Age, Growth, and Mortality of Introduced Flathead Catfish in Atlantic Rivers and a Review of Other Populations

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Abstract.—Knowledge of individual growth and mortality rates of an introduced fish population is required to determine the success and degree of establishment as well as to predict the fish's impact on native fauna. The age and growth of flathead catfish *Pylodictis olivaris* have been studied extensively in the species' native and introduced ranges, and estimates have varied widely. We quantified individual growth rates and age structure of three introduced flathead catfish populations in North Carolina's Atlantic slope rivers using sagittal otoliths, determined trends in growth rates over time, compared these estimates among rivers in native and introduced ranges, and determined total mortality rates for each population. Growth was significantly faster in the Northeast Cape Fear River (NECFR) than in the Lumber and Neuse rivers. Fish in the NECFR grew to a total length of 700 mm by age 7, whereas fish in the Neuse and Lumber river populations reached this length by 8 and 10 years, respectively. The growth rates of fish in all three rivers were consistently higher than those of native riverine populations, similar to those of native reservoir populations, and slower than those of other introduced riverine populations. In general, recent cohorts (1998–2001 year-classes) in these three rivers exhibited slower growth among all ages than did cohorts previous to the 1998 year-class. The annual total mortality rate was similar among the three rivers, ranging from 0.16 to 0.20. These mortality estimates are considerably lower than those from the Missouri and Mississippi rivers, suggesting relatively low fishing mortality for these introduced populations. Overall, flathead catfish populations in reservoirs grow faster than those in rivers, the growth rates of introduced populations exceed those of native populations, and eastern United States populations grow faster than those in western states. Such trends constitute critical information for understanding and managing local populations.

Quantification of age and growth is a vital component for understanding the ecology and life history of any fish species. This is especially important for an introduced species like flathead catfish *Pylodictis olivaris* in the Atlantic slope and elsewhere in the United States. Knowledge of the individual growth rates and age structure of an introduced population is required to determine the success and degree of establishment as well as to predict the fish's impact on native fauna. Growth rate information can also be used to compare dynamics among water bodies, years, and fish sizes; describe trends over time; examine total mortality rates; and determine the general status of a population.

Flathead catfish age and growth have been studied

sufficiently to allow elucidation of trends among geographic regions, aquatic habitats (rivers and reservoirs), and native and introduced populations (Tables 1–3). In native riverine populations of flathead catfish, the maximum reported age ranged from 5 years in the Neosho River, Kansas (Minckley and Deacon 1959), to 28 years in the Tallapoosa River, Alabama (Nash 1999). Growth to quality size (510 mm; Quinn 1991) may be obtained between 3 years (Francis 1993) and 9 years (Nash 1999). Memorable-size flathead catfish (860 mm; Quinn 1991) range in age from 8 years (Cross and Hastings 1956; Francis 1993) to 22 years (Nash 1999); however, most populations yield fish of that size by age 12. Fish over age 13 or 1,000 mm are rare to nonexistent in most populations; the maximum reported length was 1,118 mm from a fish captured in the Kansas River, Kansas (Cross and Hastings 1956). The Tallapoosa River population studied by Nash (1999) was perceived to grow considerably slower and live longer than any other native population.

Most investigators have used pectoral spines to age flathead catfish, and the results may be variably biased, especially for older fish. Nash and Irwin (1999) compared otoliths and pectoral spines for use in aging flathead catfish and determined that otoliths yielded more accurate age estimates due to annuli being more

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TABLE 1.—Average back-calculated total length at age for native flathead catfish from selected riverine populations.

Location and statistic	Total length (mm) at age													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tennessee River, Alabama	93	157	199	239	318	384	367	451	387					
Black Warrior River, Alabama	122	211	271	392	474	503	697		879					
Coosa River, Alabama	109	168	204	391	492	517	610	545	571	684				
Alabama River, Alabama	110	189	265	433	534	544	560		785					
Tallapoosa River, Alabama	147	208	261	307	351	398	427	484	510	513	535	540	565	589
Missouri River, Missouri	119	188	251	310	368	419	490	526	597	645	673	688		
Minnesota River, Minnesota	96	195	319	436	520	584	649	703	752	798	932	875	924	947
Big Black River, Mississippi	199	299	407	498	590	666	801	869	1,040	1,085				
Tallahatchie River, Mississippi	214	326	479	575	671	806	939	1,001	1,059					
Rio Grande River, Texas	61	124	232	350	485	590	673	757	914					
Missouri River, Nebraska	75	188	321	411	487	541	536							
Des Moines River, Iowa	142	269	393	469	550	600	674	714						
Big Blue River, Kansas	142	262	366	483	630		701	772						
Neosho River, Kansas	96	227	319	390	438									
Salt River, Missouri	76	155	231	300	348	422	452	503	599					
Verdigris River, Oklahoma	91	155	206	274	320	373	419	523	584	615				
Kansas River, Kansas	210	254	400	622	648	819	851	1,022	1,118	889				
Mississippi River, Illinois–Missouri ^a	191	304	406	457	482	559	660	787	851			914		
Mississippi River, Iowa–Illinois ^a	165	267	305	394	432	508	596	635	699	826	864		902	953
Mean	129.4	218.2	307.1	406.9	481.0	543.1	616.8	677.1	756.3	747.0	713.4	754.4	744.5	768.0
SE	10.9	13.3	18.8	22.8	24.9	31.9	36.4	45.4	56.3	63.9	90.5	86.8	116.2	120.3

^aData estimated from figure.

distinguishable, especially for older fish (i.e., over age 5). Pectoral spines consistently underestimated ages of older fish due to the erosion of the central lumen, which led to loss of annuli. Only several recent studies have estimated ages of flathead catfish with otoliths (e.g., Mayo and Schramm 1999; Nash 1999; Grabowski et al. 2004). Pectoral spines were used by all others (Tables 1–3) except for Pate (1980), who examined vertebrae. Thus, caution regarding the accuracy of reported ages should be exercised when interpreting results among studies, but examination of trends for young fish may be suitable for comparisons among populations.

Flathead catfish mortality has rarely been studied in the species' native range, and we found no total mortality rates reported for populations in the fish's

introduced range. The only published mortality rate estimated for an introduced population was that by Quinn (1993), who estimated annual fishing mortality for Flint River, Georgia, flathead catfish to be 14–25%. Summerfelt et al. (1972) used the Robson–Chapman estimator in Lake Carl Blackwell, Oklahoma, and reported annual total mortality rates of 31–49%. Robinson (1997) estimated annual total mortality rates over several years from catch curves in the Missouri and Mississippi rivers. Annual total mortality averaged 56% (range = 51–67%) in the Missouri River near Easley, Missouri, and 49% (range = 43–54%) in the Mississippi River at Crystal City, Missouri. Flathead catfish population modeling by Robinson (1997) suggested that a reduction of total mortality to 40% would increase the numbers of large fish and improve

TABLE 2.—Average back-calculated total length at age for native flathead catfish from selected reservoir populations.

Location and statistic	Total length (mm) at age									
	1	2	3	4	5	6	7	8	9	10
Lake Carl Blackwell, Oklahoma	58	117	198	309	446	549	623	678	714	738
Millford Reservoir, Kansas	164	230	316	412	517	591	700	796	837	869
Bluestone Reservoir, West Virginia	216	351	478	571	626	680	730	744	762	786
Watts Bar Reservoir, Tennessee	239	353	475	579	643	780	907	985	1,021	1,074
Norris Reservoir, Tennessee	132	239	351	472	589	671	737	790	841	879
Grand Lake, Oklahoma (Neosho Arm)	140	259	381	490	584	655	719	785	879	945
Grand Lake, Oklahoma (main body)	86	160	241	323	384	439	485	518		
Boomer Lake, Oklahoma		287	460	638	742	826	884	927	968	1,003
Mean	147.9	249.5	362.5	474.2	566.3	648.8	723.1	777.9	860.2	899.2
SE	24.6	29.5	37.8	42.5	40.3	43.8	47.7	50.8	40.7	44.6

TABLE 1.—Extended.

Location and statistic	Total length (mm) at age														Reference
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
Tennessee River, Alabama															Grussing et al. (2000)
Black Warrior River, Alabama															Grussing et al. (2000)
Coosa River, Alabama															Grussing et al. (2000)
Alabama River, Alabama															Grussing et al. (2000)
Tallapoosa River, Alabama	589	598	619	650	673	764	858	880	900	922	947	953	968	990	Nash (1999)
Missouri River, Missouri															Robinson et al. (1997)
Minnesota River, Minnesota	970	1,016	1,045	1,060	1,054										Stauffer et al. (1996)
Big Black River, Mississippi															Francis (1993)
Tallahatchie River, Mississippi															Francis (1993)
Rio Grande River, Texas															Pate (1980)
Missouri River, Nebraska															Holz (1969)
Des Moines River, Iowa															Mayhew (1969)
Big Blue River, Kansas															Minckley and Deacon (1959)
Neosho River, Kansas															Minckley and Deacon (1959)
Salt River, Missouri															Purkett (1958)
Verdigris River, Oklahoma															Jenkins and Finnell (1957)
Kansas River, Kansas															Cross and Hastings (1956)
Mississippi River, Illinois–Missouri ^a	1,041														Barnickol and Starrett (1951)
Mississippi River, Iowa–Illinois ^a	953														Barnickol and Starrett (1951)
Mean	780	807	832	855	864	764	858	880	900	922	947	953	968	990	
SE	269	296	301	290	269										

population size structure. Winkelman (2002) examined the effects of hand grappling (noodling) for the flathead catfish populations in Lakes Carl Blackwell and McMurty, Oklahoma, and reported annual total mortality rates of 17% and 16%, respectively.

The objectives of our research were to (1) quantify individual growth rates and age structure of introduced flathead catfish populations in three Atlantic coastal plain rivers of North Carolina, (2) determine trends in growth rate over time, (3) determine total mortality rates for each population, (4) compare growth and mortality estimates among rivers, and (5) compare our findings with those from rivers and reservoirs in both the native and introduced ranges to elucidate trends among populations. Based on a nonexhaustive literature review, we predicted that flathead catfish growth

rates in North Carolina coastal plain rivers would be high compared to those of native populations and similar to other introduced populations in the south-eastern USA.

Methods

North Carolina Atlantic rivers.—We selected three North Carolina Atlantic coastal plain river systems for study. Flathead catfish have been introduced into each watershed. The Northeast Cape Fear River (NECFR) supports the oldest population (about 30 years), the Neuse River supports a more recent population (about 20 years), and the Lumber River is the site of the most recent (<10 years) introduction (Kwak et al. 2004). The Neuse River is formed by the confluence of the Flat and Eno rivers; it varies widely in depth and width

TABLE 2.—Extended.

Location and statistic	Total length (mm) at age									Reference
	11	12	13	14	15	16	17	18	19	
Lake Carl Blackwell, Oklahoma	761	785	794							Turner (1982)
Milford Reservoir, Kansas	894	909	926	942	915	925				Layher and Boles (1979)
Bluestone Reservoir, West Virginia	798	751	675	682						Edmundson (1974)
Watts Bar Reservoir, Tennessee	1,100									Hargis (1966)
Norris Reservoir, Tennessee	947	991	1,008	1,013	1,036	1,067				Carroll and Hall (1964)
Grand Lake, Oklahoma (Neosho Arm)	1,013	1,074								McCoy (1953)
Grand Lake, Oklahoma (main body)										McCoy (1953)
Boomer Lake, Oklahoma	1,031	1,072	1,090	1,092	1,102	1,074	1,072	1,085	1,067	McCoy (1953)
Mean	934.9	930.3	898.5	932.3	1,017.8	1,022.1	1,071.9	1,084.6	1,066.8	
SE	47.2	57.2	74.2	88.9	54.8	48.6				

TABLE 3.—Average back-calculated total length at age for introduced flathead catfish from selected riverine populations.

Location and statistic	Total length (mm) at age								
	1	2	3	4	5	6	7	8	9
Neuse River, North Carolina	191	306	407	490	566	623	676	710	741
Northeast Cape Fear River, North Carolina	154	257	351	498	599	654	701	757	790
Lumber River, North Carolina	160	258	345	436	507	586	627	643	675
Altamaha River, Georgia ^a	154	265	370	478	568	612	664	680	713
Ocmulgee River, Georgia	270	398	509	605	691	759	821	889	947
Edisto River, South Carolina	260	360	550	769	970	1,153	1,067	1,030	
Little River and Long Cane, South Carolina		510	731	789	883	864	1,018	1,004	961
Great Pee Dee River, South Carolina	255	419	539	560	642	671	761	712	832
Flint River, Georgia	203	352	497	613	710	774	833	935	1,000
Cape Fear River, North Carolina	155	311	479	580	640	711	812	907	
Colorado River, Arizona–California	106	195	382	455	586	710	798		
Verde River, Arizona	118	223	362	470	621	747	785		
Coachella Canal, California	123	240	382	487	578	665	732	800	
Mean	181.4	319.2	461.2	562.7	666.1	743.1	802.6	838.7	849.4
SE	17.9	26.7	32.7	33.7	38.8	43.0	37.1	42.1	46.5

^a Fish lengths reported as fork length (mm); data not included in means, SE, or Figure 4.

along 443 river kilometers (rkm) before flowing into Pamlico Sound. The NECFR, located in the Cape Fear River drainage, is a relatively deep river (average depth = 3.0 m), possesses some tidal influence, and has an average width of 45 m. It rises in Wayne County and flows southeast for 209 rkm to the Cape Fear River at Wilmington. The Lumber River is a blackwater river with an average width of 37 m and an average depth of 0.9 m. It is located in the Pee Dee River watershed and flows 201 rkm from south-central North Carolina to the Little Pee Dee River near Nichols, South Carolina.

Fish collection and age estimation.—We collected flathead catfish ($N = 114$) from the Neuse River near Kinston during September–October 2001 and from the river near Raleigh during April–May 2003. We also collected fish ($N = 94$) from the NECFR downstream of Burgaw during August–September 2002 and May 2003 and from the Lumber River ($N = 36$) near Fairmont at Lumber River State Park in May 2003. We used a boat-mounted, low-frequency, pulsed DC electrofisher to capture flathead catfish at all sites and returned them to the laboratory for processing. All fish were sacrificed by submersion in an ice bath or an overdose in a clove oil solution.

We measured total length (± 1 mm) and weight (± 1 g), sexed each fish if possible by direct observation of the gonads, and assigned an identification number to each fish. Sagittal otoliths were removed from all flathead catfish by sectioning the supraoccipital bone with a fillet knife, hacksaw, or circular saw depending on fish size, and otoliths were stored in coin envelopes. Otoliths were prepared similarly to the methods of Maceina (1988) and Nash (1999), except with a few modifications. Otoliths were removed from envelopes, cleaned as necessary, and placed directly on a hot plate

for approximately 5 min. Crystalbond was melted onto a microscope slide in a dime-size pile, and the otolith was inserted anterior side up. The otoliths were polished with 600-grit sandpaper and were viewed under a compound microscope (100 $\times$; Figure 1). A subsample of otoliths was read independently by two readers who were naive of the fish's total length or weight; the remainder was read by a single reader. Any discrepancies in age estimation were reconciled with a concert read.

Back-calculation.—Back-calculation of length at age was completed by use of the Fraser–Lee direct proportion method (Carlander 1982). When available, five fish were randomly selected from each age-class within each river. We measured otolith radius by use of Image Pro Analysis Software (Media Cybernetics 2002). The total radius was equal to the distance between the center of the nucleus and the edge of the otolith. Annual growth was measured from the anterior edge of one annulus to the anterior edge of the adjacent annulus. Fish collected during fall were assigned an age to the final visible annulus, while the age of fish collected during spring was estimated by including the edge of the otolith as the final annulus. Figure 1 represents a flathead catfish otolith image typical of older fish in our study, and annuli are indicated on the figure.

Growth analysis.—We fitted a von Bertalanffy growth equation with an additive error structure (Ricker 1975) to age data collected from each population. Nonlinear least-squares regression (NLIN procedure in the Statistical Analysis System; SAS Institute 1994) was used to fit the equation

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

where L_t is the predicted length at a given time, L_∞ is

TABLE 3.—Extended.

Location and statistic	Total length (mm) at age								Reference
	10	11	12	13	14	15	16	17	
Neuse River, North Carolina	798	851	858	977	1,020				Current study
Northeast Cape Fear River, North Carolina	854	905	961	1,018	1,029	1,066	1,108	1,150	Current study
Lumber River, North Carolina	747	796	965						Current study
Altamaha River, Georgia ^a	717	755	849	901	879	922	647		Gabrowski et al. (2004)
Ocmulgee River, Georgia	1,012	1,081	1,178	1,321	1,665	1,761	1,800		Nash (1999)
Edisto River, South Carolina									Bulak and Leitner (1999)
Little River and Long Cane, South Carolina	1,129	984	940		940				Bulak and Leitner (1999)
Great Pee Dee River, South Carolina	770	713		901	1,101				Bulak and Leitner (1999)
Flint River, Georgia									Quinn (1989)
Cape Fear River, North Carolina									Guier et al. (1984)
Colorado River, Arizona–California									Young and Marsh (1990)
Verde River, Arizona									Young and Marsh (1990)
Coachella Canal, California									Pisano et al. (1983)
Mean	885.0	888.3	980.4	1,054.1	1,151.0	1,413.7	1,454.1	1,150.0	
SE	62.3	53.9	53.0	92.2	131.0	347.3	141.2		

the average maximum size in the population, k is the growth coefficient, t is time (years), and t_0 is the hypothetical age (years) when the mean fish total length is zero. We then compared growth rates by estimating the mean length at age 1 through the maximum age in each population based on this growth model. A nonparametric F -test for comparing parameters from nonlinear models was used to test for growth

differences between the populations based on the von Bertalanffy growth parameters (Ratkowsky 1983). This procedure involves testing the hypothesis that a common growth curve is adequate to fit data from each of the three study populations. If the common growth curve hypothesis is rejected, then a series of more-restrictive models and hypotheses that omit parameters and populations are compared to elucidate differences

FIGURE 1.—Image of a sectioned otolith extracted from a female flathead catfish (1,055 mm total length; 21,300 g) collected on 7 May 2003 from the Northeast Cape Fear River, North Carolina. Estimated age is 14 years.

FIGURE 2.—Catch curves for flathead catfish collected in the (a) Neuse River, (b) Northeast Cape Fear River, and (c) Lumber River, North Carolina, during 2001–2003.

in growth parameters among populations. Our sample sizes of fish with known sex were not sufficient to compare growth rates between sexes. However, other researchers detected no significant difference in growth between sexes for an introduced riverine population of flathead catfish (Grabowski et al. 2004), and thus we included all collected fish in a single group for growth analyses.

Mortality estimation.—The mode of the $\log_e$ (number of fish collected + 1) versus age plot (i.e., catch curve) was used to determine the age at which flathead catfish fully recruited to the gear (Figure 2). In-

stantaneous total mortality rate (Z) was estimated by the slope of a linear regression fitted to the descending right limb of each catch curve (Figure 2) (Ricker 1975; Seber 1982). The annual total mortality rate ($A = 1 - e^{-Z}$) was then calculated based on the estimate of Z (Ricker 1975). The mode of the age-frequency plot used to represent age at full recruitment (i.e., threshold age; Seber 1982) varied among populations (Figure 2). The distribution was multimodal for Lumber River flathead catfish (ages 1, 5–6, and 9; Figure 2c), and we initiated the catch curve at age 5 for that population. Such irregularities represent variation in fish recruit-

TABLE 4.—Flathead catfish size and age summary, growth parameters (95% confidence limits in parentheses), and mortality estimates for three North Carolina rivers sampled in 2001–2003. (L_{∞} = asymptotic length; k = growth coefficient; t_0 = hypothetical age at which fish length = 0; Z = instantaneous total mortality rate; A = annual total mortality rate).

Variable	River		
	Lumber	Northeast Cape Fear	Neuse
Sample size	36	94	114
Age (years)			
Mean	5.7	3.7	4.6
SD	3.1	2.9	3.1
Range	0–12	1–17	1–14
Total length (mm)			
Mean	508	397	515
SD	237	250	227
Range	124–965	123–1,150	150–1,165
Growth parameters			
L_{∞} (mm)	1,233 (447, 2,019)	1,423 (1,206, 1,640)	961 (843, 1,079)
k	0.09 (–0.01, 0.19)	0.11 (0.08, 0.14)	0.20 (0.13, 0.27)
t_0 (years)	–0.42 (–1.46, 0.62)	0.45 (0.15, 0.75)	–0.03 (–0.50, 0.44)
Mortality parameters			
Z	–0.208 (–0.401, –0.015)	–0.170 (–0.275, –0.065)	–0.221 (–0.301, –0.141)
A	0.188	0.156	0.198

ment among years and do not greatly affect the value of the catch curve (Ricker 1975).

Results

Age and Growth

Flathead catfish of wide age and size ranges were collected in each river (Table 4). Those from the NECFR exhibited the fastest growth rates, but only 10 fish older than age 5 were collected, thus limiting analyses of older fish (Table 5). The four most recent age-classes (1998–2001) showed slower growth than those cohorts previous to the 1998 year-class, while the 1996 year-class consistently showed the fastest growth among all cohorts in that river. Growth rates were rapid through age 5; fish generally grew at least 100 mm/year during that period. Growth rates were fairly constant between ages 6 and 13, averaging about 50 mm/year, but slowed slightly beyond those ages (Table 5).

Back-calculated growth of Neuse River flathead catfish revealed slower growth to age 1 for the five most recent year-classes (1996–2000) than for year-classes previous to 1996 (Table 6). Growth to successive ages was similar among all age-classes except the 1989 year-class, which consistently grew slower owing to an artifact of one slow-growing fish. Annual growth increments steadily declined through age 5 but remained similar between ages 6 and 11 (Table 6). Low sample sizes for age-12 and older fish hindered comparisons beyond age 11.

Flathead catfish of the Lumber River showed fairly similar growth rates among all age- and size-classes, and slightly slower growth was found for the 1992, 1994, 2000, and 2001 year-classes (Table 7). Similar to the NECFR population, the 1996 cohort in the Lumber River exhibited the fastest growth rates among all age-classes. The growth rate declined sharply between ages 1 and 2 and varied between 72 and 98 mm/year through age 6. Growth rates in the Lumber River were the slowest among the three populations studied.

Von Bertalanffy growth models generally fit the NECFR and Neuse River populations fairly well through age 8 (Table 4; Figure 3). Lower sample sizes and greater variation in growth rate at large sizes reduced model fit at older ages. Growth rates among rivers were significantly different in an overall comparison ($F_{6,232} = 12.6$, $P < 0.0001$) as well as in pairwise comparisons (Neuse River versus NECFR: $F_{3,202} = 30.4$, $P < 0.0001$; Neuse River versus Lumber River: $F_{3,146} = 32.8$, $P < 0.0001$; NECFR versus Lumber River: $F_{3,144} = 27.1$, $P < 0.0001$). Back-calculated and von Bertalanffy-modeled growth rates were very similar between ages 1 and 11 in the Lumber River (Figure 3). Back-calculated growth was similar to modeled growth in the NECFR until age 6, when back-calculated growth slowed. Back-calculated growth was generally slower than modeled growth in the Neuse River between ages 3 and 10 but was higher for ages 13 and 14. The von Bertalanffy growth model

TABLE 5.—Average back-calculated total length (TL [mm]) of flathead catfish collected from the Northeast Cape Fear River, North Carolina, 2002–2003.

Year-class and summary TL statistic ^a	N	Mean TL at capture	TL range	TL at age							
				1	2	3	4	5	6	7	8
2001	10	152	123–197	128							
2000	20	223	140–361	132	219						
1999	34	312	209–579	136	224	293					
1998	10	488	385–569	175	289	372	444				
1997	9	663	610–710	208	351	457	548	624			
1996	2	697	678–716	222	372	465	558	630	716		
1995	3	750	633–914	199	294	406	498	571	646	702	
1994	0										
1993	1	995	995	216	355	463	540	625	717	802	879
1992	0										
1991	0										
1990	0										
1989	2	1,098	1,080–1,115	223	345	426	493	566	642	705	768
1988	2	1,056	1,055–1,057	164	275	380	459	524	590	645	694
1987	0										
1986	0										
1985	1	1,150	1,150	216	348	453	523	585	641	697	739
Weighted mean TL at age				153.5 (8.0)	257.4 (11.4)	350.9 (14.5)	498.4 (14.6)	599.0 (16.8)	653.9 (25.6)	700.7 (28.6)	757.1 (28.2)
Mean annual increment				153.5 (8.0)	103.9 (13.9)	93.5 (18.4)	147.5 (20.6)	100.6 (22.3)	54.9 (30.7)	46.8 (38.4)	56.4 (40.2)

^a Values in parentheses are SEs; those for the mean annual increment were calculated by pooling variance estimates of weighted mean TL at age according to Zar (1996).

estimated the largest theoretical size for the NECFR population followed by the Lumber and Neuse river populations, and growth coefficients varied among rivers, indicating differing rates of increase in fish length and differing shapes of growth curves.

Mortality

Mortality estimates derived from catch curves were relatively consistent among rivers (Table 4). Instantaneous total mortality rates ranged from 0.17 to 0.22, and annual total mortality rates ranged from 0.16 to 0.20 (i.e., 16–20%). Low catch rates of older fish (ages 8 and older) and variation among cohorts decreased the precision of our mortality estimates, and 95% confidence intervals averaged ±60% of the associated Z estimates. We detected no significant difference in Z among populations by analysis of covariance ($F_{2,20} = 1.23$, $P = 0.29$), and 95% confidence intervals for all estimates overlapped the means of the other two estimates.

Discussion

We observed a large range in sizes at each age within and among the rivers we sampled. For example, the total length of age-3 fish from the Neuse River ranged from 285 to 560 mm, and 600-mm fish from the Neuse River spanned ages from 3 to 9 years (Figure 3). These large variations could be attributable to differential growth or mortality rates among cohorts or age

estimation error. Larger sample sizes of fish for age analysis would further determine the source of this wide variation, but results from other populations suggest that high within-population variance in growth rate is common for this species (Cross and Hastings 1956; Layher and Boles 1980; Winkelman 2002; Grabowski et al. 2004).

Growth

Growth comparisons among flathead catfish populations within a study or among published results should consider the bony structure used for age estimates. Pectoral spines have frequently been used to age flathead catfish and are considered the hard part of choice for the majority of studies, due to logistic simplicity and nonlethal effects. However, Nash and Irwin (1999) demonstrated potential bias and reduced precision in flathead catfish age analysis based on pectoral spines versus otoliths. Our research is one of only a few studies conducted on flathead catfish that did not rely upon spines or vertebrae as aging structures, and many previous studies may be variably biased, especially for results on older fish (ages over 5 years; Nash and Irwin 1999). However, annulus formation in the articulating process of the pectoral spine was validated for flathead catfish to age 5 (Turner 1982), and age estimates derived from the pectoral spine articulating process are more accurate and precise than those derived from pectoral spine basal recess

TABLE 5.—Extended.

Year-class and summary TL statistic ^a	TL at age								
	9	10	11	12	13	14	15	16	17
2001									
2000									
1999									
1998									
1997									
1996									
1995									
1994									
1993	949								
1992									
1991									
1990									
1989	836	908	959	1,023	1,082				
1988	749	812	872	924	978	1,035			
1987									
1986									
1985	781	829	864	913	969	1,018	1,066	1,108	1,150
Weighted mean	790.1	854.2	905.4	961.2	1,017.8	1,029.1	1,066.4	1,108.2	1,150.0
TL at age	(31.4)	(24.2)	(23.5)	(26.7)	(28.3)	(13.0)			
Mean annual	33.0	64.0	51.2	55.8	56.6	11.3	37.3	41.8	41.8
increment	(42.2)	(39.6)	(33.7)	(35.6)	(38.9)	(31.1)	(13.0)		

sections (Nash and Irwin 1999). Furthermore, ages estimated from pectoral spines for young fish are relatively accurate, and the general direction of bias in older fish ages is known (underestimates of older fish based on spines; Nash and Irwin 1999). Therefore, age estimates derived from pectoral spines in previous studies remain useful for discerning patterns among

flathead catfish populations when proper scrutiny is used in their interpretation.

In general, the observed growth of introduced flathead catfish populations in North Carolina rivers is slower than that of other introduced populations throughout the southeastern United States but faster than that of most native riverine populations (Tables 1,

TABLE 6.—Average back-calculated total length (TL [mm]) of flathead catfish collected from the Neuse River, North Carolina, 2001–2003.

Year-class and summary TL statistic ^a	N	Mean TL at capture	TL range	TL at age													
				1	2	3	4	5	6	7	8	9	10	11	12	13	14
2000	11	191	150–222	134													
1999	24	302	240–380	191	270												
1998	21	448	285–588	189	309	391											
1997	17	548	375–638	188	303	389	467										
1996	5	628	570–679	186	314	419	499	576									
1995	7	669	593–742	222	364	455	529	586	641								
1994	9	697	554–918	220	339	432	520	596	659	717							
1993	5	820	690–918	209	342	448	530	596	660	714	767						
1992	5	695	600–1,050	219	323	395	467	520	571	630	680	721					
1991	2	785	646–924	204	316	398	462	529	581	631	682	731	771				
1990	1	1,165	1,165			583	657	724	791	865	924	1,007	1,057	1,115			
1989	6	857	577–1,115	200	284	365	429	494	549	609	661	712	759	804	848		
1988	0																
1987	1	1,020	1,020		318	398	463	535	608	658	709	767	825	868	919	977	1,020
Weighted mean					191.5	306.4	407.3	489.9	566.2	622.9	676.2	710.1	740.8	798.0	850.7	858.0	977.0
TL at age					(6.1)	(7.9)	(10.8)	(13.3)	(16.4)	(21.3)	(28.0)	(37.5)	(52.2)	(60.6)	(75.3)	(78.9)	
Mean annual					191.5	115.0	100.8	82.6	76.3	56.7	53.3	33.8	30.7	57.2	52.7	7.3	119.0
increment					(6.1)	(10.0)	(13.4)	(17.1)	(21.1)	(26.8)	(35.2)	(46.9)	(64.3)	(80.0)	(96.7)	(109.1)	(78.9)

^a Values in parentheses are SEs; those for the mean annual increment were calculated by pooling variance estimates of weighted mean TL at age according to Zar (1996).

TABLE 7.—Average back-calculated total length (TL [mm]) of flathead catfish collected from the Lumber River, North Carolina, during May 2003.

Year-class and summary TL statistic ^a	N	Mean TL at capture	TL range	TL at age											
		1		2	3	4	5	6	7	8	9	10	11	12	
2002	6	142	124–189	142											
2001	1	190	190	122	190										
2000	2	276	263–289	127	206	276									
1999	2	384	350–417	149	244	317	384								
1998	5	426	388–475	142	229	308	367	424							
1997	5	633	469–772	185	289	367	495	564	631						
1996	4	725	689–770	186	310	416	517	596	658	725					
1995	3	696	636–783	187	285	378	455	525	580	633	692				
1994	6	667	514–802	159	232	314	402	467	519	567	616	667			
1993	0														
1992	1	680	680				349	421	465	519	564	608	644	680	
1991	1	965	965	177	319	425	496	567	620	682	735	788	850	912	965
Weighted mean TL at age				159.9 (8.2)	258.1 (12.7)	345.1 (14.1)	435.8 (15.8)	507.4 (18.4)	586.1 (22.7)	626.8 (22.9)	643.1 (26.6)	675.0 (29.3)	747.1 (103.0)	795.9 (115.9)	965.0
Mean annual increment (mm)				159.9 (8.2)	98.2 (15.1)	87.0 (18.9)	90.7 (21.2)	71.6 (24.2)	78.7 (29.2)	40.7 (32.2)	16.3 (35.1)	32.0 (39.5)	72.0 (107.0)	48.9 (155.1)	169.1 (115.9)

^a Values in parentheses are SEs; those for the mean annual increment were calculated by pooling variance estimates of weighted mean TL at age according to Zar (1996).

3). Growth to quality size generally occurred by age 5 in our study but was attained as early as age 3 in another Atlantic slope introduced population in the Ocmulgee River, Georgia (Nash 1999). Memorable sizes were reached between ages 11 and 12 in our study rivers versus age 8 in the Ocmulgee River. Trophy-size fish (1,020 mm; Quinn 1991) were observed by age 11 in the Ocmulgee River, whereas this size was attained by age 14 in the Neuse River and NECFR (Table 3). We collected no trophy-size fish in the Lumber River.

Growth rates of North Carolina coastal plain flathead catfish are considerably faster than those reported from the Tallapoosa River, Alabama, in the only comparable native flathead catfish age and growth study that used otoliths (Nash 1999). Growth rates in our study are also faster than those reported from riverine populations throughout the Upper Midwest (Table 1); however, among other factors, this comparison may reflect counter-gradient growth variation, which would predict faster growth in more southerly latitudes. Our growth rates were most similar to reservoir flathead catfish in their native range (Table 2).

Growth rates after age 2 in the Cape Fear River (Guier et al. 1984) were much higher than those reported here (Table 3). This may be partially attributed to the use of pectoral spines (versus otoliths) to estimate ages or could reflect actual spatial or temporal variation. However, there is compelling evidence to suggest that fish in the earlier study grew faster as a result of their more-recent establishment than the populations we studied in the Neuse River and NECFR. Guier et al. (1984) reported that flathead

catfish were first introduced into the Cape Fear River in 1966, only 13 years before their study. As an introduced population expands and decimates its initial food supply, growth is likely to slow due to intraspecific competition and other density-dependent factors. Layher and Boles (1980) reported that flathead catfish became almost entirely piscivorous at 500 mm, as did the flathead catfish in our three study rivers (Pine 2003; Pine et al. 2005). Flathead catfish in the Guier et al. (1984) study showed growth that was accelerated relative to fish in our study beginning at around age 3, when flathead catfish averaged 497 mm and presumably became obligate piscivores. Quinn (1989) reported markedly slower growth rates in the Flint River during a 1985 study than was observed in previous work from the 1970s. Similar trends may develop in other introduced flathead catfish populations, where growth rates may slow and approach those of native populations over time.

Trends among Populations

Comparisons among growth rates reported for flathead catfish in rivers versus reservoirs and native versus introduced populations reveal several trends (Figure 4). Native flathead catfish growth in reservoirs was faster on average than that of riverine populations (Tables 1, 2). Fish averaged 566 mm at age 5 in reservoirs but only 481 mm in rivers, and 700 mm was attained between ages 5 and 9 for reservoir fish and between ages 6 and 20 for riverine fish. In general, introduced riverine populations show faster growth

FIGURE 3.—Comparison of observed, von Bertalanffy (VB)—modeled, and back-calculated total length at age for flathead catfish collected in the (a) Neuse River, (b) Northeast Cape Fear River, and (c) Lumber River, North Carolina, during 2001–2003.

rates than do native riverine populations (Tables 1, 3; Figure 4).

While the data resolution among studies precluded specific statistical comparisons, an examination of means and confidence intervals suggests that growth rates between native and introduced riverine populations are statistically different (Figure 4). For all ages up to age 9, the confidence intervals for mean length at age for native riverine populations do not overlap those

corresponding means for introduced riverine populations (and vice versa), and means for reservoir fishes are intermediate to those for riverine fishes. At ages 9 and 10, the means of fish length for introduced river populations and those of native reservoirs converge, which may either suggest ecological variation or be an artifact of methodological differences in structures used for age estimation. The trends that we have detected among studies suggest that while differences in

FIGURE 4.—Mean total length at age (and 95% confidence intervals) of introduced riverine, native riverine, and native reservoir flathead catfish populations in the USA, indicating variable growth rates between native and introduced populations and between riverine and reservoir populations (see Tables 1–3 for summary according to population).

flathead catfish growth among aquatic habitats (rivers and reservoirs) and native and introduced populations may not be consistently statistically significant, they are probably biologically significant, and we expect that future results will increase sample sizes and reduce confidence intervals to yield greater statistical differentiation.

Previous to our collection of a 17-year-old flathead catfish in the NECFR, the maximum age reported for an introduced riverine population (16 years) came from the Ocmulgee River, and the maximum length obtained remains 1,800 mm from that population (Nash 1999). All introduced riverine populations yielded quality-size fish by age 5 and memorable-size fish by age 8, while the Ocmulgee River population grew trophy-size fish by age 11. Introduced riverine populations in the southeastern USA (Guier et al. 1984; Quinn 1989; Bulak and Leitner 1999; Nash 1999; our results) tended to grow faster than those from the western region of the country (Pisano et al. 1983; Young and Marsh 1990; Table 3).

Our literature review defined general trends in flathead catfish growth rates wherein populations in reservoirs grow faster than those in rivers, introduced populations grow faster than native populations, and eastern U.S. populations grow faster than those in western states. Exceptions to these trends include studies by Minckley and Deacon (1959), Francis

(1993), and Stauffer et al. (1996), who reported growth rates from native populations similar to those of introduced flathead catfish (Tables 1, 3). Possible explanations include the use of spines (versus otoliths) in each of these studies (which would result in biases lower in age and higher in associated growth estimates), particular complexities in predator–prey relationships, or other differences in local environmental conditions.

Mortality

The values of *A* for flathead catfish in our study were lower than those that Robinson (1997) found for native populations in the Missouri and Mississippi rivers but similar to recent estimates from Oklahoma reservoirs (Winkelman 2002). Our estimates of *A* for these three introduced riverine populations were relatively low, ranging from 0.16 to 0.20 (Table 4). The Neuse River population exhibited relatively constant mortality over the entire range of ages sampled ($r^2 = 0.78$; Figure 2). Annual mortality in the NECFR varied by age or possibly through time, and higher mortality was observed in recent years. The size structure of flathead catfish in this river indicates that fish may consistently be harvested once they reach 600 mm. While conducting this research, we anecdotally observed a greater number of setlines (primarily attached to tree limbs) on the NECFR than on the other two rivers,

which suggests fishing mortality as a partial explanation for the temporal variation and catch curve fit among rivers.

Stochastic mortality events may partially explain variation in flathead catfish population structure among the rivers we studied. The relatively young age structure in the NECFR may have partially been a result of Hurricane Fran, which devastated much of eastern North Carolina in 1996. Large fish kills were observed in this river due to anoxic ambient conditions associated with severe flooding during and after the storm (K. Nelson, North Carolina Wildlife Resources Commission, personal communication), and such a mortality event may have reduced recruitment and the adult flathead catfish population. Furthermore, land use on the North Carolina coastal plain is predominantly agricultural and includes numerous confined poultry and swine production facilities that are known to degrade river water quality and cause fish kills via diffuse and point releases of animal waste (Mallin 2000). Such primary and cumulative impacts on riverine fish populations in this region may lead to stochastic events that result in differential mortality among cohorts and over time. Such variation among cohorts and years complicates the utility of catch curve analysis for estimating A , as the assumed condition that mortality rate is uniform with age over the range of age-classes considered may be violated to varying degrees (Ricker 1975).

Although we were unable to separate natural and fishing mortality rates from our A estimates, we suggest that fishing mortality is an important factor in maintaining the relatively low A in these populations. Our A estimates were similar to annual fishing mortality rates reported for the Flint River introduced flathead catfish population (Quinn 1993). In a radiotelemetry study associated with our research on the same three rivers (Kwak et al. 2004), only one instance of natural mortality was detected throughout the 1-year tracking study among 40 radio-tagged fish (2.5%), and five angling mortalities (12.5%) were reported during the 2-year period after fish were radio-tagged. In addition, radio signals were lost from eight fish during the 1-year tracking period. These fish may have permanently emigrated from our study areas, and some may have been undetected mortalities. The relatively low mortality rates of our radio-tagged fish are in accord with the similarly low estimates of annual fishing mortality (14–25%) reported by Quinn (1993) for another introduced flathead catfish population and support the validity of our 16–20% estimates of A derived from catch curve analyses (Table 4).

Conclusions

Our age, growth, and mortality research on these three populations of flathead catfish in North Carolina coastal plain rivers represents one of several studies of such introduced populations for which data accuracy and precision are presumed to be reasonable to form scientific conclusions. Our literature review and compilation revealed important trends in flathead catfish growth rates as related to population origin (native or introduced), habitat (lentic or lotic), and geography (region of the USA). Our results conformed to the expectation that growth rates in these populations would be higher than those of native riverine populations, but growth was generally slower than that of other introduced flathead catfish populations in the southeastern USA, contrary to our prediction. Elucidating such trends among native and introduced populations, aquatic habitats, and geographic regions greatly enhances our understanding of and ability to manage this ecologically, economically, and culturally important species, and we look forward to future research to further refine these relationships.

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