that growth rates in First Bisby Lake (1.74 g year^{-1}) were greater than in Little Moose Lake Outlet (1.09 g year^{-1}).

Discussion

Our findings confirm the assertions of Westman (1941) and Applegate (1943) that the scales of the central mudminnow are of no utility in determining age. Given the consistently and
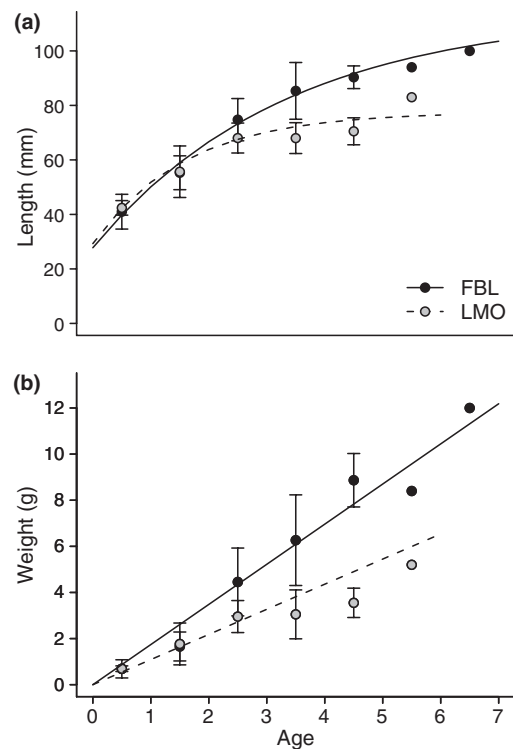

Fig. 4. Length (a) and weight (b) at age of central mudminnow populations in First Bisby Lake (n = 66) and Little Moose Lake Outlet (n = 59). Error bars represent one standard deviation from the mean. Points are offset by 0.5 years to account for approx. 6 months of somatic growth that occurred between formation of last annulus and autumn fish collection. Lines on plot a = von Bertalanffy growth functions for each population; lines on plot b = linear functions of weight at age

substantially lower ages obtained from scales compared to otoliths, it is unlikely that our scale ages represent the true age of these fish, despite the fairly precise age estimates achieved by multiple readers using scales. In general, scale circuli were not continuous, circuli did not show the characteristic crowding or 'crossing over' typically indicative of an annual interruption or slowing of growth, and many scales were not readable due to regeneration – a phenomenon that has been reported in many other fish species (Beamish and Chilton, 1982; Stolarski and Hartman, 2008). Furthermore, our findings are in agreement with the vast majority of scale–otolith comparisons, indicating that scale-derived ages are underestimates compared to oto-lith-derived ages, especially in older fish (Sikstrom, 1983; Wright and Giles, 1991; Quist et al., 2007; Muir et al., 2008). In the case of the central mudminnow, the discrepancy in ages derived from scales and otoliths was not due to difficulty in counting crowded annuli toward the edge of the scale in older fish but was instead due to difficulty in detecting the existence of annuli at all. Given that the identification of no more than three annuli on any one scale could be agreed upon by two independent readers and that only 16% of scale-derived ages agreed with otolith-derived ages, we do not believe that our designations of annuli on central mudminnow scales were true annual marks. This may be due to a lack of yearly scale annulus formation, which has been documented for other species (Beamish and McFarlane, 1983; Beckman, 2002). By contrast with scales, otoliths from the central mudminnow are mechanistically well suited for age determination. Central mudminnow otoliths are relatively large and easily extracted compared to many other species that reach similar adult sizes

(e.g. many cyprinids). While the age data presented here are not validated, they represent the first description of central mudminnow age and growth using reliable hard part analysis.

The role of the central mudminnow as a forage fish and competitor in a variety of aquatic systems substantiates the importance of describing growth relationships across a range of habitats for this species (Peckham and Dineen, 1957; Tonn, 1985; Tonn and Paszkowski, 1987). Indices of growth including L_∞, growth rate (g year^{-1}), and size at age of older individuals were greater in the lake population than in the stream population. Other studies have described similar trends for lake vs stream populations for multiple fish species (Carlander, 1977; Noltie, 1988; Quist and Guy, 2001). Reasons for the differences in growth among the waters in our study are not known, but may be due to the availability of food resources or the stream environment being less stable and physiologically more demanding than the lake environment (Noltie, 1988).

Female central mudminnow were larger than males in both populations when compared at age 2. Westman (1941) found a similar relationship for three populations of central mudminnow in New York State, and greater growth of females is common among teleosts. Female maturation was also found to occur at an older age, which again was in agreement with Westman's (1941) observation that most males had matured by age 1, whereas fewer females had matured by this age. We found no females in either population older than age 3; however age 4 and older fish represented only 8% of the sample from First Bisby Lake and 5% of the sample from Little Moose Lake Outlet. The lack of females age 3 or older could reflect some sex-specific life history trait, a lack of susceptibility of older females to our sampling gear, or simply the absence of older age classes in our study waters.

The length–weight relationship developed for the studied populations indicates a tendency for slightly allometric growth ($b = 3.175$, slightly greater than 3.0), with an increase in relative body thickness or plumpness with increasing length (Froese, 2006). By comparison, the b parameter for a closely related species, the eastern mudminnow (Umbra pygmaea), was calculated to be 3.550 by Dederen et al. (1986).

The von Bertalanffy growth function provided an accurate description of somatic growth for the central mudminnow at the ages encountered. However, the estimated parameter t_0 was low in both cases, causing the growth curve to cross the y-axis at an abnormally high value. Because this species has a very brief egg stage (approx. 6 days) (Westman, 1941; Peckham and Dineen, 1957), t_0 should be close to zero. However, forcing the curve through the origin would result in an increased K, decreased L_∞ and an overall poor fit to the data. The von Bertalanffy growth function has been demonstrated to be a poor representation of growth at early life stages (Ricker, 1975; Lester et al., 2004) because it is unable to account for the changes in energy allocation and growth associated with maturity (Day and Taylor, 1997; Czarnoleski and Kozlowski, 1998). Our data showed that some individuals in the population were maturing as young-of-year and most individuals were mature by the autumn of their second year (age 1). Therefore, the von Bertalanffy function should be useful for modeling the growth of this species over the vast majority of its lifespan.

Management on the ecosystem level requires a basic knowledge of the biology of game, non-game and commercial fish species, including age structure and growth information. The life history and ecology of the central midminnow have been studied in various levels of detail, providing only a partial understanding of the ecological role of this species. They are known to prey primarily on aquatic macroinvertebrates, but will also consume fish as adults (Chilton et al., 1984). At high densities, central mudminnows may affect the structure of littoral macroinvertebrate communities (Brown and DeVries, 1985), however their effect on littoral fish communities is unknown. Central mudminnows may also serve as important prey items in some systems (Tonn, 1985; Ward et al., 2008) but not in others (Weidel et al., 2000, 2007). The age structure of a population may affect the degree to which any or all of these relationships are manifested. Chilton et al. (1984) found that only adult female central mudminnows were piscivorous during winter and that age 2+ females were nearly entirely piscivorous during this season. Thus, the size and age structure of a large adult female population could strongly influence the ability of other competing fish species to become established or maintain populations under some conditions. Without basic, reliable knowledge of age and growth characteristics, inter-specific or community-level influences of central mudminnow populations may be unapparent or misinterpreted.

The need for the use of reliable ageing structures, such as otoliths, for small, non-game species is further exemplified by our results as they pertain to the later maturation of central mudminnow females and the lack of females older than age 3. The use of scales or length frequency analysis would not have allowed for detection of these conditions. Growth in this species, and presumably other small, relatively short-lived species, is variable, and adult size is reached quickly, so there is considerable overlap in age-class size. Our sampling of the two study populations did not allow definitive conclusions regarding the lack of older females in our samples, however, the use of otoliths as ageing structures has allowed for identification of this condition and provides a means by which to investigate the longevity of female central mudminnow in the future. We suggest that determination of reliable means of ageing other small, non-game fishes may lead to the discovery of unique life-history traits for a wide variety of species that have not been previously described. Such findings may ultimately prove useful in protecting and enhancing populations of threatened or endangered species and in efforts to manage for biologically diverse fish communities.

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