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Population Dynamics of Flathead Catfish in the Lower Minnesota River

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INTRODUCTION

Minnesota is at the northern edge of the Flathead Catfish *Pylodictis olivaris* native range, which extends southward in the Mississippi and Rio Grande drainages into Mexico (Lee and Terrell 1987; Jackson 1999). The natural distribution of the Flathead Catfish in Minnesota is limited to the Mississippi River drainage downstream from St. Anthony Falls, the St. Croix River drainage downstream from Taylor's Falls, and the Minnesota River drainage downstream from Granite Falls (Eddy and Underhill 1974; Kirsch et al. 1985; Underhill 1989).

The Flathead Catfish is one of the most important game fish in the Minnesota River (Stauffer et al. 1996), and the fishery is likely to become an even more valuable resource in the future as catfish angling gains in popularity (Arterburn et al. 2002). In addition to being an important game fish, the Flathead Catfish is the apex predator in the Minnesota River. Introduced Flathead Catfish populations have suppressed prey fish communities in Minnesota and elsewhere in North America (Davis 1985; Dobbins et al. 1999; Jackson 1999; Odenkirk et al. 1999). In the Minnesota River, the native Flathead Catfish may also play a keystone role in top-down structuring of the fish community by consuming substantial biomass of less desirable species such as Common Carp *Cyprinus carpio* (Davis 1985).

The Flathead Catfish population in the Minnesota River has experienced a long history of conservative fishing regulations. For many years Minnesota catfish anglers have been limited to a single attended line with one hook or lure; set lines, jug fishing, noodling, etc. are not legal. From 1966-2002 the possession limit on the Minnesota River was 5 combined Channel Catfish *Ictalurus punctatus* and Flathead Catfish. Since 2003, the possession limit for Flathead Catfish has been two with only one of these over 24 in, and since 2015 the season has been closed from December 1 through March 31 to protect concentrations of overwintering fish. There is no commercial fishing for catfish in the Minnesota River. Exploitation rates of Flathead Catfish in the Minnesota River have not been quantified, but they were suspected to be low due to the restrictive regulations, traditional Minnesota angler preferences for other species, and specialized angling methods typically required to catch Flathead Catfish. However, anecdotal evidence indicates that a growing number of anglers have been targeting large Flathead Catfish in recent years, and there is concern this could lead to a decline in the quality of the fishery if current regulations are inadequate to prevent substantial numbers of these large fish from being harvested.

Prior to this study, limited information was available on Minnesota River Flathead Catfish population characteristics (Stauffer et al. 1996; Stauffer and Koenen 1999; Minnesota Department of Natural Resources, unpublished data). Results of Stauffer et al. (1996) indicated a lightly exploited population with a high-quality size structure and consistent recruitment; however, there was concern that the situation might have changed since their data were collected, and also their sampling was only conducted upstream from New Ulm. Obtaining more detailed and current information farther downstream was important to Minnesota fisheries managers because of differences in the fishery of the lower river such as higher stream order, greater potential influence of emigration to and immigration from the Mississippi River, more urbanization, and greater angling effort.

Similar to other populations in the northern part of the species' range (Vokoun and Rabeni 2005; Gelwicks and Simmons 2011; Piette and Niebur 2011), Flathead Catfish in the Minnesota River may migrate many river kilometers between wintering and spawning habitats, but tend to establish small post-spawning home ranges during late summer (Stauffer et al. 1996; Shroyer 2011). I sampled during the late-summer post-spawning period because it represents a time when fish are essentially non-migratory and dispersed throughout suitable summer habitat; in addition, flows are usually relatively low and stable, minimizing potential effects of flow variation on capture efficiency.

In the Minnesota River, low-frequency electrofishing was shown to be effective at sampling juvenile Flathead Catfish, and trotlining was effective at sampling adult fish (Stauffer and Koenen 1999). Therefore, Stauffer and Koenen (1999) recommended a combination of low-frequency electrofishing and trotlining to sample the entire size range of flathead catfish in the Minnesota River. However, preliminary work during 2010 and 2011 showed that large-diameter, small-mesh unbaited hoop nets were effective at sampling a wide size range of Flathead Catfish in the lower Minnesota River during late summer. Hoop netting has the advantages of being less labor intensive than either low-frequency electrofishing or trotlining, less weather- and flow-dependent than electrofishing, and much safer than trotlining. Therefore, I chose to sample with hoop nets both because of their preliminary efficiency and to further evaluate the gear type in the Minnesota River.

Capture-recapture experiments have rarely been attempted for riverine Flathead Catfish, and with the exception of Pine (2003), they have all relied on traditional closed-population methods such as the Schnabel multiple census (Ricker 1975), with no consideration of potentially more appropriate closed-population models such as those described by Otis et al. (1978), and usually with little or no justification for assuming both geographic and demographic closure (e.g., Scott 1950; Morris et al.1971; Quinn 1988; Dobbins et al. 1999; Daugherty and Sutton 2005). The tendency has been to focus on the assumption of geographic closure (e.g., Quinn 1988; Dobbins et al. 1999; Daugherty and Sutton 2005) while ignoring the equally important assumption of demographic closure (i.e., negligible recruitment and mortality). In this study I use a rigorous approach similar to that of Pine (2003): considering alternative closed-population and open-population models with different assumptions; assessing model parsimony and goodness of fit; and discussing effects of potential violations of assumptions.

METHODS

We sampled Flathead Catfish from four reaches in the lower Minnesota River (Table 1; Figure 1) during August of 2013, 2014, and 2015 (Table 2) when discharge was 33-122 m^3/s at the nearest U.S. Geological Survey stream gauges (Figure 2). Sampling was also planned for the same four reaches during 2016, but due to boat landings blocked by deposited sediment as the river receded from unusually high stages during the first week of August, followed almost immediately by exceptionally high discharge for the rest of the month (Figure 2), we were only able to sample the LeSueur reach. The LeSueur and Jordan reaches were rural locations with mostly unmodified banks and abundant coarse woody structure. The Mankato reach was an urban location with predominantly riprapped banks and little coarse woody structure. The Shakopee reach was in the Twin Cities Metro Area, with moderately abundant coarse woody structure, a potentially strong influence of the Mississippi River fish community, and a large potential angler population nearby. The order in which reaches were sampled was chosen randomly the first year, and then the order was rotated in each subsequent year to avoid producing misleading differences in catches among reaches due to any consistent trends in river conditions or fish behavior from early to late August.

TABLE 1. Geographic coordinates of the study reaches in the lower Minnesota River.

Reach	Downstream end	Upstream end
Shakopee	44.80153°, -93.53676°	44.79382°, -93.58024°
Jordan	44.69487°, -93.64488°	44.68638°, -93.67834°
LeSueur	44.45985°, -93.92409°	44.43528°, -93.93355°
Mankato	44.18057°, -94.00375°	44.16469°, -94.03647°

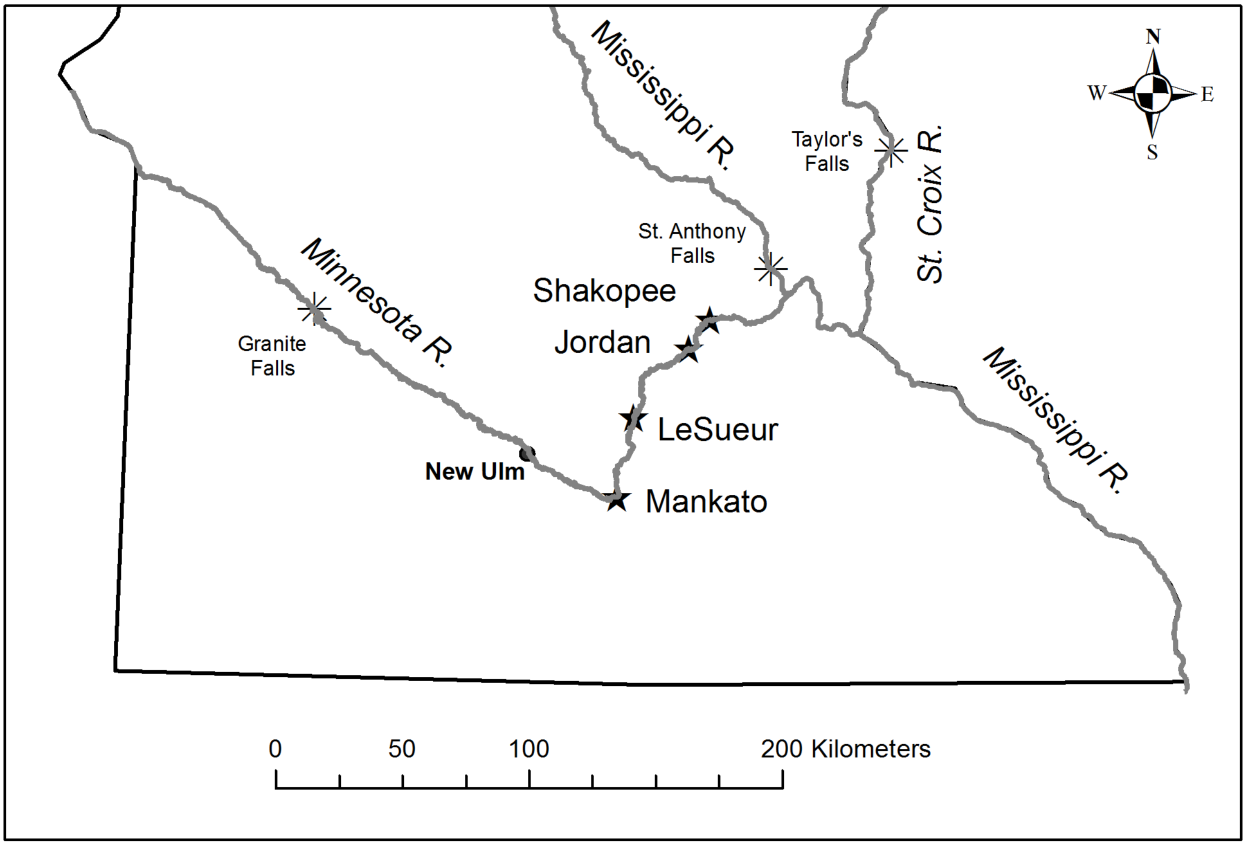

FIGURE 1. Locations of the four study reaches (starred) and other geographic features in southern Minnesota.

TABLE 2. Dates of sampling each study reach in the lower Minnesota River during August, 2013-2015.

Reach	2013	2014	2015	2016
Jordan	8/5-8/9	8/11-8/15	8/17-8/21	NA
Mankato	8/12-8/16	8/18-8/22	8/24-8/28	NA
LeSueur	8/19-8/23	8/25-8/29	8/3-8/7	8/8-8/11
Shakopee	8/26-8/30	8/6-8/8	8/10-8/14	NA

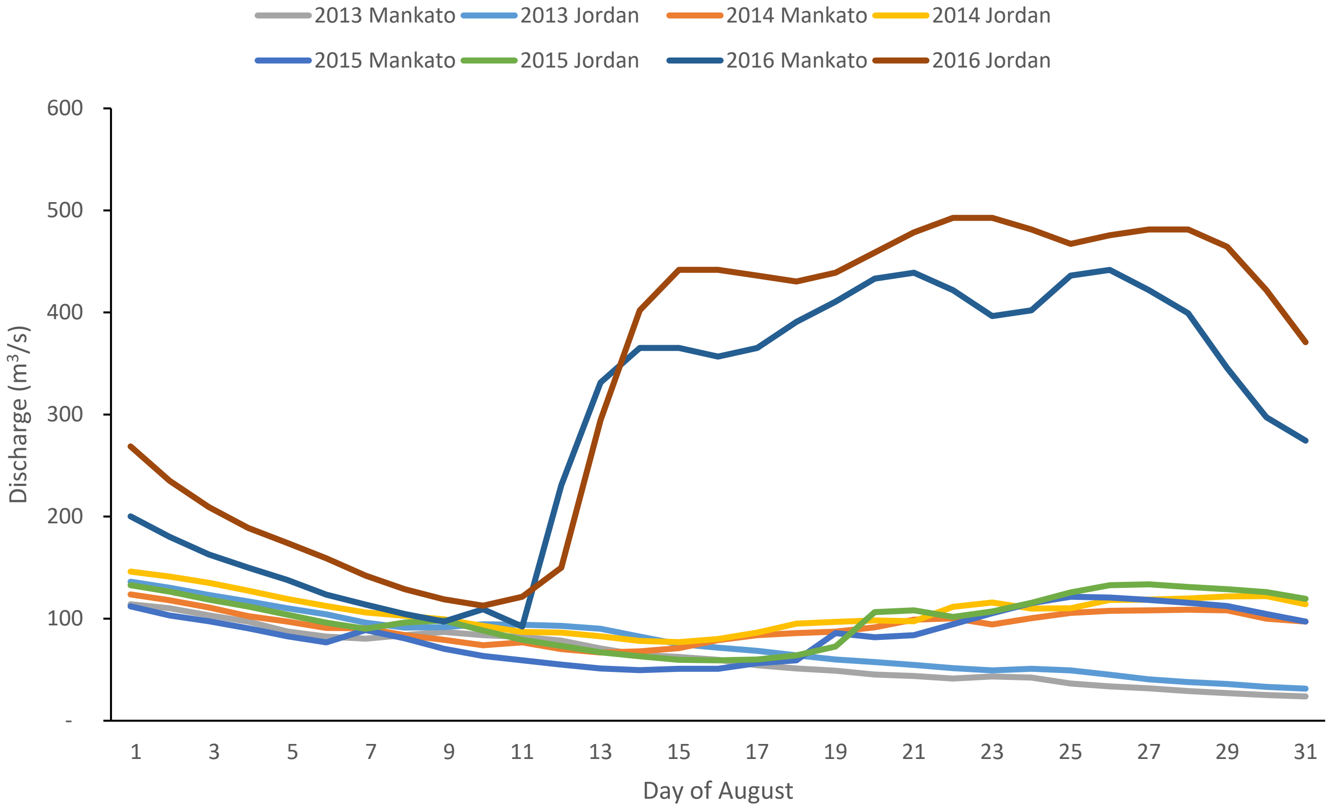

FIGURE 2. Discharge (m^3/s) of the Minnesota River at 12 am Central Daylight Time during each day of August, 2013-2016 at two U.S. Geological Survey gauges. The 2016 data are provisional.

Within each 4-km reach, we fished 15 large unbaited hoop nets for four consecutive nights, except the Shakopee reach in 2014 when there were only two effective nights of effort due to major problems with the net sets the first two nights; and the LeSueur reach in 2016 when we had to retrieve the nets after three nights due to an excessive increase in discharge. The hoop nets had a total length of 4.9 m; seven fiberglass hoops tapering from 1.2 m at the front to 1.0 m at the back; 2.5-cm-square knotted mesh of size 15 twine with black asphalt net coat treatment; hand-tapered finger-size throats on the second and fourth hoops, with the first throat tied to the fifth hoop; and a rope bridle across the mouth of the net. The nets were spaced as uniformly as possible throughout each reach while attempting to set in locations favorable for maximizing catches of Flathead Catfish (e.g., near vertical banks and coarse woody structure on outside bends). Potential net locations were initially investigated with a Lowrance® Elite-5 DownScan Imaging™ sonar to minimize snagging on submerged woody structure. Each net was deployed with a 4.5-9.1 kg navy anchor (and usually an anchor chain) attached to the cod end with a 4.5-m rope and snap swivel; the mouth of the net extending downstream (unanchored); and a marker buoy attached to the bridle with a 9-m rope and snap swivel. Water depths at the front hoop ranged from 0.8 to 5.0 m (median = 2.0 m). Nets were set one morning and lifted the next morning. Water temperatures when nets were set or lifted ranged from 18.0° to 28.0° C (median = 24.1° C). Nets were generally reset in the same locations each day, but occasionally a net was moved after the first set or two due to problems with snags, excessive current velocities, or eddies. Most nets were set in virtually the same locations each year, but a few had to be relocated short distances within the study reaches because previous locations were no longer favorable for hoop nets.

Upon retrieval of each hoop net, all captured Flathead Catfish were placed in a stock tank of fresh river water. After 2013, bottled oxygen was bubbled from a diffuser and salt was added to the stock tank to reduce stress. All newly-captured Flathead Catfish ≥ 25 cm TL (except six larger fish captured on the last day of sampling during 2015) were implanted with a glass-encapsulated 12 mm X 2 mm, 134.2 kHz, FDXB PIT tag in the cephalic portion of the adductor mandibularis muscle immediately posterior to the left eye. This tagging location was used to virtually eliminate the possibility of accidental human ingestion, and it had been shown to have a high retention rate (Daugherty and Buckmeier 2009). Tags were scanned immediately after implantation to insure they were functional, and each tagged fish had the entire adipose fin removed as a secondary mark to enable estimation of the tag loss rate. All Flathead Catfish were scanned for a previously-implanted PIT tag and measured the first time they were captured in a given year. In 2013 an entire pectoral spine was removed from each newly-tagged fish for age and growth analysis, except for one fish that was captured with both spines broken, and five large fish when attempts to remove entire spines without substantial injury to the fish were unsuccessful. Pectoral spines were quickly and easily removed from small Flathead Catfish with little apparent injury to the fish, but it was difficult to disarticulate the spines from large Flathead Catfish (over about 80 cm). Although disarticulation and removal of entire pectoral spines from catfish is common practice (e.g., Stauffer et al. 1996) and reportedly nonlethal to Channel Catfish (Stevenson and Day 1987; Michaletz 2005), removing the spine from a large Flathead Catfish was often time consuming and considered overly stressful and harmful to the fish. Spine removal from the larger Flathead Catfish often required cutting around the articulating process to sever tough connective tissue, followed by strenuous wiggling and twisting of the spine with pliers, which resulted in a large, sometimes profusely bleeding wound. This procedure probably contributed to behavioral effects or even post-release mortality that could have affected the capture-recapture results. Therefore, after 2013, pectoral spines were only removed from newly-tagged fish < 71 cm TL. Fish were released within 100 m of their capture locations, but not in immediate proximity to deployed nets.

Hoop net CPUE was calculated as both catch per net-night and catch per night (15 net-nights), but catch per night was used in modeling and hypothesis testing because its sampling distribution was more symmetrical and did not include zeroes. The size structure of the catch was summarized using the standard length categories for Flathead Catfish recommended by Bister et al. (2000): Stock ≥ 35 cm; Quality ≥ 51 cm; Preferred ≥ 71 cm; Memorable ≥ 86 cm; and Trophy ≥ 102 cm.

The hoop netting and PIT tagging were planned as a robust design experiment using within-year data to obtain closed-population abundance estimates and among-year data to estimate apparent survival after accounting for any temporary emigration (Williams et al. 2002). Alternatively, conventional open-population estimates of abundance, apparent survival, and recruitment + immigration were obtained from POPAN Jolly-Seber models (Schwarz et al. 1993; Schwarz and Arnason 1996). Models were fitted in Program MARK Version 6.1 (Program MARK 2017). Closed-population models were limited to the "Full Likelihood *p* and *c*" option within Program MARK because the data did not support more complex models. Potentially useful models were selected based on estimability of parameters, bias-corrected Akaike information criteria (AICc), and examination of residual plots. Models were considered to fit reasonably well if none of the deviance residuals were outside the bounds of ± 2 when c-hat was set to the default value of 1. Program MARK Version 6.1 did not produce meaningful residual plots for POPAN Jolly-Seber models, so I examined residual plots for the equivalent Link-Barker Jolly-Seber models instead. Both closed-population and open-population models were fitted to various length groups (at the time of marking) to account for potential length-based heterogeneity in capture probabilities and to allow comparing abundance estimates for individual length groups to length frequencies of the hoop net catches. Closed-population models were fitted separately to each reach, but reaches were pooled for open-population models to maximize the precision of parameter estimates.

Pectoral spines and attached tissue were air-dried for several days after collection and then stored in labeled coin envelopes until cleaning and sectioning. The cleaning process involved:

1) Pulling off any easily removable skin, muscle, or connective tissue and clipping off the excess distal end of the spine with side-cutting pliers.
2) Soaking the spine in an individually labeled vial overnight in a solution of approximately 75 mL of Biz® detergent booster dissolved in 1 L of water.
3) Removing the softened skin, muscle, and connective tissue using a scalpel, forceps, and side-cutting pliers.
4) Rinsing the spine three times with water, then soaking the spine overnight in its vial with a 50:50 ammonia: water solution.
5) Rinsing the spine three times with water, then placing it back in its vial with 50% isopropyl alcohol until sectioning.

After thorough cleaning, spines were cross-sectioned through the approximate center of the articulating process to avoid losing early annuli to the central lumen (Turner 1982). At least two 0.030-in-thick sections were cut from each spine using a Buehler IsoMet® low-speed saw, 15 HC - 4 in wafering blade, and IsoCut® fluid. After sectioning, all pieces of each spine were blotted with paper towels and placed back in a labeled coin envelope until age determination. Then two spine sections from each fish were placed on a glass microscope slide and covered with immersion oil or baby oil, making sure both sides of each section were coated. The slides were then viewed on a black background under a dissecting microscope with light from twin high-intensity gooseneck light sources adjusted at low angles to the slide to optimize the visibility of annuli. Both spine sections were examined and cross-referenced while enumerating annuli. Examination of spines from smaller, younger fish helped verify the location of the first annulus in larger, older fish. The edge of the spine was generally interpreted as current-year growth in smaller, younger fish. In larger, older fish there generally appeared to be an annulus at or very near the edge of the spine. In some cases when interpretation of the edge was uncertain, I made my best judgment based on the pattern in the last few previous growth increments. Since spines tend to underestimate age relative to otoliths (Nash and Irwin 1999; Olive et al. 2011; Steuck and Schnitzler 2011), if in doubt about interpretation of a spine I assigned the older potential age. The best spine section from each fish was digitally photographed for reference and measurement using a camera tube attached to the dissecting scope. Measurements of spine radii to the edge and to the last annulus were obtained from digital images using ImageJ 1.48v software (ImageJ 2017). Radii were measured along the center of the extension of the anterior edge of the pectoral spine, as illustrated and described by Turner (1982). Spines that were obviously deformed or had indistinct centers were not measured. A regression of fish length versus spine radius for the 2013 sample was linear ($R^2 = 0.914$) with an intercept not significantly different from zero ($P = 0.806$); therefore, I used the direct proportion method (DeVries and Frie 1996) to back-calculate fish length at last annulus for measured spines that exhibited current-year growth. Since sampling was conducted in August after some fish exhibited substantial current-year growth, lengths at last annuli rather than lengths at capture were used to fit a von Bertalanffy growth curve that was standardized to lengths at the beginning of the growing season.

A catch curve (Ricker 1975) was constructed from *ln*(catch+1) of each age class from the pooled 2013 catch-at-age data. Only ages 5 and older were used to estimate mortality and recruitment variability because younger ages were on the ascending limb of the catch curve. An ordinary least squares linear regression model was fitted to *ln*(catch+1) vs. ages 5-32. The absolute value of the slope of the regression equation was the estimate of instantaneous mortality rate Z; survival rate $S = e^{-Z}$; and total annual mortality rate $A = 1 - S$ (Ricker 1975). Studentized residuals from the linear regression model were used as a measure of recruitment variability (Maceina 1997).

RESULTS[1]

General Catch Statistics

The Flathead Catfish catch per net-night averaged 1.2, but the frequency distribution was highly skewed (Figure 3). Almost 50% of the net-nights caught none, and 75% caught two or fewer; however, catches were as high as 12 per net-night. The catch per night (15 net-nights) was more symmetrically distributed (Figure 4). Nightly catches varied from 6 to 41, with a median of 17. A multiple linear regression model of log-transformed nightly catches with reach, year, night within the sampling period, day of the month, and discharge as predictor variables (Table 3) revealed strong effects of reach, night within the week (catches tended to decline over time; Figure 5A) and day of the month (catches tended to increase throughout August; Figure 5B). Mean nightly catches at Mankato were 23.5 versus only 12.9 at Jordan, but no other differences among reaches were significant ($P \le 0.05$). There was no evidence for differences in nightly catch rates among years, and no evidence for an effect of discharge within the range encountered during August of 2013-2015.

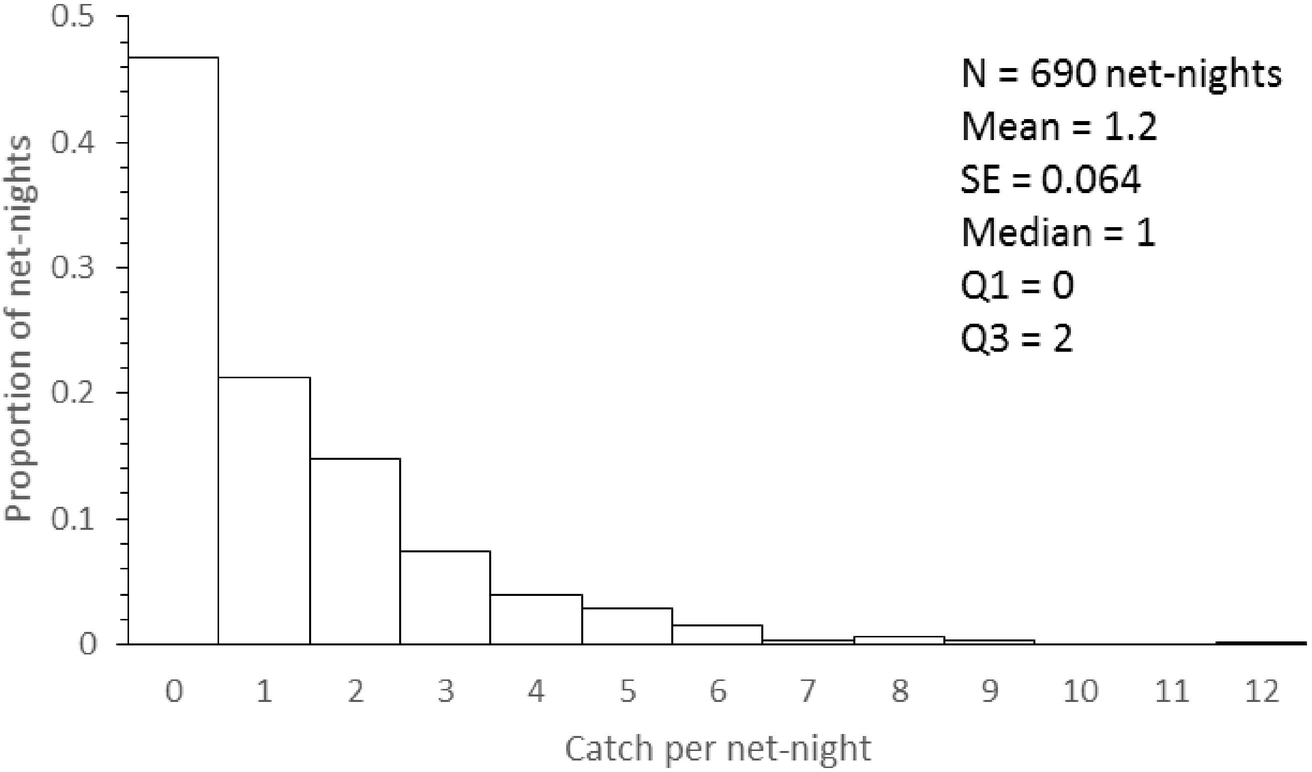

FIGURE 3. Distribution of Flathead Catfish hoop net catch per net-night in four reaches of the lower Minnesota River during August, 2013-2015.

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[1] Because of the very limited sampling that could be completed in 2016, only 2013-2015 results are presented.

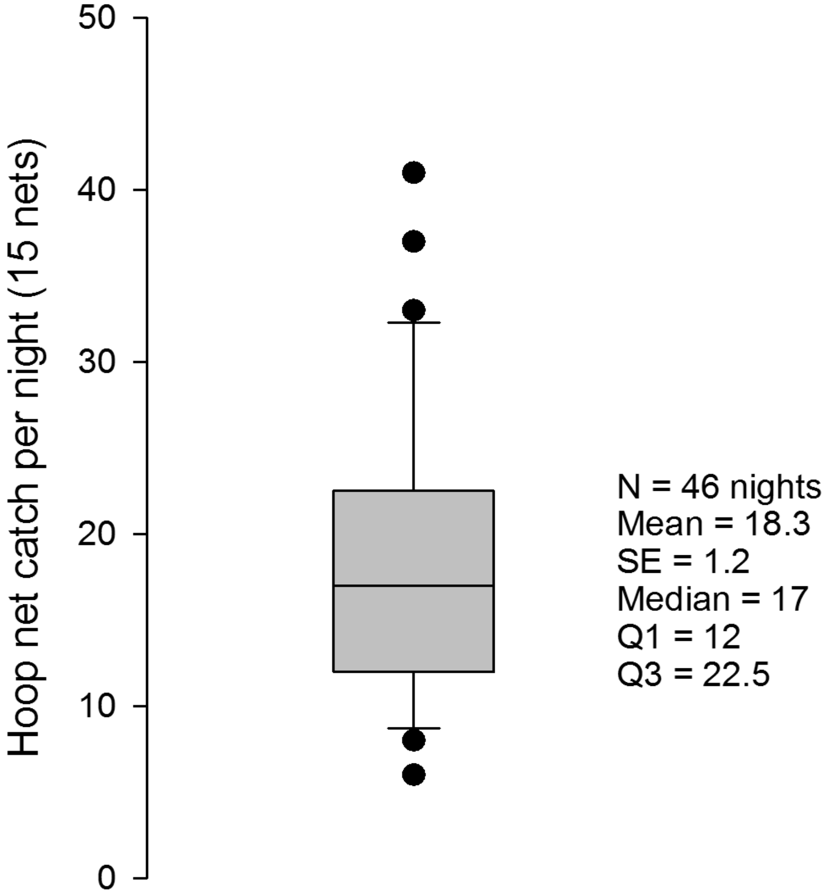

FIGURE 4. Box plot of hoop net catch per night of Flathead Catfish in four study reaches of the lower Minnesota River during August, 2013-2015. Effort per night was always 15 nets. The boundaries of the box indicate the 25th percentile (Q1) and 75th percentile (Q3), and the line within the box indicates the median. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, and dots outside the whiskers represent outliers.

TABLE 3. Analysis of variance for a multiple linear regression model with log-transformed nightly hoop net catch as the response variable and reach, year, night within the sampling period (1-4), sampling date (August 1-31), and discharge as predictor variables.

	df	SS	MS	*F*	*P*
Reach	3	1.9645	0.6548	4.8173	0.0064
Year	1	0.0019	0.0019	0.0138	0.9072
Night	1	0.8351	0.8351	6.1432	0.0180
Date	1	1.5153	1.5153	11.1471	0.0020
Discharge	1	0.0618	0.0618	0.4544	0.5046
Residuals	36	4.8938	0.1359		

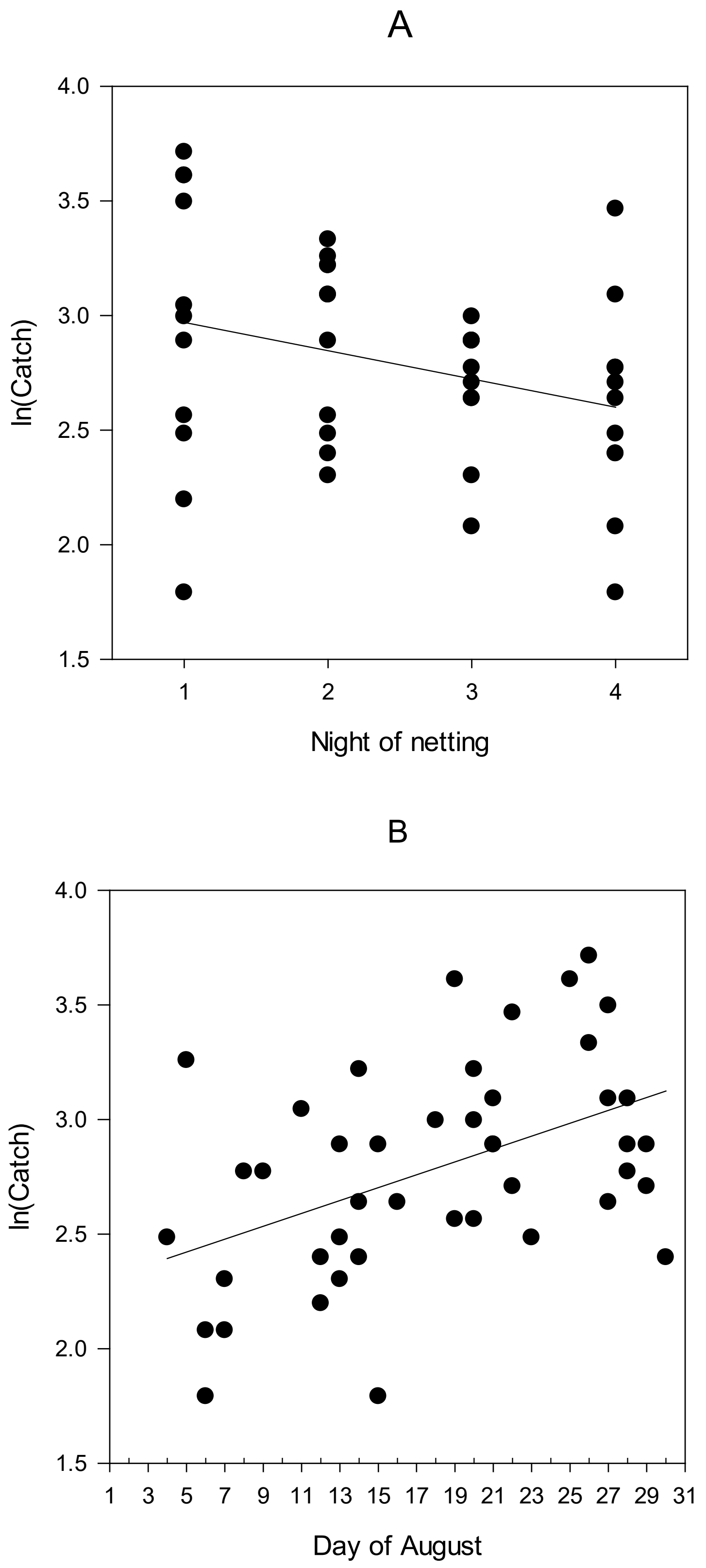

FIGURE 5A & 5B. Natural log of the nightly hoop net catch of Flathead Catfish in 2013-2015 versus the night of netting (A) and the day of August (B).

Flathead catfish captured in the hoop nets ranged from 19.1 to 119.4 cm, with a median of 75.8 cm (Figure 6). Proportional size distributions (Guy et al. 2007), calculated from pooled catches for all years and reaches, were: PSD = 90; PSD-P = 59; PSD-M = 35; PSD-T = 9; PSD S-Q = 10; PSD Q-P = 31; PSD P-M = 23; and PSD M-T = 27. When reaches were pooled, overall length frequencies of the catch differed among years (Chi-squared = 29.531 with 8 df; *P* < 0.001; Table 4). Frequencies of Flathead Catfish < 51 cm were substantially lower than expected in 2013, substantially higher than expected in 2014, and slightly lower than expected in 2015; while frequencies of Flathead Catfish ≥ 102 cm were substantially higher than expected in 2013, substantially lower than expected in 2014, and the same as expected in 2015. However, frequencies of the three middle length classes did not substantially differ among years, and each year, the highest catches were of the 51-70 cm length class. When years were pooled, overall length frequencies of the catch differed among reaches (Chi-squared = 32.378 with 12 df; *P* = 0.001; Table 5). Frequencies of Flathead Catfish < 51 cm were substantially higher than expected at LeSueur and substantially lower than expected at Mankato. In the three middle length classes, relative frequencies varied among reaches. There was little difference among reaches in relative frequencies of Flathead Catfish ≥ 102 cm, except they made up a lower than expected proportion of the catch at LeSueur.

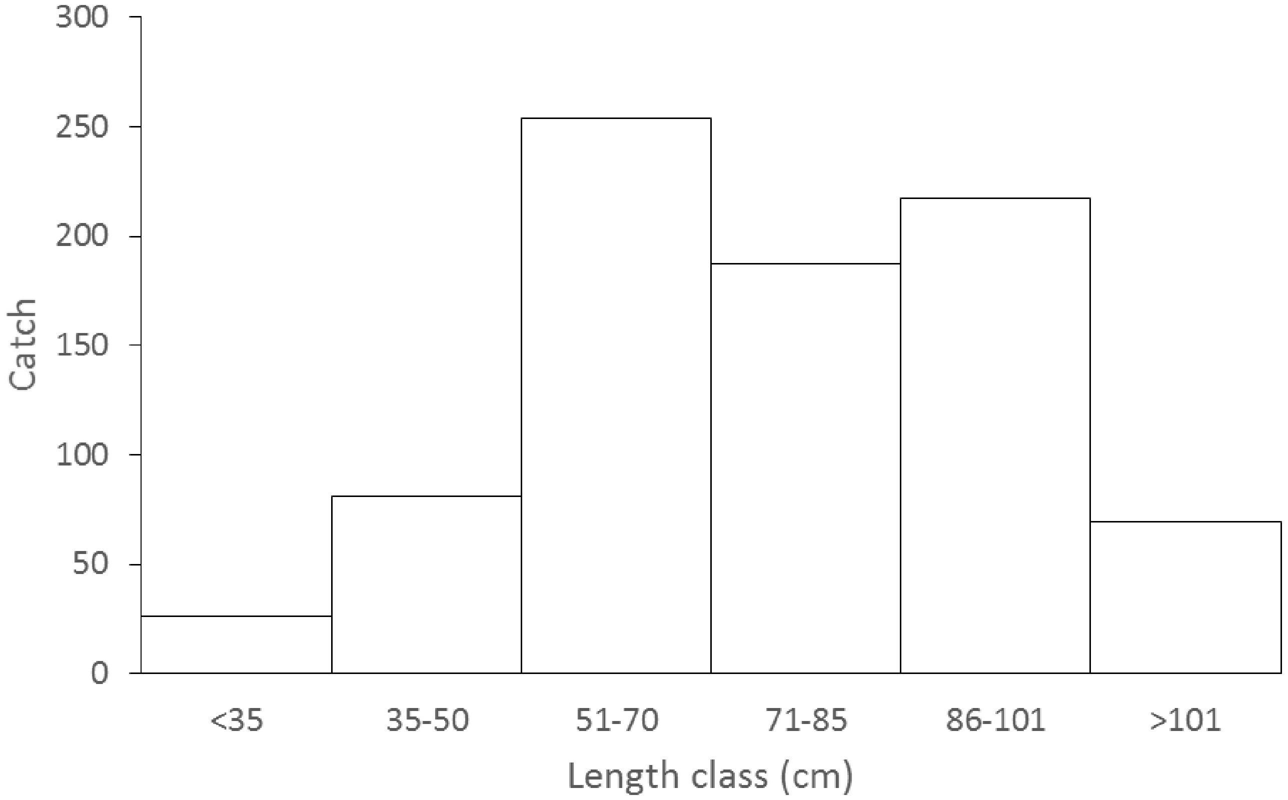

FIGURE 6. Length frequency of the hoop net catch of Flathead Catfish in four study reaches of the lower Minnesota River during August, 2013-2015.

TABLE 4. Observed (and expected) August hoop net catches of Flathead Catfish in the lower Minnesota River, by length class, in each of three years. Expected values represent the average proportional distribution among years.

Length class (cm)	2013	2014	2015
<51	17 (34)	59 (38)	31 (35)
51-70	85 (80)	87 (90)	82 (84)
71-85	61 (59)	61 (66)	65 (62)
86-101	70 (69)	73 (77)	74 (72)
>101	31 (22)	15 (24)	23 (23)

TABLE 5. Observed (and expected) August hoop net catches of Flathead Catfish in the lower Minnesota River, by length class, in each of four reaches. Expected values represent the average proportional distribution among reaches.

Length class (cm)	Shakopee	Jordan	LeSueur	Mankato
<51	22 (24)	25 (21)	35 (27)	25 (36)
51-70	48 (56)	40 (50)	73 (63)	93 (85)
71-85	55 (41)	28 (37)	32 (47)	72 (62)
86-101	43 (48)	55 (43)	56 (54)	63 (72)
>101	16 (15)	16 (14)	12 (17)	25 (23)

Age, Growth, and Catch-at-Age Data

The hoop net catch in 2013 was composed of many age classes from 1 to 32 (Figure 7). My maximum age estimate of 32 is eight years older than that reported by Stauffer et al. (1996), but similar to that reported for Pools 12 and 13 of the Upper Mississippi River based on otoliths (Steuck and Schnitzler 2011).

An ordinary least-squares linear regression model fit the 2013 catch curve reasonably well ($R^2 = 0.69$) for ages 5-32 (Figure 8), and the slope of the descending limb was highly significant ($P < 0.001$). None of the individual ages had undue influence, because the largest Cook's distance was substantially less than 1 (Weisberg 1985). The resulting estimates were $Z = 0.0940$ (95% confidence interval 0.0685-0.119), $S = 0.91$ (95% confidence interval 0.89-0.93), and $A = 0.090$ (95% confidence interval 0.066-0.11), indicating a very high annual survival rate for Flathead Catfish age 5 and older. Studentized residuals of the regression model indicated relatively consistent recruitment of the 1981-2008 year classes, with only the apparently weak 1995 and 1997 year classes as outliers with residuals beyond the bounds of ± 2 standard deviations (Figure 9). There was no long-term time trend in the residuals that would suggest biased estimates of *Z*, *S*, and *A* from the catch curve.

Modal ages in hoop net catches of Flathead Catfish < 71 cm were 6 in 2013, 3-4 and 6 in 2014, and 5 in 2015 (Figure 10). Annual variation in modal ages probably was due to fluctuations in both year class strengths and catchability of fish < 51 cm, at least 74% of which each year were younger than age 5 and not fully recruited to the hoop nets.

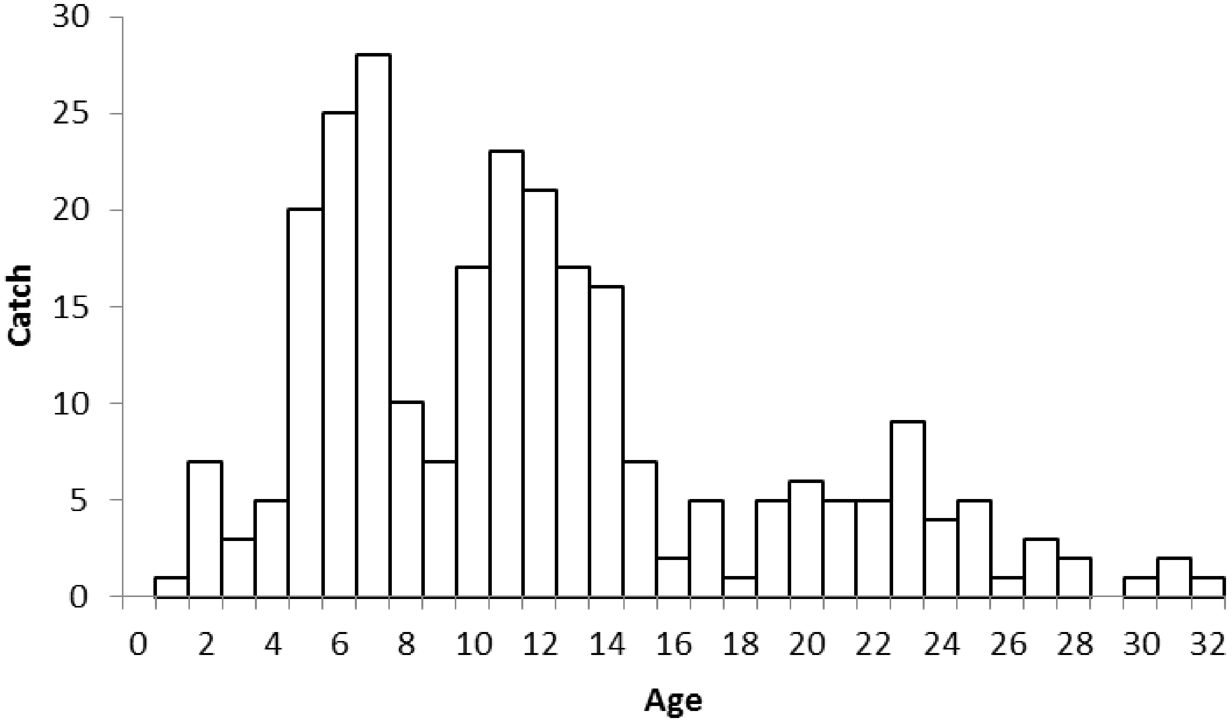

FIGURE 7. Age distribution of the hoop net catch of Flathead Catfish in four study reaches of the lower Minnesota River during August, 2013.

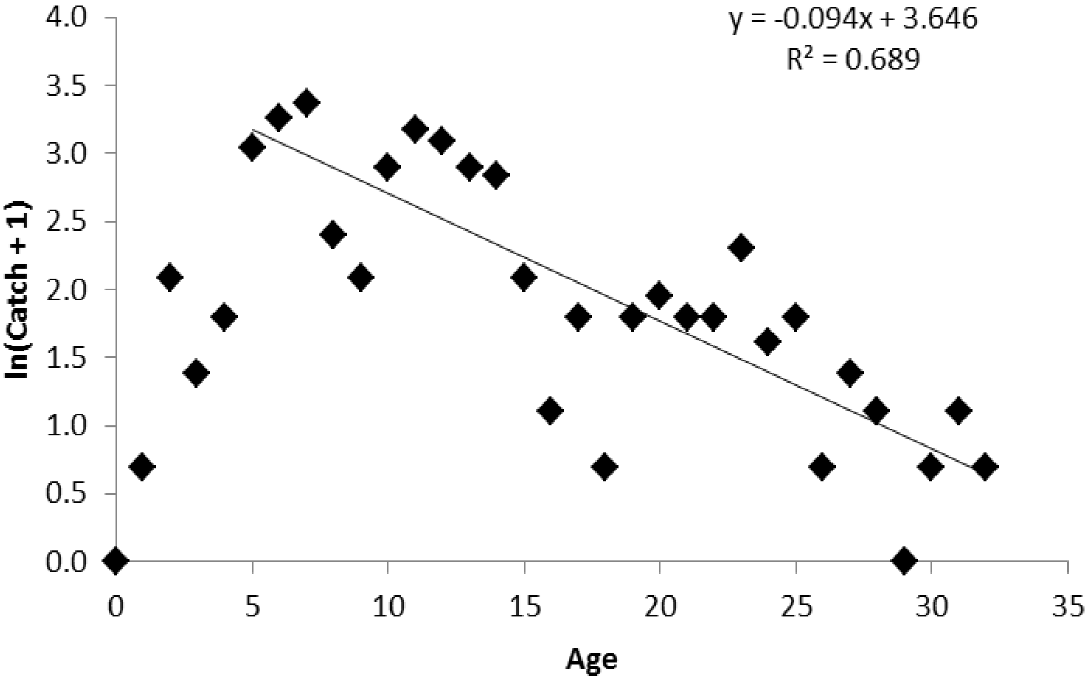

FIGURE 8. Catch curve for Flathead Catfish sampled with large hoop nets from four study reaches of the lower Minnesota River in August, 2013. Ages < 5 were excluded from the linear regression model.

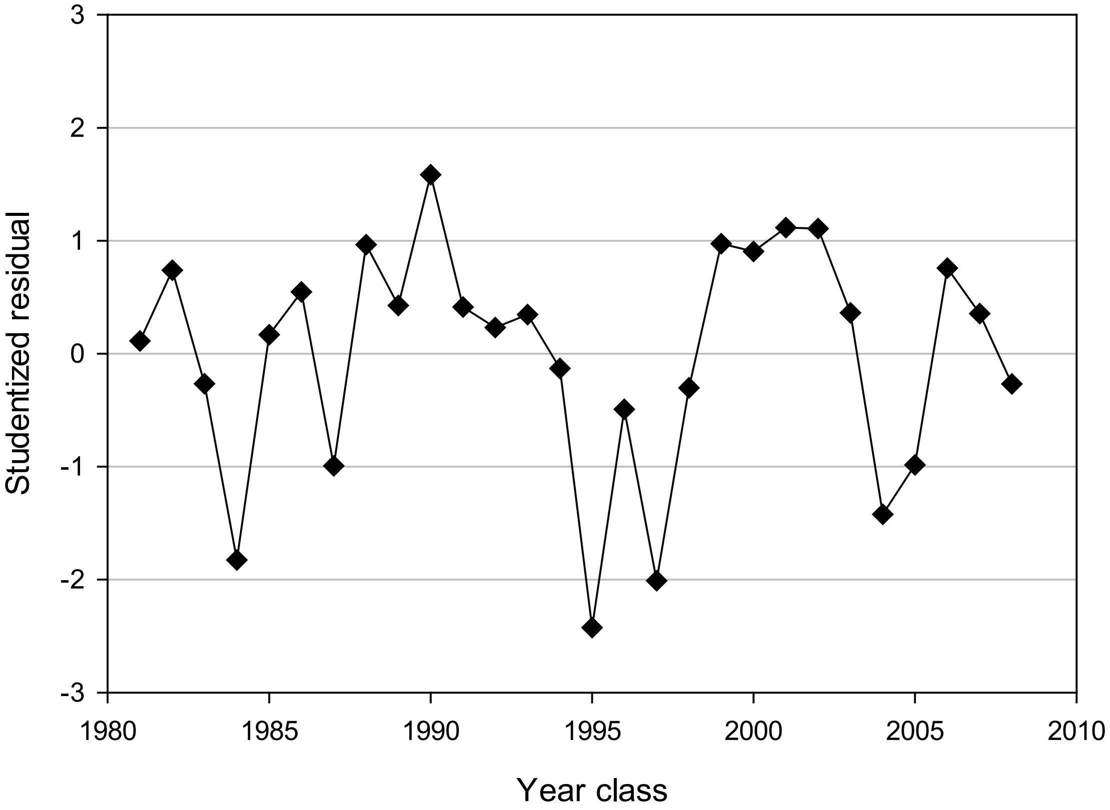

FIGURE 9. Studentized residuals of the catch curve regression model for Flathead Catfish ages 5-32 sampled with hoop nets from four study reaches of the lower Minnesota River in August, 2013.

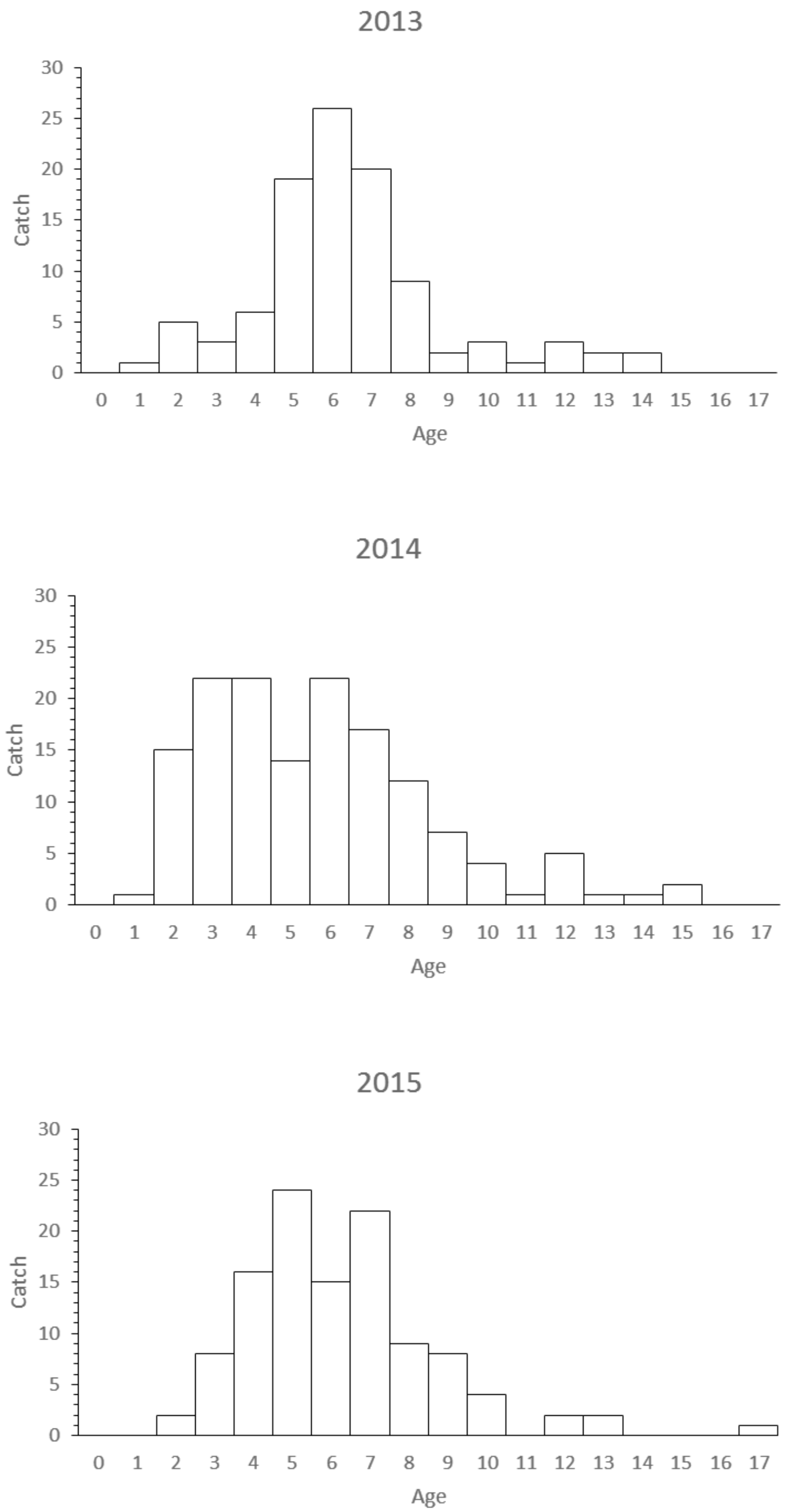

FIGURE 10. Age distribution of the hoop net catch of Flathead Catfish < 71 cm in four reaches of the lower Minnesota River during August, 2013-2015.

A von Bertalanffy growth curve for pooled 2013 lengths at last annuli fit reasonably well (R^2 = 0.80), but lengths at annuli were highly variable, especially after annulus 9 (Figure 11). The von Bertalanffy parameters were: L_∞ = 100 cm (SE = 2.3 cm); K = 0.16 yr^{-1} (SE = 0.014 yr^{-1}); and t_0 = 0.49 yr (SE = 0.34 yr). Although L_∞ represented the maximum length for the average fish, due to the high variability in individual growth combined with the presence of many old fish in the population, some individuals exceeded L_∞ (Francis 1988). My estimate of L_∞ was substantially lower, and K was substantially higher, than previous estimates by Stauffer et al. (1996) for the Minnesota River. Predicted lengths from the growth curves were very similar for the current study and Stauffer et al. (1996) for fish up to age 10, but Stauffer et al. (1996) predicted substantially greater lengths at subsequent ages (Table 6). My growth curve predicted the average Flathead Catfish in the lower Minnesota River reached stock size (35 cm) between annulus 3 and annulus 4, quality size (51 cm) at annulus 5, preferred size (71 cm) between annulus 8 and annulus 9, and memorable size (86 cm) at annulus 13, but only unusually fast-growing individuals ever reached trophy size (102 cm). Predicted lengths at ages 2-10 in the lower Minnesota River were typical for native riverine populations throughout the United States (Kwak et al. 2006). Few, if any, older fish have been reported for most populations; other native riverine populations with fish reported over age 15 include the Coosa and Tallapoosa rivers (Alabama), Mississippi River (Iowa), and Missouri River (Nebraska; Table 6). Growth up to age 18 in the Minnesota River was very similar to that reported for the Missouri River, but faster than in the Mississippi, Coosa, or Tallapoosa rivers.

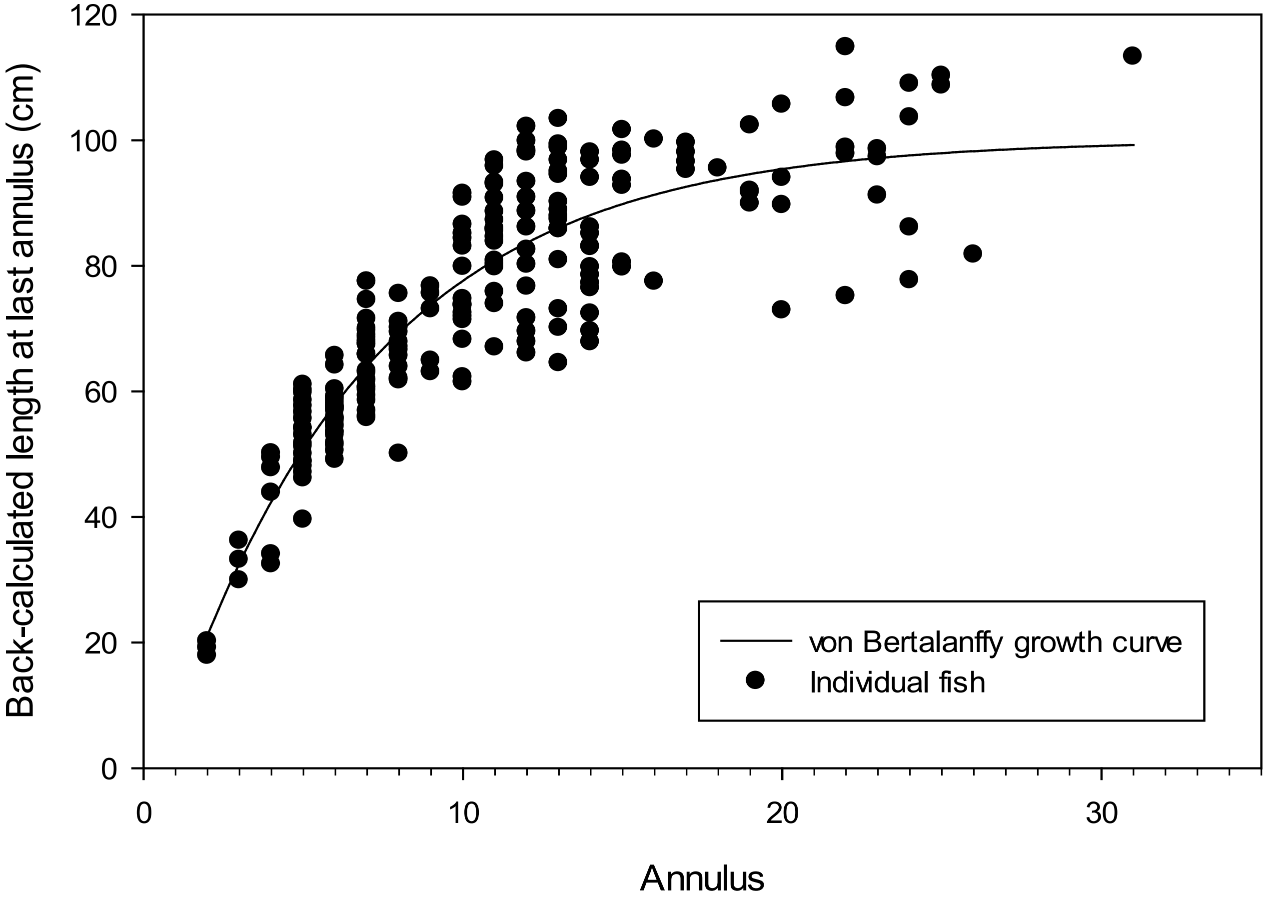

FIGURE 11. Back-calculated lengths at last annuli of Flathead Catfish sampled with large hoop nets from the lower Minnesota River in August, 2013.

TABLE 6. Mean total lengths at age for Flathead Catfish in the current study and other studies of native riverine populations with reported ages above 15.

	Mean length at age (cm)																	
	2	3	4	5	6	7	8	9	10	12	14	16	18	20	22	24	26	28
This study	21	33	42	51	58	64	69	74	78	84	88	91	94	95	97	98	98	99
Stauffer et al. (1996)	23	33	42	50	57	64	70	75	80	89	95	101	105	109	112	114		
Mississippi River, Iowa[1]	24	32	39	46	51	56	61	65	68	74	79	83	86	88	90	91	92	93
Missouri River, Nebraska[2]	18	27	36	45	52	60	64	69	78	84	89	94	94	99	102	106		
Tallapoosa River, Alabama[3]	21	26	31	35	40	43	48	51	51	54	59	60	65	76	88	92	95	99
Coosa River, Alabama[4]	16	20	24	29	40	52	49	53	54	65	69	77	87					

[1] Steuck and Schnitzler (2011): combined sexes, otoliths; [2] Morris (1971): unchannelized section; [3] Nash (1999), cited by Kwak et al. (2006); [4] Jolley and Irwin (2011): estimated from Figure 5, tailwater.

Capture-Recapture Models

Few, if any, Flathead Catfish were captured more than once within the four-night annual sampling period at a given reach (Table 7). Even when short-term recaptures occurred, closed-population models that assumed equal initial capture and recapture probabilities did not fit or produce reasonable abundance estimates. Therefore, I focused on variations of models that allowed recapture probabilities to be very low or zero and did not use recaptures for abundance estimation. These models implied that Flathead Catfish were essentially removed from the catchable population in the short term due to extreme trap shyness, resulting in the tendency for catches to decline over the four nights of sampling. The simplest model [*p*(.)*c*(.); equivalent to behavioral response model M_b of Otis et al. (1978)] assumed a constant initial capture probability *p* and a constant recapture probability *c*. A more general model [*p*(1222)*c*(.)] allowed *p* to be different during the first night of netting than during the three subsequent nights; a second more general model [*p*(1122)*c*(.)] allowed *p* to be different during the first two nights than during the second two nights. The models with limited time variation in *p* were justified biologically because any instances of net sets not fishing properly due to snags, etc. were usually resolved after the first lift or two, often causing an increase in effective effort.

Otis et al. (1978) found that in simulated closed-population capture-recapture experiments with behavioral responses to capture, abundance estimates were reasonably unbiased if p was at least 0.2. Consistent with their results, when my model p(.)c(.) fit well and gave the most precise abundance estimates of the three alternative models, point estimates of p ranged from 0.22 to 0.53 (Table 8). When the models with limited time variation in p fit well and gave the most precise abundance estimates, point estimates of p(1) ranged from 0.028 to 0.45; p(2) ranged from 0.20 to 0.76; and p(2)> p(1). When valid closed-population abundance estimates were possible, they were quite low (Table 9) because modest numbers of Flathead Catfish were captured and estimated nightly initial capture probabilities were quite high.

TABLE 7. Numbers of flathead catfish newly released and recaptured over four consecutive nights of hoop netting at each of four study reaches in the lower Minnesota River during August, 2013-2015. Only recaptures from the same annual sampling period are shown.

	Shakopee		Jordan		LeSueur		Mankato	
Year	Released	Recaptured	Released	Recaptured	Released	Recaptured	Released	Recaptured
2013	84	0	45	0	58	0	74	1
2014	49	0	41	0	96	0	109	3
2015	51	2	75	0	54	0	89	0

TABLE 8. Estimated nightly initial capture probabilities p (and 95% confidence intervals) of various length categories of Flathead Catfish in four reaches of the lower Minnesota River during four consecutive nights of hoop netting in August, 2013-2015. Superscripts indicate the models used for estimation. Results shown are from models with no deviance residuals outside the bounds of ± 2 when c-hat was set to the default value of one. If more than one model fit well, the model with the most precise abundance estimate was chosen.

				Length category (cm)		
Year	Reach	< 51	≥ 51	51-70	< 71	≥ 71
2013	Shakopee	$p(.)$: 0.35 (0.063-0.82)[a]	$p(1)$: 0.37 (0.26-0.49)[c] $p(2)$: 0.53 (0.22-0.82)	NA	NA	$p(.)$: 0.47 (0.33-0.62)[a]
	Jordan	NA	NA	$p(1)$: 0.23 (0.074-0.53)[b] $p(2)$: 0.40 (0.093-0.82)	$p(1)$: 0.28 (0.14-0.49)[c] $p(2)$: 0.69 (0.16-0.96)	NA
	LeSueur	$p(.)$: 0.23 (0.007-0.92)[a]	NA	$p(1)$: 0.14 (0.008-0.77)[c] $p(2)$: 0.21 (0.003-0.96)	NA	$p(1)$: 0.19 (0.083-0.38)[b] $p(2)$: 0.46 (0.20-0.74)
	Mankato	NA	$p(1)$: 0.18 (0.096-0.31)[b] $p(2)$: 0.31 (0.14-0.57)	$p(1)$: 0.30 (0.15-0.50)[c] $p(2)$: 0.56 (0.095-0.94)	$p(1)$: 0.25 (0.08-0.55)[c] $p(2)$: 0.41 (0.032-0.94)	$p(1)$: 0.19 (0.095-0.34))[b] $p(2)$: 0.35 (0.15-0.63)
2014	Shakopee	NA	NA	NA	NA	NA
	Jordan	NA	$p(1)$: 0.35 (0.22-0.51)[c] $p(2)$: 0.76 (0.24-0.97)	NA	$p(1)$: 0.20 (0.11-0.36)[c] $p(2)$: 0.73 (0.31-0.94)	$p(1)$: 0.32 (0.14-0.57)[b] $p(2)$: 0.54 (0.21-0.84)
	LeSueur	$p(.)$ 0.49 (0.27-0.71)[a]	$p(1)$: 0.32 (0.20-0.47)[c] $p(2)$: 0.43 (0.16-0.75)	$p(.)$ 0.42 (0.24-0.62)[a]	$p(.)$: 0.42 (0.28-0.58)[a]	$p(1)$: 0.29 (0.17-0.44)[c] $p(2)$: 0.52 (0.18-0.84)
	Mankato	NA	NA	NA	NA	NA
2015	Shakopee	NA	$p(1)$: 0.27 (0.11-0.53)[c] $p(2)$: 0.33 (0.057-0.80)	$p(1)$: 0.23 (0.069-0.56)[c] $p(2)$: 0.45 (0.053-0.92)	$p(1)$: 0.29 (0.13-0.52)[c] $p(2)$: 0.49 (0.11-0.89)	$p(.)$: 0.32 (0.14-0.58)[a]
	Jordan	NA	NA	$p(1)$: 0.33 (0.17-0.55)[c] $p(2)$: 0.62 (0.092-0.96)	$p(.)$: 0.23 (0.058-0.60)[a]	NA
	LeSueur	$p(1)$: 0.20 (0.044-0.59)[b] $p(2)$: 0.45 (0.083-0.88)	$p(1)$: 0.21 (0.12-0.36)[b] $p(2)$: 0.59 (0.39-0.77)	$p(1)$: 0.34 (0.14-0.62)[b] $p(2)$: 0.44 (0.11-0.83)	$p(1)$: 0.26 (0.10-0.51)[b] $p(2)$: 0.35 (0.086-0.75)	$p(1)$: 0.14 (0.052-0.32)[b] $p(2)$: 0.71 (0.48-0.87)
	Mankato	NA	NA	$p(1)$: 0.22 (0.11-0.39)[b] $p(2)$: 0.43 (0.19-0.70)	$p(1)$: 0.23 (0.13-0.38)[b] $p(2)$: 0.54 (0.33-0.74)	$p(1)$: 0.37 (0.24-0.54)[c] $p(2)$: 0.46 (0.17-0.78)

[a] Model $p(.)c(.)$ -- constant initial capture probability p and constant recapture probability c.

[b] Model $p(1222)c(.)$ -- initial capture probability p may be different on the first night than on subsequent nights; constant recapture probability c.

[c] Model $p(1122)c(.)$ -- initial capture probability p may be different on the first two and second two nights; constant recapture probability c.

TABLE 8 continued.

				Length category (cm)		
Year	Reach	71-85	< 86	≥ 86	86-101	> 101
2013	Shakopee	*p*(1): 0.45 (0.28-0.64)[b] *p*(2): 0.58 (0.27-0.83)	*p*(.): 0.22 (0.088-0.45)[a]	*p*(.): 0.52 (0.33-0.71)[a]	*p*(.): 0.53 (0.31-0.75)[a]	NA
	Jordan	*p*(1): 0.028 (0.002-0.32)[c] *p*(2): 0.34 (0.013-0.95)	*p*(1): 0.12 (0.034-0.36)[c] *p*(2): 0.37 (0.044-0.88)	NA	NA	NA
	LeSueur	*p*(.): 0.35 (0.063-0.82)[a]	NA	*p*(1): 0.21 (0.079-0.44)[b] *p*(2): 0.42 (0.14-0.77)	NA	*p*(.): 0.38 (0.035-0.91)[a]
	Mankato	*p*(1): 0.20 (0.064-0.47)[b] *p*(2): 0.62 (0.28-0.87)	*p*(1): 0.18 (0.084-0.35)[b] *p*(2): 0.36 (0.14-0.67)	*p*(1): 0.18 (0.067-0.41)[b] *p*(2): 0.28 (0.068-0.68)	*p*(1): 0.24 (0.070-0.56)[c] *p*(2): 0.39 (0.033-0.92)	*p*(1): 0.21 (0.067-0.49)[b] *p*(2): 0.58 (0.23-0.86)
2014	Shakopee	NA	NA	NA	NA	NA
	Jordan	NA	*p*(1): 0.23 (0.12-0.38)[c] *p*(2): 0.64 (0.21-0.92)	*p*(.): 0.35 (0.11-0.70)[a]	*p*(.) 0.30 (0.070-0.71)[a]	NA
	LeSueur	*p*(1): 0.38 (0.16-0.65)[b] *p*(2): 0.48 (0.13-0.85)	*p*(.): 0.40 (0.27-0.54)[a]	*p*(1): 0.23 (0.090-0.48)[c] *p*(2): 0.40 (0.071-0.85)	*p*(1): 0.27 (0.11-0.53)[c] *p*(2): 0.41 (0.073-0.86)	NA
	Mankato	*p*(.): 0.27 (0.095-0.58)[a]	NA	NA	NA	NA
2015	Shakopee	*p*(.): 0.40 (0.14-0.73)[a]	*p*(1): 0.30 (0.17-0.49)[c] *p*(2): 0.50 (0.16-0.84)	*p*(1): 0.32 (0.14-0.57)[b] *p*(2): 0.54 (0.21-0.84)	*p*(.): 0.44 (0.18-0.74)[a]	*p*(.): 0.36 (0.045-0.87)[a]
	Jordan	*p*(1): 0.24 (0.094-0.48)[c] *p*(2): 0.61 (0.080-0.97)	*p*(1): 0.16 (0.034-0.50)[b] *p*(2): 0.20 (0.022-0.72)	NA	*p*(1): 0.18 (0.067-0.40)[c] *p*(2): 0.40 (0.078-0.84)	NA
	LeSueur	*p*(.): 0.28 (0.048-0.76)[a]	*p*(1): 0.24 (0.11-0.43)[b] *p*(2): 0.38 (0.14-0.70)	NA	NA	NA
	Mankato	*p*(.): 0.34 (0.16-0.59)[a]	NA	*p*(.): 0.43 (0.21-0.68)[a]	*p*(.): 0.49 (0.25-0.73)[a]	NA

[a] Model *p*(.)*c*(.) -- constant initial capture probability *p* and constant recapture probability *c*.

[b] Model *p*(1222)*c*(.) -- initial capture probability *p* may be different on the first night than on subsequent nights; constant recapture probability *c*.

[c] Model *p*(1122)*c*(.) -- initial capture probability *p* may be different on the first two and second two nights; constant recapture probability *c*.

TABLE 9. Closed-population abundance estimates (and 95% confidence intervals) of various length categories of Flathead Catfish in four reaches of the lower Minnesota River during four consecutive nights of hoop netting in August, 2013-2015. Superscripts indicate the models used for abundance estimation. Results shown are from models with no deviance residuals outside the bounds of ± 2 when *c*-hat was set to the default value of one. If more than one model fit well, the model with the most precise abundance estimate was chosen.

		Length category (cm)									
Year	Reach	< 51	≥ 51	51-70	< 71	≥ 71	71-85	< 86	≥ 86	86-101	> 101
2013	Shakopee	8 (7-27)^{a}	84 (78-117)^{c}	NA	NA	59 (56-73)^{a}	29 (28-40)^{b}	90 (65-189)^{a}	28 (27-38)^{a}	19 (19-29)^{a}	NA
	Jordan	NA	NA	17 (15-44)^{b}	26 (20-68)^{a}	NA	18 (11-122)^{c}	38 (28-139)^{c}	NA	NA	NA
	LeSueur	7 (5-56)^{a}	NA	46 (26-386)^{c}	NA	31 (28-53)^{b}	8 (7-27)^{a}	NA	24 (21-50)^{b}	NA	4 (4-18)^{a}
	Mankato	NA	101 (81-179)^{b}	25 (23-52)^{c}	29 (24-96)^{c}	64 (53-116)^{b}	15 (15-25)^{b}	49 (41-95)^{b}	50 (37-132)^{b}	26 (21-90)^{c}	14 (14-25)^{b}
2014	Shakopee	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Jordan	NA	26 (26-36)^{c}	NA	24 (23-36)^{c}	19 (18-32)^{b}	NA	29 (27-49)^{c}	17 (14-40)^{a}	17 (13-49)^{a}	NA
	LeSueur	22 (21-33)^{a}	88 (78-139)^{c}	36 (33-53)^{a}	59 (55-78)^{a}	48 (44-80)^{c}	16 (15-32)^{b}	78 (71-101)^{a}	35 (29-91)^{c}	29 (25-72)^{c}	NA
	Mankato	NA	NA	NA	NA	NA	37 (29-84)^{a}	NA	NA	NA	NA
2015	Shakopee	NA	56 (45-141)^{c}	15 (13-47)^{c}	24 (21-50)^{c}	37 (31-70)^{a}	13 (12-30)^{a}	37 (34-65)^{c}	19 (18-32)^{b}	14 (13-27)^{a}	5 (5-22)^{a}
	Jordan	NA	NA	18 (17-36)^{c}	35 (25-103)^{a}	NA	14 (13-33)^{c}	63 (39-273)^{b}	NA	38 (30-100)^{c}	NA
	LeSueur	10 (9-28)^{b}	47 (45-59)^{b}	18 (16-38)^{b}	31 (26-74)^{b}	29 (29-36)^{b}	13 (10-47)^{a}	42 (36-80)^{b}	NA	NA	NA
	Mankato	NA	NA	42 (37-69)^{b}	47 (44-62)^{b}	57 (52-88)^{c}	36 (31-64)^{a}	NA	23 (21-38)^{a}	18 (17-29)^{a}	NA

[a] Model $p(.)c(.)$ -- constant initial capture probability p and constant recapture probability c.

[b] Model $p(1222)c(.)$ -- initial capture probability p may be different on the first night than on subsequent nights; constant recapture probability c.

[c] Model $p(1122)c(.)$ -- initial capture probability p may be different on the first two and second two nights; constant recapture probability c.

No Flathead Catfish < 51 cm at the time of tagging were recaptured in subsequent years, so open-population Jolly-Seber models were limited to fish ≥ 51 cm at the time of tagging. In addition, open-population models were only fitted to fish ≥ 51 cm, ≥ 71 cm, and ≥ 86 cm at the time of tagging because sample sizes were too low in other length categories for models to be meaningful. Many more recaptures occurred after 1-2 years at large than during the four-night annual sampling periods (Table 10). For each of the three length categories with adequate sample sizes, the best models in terms of AIC_c and estimability of parameters assumed constant annual apparent survival, constant annual capture probability, and constant annual recruitment + immigration. Residual plots for these models indicated good fits to the data. Annual apparent survival estimates (i.e., actual survival minus permanent emigration) were similar among length categories (Table 11). Estimated annual capture probabilities from the open-population models (Table 11) were substantially lower than most corresponding closed- population estimates of nightly initial capture probabilities (Table 8), although still approaching 0.20. Open-population abundance estimates (Table 12) represented totals for the four study reaches and thus were expected to be approximately four times the corresponding closed-population abundance estimates for individual reaches (Table 9); however, the differences were substantially more than expected. There was no evidence for differences in abundance among years. Abundance estimates represented 16 river km, so average abundance per km was simply N-hat/16. The estimated average Flathead Catfish densities in the study reaches in August 2013-2015 were approximately 90 fish/km ≥ 51 cm, 50 fish/km ≥ 71 cm, and 30 fish/km ≥ 86 cm (Table 12). Estimated net annual recruitment + immigration (Table 11) averaged approximately 46% of the abundance estimates for Flathead Catfish ≥ 51 cm, 47% for Flathead Catfish ≥ 71 cm, and 42% for Flathead Catfish ≥ 86 cm.

One of the assumptions of Jolly-Seber models is that all emigration is permanent; if temporary emigration occurs, then abundance, recruitment, and survival estimates may be biased (Kendall et al. 1997). In my open-population models, the only possibility of temporary emigration was if fish initially captured in 2013 were not available for capture in 2014 (e.g., they were outside the study reaches), but were available for capture in 2015. Pollock's robust design can be used to test for temporary emigration and obtain unbiased parameter estimates if necessary (Kendall et al. 1997). In this study, fitting of robust design models was limited to Flathead Catfish length categories with valid closed-population abundance estimates each year for a given reach. In these cases, I fit robust design models with the same closed-population components as in Table 9; constant annual survival; and either constant Markovian, constant random, or no temporary emigration. Comparisons of AIC_c values for alternative robust design models provided little support for models with temporary emigration; therefore, there was no evidence that the Jolly-Seber assumption of only permanent emigration was violated.

TABLE 10. Numbers of Flathead Catfish released and recaptured* during 2013-2015 in four study reaches of the lower Minnesota River, by length category.

Length category	Release year	Number released	Number recaptured 2014	2015	Total
≥ 51 cm	2013	243	16	10	26
	2014	236		28	28
≥ 71 cm	2013	158	11	7	18
	2014	149		19	19
≥ 86 cm	2013	98	7	5	12
	2014	87		12	12

*Numbers of recaptures exclude five fish that lost their tags.

TABLE 11. Apparent survival (Phi), annual capture probability (*p*), and net annual recruitment + immigration (B-hat) estimated from POPAN Jolly-Seber models of three length categories of Flathead Catfish released and recaptured at four pooled 4-km study reaches of the lower Minnesota River in 2013-2015. Models assumed constant annual Phi, *p*, and probability of entry. Adjusted estimates account for tag loss.

Length category	Parameter	Estimate	SE	95% confidence bounds Lower	Upper	Adjusted estimate
≥ 51 cm	Phi	0.524	0.144	0.262	0.775	0.582
	p	0.176	0.062	0.084	0.331	
	B-hat	637	85	491	827	573
≥ 71 cm	Phi	0.521	0.169	0.223	0.804	0.579
	p	0.190	0.080	0.078	0.393	
	B-hat	386	63	281	530	348
≥ 86 cm	Phi	0.548	0.213	0.184	0.867	0.609
	p	0.192	0.098	0.064	0.450	
	B-hat	206	42	139	307	182

TABLE 12. Annual abundance (N-hat) and density (N-hat/km) estimates from POPAN Jolly-Seber models of three length categories of Flathead Catfish at four pooled 4-km study reaches of the lower Minnesota River in 2013-2015. Models assumed constant annual apparent survival, constant annual capture probability, and constant annual probability of entry.

Length category	Year	N-hat	SE	95% confidence bounds Lower	Upper	N-hat/km	SE	95% confidence bounds Lower	Upper
≥ 51 cm	2013	1408	504	713	2782	88	32	45	174
	2014	1374	488	699	2701	86	31	44	169
	2015	1359	481	693	2664	85	30	43	167
≥ 71 cm	2013	848	358	383	1877	53	22	24	117
	2014	826	348	374	1824	52	22	23	114
	2015	816	344	370	1801	51	22	23	113
≥ 86 cm	2013	520	265	203	1332	33	17	13	83
	2014	490	252	190	1264	31	16	12	79
	2015	475	242	185	1219	30	15	12	76

Another assumption of Jolly-Seber models is that tags are not lost. If there is tag loss, estimates of survival and recruitment (but not abundance) are biased (Arnason and Mills 1981). In this study, 5 of 59 Flathead Catfish recaptured after 1-2 years at large did not have detectable PIT tags, for an overall loss or malfunction rate of 8%. Therefore, I used equations (2.9) and (2.12) of Arnason and Mills (1981) to adjust the Jolly-Seber estimates of Phi and B-hat (Table 11) for tag loss. Tag loss resulted in negatively biased apparent survival and positively biased B-hat. However, the adjusted estimates were well within the 95% confidence bounds of the unadjusted estimates, so bias due to tag loss was relatively inconsequential.

Four tagged fish (all ≥ 71 cm) were found dead 1-2 days after capture and spine removal in 2013, and these fish were counted as losses on capture in the Jolly-Seber models (Cooch and White 2017). Because of concern about potential unobserved post-release mortality due to spine removal from fish ≥ 71 cm in 2013, I simulated effects on Jolly-Seber parameter estimates in Program MARK by assigning additional percentages of the 2013 catch of fish ≥ 71 cm to losses on capture, and then running the same POPAN model to obtain new parameter estimates. Substantial unobserved post-release mortality in 2013 would have resulted in negatively biased estimates of apparent survival and abundance, and positively biased estimates of *p* and B-hat. Estimates of abundance and *p* would have been affected much less than estimates of apparent survival and B-hat; even if post-release mortality had been as high as 50% in 2013, adjusted estimates of abundance and *p* would have been well within the 95% confidence bounds of the unadjusted estimates (Table 13).

Total catches over the four nights of sampling per reach per year were strongly correlated with closed-population abundance estimates because when a valid closed-population estimate was obtained, the cumulative catch accounted for most of the estimated abundance (Figure 12). Numbers of nets and numbers of nights per reach were constant (except for Shakopee in 2014), so the correlation was virtually the same with either catch/net or catch/night. Annual open-population abundance estimates (Table 12) and corresponding catches did not vary substantially among years, and only three years of data were available. Additional years of data encompassing more annual variation would be necessary for a meaningful evaluation of potential correlations between catch rates and annual open-population abundance estimates.

TABLE 13. Comparison of actual parameter estimates from POPAN Jolly-Seber models of Flathead Catfish ≥ 71 cm (assuming 0% unobserved losses on capture) with hypothetical parameter estimates resulting from simulating 50% losses on capture in 2013. Models assumed constant annual apparent survival, constant annual capture probability, and constant annual probability of entry.

	Percentage of unobserved losses on capture in 2013							
	0%				50%			
Parameter	Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper
Phi	0.521	0.169	0.223	0.804	0.769	0.255	0.167	0.982
p	0.190	0.080	0.080	0.393	0.172	0.074	0.070	0.364
B-hat	386	63	281	530	239	142	82	702
N-hat(2013)	848	358	383	1877	930	397	417	2073
N-hat(2014)	826	348	374	1824	892	387	396	2012
N-hat(2015)	816	344	370	1801	925	395	415	2062

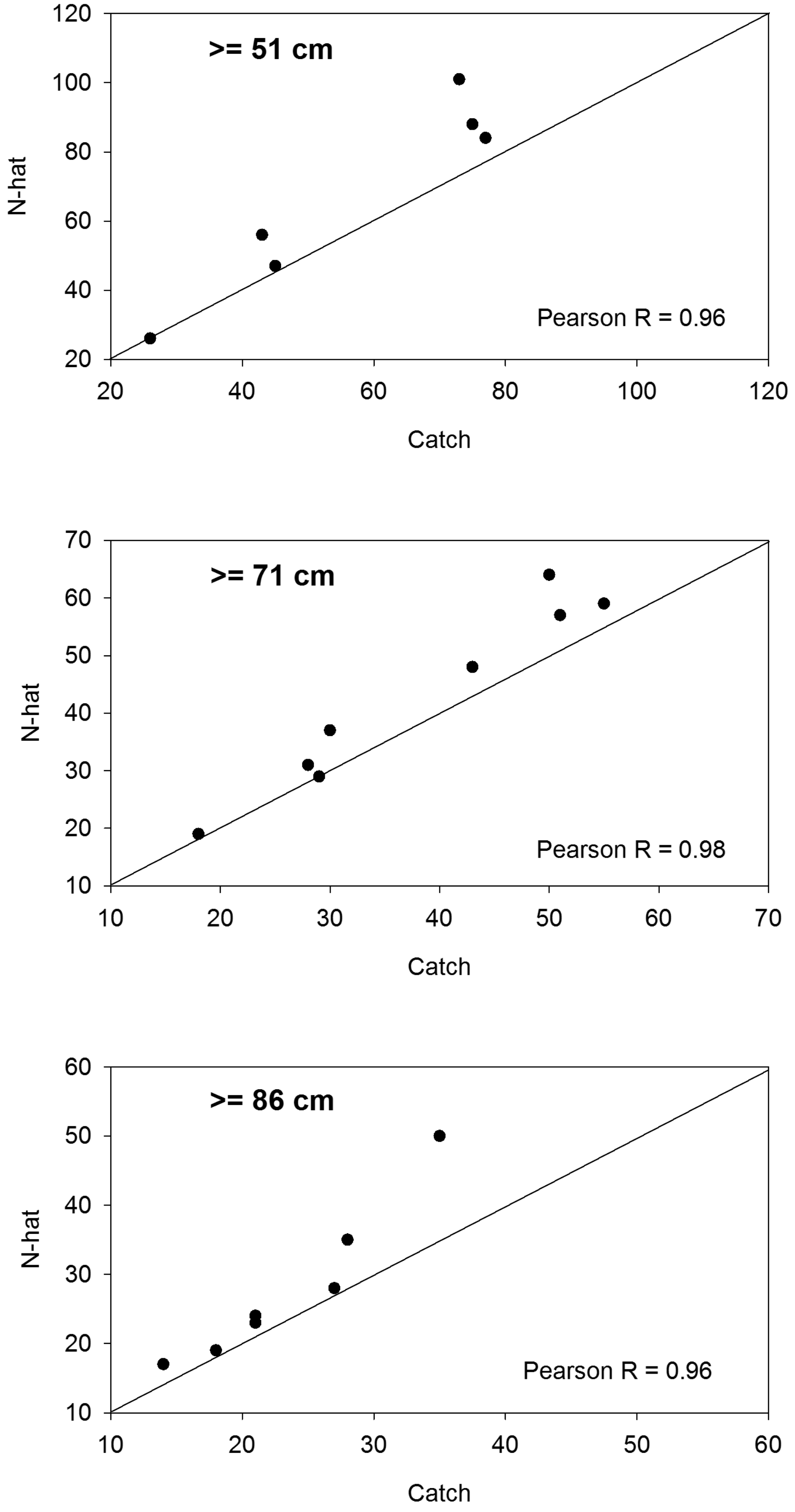

FIGURE 12. Closed-population abundance estimates (N-hat) versus hoop net catches of three length classes of Flathead Catfish in four study reaches of the lower Minnesota River during August of 2013-2015. Diagonal lines represent 1:1 correspondence.

DISCUSSION

Mean hoop net catches per net-night in the lower Minnesota River were much higher than the 75th percentile of reported values summarized by Bodine et al. (2013), indicating that our sampling methods were exceptionally efficient or the Flathead Catfish population was exceptionally abundant. A strong tendency for declining nightly catches of Flathead Catfish in nets repeatedly lifted and reset in the same locations suggested that our sampling was often efficient enough to deplete the supply of new fish that were vulnerable to the nets during each four-night annual sampling period in a given reach. Stauffer and Koenen (1999) reported that hoop nets were not effective at capturing Flathead Catfish in the Minnesota River. However, their lack of success probably was due to using nets that were too small (76 cm diameter with 19 mm mesh) and of a design that did not fish properly in a river (Stauffer et al. 1996). Recent sampling with large hoop nets in the same reaches they sampled with small hoop nets has resulted in catch rates very similar to those observed during this study (Tony Sindt, Minnesota Department of Natural Resources, personal communication). Large-diameter, small-mesh hoop nets efficiently captured a greater length range of Flathead Catfish than trot lines (Stauffer and Koenen 1999), without the necessity of obtaining and transporting large quantities of appropriately-sized live baitfish, and without the danger to staff inherent with handling large hooks anchored in strong current. However, Flathead Catfish were not fully recruited to our hoop nets until they reached 51 cm, even though the 2.5-cm-bar mesh was capable of retaining individuals as small as 19 cm. Therefore, low-frequency electrofishing is likely a more efficient means of capturing juveniles (Stauffer and Koenen 1999). The size selectivity of the hoop nets may have been partly due to setting nets in habitats that were used more frequently by larger fish. It is also possible that small Flathead Catfish tended to avoid entering nets that already contained larger conspecifics, due to the danger of aggression or cannibalism. Overall hoop net catch rates were similar among the three years of sampling. However, there was significant variation in length distributions among years, primarily due to a greater proportion of fish < 51 cm in 2014. There also was significant variation in length distributions among reaches, possibly due to differences in habitat preferences among length classes. Although the large hoop nets were of limited value for sampling juveniles directly, the catch curve based on fish age 5 and older indicated that recruitment to the adult population has been quite consistent for many years.

My study design allowed for comparison of closed-population and open-population capture-recapture abundance estimates. A capture-recapture abundance estimate is not necessarily a “population estimate,” but only an estimate of the number of animals that are vulnerable to the sampling methods (Seber 1982: p. 72). Interpreting an abundance estimate as a population estimate requires the assumption that one is sampling the entire biological population (or a defined sub-population), but this assumption is not always valid. For example, Kelso and Shuter (1989) found that closed-population removal models based on intensive gill netting substantially underestimated the total population of trout *Salvelinus* spp. and *Oncorhynchus mykiss* in a small lake, even though their models fit the data well. They believed the discrepancy was due to changing catchability as a result of sampling by a single, passive, size-selective gear in a heterogeneous habitat subject to significant environmental changes; a scenario remarkably similar to my hoop net sampling of Flathead Catfish in the Minnesota River. In this study, although the spacing of hoop nets along each study reach approximated the previously documented mean weekly net movements of adult Flathead Catfish at the same time of year in the LeSueur reach (Shroyer 2011), it is likely that some individuals did not move enough during an annual four-night sampling period to have any chance of encountering a net and being captured. Therefore, similar to the results of Scott (1950) from hoop net and wire basket catches in the Coosa River, Alabama, my closed-population abundance estimates probably only represented a portion of the Flathead Catfish that were actually present in the study reaches each August. In addition, since very few, if any, fish were recaptured within an annual sampling period, closed-population abundance estimates were only possible when nightly catches tended to decline over the four nights of annual sampling, analogous to removal methods. When nightly catches did not decline, it could have been due to increased movement within the reach resulting in higher probability of encountering nets, or substantial short-term immigration resulting in violation of the closed-population assumption. Open-population abundance estimates based on all three years of capture and recapture data generally indicated substantially higher Flathead Catfish densities than corresponding closed-population estimates. The open-population estimates probably better represented actual abundance not only because they did not assume short-term closure, but also because marked fish had time to move and mix with unmarked fish during the one-year intervals between sampling periods.

Density estimates for the Minnesota River are difficult to compare directly with other riverine populations because of differences in length ranges of the fish sampled and potential biases of most other estimates. Morris et al. (1971) estimated densities of Flathead Catfish in the Missouri River, Nebraska to be 17 fish/km ≥ 20 cm in the unchannelized section and 9 fish/km ≥ 20 cm in the channelized section using a modified Schnabel method, but their methods may have resulted in substantial bias because they only sampled brush piles and bank stabilization structures. Quinn (1988) used traditional Schnabel and Schumacher-Eschmeyer closed-population methods for Flathead Catfish ≥ 30.5 cm that were captured and recaptured between May and November 1985 in the Flint River, Georgia, resulting in density estimates of approximately 160 fish/km ≥ 30.5 cm. However, their estimates may have been substantially biased due to recruitment and mortality over the 6-month sampling period. Dobbins et al. (1999) probably came closer to meeting closed-population assumptions with their Schnabel estimates of 35-58 fish/km ≥ 38 cm TL in the Apalachicola River, Florida. Daugherty and Sutton (2005) estimated density at 145 fish/km in the St. Joseph River, Michigan, but it was unclear what length range this applied to, and the estimate may have been substantially biased due to violation of demographic closure during excessively long sampling periods. Kaeser et al. (2011) used traditional Petersen closed-population methods to estimate abundance of Flathead Catfish ≥ 30.5 cm in the Flint River and Ichawaynochaway Creek, Georgia in 2007 and the Altamaha River, Georgia in 1995 and 2009. Their assumption of geographic closure was reasonable, but it was unclear whether sampling periods were short enough for the assumption of demographic closure to be valid. Their density estimates for the Flint River and Ichawaynochaway Creek were only about 30 fish/km and 10 fish/km, respectively; while estimates for the Altamaha River were about 200 fish/km in 1995 and 60 fish/km in 2007. The only previous capture-recapture study that rigorously addressed both geographic and demographic closure was that of Pine (2003). His density estimates of Flathead Catfish > 12.5 cm were only 4-31 fish/km for introduced populations in three North Carolina coastal plain rivers based on robust design models. My density estimates for Flathead Catfish ≥ 51 cm were approximately 90 fish/km based on open-population Jolly-Seber models, which along with the exceptionally high catch rates indicate very high abundance of adult Flathead Catfish in the lower Minnesota River.

This study suggested long-term open-population experiments may be more useful than short-term closed-population experiments for riverine Flathead Catfish due to the difficulty of obtaining a large enough sample in a short enough time before assumptions of geographic and demographic closure are violated, along with potential problems such as short-term trap shyness and inadequate short-term mixing of marked and unmarked fish. Unlike Pine (2003), I did not need to account for temporary emigration. This was partly due to the limited possibility of temporary emigration in a study with only three primary periods, but also because my sampling occurred at a time of year when Flathead Catfish exhibited high site fidelity, and my study reaches were much larger than the typical home range size (Shroyer 2011). Three primary periods (not necessarily annual or evenly spaced) are the minimum for open-population models, but future studies should be planned for more than the minimum to increase precision of estimates and allow for potential loss of planned sample periods due to adverse river conditions. Studies should be designed to minimize the possibility of temporary emigration, but should incorporate the robust design so that temporary emigration can be detected and dealt with if necessary.

Flathead Catfish in this study were extremely trap shy for at least three nights after initial capture in hoop nets. Pine (2003) also found evidence of trap shyness during repeated electrofishing samples. Except for Pine (2003), all previously reported closed-population abundance estimates for riverine Flathead Catfish have assumed equal initial capture and recapture probabilities. If the fish in these studies actually were trap shy, then the abundance estimates were positively biased. Because of the apparent tendency for short-term trap shyness in Flathead Catfish, future closed-population capture-recapture studies always should consider models with behavioral effects on recapture probabilities.

An assumption of Jolly-Seber models is that marked and unmarked animals have the same capture probability (Seber 1982: p. 196). If Flathead Catfish were still trap shy after 1-2 years at large (i.e., “permanently” trap shy), then Jolly-Seber capture probabilities were negatively biased and abundance estimates were positively biased (Williams et al. 2002). However, the fact that many more fish were recaptured after 1-2 years at large than during the four-night annual sampling periods suggests that trap shyness was primarily a short-term behavioral response, perhaps due to restricted movement while recovering from the stress of capture, tagging, and spine removal. Since Jolly-Seber estimates of capture probabilities were relatively high, it seems unlikely that many marked fish “remembered” to avoid hoop nets in subsequent years.

The 8% long-term loss or malfunction rate of PIT tags in this study was surprisingly high relative to the 1.5% rate reported for the same implantation location by Daugherty and Buckmeier (2009). Several factors may have contributed to the difference. The tags used in this study were longer than the 8.5 mm X 2.1 mm tags that they evaluated, perhaps increasing the probability of loss. Their initial sample size (72 tagged fish) was much smaller than mine (479 tagged fish ≥ 51 cm), although they recovered 68 fish at the end of their study versus 59 recaptured during this one. Their long-term loss rate was determined after 300 days in the unnatural environment of two 0.24-ha earthen ponds, whereas mine was determined after 1-2 years in the natural environment of a free-flowing river where more active fish behavior could have increased the probability of tag loss or breakage. If I were to do another similar study with riverine Flathead Catfish, I would implant food-safe PIT tags in the dorsal musculature in an attempt to achieve improved long-term retention.

Point estimates of apparent survival from the Jolly-Seber models were much lower than the 91% actual survival estimate from the catch curve. Almost 80% of telemetry-tagged Flathead Catfish survived and returned to the LeSueur reach from late summer, 2008 to late summer, 2009 (Shroyer 2011), which is near the upper 95% confidence bounds of apparent survival estimates from the Jolly-Seber models; however, the Jolly-Seber estimates were negatively biased by tag loss and possibly by unobserved post-release mortality in 2013. The difference between actual survival and apparent survival is an estimate of the annual permanent emigration rate. Given the imprecision and potentially substantial bias of the Jolly-Seber apparent survival estimates, and the independent estimate of nearly 80% apparent survival based on telemetry, my best estimate of the annual permanent emigration rate from the 4-km study reaches during August is only about 10%.

Most other Flathead Catfish populations apparently experience substantially higher annual mortality rates than the Minnesota River population, corresponding with the relative rarity of old fish (Kwak et al. 2006). However, earlier studies probably tended to underestimate ages and survival rates, especially when basal recess spine sections were used for age determination (Turner 1982). Recent studies using otoliths for age determination estimated annual survival of lightly exploited populations similar to that in the Minnesota River (Marshall et al. 2009; Jolley and Irwin 2011; Winkelman 2011).

Flathead Catfish in the Minnesota River are an uncommon example of a fish population with a very high annual survival rate and relatively consistent recruitment for many years. There was no evidence that population dynamics were substantially different in the lower river in 2013-2015 than they were upstream from New Ulm 20 years earlier (Stauffer et al. 1996). The Minnesota River population of Flathead Catfish grew similarly to other native riverine populations throughout the United States at young ages, but did not reach large sizes until relatively old ages. Nonetheless, length distributions of the hoop net catch indicated very high proportions of large fish in the Minnesota River relative to other populations based on comparable hoop net samples (Ford et al. 2011), trot line samples (Arterburn 2001), or recreational and commercial catches (Marshall et al. 2009; Brown 2011; Travnichek 2011; Winkelman 2011). Flathead Catfish in the Minnesota River commonly survived long enough to reach memorable size, but the existence of a substantial proportion of trophy-size fish depended on the very high annual survival rate that allowed unusually fast-growing individuals to reach old ages. Therefore, the size structure of this population is vulnerable to any substantial increase in total mortality, and very conservative fishing regulations are warranted if maintaining the current trophy fishery is a high priority.

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