Reproductive Development in the Sicklefin Chub in the Missouri and Lower Yellowstone Rivers

DOUGLAS J. DIETERMAN[1], ERIC ROBERTS[2], PATRICK J. BRAATEN, and DAVID L. GALAT

School of Natural Resources, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO (DJD, ER)
U.S. Geological Survey, Fort Peck Project Office, Government Administration Building, East Kansas Street, Fort Peck, MT (PJB)
U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO (DLG)

ABSTRACT -- We describe aspects of sicklefin chub (*Macrhybopsis meeki*) reproductive development from three study areas encompassing greater than 2,700 km of the Missouri and Lower Yellowstone rivers. The sicklefin chub was collected between late July and early October in 1996 and 1997. A total of 193 sicklefin chub was collected and examined for reproductive characteristics. Twenty-nine sicklefin chub were found to be reproductively mature females. Some sicklefin chub matured at age 2, but most matured at age 3 and all matured by age 4. Females first became mature at 70 to 79 mm total length (TL) in the Upper Missouri River reach in central Montana, 80 to 89 mm TL in the Missouri and Lower Yellowstone rivers in eastern Montana-western North Dakota, and 90 to 99 mm TL in the lower Missouri River in Nebraska, Iowa, Kansas, and Missouri. Gonad mass of gravid females averaged 6.9% of total body mass and ranged from 1.7 to 13.5%. Total number of oocytes per female, ranged from 7 to 1,561. Reproductive development

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[1]Corresponding author. Current address: Minnesota Department of Natural Resources, Lake City Fisheries Research Office, 1801 South Oak St., Lake City, MN 55041. E-mail address: Douglas.dieterman@dnr.state.mn.us
[2]Current address: Montana Fish, Wildlife, and Parks, 930 West Custer Ave, Helena, MT 59620.

of the sicklefin chub appeared to be group synchronous or asynchronous indicating multiple spawnings during a spawning season. This variability in spawning mode required cautious interpretation of gonadosomatic index values and oocyte counts as estimates of total fecundity, because some females might have released a cohort of oocytes prior to their capture.

Key words: age at maturity, fecundity, *Macrhybopsis meeki*, Missouri River, reproduction, sicklefin chub, size at maturity, Yellowstone River.

The sicklefin chub (*Macrhybopsis meeki*) is a small minnow of large, turbid rivers in the central United States. It historically inhabited the entire mainstem Missouri River and Mississippi River downstream from the Missouri River's confluence (Pflieger 1997). Sicklefin chub declined in the Missouri River following construction of reservoirs along the middle one-third of the river (Werdon 1993, Hesse 1994, Galat et al. 2005). These reservoirs reduced turbidity, altered natural thermal and hydrologic regimes, and fragmented fish populations (Morris et al. 1968, Keenlyne et al. 1994, Galat and Lipkin 2000). In 1994, the United States Fish and Wildlife Service (USFWS) identified the sicklefin chub as a Federal Category 1 candidate species for listing under the Endangered Species Act of 1973 because of its reduced range. Range reduction likely was due to destruction and modification of habitat, such as altered thermal regimes, which might have impacted temperature dependent spawning cues, predation, and competition from non-native fishes (USFWS 1995). By 2000, the sicklefin chub was thought to occupy only 54% of its former range within the Missouri River system in three reproductively isolated populations (USFWS 2001). Although a petition for Federal listing of the sicklefin chub as endangered was denied (USFWS 2001), it currently is listed as critically imperiled or imperiled in six of the seven mainstem Missouri River states (NatureServe 2005).

Fundamental life history information can aid in the recovery of declining species. Currently, the life history of the sicklefin chub is poorly known. Baltz (1990) considered reproduction to be an essential life history aspect requiring study. Specifically, he listed four areas of primary concern: (1) age and size at maturity; (2) fecundity estimates; (3) spawning season, including environmental cues such as stream discharge and water temperature; and (4) spawning habitat.

Grisak (1996) studied the sicklefin chub in the Missouri River in central Montana and reported on some aspects of its reproduction. He collected gravid females and ripe males in 1994 and 1995 and reported sexual maturity at ages 2 to 4. Five gravid females and one ripe male were collected between 5 and 17 August 1994, when water temperatures averaged 21.7°C (range 19.7 to 22.7°C). Eleven gravid females were collected between 18 and 31 July 1995, when water temperatures averaged 21.3°C (range 20.5 to 22.5°C). Twenty-two ripe males were collected between 19 July and 16 August 1995, when water temperatures averaged 22.3°C (range 18 to 28°C).

These results suggest that the sicklefin chub might have a protracted spawning season in the Missouri River. A protracted spawning season could result from each female spawning multiple times (i.e., multiple or repeated spawner) or the population might exhibit asynchrony in gonadal development (de Vlaming 1983). For example, different aged fish might spawn at different times (Mills 1987) or different populations spawn at different times at different latitudes (Leggett and Carscadden 1978). Patterns of oocyte development can be discerned by plotting the frequency of oocytes in an ovarian sample as a function of oocyte diameter. Wallace and Selman (1981) found that three basic patterns of oocyte development can be revealed by examination of oocyte size distributions. Development is termed "synchronous" if all oocytes, once formed, grow in unison, and thus oocyte size-frequency distribution consists of a single mode. This mode of development is characteristic of semelparous fishes like anadromous salmon (*Oncorhynchus* spp.) and eels (*Anguilla* spp.).

"Group-synchronous" oocyte development occurs when at least two size classes of oocytes (i.e., bi-or multi-modal size distributions) can be distinguished in the ovary of a single female at some time during the spawning season. Each mode of similar-sized eggs is spawned at one time but several cycles of egg development and spawning can occur. An entire year might be required for one cycle to be completed in annual spawning fishes or it might only take a few weeks for fishes that spawn at multiple discrete times within one spawning season. This is the most common ovarian development type among teleost fishes (de Vlaming 1983).

Lastly, "asynchronous" oocyte development occurs when oocytes of all stages of development might be present (Murua and Saborido-Rey 2003). The oocyte size-frequency distribution is continuous except in ripe ovaries, where there might be a clear separation between ripe and yolked oocytes. Asynchronous spawning fishes continually develop and release oocytes. In some species, individuals might spawn a few eggs every day throughout a spawning season.

Asynchronous spawners presumably undergo multiple spawnings over a protracted spawning season, whereas group synchronous spawners might or might not spawn multiple times during the spawning season. However, the actual number of spawnings and the number of eggs released during each act cannot be assessed from oocyte size-frequency distributions alone, but must be determined from direct observations of spawning females (West 1990).

Although some information on sicklefin chub reproduction has been reported, information is lacking on its type of ovarian development and fecundity by size class. Also, size and age at maturity in the Missouri River at locations outside of Montana are lacking. The purpose of our study was to present preliminary information on the reproductive development of the sicklefin chub based on specimens collected as part of a study examining habitat use and population structure of benthic fishes in the Missouri and Lower Yellowstone rivers (Pierce et al. 2003, Berry et al. 2005). Our objectives were to determine: (1) age and size at maturity, (2) total number of oocytes and gonadosomatic indices (GSI), and (3) type of ovarian development for sicklefin chubs.

STUDY AREA

The Missouri River originates at the confluence of the Jefferson, Gallatin, and Madison rivers in western Montana and flows 3,768 km to its confluence with the Mississippi River near St. Louis, Missouri. The drainage basin encompasses 1,327,000 km^2 in portions of 10 states and four physiographic provinces; the Rocky Mountains, Great Plains, Central Lowlands, and Interior Highlands (Robinson 1986). The freeze-free season ranges from about 40 days in the extreme upper basin to greater than 120 days in the lower basin (Hesse et al. 1989).

Individuals of the sicklefin chub were collected from three river reaches separated by mainstem impoundments. The Upper Missouri River reach (UMR) was the Missouri River upstream from Fort Peck Dam, Montana, between river kilometer (rkm) 3,141.0 and 3,029.0. The Upper Inter-Reservoir reach (UIR) encompassed portions of the Missouri River between Fort Peck Dam and the headwaters of Lake Sakakawea, North Dakota (rkm 2,736.9 to 2,497.2) and the lower 114 rkm of the Yellowstone River, Montana. The third reach, Lower Missouri River (LMR), included the most downstream 958 rkm of the mainstem Missouri River below Gavins Point Dam, South Dakota, flowing through Iowa, Nebraska, Kansas, and Missouri. The UMR and UIR reaches were characterized by wide channels with islands, sand bars, and side channels. Tributary inputs and absence of an upstream impoundment on the Yellowstone River permit a semblance of the historical flow regime with high spring flows and low stable summer flows (Galat and Lipkin 2000). The LMR reach flowes through a single, often rock-lined channel confined by navigation structures and levees and has flows regulated to maintain navigation, reduce flood peaks, and provide hydroelectric energy production (Hesse et al. 1989).

METHODS

Individuals of the sicklefin chub were collected between late July and early October in 1996 and 1997 following standardized collection procedures (Sappington et al. 1996, 1997). Shallow water habitats, less than 1.2 m deep, were sampled with a 10.7 m long by 1.8 m high seine with 5 mm mesh and a 1.8 by 1.8 by 1.8 m center bag. Deep-water habitats, greater than 1.2 m, were sampled with a 2 m wide by 0.5 m high benthic trawl with a 3.2 mm inner mesh net. Water temperature

(°C) was measured at the surface at each collection site with a YSI Model 30 conductivity/water temperature meter. All specimens were fixed in 10% neutral buffered formalin and then transferred to 80% ethanol. Total length (TL) in millimeters and total body mass to the nearest 0.1 g were measured on preserved specimens in the lab. Scales were removed from these fish for aging and aged by following methods described in Braaten and Guy (2002). Scales were removed from an area between the lateral-line and dorsal fin insertion and mounted between glass slides. Scales were viewed at 50X magnification under transmitted light and two readers independently aged all fish. If readers did not agree on an age after two independent examinations, the fish was omitted. Annuli were determined most often by crowded circuli, indicative of slowing growth, or less frequently, by the presence of cut-over incomplete circuli. Although assigned ages were verified with our use of two independent readers, ages were not validated with formal methods such as recapture of previously marked, known-age individuals. We examined the following aspects of sicklefin chub reproductive development: age and size at sexual maturity; total number of oocytes present, GSI values, and oocyte size-frequency distributions for gravid females.

Gonads were classified as immature or mature based on gross examination of preserved tissues under a dissecting microscope following descriptions in Bagenal and Braum (1968), Lehtinen and Layzer (1988), and Crim and Glebe (1990) and by histological examination based on descriptions in Crim and Glebe (1990) and Takashima and Hibiya (1995), if gross examination was uncertain. Gonads for histological examination were prepared following standard histological methods and were stained with Mayer's hematoxylin and eosin (H&E) (Humanson 1967, Hinton 1990). Gonads were classified as immature if they were (1) visually transparent, very small, not visible to the naked eye and often difficult to identify under the dissecting microscope or (2) were larger, usually visible to the naked eye, and opaque but contained no mature cells. The extremely small size of the former precluded their histological preparation and sexual determination, whereas, histological examination of the latter, revealed only immature egg or sperm cells (e.g., primary oocytes or spermatocytes). Mature gonads were large and visible to the naked eye. Mature testes were white colored. Gravid ovaries were orange colored with numerous fully developed eggs present that were easily seen with the naked eye. Eggs were round and typically white-yellow colored. Ovaries subsequently were placed in Gilson's fluid following weighing to facilitate egg separation. Mature ovaries, based on histological examination, contained primary and tertiary yolk granule oocytes and often empty follicles indicating that some oocytes had been ovulated (Crim and Glebe 1990). Flaccid ovaries, either empty or nearly empty with little internal tissue present were considered spent. A few ova were present in some spent ovaries. All individuals classified as mature or spent were considered sexually mature adults.

The GSI was calculated as the ratio of ovarian mass to total body mass (Crim and Glebe 1990). Gonad mass was measured to the nearest 0.01 g after they had been blotted dry with a paper towel. Number of oocytes present was determined by using a dissecting microscope to make direct counts of oocytes from gravid females. The type of ovarian development was evaluated by examining size-frequency histograms of oocyte diameters of a random subsample of about 400 ova from each gravid female.

RESULTS

We collected and examined 193 individuals of the sicklefin chub. Fifty-one individuals were collected from the UMR reach, 85 from the UIR reach, and 57 from the LMR reach (Tables 1 and 2). Total lengths of all specimens ranged from 16 to 118 mm and ages were between 0 and 4 years old. The ratio of males to females was 0.85:1 for all specimens whose sex was determined (Tables 1 and 2). Only 29 specimens were reproductively mature females. Sixteen of these 29 females were gravid with large numbers (228 to 1,561) of eggs present, whereas three other females had only a small number (7, 27, and 189) of mature oocytes present (Table 3). These three females were classified as gravid also because their oocytes were large in size and easily seen. The remaining 10 mature females were considered

Table 1. Percent of mature fish at ages for sicklefin chub (*Macrhybopsis meeki*) collected from three reaches of the Missouri and lower Yellowstone rivers, July to October, 1996 and 1997. Numbers in parentheses are number of fish examined for each reach, age group, and sex. The UMR reach is the Missouri River upstream from Fort Peck Reservoir, Montana. The UIR reach includes the Missouri River between Fort Peck Dam and Lake Sakakawea and the lower Yellowstone River in eastern Montana and western North Dakota. The LMR reach is the lower Missouri River in Iowa, Nebraska, Kansas, and Missouri.

	UMR reach		UIR reach		LMR reach	
Age group	Female	Male	Female	Male	Female	Male
0	0%(9)*		(0)	(0)	0%(32)*	
1	0% (1)	0% (2)	(0)	0% (2)	0%(3)	0%(8)
2	5%(21)	23%(13)	25%(24)	17%(30)	17%(6)	67%(6)
3	100% (2)	(0)	92%(13)	100%(10)	100%(1)	100%(1)
4	100% (1)	(0)	100% (5)	100% (1)	(0)	(0)

*sex not determined.

spent. Eighteen of 19 gravid females were collected between the last week of July and mid-August when water temperatures averaged 21.6°C (Table 3). However, water temperatures were quite variable during sampling, ranging from 16.7 to 25.4°C (Table 3).

Sexual maturation

All collected individuals of sicklefin chub less than 2 years old were immature, whereas all 3 year old and older individuals, except one, were classified as mature (Table 1). Less than 50% of females in all three populations and of males in the UMR and UIR reaches were sexually mature at age 2. No age 4 and only two age 3 individuals were collected in the channelized LMR reach. Females first became sexually mature at 70 to 79 mm TL in the UMR, 80 to 89 mm TL in the UIR reach and at 90 to 99 mm TL in the channelized LMR reach (Table 2).

Table 2. Percent of mature sicklefin chub (*Macrhybopsis meeki*) for 10 mm length groups for three reaches of the Missouri and lower Yellowstone rivers, July to October, 1996 and 1997. Numbers in parentheses are total number of fish examined for each reach, length group, and sex. The UMR reach is the Missouri River upstream from Fort Peck Reservoir, Montana. The UIR reach includes the Missouri River between Fort Peck Dam and Lake Sakakawea and the lower Yellowstone River in eastern Montana and western North Dakota. The LMR reach is the lower Missouri River in Iowa, Nebraska, Kansas, and Missouri.

	UMR reach		UIR reach		LMR reach	
Length group TL (mm)	Female	Male	Female	Male	Female	Male
< 30	(0)	(0)	(0)	(0)	0%(18)*	
30-39	0% (2)	(0)	(0)	(0)	(0)	(0)
40-49	0% (7)	(0)	(0)	(0)	0%(3)	0%(4)
50-59	(0)	0% (2)	(0)	(0)	0%(1)	0%(1)
60-69	0% (5)	0% (3)	0% (2)	0% (2)	(0)	0%(4)
70-79	8%(12)	33% (9)	0%(10)	0%(10)	0%(1)	(0)
80-89	14% (7)	0% (2)	46%(13)	33%(18)	0%(3)	100%(1)
90-99	(0)	(0)	86% (7)	100% (5)	50%(2)	80%(5)
≥ 100	100% (2)	(0)	100%(11)	100% (5)	100%(1)	(0)

*sex not determined.

Table 3. Fish identification (ID) number, collection reach, date, water temperature at time of capture, age, total length (TL), gonadosomatic index value (GSI), total number of oocytes, and number of egg diameters measured for 19 gravid females of the sicklefin chub (*Macrhybopsis meeki*) collected in the Missouri and lower Yellowstone rivers, July to October 1996 and 1997. The UMR reach is the Missouri River upstream from Fort Peck Reservoir, Montana. The UIR reach includes the Missouri River between Fort Peck Dam and Lake Sakakawea and the lower Yellowstone River in eastern Montana and western North Dakota. The LMR reach is the lower Missouri River in Iowa, Nebraska, Kansas, and Missouri.

Fish ID number	Collection reach	Collection date	Water temperature (°C)	Age	TL (mm)	GSI	# oocytes	# of eggs measured
29	UMR	7/27/96	22.9	3	106	10.3	1,115	416
185	UMR	8/11/97	24.5	3	90	10.0	1,055	390
184	UMR	8/11/97	24.5	4	117	11.0	1,561	512
5	UIR	8/7/96	17.2	3	86	13.5	1,473	302
4	UIR	8/13/96	24.0	3	104	2.2	487	375
11	UIR	9/11/96	14.3	3	93		641	410
148	UIR	8/7/97	25.2	3	93	5.3	228	228
145	UIR	8/7/97	25.2	4	102	1.9	7	7
146	UIR	8/7/97	25.2	4	105	1.7	27	27
144	UIR	8/7/97	25.2	4	105	2.9	189	189
160	UIR	8/7/97	24.9	4	107	5.2	495	389
169	UIR	8/13/97	17.1	2	88	9.0	444	403
173	UIR	8/13/97	16.7	2	90	5.5	388	388
170	UIR	8/13/97	17.4	3	107	7.2	421	421

Table 3, continued.

Fish ID number	Collection reach	Collection date	Water temperature (°C)	Age	TL (mm)	GSI	# oocytes	# of eggs measured
179	UIR	8/14/97	17.6	2	90	5.3	411	411
180	UIR	8/14/97	17.6	2	99	4.6	419	419
168	UIR	8/15/97	16.8	3	104	7.6	617	413
71	LMR	8/13/96	25.4	3	112	8.1	1,104	406
200	LMR	7/31/97		2	92	12.5	702	469

Number of oocytes, gonadosomatic index, and ovarian development

Gonad mass of gravid females averaged 6.9% (SD = 3.6%) of total body mass and ranged from 1.7 to 13.5% (Table 3). However, fish identification numbers 145, 146, and possibly 144 might have been spent due to their nearly empty and flaccid ovaries. Excluding these fish, total number of oocytes present ranged from 228 to 1,561 (Table 3). Several specimens between 86 and 112 mm TL were collected in mid-August from different reaches and all had greater than 1,000 ova (fish 5, 71, 185), whereas other specimens of similar lengths contained fewer than 500 ova (fish 4, 173, 179) and had possibly released one or more clutches before capture. Consequently, number of oocytes per female was correlated only weakly with total length ($r = 0.26$, $P = 0.28$, $n = 16$). Egg diameter size-frequency histograms were generally unimodal, (Fig. 1). However, two gravid females showed a bimodal distribution in egg diameters (fish 184 and 11, Fig. 1).

DISCUSSION

Roff (1981) recommended using the lowest age or size at which one-half of a cohort reproduces as the definition of age or size at maturity for a population. Based on these criteria, reproductive maturity of sicklefin chub in the Missouri River tentatively occurs at age 3 and for fish exceeding 90 mm TL.

No spent female sicklefin chubs were collected in the LMR reach. Few gravid females (21% of total females collected) and low numbers of spent females in our collections might indicate post-spawn mortality. Trautman (1981) noted large numbers of dead, recently spawned individuals of the related silver chub (*M. storeriana*) washed up on the shores of Lake Erie during the spawning season in June and July in Ohio. If confirmed, the larger size at maturity for females of the sicklefin chub in the LMR reach coupled with a potential for post-spawn mortality could represent a population bottleneck in the lower river. Females of the sicklefin chub would need to grow and survive until they reach 90 mm TL to spawn in the lower river, but if substantial numbers of females die following spawning, most females of the sicklefin chub might only live to spawn once in the LMR reach. Alternatively, in upstream reaches, more females might be able to release eggs because smaller-sized females can spawn there. Some of these females might die from post-spawn mortality but some either survive to larger sizes or else similar-sized conspecifics do not reproduce, but instead, survive to spawn the following year. This would explain the wider size range of mature females in the UMR and UIR reaches compared with the LMR reach (Table 2).

Uneven sex ratios can reduce the genetically effective size (N_e) of small populations (Nelson and Soulé 1987, Meffe and Carroll 1997). We found females of the sicklefin chub (54%) to be more common than males (46%), a pattern common

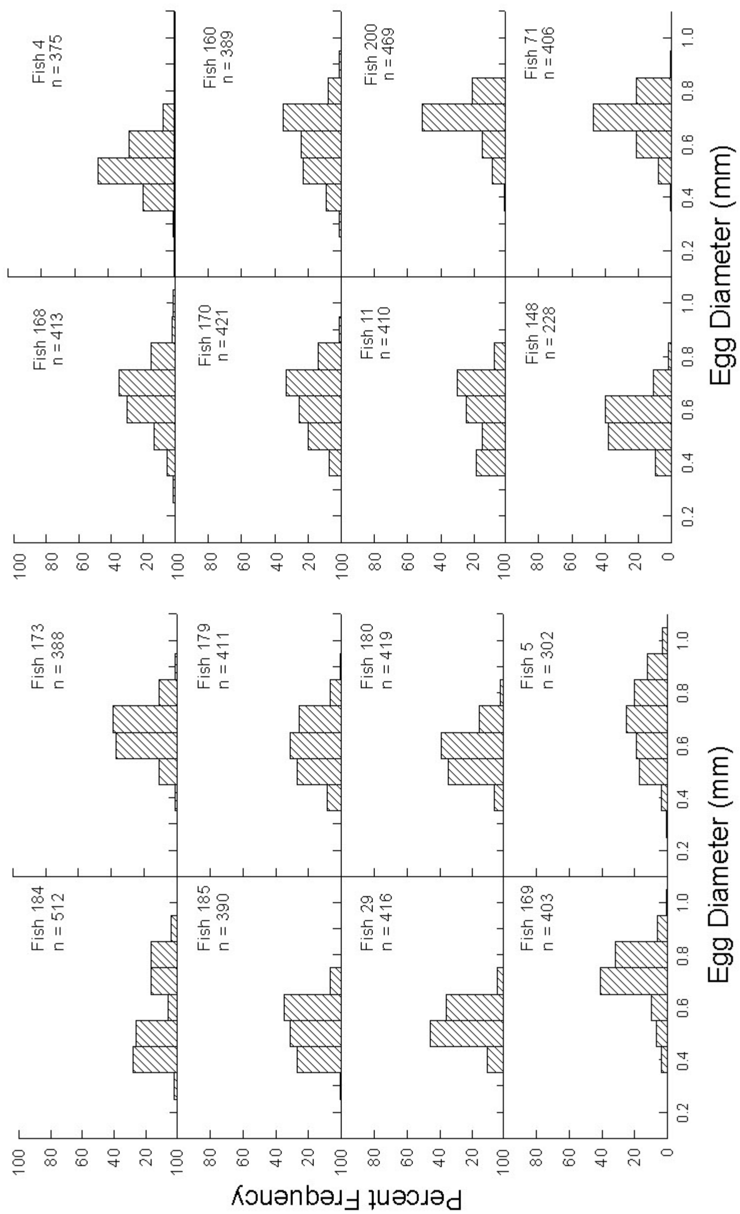

Figure 1. Size-frequency distributions of egg diameters (mm) for gravid females of the sicklefin chub (*Macrhybopsis meeki*) collected from the Missouri and Lower Yellowstone rivers, July to October, 1996 and 1997. Fish identification number and number (n) of eggs listed in each panel.

among many freshwater fishes (Bennett 1970). For example, Gould (1985) reported 51% of flathead chub (*Platygobio gracilis*) collected in selected Montana streams to be female, whereas 49% were male. A genetically adequate sex ratio for a population likely varies by species, but Meffe and Carroll (1997) provide a simple formula for calculating N_e based on the numbers of breeding males and females in a population. We do not know of any published estimates of sex ratios for sicklefin chub and therefore recommend using our ratio as a baseline for future studies. However, we acknowledge that some factors can affect these estimates, such as collecting fish in disproportion to their sex ratio. For example, if our largest numbers were collected in a particular habitat and most males where in some other habitat not well sampled, we might not have collected them in true proportion to their abundance in the entire river. Alternatively, sex can be miss-classified if gonads from immature fish or early seasonal development are used, although we tried to alleviate this by omitting immature fish from our sex ratio determination. Spawning sicklefin chub under controlled conditions and rearing the young might be necessary to help resolve estimates of true sex ratios.

Our results on ovarian development in conjunction with other information supported classifying the sicklefin chub as a group-synchronous or possibly an asynchronous spawner. Two individuals appeared to show group-synchronous ovarian development as indicated by a somewhat bimodal oocyte size-frequency distribution, whereas all other females exhibited a unimodal oocyte size-frequency distribution that would imply synchronous development. However, the wide range of number of oocytes per female for individuals of similar length (e.g., fish identification numbers 185, 173, and 179; Table 3) suggested some individuals might have released one or more clutches before capture. The first appearance of larval sicklefin/sturgeon chub (i.e., it is not presently possible to distinguish these two species at larval stages) in mid June in the LMR (Tibbs and Galat 1997) is consistent with our finding that some or all of the females collected in August already might have released one or more batches of eggs (i.e., multiple spawners), or that different fractions of the population spawn at different times. Others have reported collecting sicklefin/sturgeon chub larvae from mid-June through mid-September in various years in the LMR (Galat et al. 2004, Reeves 2005), which would indicate multiple spawning periods also. Finally, our observations of large diameter oocytes in sicklefin chub ranging from two to four years old indicated that individuals likely spawn more than once in their lifetime, which suggests that the species is iteroparous as are most cyprinids (Helfman et al. 1997). The bimodal oocyte size-frequency distribution in two fish, seasonal lateness of our collections, variable number of oocytes present per female, and large oocyte diameters in many females (Fig. 1, Table 3), coupled with a 3-month period when larval sicklefin/sturgeon chub have been collected by others argues against the species having synchronous ovarian development and for sicklefin chub exhibiting group-synchronous or asynchronous ovarian development. If so, the maximum number of oocytes we recorded (1,561) would be an underestimate of fecundity if individual sicklefin chub are multiple spawners and this female had released eggs previously. This is why we reported numbers of oocytes recorded per female, rather than referring to it as fecundity. Fecundity of the closely related sturgeon chub (*Macrhybopsis gelida*) was reported to range from 2,000 to approximately 5,300 immature and mature oocytes, but was based on only eight fish (Stewart 1981, Werdon 1992).

Group-synchronous or asynchronous ovarian development indicates that the species can spawn over a protracted spawning period, which is consistent with other fishes inhabiting highly variable environments, such as the Missouri River. Fishes with a limited spawning season, based on a narrow range of environmental cues, might risk loss of an entire year class if those proximate spawning cues are not realized in a given year. Even if a species successfully spawns, subsequent harsh environmental conditions, such as flooding, might kill all newly spawned eggs or larvae (Harvey 1987). Thus, in highly variable environments the most successful species might be those exhibiting protracted spawning seasons to ensure some individuals are able to survive sporadic harsh conditions (Matthews 1998). Numerous short-lived fishes inhabiting the variable streams and rivers of the Great Plains Region exhibit protracted spawning seasons (Starrett 1950, Fausch and Bestgen 1997, Dodds et al. 2004). Therefore, not surprisingly the sicklefin chub appears to have a similar reproductive strategy.

In summary, our results for sicklefin chub collected throughout most of the length of the Missouri River indicated that at least some individuals mature at age 2, but most mature at age 3. Females can produce over 1,000 oocytes that might compose more than 10% of their total body mass. Large differences in numbers of oocytes among similar sized individuals, the presence of bimodal egg size frequency peaks in some individuals, and the long period when larvae have been reported in the lower Missouri River lead us to hypothesize that the species is a protracted spawner and perhaps some individuals might be multiple spawners. These results are preliminary and should therefore not be over interpreted. They need to be more rigorously evaluated by collecting larger sample sizes of females of the sicklefin chub earlier and later in the year and conducting more detailed histological analyses of ovarian development. Laboratory studies, where spawning is induced (e.g., Platania and Altenbach 1998), can help determine their spawning mode, reproductive behavior, and egg type (e.g., demersal vs. pelagic). Such fundamental information on reproductive development and strategies is required for successful management of this and other imperiled small-bodied, big river fishes.

ACKNOWLEDGMENTS

We are grateful to the members of the Missouri River Benthic Fishes Consortium for collecting most of the specimens reported here. Jason Vokoun and Greg Wallace assisted with some field collections. We also thank Diana Papoulias and Mandy Annis, United States Geological Survey, Columbia Environmental Research Center, and Jennifer Johnson, United States Fish and Wildlife Service for their expertise on fish ovarian development, technical support, and use of equipment during histological preparation and examination of gonads. Diana Papoulias and Jennifer Johnson critically examined earlier drafts of our paper. Our research was funded by the United States Army Corps of Engineers and the United States Bureau of Reclamation. Our paper is a contribution of the Consortium and of the Missouri Cooperative Fish and Wildlife Research Unit (United States Geological Survey, Biological Resources Division; Missouri Department of Conservation; University of Missouri; and the Wildlife Management Institute cooperating).

LITERATURE CITED

Bagenal, T. B., and E. Braum. 1968. Eggs and early life history. Pp. 159-181 *in* Methods for assessment of fish production in fresh waters (W. E. Ricker, editor). International Biological Programme Handbook 3. Blackwell Scientific Publications, Oxford, England.

Baltz, D. M. 1990. Autecology. Pp. 585-607 *in* Methods for fish biology (C. B. Schreck and P. B. Moyle, editors). American Fisheries Society, Bethesda, Maryland.

Bennett, G. W. 1970. Management of lakes and ponds. Second edition. Robert E. Krieger Publishing Company, Malabar, Florida.

Berry, C. R., M. L. Wildhaber, and D. L. Galat. 2005. Fish distribution and abundance. Volume 3. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone Rivers. United States Geological Survey, Cooperative Research Units, South Dakota State University, Brookings. Available at: http://infolink.cr.usgs.gov/Science/BenthicFish/index.htm (Accessed 1 August 2005).

Braaten, P. J., and C. S. Guy. 2002. Life history attributes of fishes along the latitudinal gradient of the Missouri River. Transactions of the American Fisheries Society 131: 931-945.

Crim, L. W., and B. D. Glebe. 1990. Reproduction. Pp. 529-553 *in* Methods for fish biology (C. B. Schreck and P. B. Moyle, editors). American Fisheries Society, Bethesda, Maryland.

de Vlaming, V. L. 1983. Oocyte development patterns and hormonal involvements among teleosts. Pp. 176-287 *in* Control processes in fish physiology (J. C. Rankin, T. J. Pritcher and R. T. Duggan, editors). Croom Helm, London, England.

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54:205-216.

Fausch, K. D., and K. R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pp. 131-167 *in* Ecology of Great Plains vertebrates and their habitats (F. L. Knopf and F. B. Samson, editors). Springer-Verlag, New York, New York.

Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. Pp. 249-291 *in* Historical changes in large river fish assemblages of the Americas (J. N. Rinne, R. M. Hughes, and B. Calamusso, editors). American Fisheries Society Symposium 45, Bethesda, Maryland.

Galat, D. L., and R. Lipkin. 2000. Restoring the ecological integrity of great rivers: historical hydrographs aid in defining reference conditions for the Missouri River. Hydrobiologia 422/423:29-48.

Galat, D. L. G. W. Whitledge, and G. T. Gelwicks. 2004. Influence of lateral connectivity on larval fish assemblage structure and habitat use in lower Missouri River floodplain waterbodies. Final Report to Missouri Department of Conservation. Missouri Cooperative Fish and Wildlife Research Unit, Columbia.

Gould, W. 1985. Aspects of the biology of the flathead chub (*Hybopsis gracilis*) in Montana. Great Basin Naturalist 45:332-336.

Grisak, G. G. 1996. The status and distribution of the sicklefin chub in the Middle Missouri River, Montana. M.S. Thesis. Montana State University, Bozeman.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851-855.

Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The diversity of fishes. Blackwell Science, Inc., Malden, Massachusetts.

Hesse, L. W. 1994. The status of Nebraska fishes in the Missouri River, 5. selected chubs and minnows (Cyprinidae): sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), silver chub (*M. storeriana*), speckled chub (*M. aestivalis*), flathead chub (*Platygobio gracilis*), plains minnow (*Hybognathus placitus*), and western silvery minnow (*H. argyritis*). Transactions of the Nebraska Academy of Science 21:99-108.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present and future stresses. Pp. 352-371 *in* Proceedings of the International Large River Symposium (D. P. Dodge, editor). Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Hinton, D. E. 1990. Histological techniques. Pp. 191-211 *in* Methods for fish biology (C. B. Schreck and P. B. Moyle, editors). American Fisheries Society, Bethesda, Maryland.

Humanson, G. L. 1967. Animal tissue techniques, second edition. W. H. Freeman and Company, San Francisco, California.

Keenlyne, K. D., C. J. Henry, A. Tews, and P. Clancey. 1994. Morphometric comparisons of Upper Missouri River sturgeons. Transactions of the American Fisheries Society 123:779-785.

Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alsoa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35:1469-1478.

Lehtinen, S. F., and J. B. Layzer. 1988. Reproductive cycle of the plains minnow, *Hybognathus placitus* (Cyprinidae), in the Cimarron River, Oklahoma. Southwestern Naturalist 33:27-33.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York, New York.

Meffe, G. K., and C. R. Carroll. 1997. Genetics: conservation of diversity within species. Pp. 161-201 *in* Principles of conservation biology, second edition (G. K. Meffe and R. C. Carroll, editors). Sinauer Associates, Inc., Sunderland, Massachusetts.

Mills, C. A. 1987. The history of the minnow *Phoxinus phoxinus* (L.) in a productive stream. Freshwater Biology 17:53-67.

Morris, L. A., R. N. Langemeier, T. R. Russell, and A. Witt, Jr. 1968. Effects of main stem impoundments and channelization upon the limnology of the Missouri River, Nebraska. Transactions of the American Fisheries Society 97:380-388.

Murua, H., and F. Saborido-Rey. 2003. Female reproductive strategies of marine fish species of the North Atlantic. Journal of the Northwest Atlantic Fishery Science 33:23-31.

NatureServe. 2005. NatureServe Explorer: An online encyclopedia of life [web application]. Version 1.8. NatureServe, Arlington, Virginia. Available at: http://www.natureserve.org/explorer (Accessed 1 June, 2005).

Nelson, K., and M Soulé. 1987. Genetical conservation of exploited fishes. Pp. 345-368 *in* Population genetics and fishery management (N. Ryman and F. Utter, editors). University of Washington Press, Seattle, Washington.

Pflieger, W. L. 1997. The fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City, Missouri.

Pierce, C. L., C. S. Guy, P. J. Braaten, and M. A. Pegg. 2003. Fish growth, mortality, recruitment, condition, and size structure. Volume 4. Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. United States Geological Survey, Cooperative Research Unit, Iowa State University, Ames. Available at: http://infolink.cr.usgs.gov/Science/BenthicFish/index.htm (Accessed 1 August 2005).

Platania, S. P., and C. S. Altenbach. 1998. Reproductive strategies and egg types of seven Rio Grande basin cyprinids. Copeia 1998:559-569.

Reeves, K. S. 2005. Habitat use by larval fishes in the lower Missouri River. Ph.D. Dissertation. University of Missouri, Columbia.

Robinson, H. W. 1986. Zoogeographic implications of the Mississippi River Basin. Pp. 267-285 *in* The zoogeography of North American freshwater fishes (C. H. Hocutt and E. O. Wiley, editors). John Wiley and Sons, New York, New York.

Roff, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Canadian Journal of Fisheries and Aquatic Sciences 38:968-977.

Sappington, L., D. Dieterman, and D. Galat (editors). 1996, 1997. Standard operating procedures to evaluate the population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone Rivers. Columbia Environmental Research Center, Biological Resources Division, United States Geological Survey, Columbia, Missouri. Available at: www.cerc.cr.usgs.gov/pubs/pubs.html (Accessed 18 May 2005).

Starrett, W. C. 1950. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. Ecology 32:13-27.

Stewart, D. D. 1981. The biology of the sturgeon chub (*Hybopsis gelida* Girard) in Wyoming. M.S. Thesis. University of Wyoming, Laramie.

Takashima, F., and T. Hibiya. 1995. An atlas of fish histology, normal and pathological features. Second edition. Kodansha Ltd, Tokyo, Japan.

Tibbs, J. E., and D. L. Galat. 1997. Larval, juvenile, and adult small fish use of scour basins connected to the Lower Missouri River. Final Report, Missouri Department of Conservation, Columbia, Missouri.

Trautman, M. B. 1981. The fishes of Ohio. Revised edition. Ohio State University Press, Columbus, Ohio.

USFWS (United States Fish and Wildlife Service). 1995. Endangered and threatened wildlife and plants; Notice of 90-day finding on the petition to list the sturgeon chub and sicklefin chub as endangered. Federal Register 60:3613-3615.

USFWS (United States Fish and Wildlife Service). 2001. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the sicklefin chub (Macrhybopsis meeki) and sturgeon chub (*Macrhybopsis gelida*) as endangered. Federal Register 66:19910-19914.

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. American Zoologist 21:325-343.

Werdon, S. J. 1992. Population status and characteristics of *Macrhybopsis gelida*, *Platygobio gracilis* and *Rhinichthys cataractae*. M.S. Thesis. South Dakota State University, Brookings.

Werdon, S. J. 1993. Status report on sicklefin chub (*Macrhybopsis meeki*), a candidate endangered species. United States Fish and Wildlife Service, Ecological Services, Bismarck, North Dakota.
West, G. 1990. Methods of assessing ovarian development in fishes: a review. Australian Journal of Marine and Freshwater Research 41:199-222.

Received: 21 November 2005 *Accepted: 2 October 2006*

Associate Editor for Ichthyology: Brian G. Blackwell