Variable growth and longevity of yellow bullhead (*Ameiurus natalis*) in the Everglades of south Florida, USA

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Summary

Yellow bullhead (Ictaluridae: *Ameiurus natalis*) is the most abundant ictalurid catfish in the Everglades of southern Florida, USA, and, as both prey and predator, is one of many essential components in the ecological-simulation models used in assessing restoration success in the Everglades. Little is known of its biology and life history in this southernmost portion of its native range; the present study provides the first estimates of age and growth from the Everglades. In total, 144 yellow bullheads of 97–312 mm total length (TL) were collected from canals and marshes of the Everglades between April 2000 and January 2001, and from October 2003 to February 2005. Fish were aged using cross-sections of pectoral spines and ranged from 1–12 years, with the maximum age almost twice that of any yellow bullhead previously reported. Yellow bullheads from south Florida grew relatively rapidly during their first 3 years, but after age 5 growth slowed and fish approached an asymptote of ∼214 mm TL. Compared to other populations in the United States, yellow bullhead in the Everglades grew relatively slowly, were smaller at age overall, but survived to older ages.

Introduction

A major effort is underway to restore historical ecological functions of the Everglades ecosystem in southern Florida by altering current hydrological management practices. The restoration process employs ecological-simulation models, such as the Across Trophic Level System Simulation (ATLSS), to guide and evaluate restoration alternatives. Because fishes are major prey and predator components of wetland food webs in southern Florida, they have been recognized as key indicators for measuring restoration success (Loftus et al., 2001; Trexler et al., 2001). Fish life-history traits, such as age and growth, must be known to build effective models of fish populations and communities, yet those traits remain poorly studied for many fish species in the Everglades.

The yellow bullhead (*Ameiurus natalis*) is native to eastern North America, with the Everglades comprising the southernmost portion of its native range (Loftus and Kushlan, 1987; Page and Burr, 1991). While the yellow bullhead is omnivorous over much of its range (Scott and Crossman, 1973; Becker, 1983; Laerm and Freeman, 1986; Sheldon and Meffe, 1993; Ross, 2001), it is mainly predatory in the Everglades system (Loftus, 2000). Its growth rates appear to vary according to environmental conditions (Schoffman, 1955; Ross, 2001; Boschung and Mayden, 2004). Although yellow bullhead is the most abundant ictalurid catfish in the Everglades (Loftus and Kushlan, 1987; Nelson and Loftus, 1996), there is no information on the age and growth for the species in southern Florida. This lack of information severely limits the ability of management agencies to predict effects on the population dynamics or resiliency of yellow bullhead populations in relation to changes in environmental conditions with altered hydrology.

The aim of the present study was to describe and model the age and growth of yellow bullhead from the Everglades. In addition, growth of yellow bullhead from the Everglades was compared with other regions to provide a more complete understanding of the variation and limits of yellow bullhead growth.

Materials and methods

Fish collections

Yellow bullheads were collected from boxcut canals and freshwater sloughs of the Everglades (Fig. 1). Fish were sampled during daytime using a boat-mounted, DC electrofishing unit with two-anode arrays, and a hull-cathode Smith-Root® generator-powered pulsator 9.0, with pulse frequencies ranging from 30 to 60 pulses per second. Fish were collected in April, July, October, and December of 2000, and in January 2001, from three canals: Tamiami Canal (C-4), Snake Creek Canal (C-9), and Canal L-31W (Fig. 1). All canals had limestone sides and bottoms with sand or marl sediment over the rock, and minimal submerged and emergent vegetation. During each sampling period, a 1-km segment of canal was sampled (ultimately covering a continuous reach of 4 km within each of the three canals). Despite the effort, few yellow bullheads were captured from canals: therefore, most fish for this study were collected during bimonthly sampling events from October 2003 to February 2005, mainly from sites within Everglades National Park (ENP) (Fig. 1). The same electrofishing system was mounted on an airboat (Chick et al., 1999) to collect bullheads along 100-m transects in shallow, densely vegetated marshes and open-water alligator ponds (Gunderson and Loftus, 1993).

Yellow bullheads were measured for total length (TL) and/or standard length (SL) (±1 mm) and weighed (±0.00 g). Total length was estimated for all fish measured only for SL by using a highly predictive ($r^2 = 0.99$) regression equation relating TL to SL based on previous measurement of a large number of yellow bullhead from south Florida (TL = 1.2034[SL] + 2.9847; L. G. Nico, unpublished data).
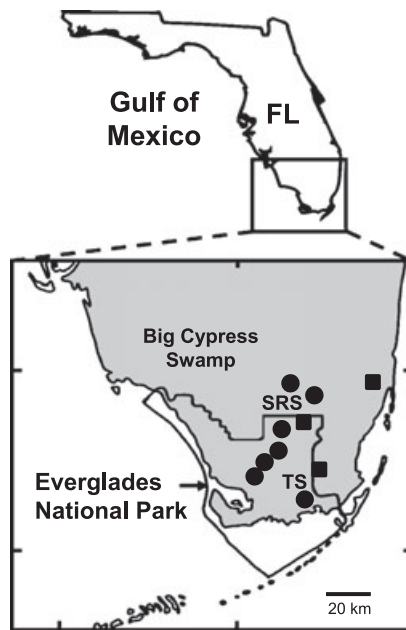
Fig. 1. Sampling sites for yellow bullheads (*Ameiurus natalis*) in marshes and alligator holes (filled circles) and canals (filled squares) in the Everglades of southern Florida, where SRS = Shark River Slough and TS = Taylor Slough

Both pectoral spines were removed at their articulation point, cleaned by immersion in hot water to remove skin and tissue, and stored dry.

Pectoral-spine processing

Pectoral spines were measured for length from the midpoint of the ventral process to the distal tip of the spine using calipers (Ultra-Cal Mark III, Fred V. Fowler Company, Newton, MA). Spine length was regressed on fish TL to determine if the growth of the pectoral spine was correlated with fish growth. The left pectoral spine was then prepared for ageing using modifications of Crumpton et al. (1987) and Nash and Irwin (1999). The spine was first mounted on a fully frosted slide with adhesive (Superglue, Loctite® Corporation, Rocky Hill, CT). Spines were cross-sectioned in ∼0.3-mm increments using a Buehler Isomet 1000 Variable-Speed Saw (Buehler®, IL) with a diamond-wafering blade (7.6 cm diameter by 0.15 mm wide). Sectioning started at the ventral process, continued past the articulating process, and was completed when sections distal to the basal recess were obtained (∼3–5 sections depending on the size of the spine). This process enabled the proximal sections to be examined for the appearance of annuli that otherwise might have been occluded by the lumen of sections more distal to the articulating process (similar to Buckmeier et al., 2002). Spine sections were washed in distilled water, air-dried, and permanently mounted on labeled slides using Flo-Texx® (Lerner Laboratories, New Haven, CT). Mounted spine sections were viewed on a black background with reflected light using a Leica® MZ12 stereomicroscope and fiber-optic light pipes. Annuli were discernible as alternating opaque and translucent zones and the translucent zones were enumerated for age estimates. The condition of the growth on the edge of the spine (translucent vs opaque) was also noted, as was the amount of growth. Categorizing the growth at the edge of the spine was necessary to assign fish to correct age classes for later comparison of age estimates between readers (see below).

To check the presence and location of the first annulus in the pectoral spines, a length-frequency histogram was derived for yellow bullhead sampled in the study. Spawning of yellow bullhead typically occurs between April and June (Harlan and Speaker, 1956; Scott and Crossman, 1973; Boschung and Mayden, 2004). Consequently, fish captured in the spring (prior to the anticipated spawning season), and that fell into the first mode of the length-frequency distribution, would be fish that had been born the previous year; fish from that cohort should have been almost one year old at the time of capture. Therefore, ages of fish in the first mode of the length-frequency histogram were examined to check whether they had been correctly assigned to age class 1 by the readers.

Age estimation

Ages were assigned to yellow bullhead on the basis that each completed annulus in the pectoral spines was deposited over a 12-month period. This was based on preliminary validation of the method for yellow bullheads using oxytetracycline(OTC)-tagged fish (Murie et al., 2006), as well as both OTC-tagged fish and marginal-increment analysis of several other species from the Everglades of southern Florida (Murie, 2002).

To determine within-reader precision, all pectoral-spine sections were aged by a primary reader (DJM) during two independent ageing sessions conducted three months apart. If the two age estimates agreed then that was considered the 'resolved' age for the fish. If the two estimates did not agree, a third, independent age was obtained in a third ageing session by the primary reader; agreement between two of the three age estimates was recorded as the resolved age. If none of the age estimates agreed, the median age was used as the resolved age. To determine between-reader precision, an age-stratified subset was read independently by a second reader (DCP); both readers had previous experience in ageing fin rays and spines. During ageing, readers did not know the size of the fish, collection date, or any other previously assigned age estimates from either reader. Comparative age estimates were obtained by assigning an age class to each individual fish based on using a birthdate of 1 January (Chilton and Beamish, 1982), with the condition of the growth zone at the margin of the spine taken into consideration. This method of assigning age classes ensured that fish born into the same cohort would be assigned into the same age class, despite being collected at different times of the year or having potential differences in their growth rates (Murie and Parkyn, 2005).

Ageing precision within and between readers was estimated by calculating: (i) the percent agreement between two independent ages (e.g. number of fish aged by Reader1 and Reader 2 that do not differ, expressed as a percentage of all fish aged by both readers); (ii) the average percent error (APE) (Chilton and Beamish, 1982); and (iii) the coefficient of variation (CV) (Kimura and Lyons, 1991). Percent agreement is the most commonly used indicator of precision, but APE and CV are considered to be 'age independent' and therefore provide better precision estimates over the range of ages observed for the species. The lower the APE or CV value, the greater the precision.

Growth of yellow bullhead

Wet mass of yellow bullheads was regressed as a function of TL to determine the length-related increase in mass. The von Bertalanffy growth equation (Ricker, 1975) was used to model

fish TL at age for yellow bullheads using non-linear regression analysis (SAS Institute Inc., 1999):

$$L_t = L_\infty(1 - e^{-k[t-t_0]}) \qquad (1)m1$$

where L_t is the predicted TL (mm) at time t (age, in years), L_∞ is the estimate of average maximum length (asymptotic length, mm), k is the growth coefficient, and t_o is the theoretical age (years) when fish length would be 0. For growth analysis, individual fish were assigned an absolute age based on a spawn date of 1 June, the assumed median value for spawning in yellow bullhead that typically ranges from April through June (Harlan and Speaker, 1956; Scott and Crossman, 1973; Boschung and Mayden, 2004). This period of the year also corresponded to completion of the translucent zone in the annulus of yellow bullhead (see Results). Absolute ages therefore allowed correction for the time of year that the fish were sampled without the need to back-calculate their length.

Results

Fish collections

In total, 144 yellow bullhead were collected from southern Florida (Fig. 1), ranging in length from 97 to 298 mm TL (Fig. 2), with most (> 90%) between 100 and 230 mm TL. Few (n = 8) yellow bullheads were taken from canal habitats during 2000–2001. Most (n = 136) fish were collected from marshes and alligator ponds in 2003–2005, with the majority taken in April 2004 (n = 97) during the dry season when bullheads were concentrated.

Pectoral-spine processing

Pectoral spines of yellow bullhead showed distinct translucent and opaque zones (Fig. 3). Preliminary observations indicated that sections taken above the basal recess consistently showed fewer annuli, both in the central-lumen area and on the edge of the spine structure, so those sections were not used in ageing. Instead, ages were obtained using sections through the articulating process below the basal recess and above the ventral process, similar to Buckmeier et al. (2002).

Identification of the first annulus in the pectoral spines was supported by the length-frequency distribution of yellow bullheads comprising the first mode in the length-frequency distribution that were collected in February and April. These fish were presumed to be approaching their first birthday based
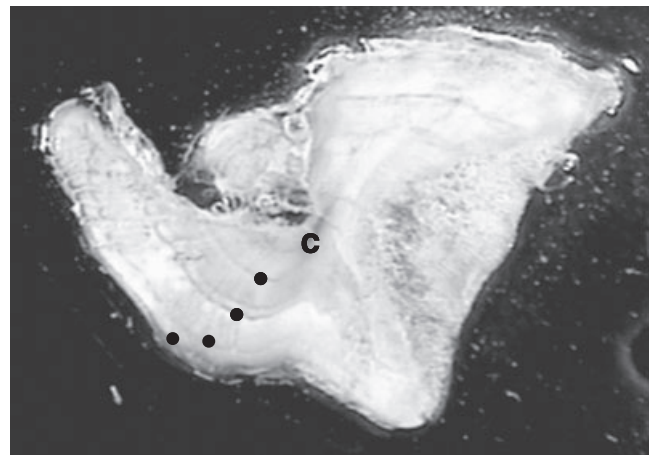
Fig. 3. Digital image of cross-section of pectoral spine from yellow bullhead (*A. natalis*) showing four annuli, with growth at the edge. Image taken under reflected light showing translucent zones of annuli (●) and core of the spine (C)

on an estimated spawning range of April through June. The fish ranged from > 95 to ~120 mm TL (Fig. 3). Of 15 yellow bullhead within this size range, 80% (n = 12) had been assigned an age of 1 year and 20% (n = 3) had been assigned to age 2. Though representing a small sample size, these results indicated that the first annulus had been interpreted correctly in the age assignments for the majority of fish.

Age estimation

Ages of yellow bullhead ranged from 1 to 12 years, with the oldest fish 220 mm TL and 132 g. The largest yellow bullhead aged was 298 mm TL and 287 g, and 5 years old. Yellow bullheads collected in February were evenly divided between having a translucent (52%) vs opaque (48%) zone at the edge of their pectoral spine. The majority of fish collected in April had a translucent zone at the edge (87%), whereas 100% of fish in August and 85% of fish in October had opaque zones at the edge. Qualitatively, this indicated that the opaque zone in the pectoral spine of individual bullheads was deposited variously between April and October; the translucent zone was formed sometime between October and April, but potentially as late as July because fish had an opaque growth zone by August.

For the primary reader, 69% (99 of 144) of pectoral-spine ages agreed between the first and second ageing session, with 92% agreeing within ±1 year. Of the 31% (n = 45) of spines not in perfect agreement within the primary reader, a third age estimate obtained during a final ageing session provided resolved ages for all but 6% (n = 9); resolved ages for these latter fish were obtained using the median age of the three age values.

Between two experienced readers, 65% (49 of 75) of the independent age readings of pectoral-spine sections of yellow bullhead were in complete agreement, 92% agreed within ±1 year, and all other readings differed by ±2 years (8%). Other measures of precision also indicated relatively low variability with CV = 8.6% and APE = 6.1%.

Growth of yellow bullhead

The relationship between pectoral-spine length (PSL) as a function of TL of yellow bullhead was described by:
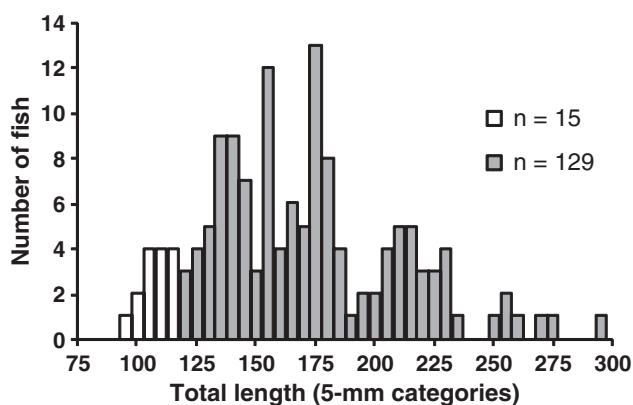

Fig. 2. Length-frequency distribution for yellow bullheads (*A. natalis*) collected from south Florida. Fish in the first length mode (white bars) were collected in February and April, prior to their first birthday

PSL $= 19.958 \text{Ln(TL)} - 80.278$ ($R^2 = 0.90$, n = 95, P < 0.001). Larger individuals had relatively longer pectoral spines, but pectoral-spine growth was not linear and the relative rate of spine growth decreased as fish TL increased. The relationship between weight (WT) and TL of yellow bullhead was allometric with an exponent < 3 and described by: WT $= 0.00004 \text{TL}^{2.9004}$ ($R^2 = 0.97$, P < 0.001).

Total length of yellow bullhead as a function of absolute age (Fig. 4) was adequately modeled using a von Bertalanffy growth equation, as indicated by model convergence and overall fit (P < 0.0001), described by:

$$L_t = 213.8(1 - e^{-0.4288[t+1.0755]})$$

where L_t is the predicted TL (mm) at time t (age, in years). In general, yellow bullheads increased in length quickly during their first 3 years, after which growth rate decreased substantially and began to plateau. After age 5, yellow bullhead growth approached an asymptotic length, estimated at 214 mm TL. Most notably, growth of yellow bullheads was extremely variable within and among all age classes. This variability was also evident in the low predictability ($R^2 = 0.48$) of the regression of pectoral-spine age as a function of spine length, which indicated that the age of individual bullhead could not be reliably predicted from its spine length.

Discussion

Yellow bullheads in the Everglades grew relatively slower and were smaller at age compared to other U.S. populations (Fig. 5). Their growth rate during the first 3 years was similar to that of populations from Oklahoma (Jenkins et al., 1952; Finnell et al., 1956) and Washington (Wydoski and Whitney, 1979), after which the latter populations attained much larger sizes with increasing age. Yellow bullheads have also been shown to have variable growth even within the same river drainage, with individuals from a tributary of the Mississippi River in western Mississippi being much smaller at ages 2–3 (< 200 mm SL, or ∼244 mm TL) compared with fish from Reelfoot Lake in the Mississippi River drainage of Tennessee (Ross, 2001); growth rate in the latter was much greater than that of yellow bullheads studied in other regions, including southern Florida. Yellow bullheads outside of Tennessee, however, have also been documented as attaining relatively
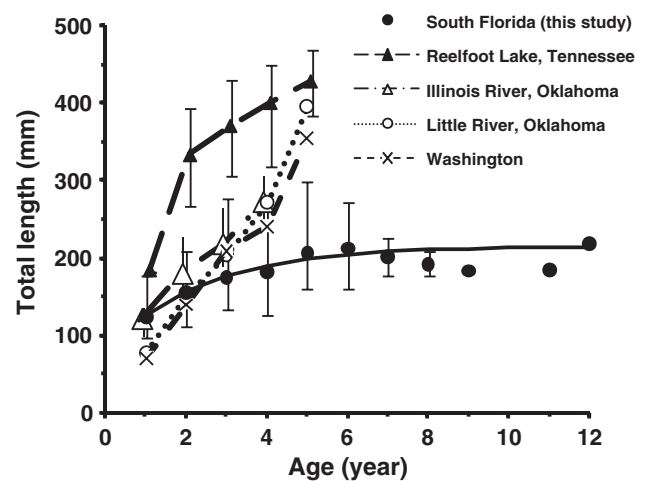
Fig. 5. Mean total length at observed age for yellow bullhead (*A. natalis*) collected from south Florida (this study), Illinois River and Tenkiller Reservoir, Oklahoma (Jenkins et al., 1952), Reelfoot Lake, Tennessee (Schoffman, 1955), Little River, Oklahoma (Finnell et al., 1956), and Washington (Wydoski and Whitney, 1979). Vertical bars denote size range of yellow bullhead at age for south Florida, Illinois River, and Reelfoot Lake and are offset from one another for clarity. Solid line = estimated von Bertalanffy growth curve for yellow bullheads from south Florida (this study)

larger sizes compared to those from southern Florida. According to the International Game Fish Association, the world all-tackle angling record for yellow bullhead is 1.92 kg (4.25 lb) for a fish caught in Mormon Lake, Arizona in 1984, although Sternberg (1987) reported an Illinois state record catch of 2.4 kg (5 lb 4 oz). In contrast, the maximum weight of any individual yellow bullhead in the present study was only 0.54 kg. Although yellow bullheads in southern Florida were characterized by slow growth and small size, they survived to a much older maximum age (12 years), which surpassed the previously reported maximum of seven years (Scott and Crossman, 1973).

The smaller size at age of yellow bullheads from southern Florida compared with yellow bullheads elsewhere in their native range indicated that the southern Florida populations are likely limited in their growth by biotic and abiotic factors. This variability in growth might be partially explained by density-dependent processes. For example, Ross (2001) reported that yellow bullheads were stunted when living in overpopulated ponds, an observation indicating food limitation. Limitations in prey resources in southern Florida also may result from intra- and interspecific competition, interference by other predators (e.g. abundant wading birds) and the oligotrophic nature of the wetlands (Turner et al., 1999). In addition, Loftus (2000) noted that feeding by many fishes in the Everglades is reduced during the spring dry season, a period when yellow bullheads and other fishes are concentrated in alligator (*Alligator mississippiensis*) holes and other aquatic refuges. Densities of large fishes in these pools are high, food resources are depleted, and water quality is typically poor (Loftus and Kushlan, 1987; Nelson and Loftus, 1996). Growth of fishes would therefore be slow under normal dry-season conditions, and exacerbated with the duration of the dry season artificially extended by current water-management practices.

In general, factors such as habitat quality and quantity influence the abundance and distribution of yellow bullhead and may also contribute to density-dependent growth
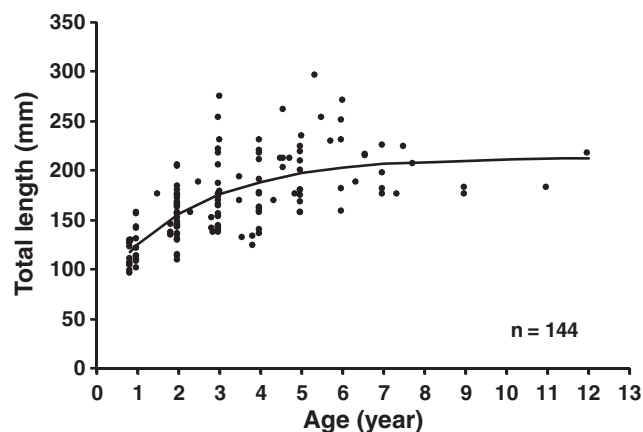

Fig. 4. Total length at capture as a function of absolute age estimate (assuming a 1 June birthdate) for yellow bullhead (*A. natalis*) from south Florida. Line represents estimated von Bertalanffy growth curve

regulation. Yellow bullheads tend to be most common in shallow, relatively clear-water portions of lakes and streams with dense vegetation (Scott and Crossman, 1973; Trautman, 1981; Laerm and Freeman, 1986; Loftus and Kushlan, 1987). The species also occurs in slow-moving waters rather than faster-flowing rivers (Scott and Crossman, 1973; Laerm and Freeman, 1986). Similarly, in south Florida, yellow bullheads were mainly taken in densely vegetated, shallow marshes, not in deepwater canals. In general, low densities and small maximum sizes are common among aquatic animals in southern Florida, patterns thought to be related to the oligotrophic nature of the local aquatic systems (Turner et al., 1999; Rice et al., 2005).

Yellow bullhead from the Everglades were aged using pectoral spines, a method that potentially underestimates ages in catfishes (Turner, 1982; Crumpton et al., 1987; Nash and Irwin, 1999; Buckmeier et al., 2002). Accurate ageing of some fish is problematic because the lumen of the spine potentially occludes the inner annuli, and the annuli at the edge of the spine section merge and become indistinguishable from one another (Nash and Irwin, 1999). For yellow bullhead in the present study, however, there may be no or little bias because spine sections were taken through the dorsal-anterior articulating process and had no or little lumen, and compacted annuli at the edge of the structure were still individually demarcated. Ageing some species of catfishes by otoliths may be a more precise (e.g. 85% agreement) and accurate method. This has been successfully applied to flathead catfish (*Pylodictis olivaris*) (Nash and Irwin, 1999), channel catfish (*Ictalurus punctatus*) (Buckmeier et al., 2002), and brown bullhead (*Ameiurus nebulosus*) (Maceina and Sammons, 2006). Attempts to age otoliths of yellow bullhead using a variety of procedures (Crumpton et al., 1987; Nash and Irwin, 1999; Buckmeier et al., 2002) were unsuccessful, with the failure of the latter method for yellow bullhead independently confirmed by D. Buckmeier (Texas Parks & Wildlife). Although ageing precision for yellow bullhead spines was relatively lower (65% agreement) than between-reader agreement using otoliths for other catfishes (85% agreement for both Nash and Irwin, 1999 and Buckmeier et al., 2002), the ageing precision did increase to 92% agreement within ± 1 year. This indicated that even minor improvements in ageing criteria would be beneficial. To date, using pectoral spines appears to be the only method of ageing yellow bullhead from the Everglades that is relatively precise and accurate.

Over the last century, human alterations of the south Florida landscape, especially the excavation of vast networks of drainage canals, have greatly changed the region's hydrology. Resulting changes in the duration and timing of seasonal flooding of the Everglades wetlands, in turn, have altered the structure of local fish communities (Trexler et al., 2005). In an attempt to reverse human-induced changes in the region's hydrology, major ecosystem restoration is underway (DeAngelis et al., 2005; CERP, 2005). One goal of the restoration effort is recovery of historic fish-community and abundance patterns (Ogden et al., 2003). Consequently, fishes are considered key indicators for measuring restoration success (Gunderson and Loftus, 1993; Trexler et al., 2001). Predicting or simulating responses by fishes to changes in hydrology from restoration requires simulation models that incorporate life-history parameters of yellow bullhead and other ecologically important fish species. Restoration of natural hydrology over the expanse of the Everglades should sustain large areas with shallow, slow-moving water and abundant vegetation,

a condition expected to positively influence age and growth and other biological processes in yellow bullheads and other native wetland organisms.

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