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AGE, GROWTH, AND LIFE HISTORY COMPARISONS BETWEEN THE INVASIVE WHITE SUCKER (*CATOSTOMUS COMMERSONI*) AND NATIVE RIO GRANDE SUCKER (*C. PLEBEIUS*)

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ABSTRACT—I compared the life histories of the invading *Catostomus commersoni* and the declining native *C. plebeius* in the upper Rio Grande of northern New Mexico to illuminate the mechanisms by which *C. commersoni* attains higher abundance than *C. plebeius*. In the first year of life, the 2 species did not differ in length, but *C. plebeius* reached greater individual mass. *Catostomus plebeius* achieved a higher intrinsic reproductive rate by maturing earlier, but *C. commersoni* attained approximately twice the net reproductive output by living longer, growing larger, and attaining 15-fold higher fecundity. While other factors undoubtedly facilitate the invasion of *C. commersoni*, I suggest that the high fecundity achieved by large *C. commersoni* contributes to its dominance in the upper Rio Grande system.

RESUMEN—Comparé la historia de vida de la especie invasiva del pez *Catostomus commersoni* y la especie nativa en declinación *Catostomus plebeius* en la parte superior del Río Bravo en el norte de Nuevo México, EEUU, para elucidar los mecanismos por los cuales *C. commersoni* alcanza mayor abundancia que *C. plebeius*. En el primer año de vida, las dos especies no difirieron en longitud, pero *C. plebeius* alcanzó una masa individual más grande. *Catostomus plebeius* alcanzó una tasa reproductiva intrínseca más grande por madurar más temprano, pero *C. commersoni* logró aproximadamente la doble producción reproductiva neta, creciendo más y alcanzando una fecundidad 15 veces más alta. Aunque otros factores sin duda facilitaron la invasión de *C. commersoni*, sugiero que la alta fecundidad lograda por las grandes de *C. commersoni* contribuye a su dominación en la parte superior del sistema del Río Bravo.

The white sucker (*Catostomus commersoni*) was first documented in the upper Rio Grande of Colorado and New Mexico in the early 1930s and has since spread throughout the upper basin, becoming a dominant member of the fish fauna in this region (unpublished records, Museum of Southwestern Biology, University of New Mexico, Albuquerque; Platania, 1991). Coinciding with the spread of *C. commersoni* has been the decline of the Rio Grande sucker (*Catostomus plebeius*), which is now absent from most of its native range in the upper Rio Grande (Calamusso et al., 2002). Although it is difficult to document competitive displacement of one species by another (Douglas et al., 1994), evidence suggests that the potential for negative interactions between these 2 species is substantial. Across its native range, *C. plebeius* is most abundant in streams that have not been invaded by *C. commersoni* (Calamusso et al., 2002). At the local scale, *C. plebeius* abundance and condition are

negatively correlated with *C. commersoni* abundance, and the 2 species overlap substantially in habitat use (Swift-Miller et al., 1999). *Catostomus commersoni* is omnivorous, consuming invertebrates when abundant, but also consuming algae and detritus when invertebrate density is low (Ahlgren, 1990), whereas *C. plebeius* is specialized for consuming perilitic algae (Smith, 1966). Despite these differences, Swift-Miller et al. (1999) found little evidence for trophic niche partitioning between the 2 species when in sympatry in the upper Rio Grande. Periphyton composed the majority of the diet in both species, and they exhibited complete overlap in the types of invertebrates consumed. In the streams of the Rio Grande drainage, both species occupy similar habitats and consume the same food items and, thus, are likely to compete for these resources when and where they are rare.

For both species, spawning commences in the spring, triggered either by a decline in peak flows

(*C. plebeius*; Rinne, 1995) or when water temperatures are between 7 and 10°C (*C. commersoni*; Hamel et al., 1997), or more likely, some combination of these factors. In a previous study in northern New Mexico, both species were found to spawn at the same time in the same reach, although genetic analysis detected a lack of hybrid offspring (McPhee and Turner, 2004). Still, competition for spawning habitat and reproductive effort wasted in the production of inviable hybrids remain possible explanations for the decline of *C. plebeius* in the presence of *C. commersoni*.

Despite similarities in habitat use and diet, the 2 species differ greatly in maximum body size attained (ca. 640 mm in total length for *C. commersoni*, Lee et al., 1980; and 160 mm standard length for *C. plebeius*, Smith, 1966). The life history and demographic implications of body size are profound (Calder, 1984). For temperate fishes, the size an individual achieves during the first growing season often determines whether it survives the first winter (Post and Evans, 1989; Schultz et al., 1998) and can affect energetic state at the beginning of the next growing season, with implications for future survival and reproductive success (Cargnelli and Gross, 1997). Furthermore, fecundity and the timing of life history events scale with body size in fishes, affecting demography as well as individual fitness. Whether *C. commersoni* is displacing or replacing *C. plebeius*, the differences in traits related to fecundity and mortality rates will affect their relative abundances and ultimately the fate of the native *C. plebeius* in the Rio Grande. Therefore, in this study, I compared life history traits of the 2 species to compare their reproductive schedules and potential reproductive output.

METHODS—Sampling took place at 4 sites in the Rio Vallecitos, a small tributary of the Rio Chama in the upper Rio Grande basin of northern New Mexico (Fig. 1). I conducted larval sampling weekly or bi-weekly, beginning 7 May 2001, when flows were low enough that sampling gear could be deployed safely and effectively, until 28 June 2001, when spring runoff had subsided and flow at the mouth of the Rio Vallecitos was approximately 0.15 m³/s (estimated from records of the U. S. Geological Survey, http://waterdata.usgs.gov/nm/nwis_gage_#08289000). Larvae were captured with 2 stationary drift nets (363 µm mesh) fished 15 min of every hour between dusk and dawn, when catostomid larvae are most likely to drift (Corbett and Powles, 1986). Larvae were preserved with 95% ethanol in the field. I sampled juvenile and adult

Catostomus irregularly from September 1999 to November 2001, resulting in 13 sample days in total; fishes were captured on 9 of these days (Appendix I). I collected juvenile and adult *Catostomus* using a backpack electrofisher (Smith-Root Model 12-B) in a single pass with one dip-netter. Reaches were unblocked and approximately 7 to 10 m in length. Fishes were euthanized by an overdose of MS-222, returned to the laboratory on ice, and stored at -80°C. I did not preserve any fishes with formalin so that they could be used in genetic studies (McPhee and Turner, 2004; unpubl. data). All individuals collected, with corresponding field notes, were housed at the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

Individuals of small size were difficult to identify visually, particularly those that had been malformed after freezing and thawing. Furthermore, the potential for hybridization between the 2 species made identification based solely on morphology unreliable. In a genetic study of hybridization between the 2 species, mitochondrial and nuclear markers were used to distinguish pure *C. commersoni* and *C. plebeius* and would be able to distinguish F1 hybrids (McPhee and Turner, 2004). For this study, the same genetic markers were used to identify larvae and young-of-year individuals and to confirm morphological identification of the older individuals. In the laboratory, standard length (SL; mm) and mass (g) were recorded from all fishes with the exception of larvae, from which total length (TL; mm) was obtained. Condition factor for juveniles and adults was calculated as $\text{mass/length}^3 \times 10^4$ (after Anderson and Gutreuter, 1983).

I used Fisher's exact test of homogeneity (Sokal and Rohlf, 1995) to test the null hypothesis that the proportion of larvae captured by sample date did not differ between species and to test the null hypothesis that proportion of individuals that were sexually mature by age class did not differ between species. Analysis of variance (ANOVA) was adjusted for multiple comparisons with the Bonferroni method (Sokal and Rohlf, 1995) to test how standard length and condition factor differed between species while accounting for differences in sample site and date. The difference in larval body length by species was compared using a one-tailed *t*-test. I conducted all statistical procedures using SAS (SAS Institute Inc., 1988).

From length-frequency histograms, I visually estimated the upper bound of the smallest mode in the distribution of standard length, which corresponds to the youngest age class (Peterson method; Jearld, 1983). Examination of hard anatomical structures was needed for larger individuals, because the length-frequency method tends to obscure divisions between age classes beyond age 2. Scales, although frequently used to age a variety of fish species, have been shown to underestimate the age of catostomids (Beamish and Harvey, 1969), whereas opercula are reliable aging structures for this group of fishes (Scoppetonne et al., 1986). Therefore, opercula were used, following the methods of Scoppetonne et al. (1986), to age individuals >50 mm SL. I removed an operculum from the right side of a fish, boiled the flesh away, and counted

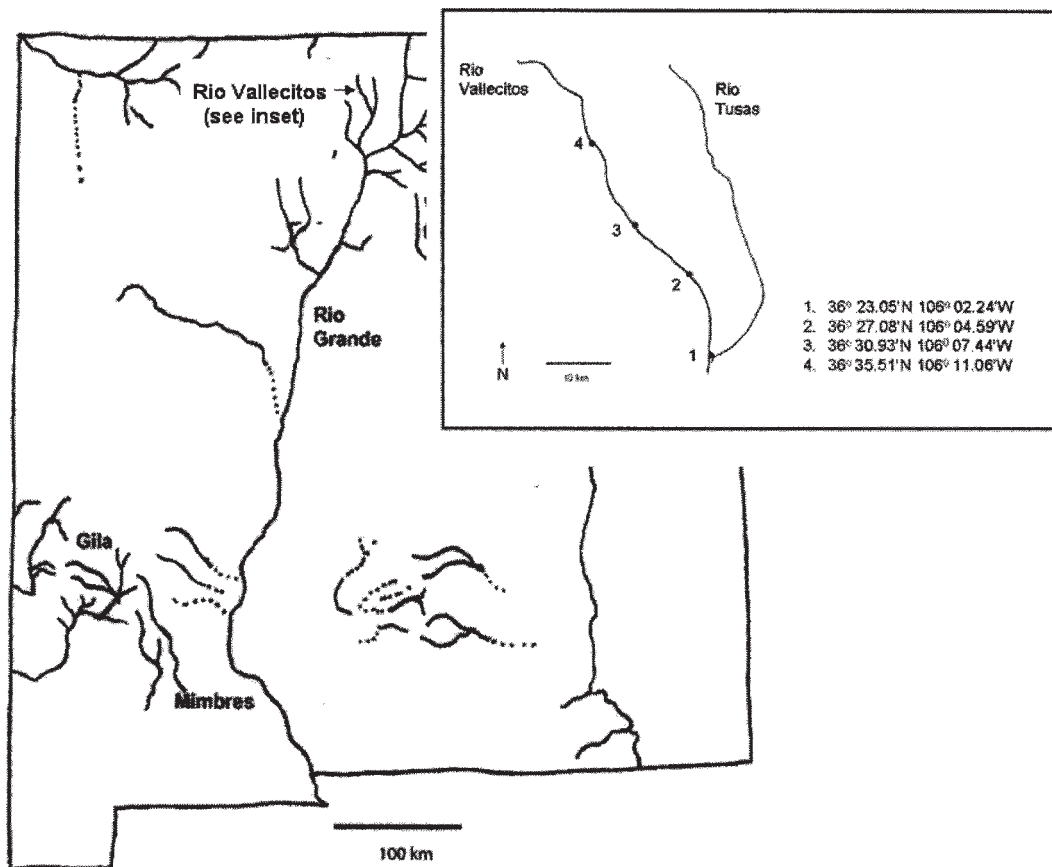


FIG. 1.—Map of sample area and sites in New Mexico.

annuli with the naked eye or with the aid of a stereomicroscope.

I calculated mean length of each age class for each species and then plotted mean length of age-class x against mean length of age-class $x + 1$. The slope of the resulting regression revealed an estimate for the average growth rate for each species (growth increment method; Walford, 1946). Differences in slope and intercept between the regressions for the 2 species were statistically compared by testing the effect of species (for intercept) and the interaction between species and size of age-class x (for the slope) in an analysis of covariance (ANCOVA; Sokal and Rohlf, 1995).

Fishes >50 mm SL were dissected and gonads were inspected visually to determine maturity and sex. Sexual maturity was assigned if gonads were developed and easily identified. I estimated fecundity by removing the egg mass from mature females, dividing it into 3 portions (anterior, middle, and posterior), and weighing each portion. The number of eggs was counted from a weighed subsample of each portion, and total fecundity was extrapolated by summing estimated egg count from each portion based on the ratio of egg count to mass of each subsample. This subsampling method was intended to minimize the error due to an

anterior-to-posterior gradient in egg size within the egg mass (M. McPhee, pers. observ.). Linear regression was used to determine the relationship between body length and fecundity (both variables log-transformed). To determine whether the intercept and slope of this relationship differed by species, the significance of species and the interaction between species and body size as predictor variables was examined with ANCOVA. Fecundity as a function of age, $m(x)$, was then estimated by calculating the fecundity of the average size per age for each species.

Catch-per-unit-effort (CPUE) was calculated as the number of individuals captured per shocking second. The probability of surviving from age $x - 1$ to age x was estimated by calculating the average CPUE of each age class for each species and then calculating $CPUE (age\ x) / CPUE (age\ x - 1)$. The product of these age-specific mortality rates up to age x gave $l(x)$, the probability of surviving from birth to age x (Stearns, 1992). Because drift-net effort was not directly comparable to shocking effort, I excluded larvae from this analysis. The data did not permit calculation of survival from fertilization to age 1. Instead, exponential curves were fitted to the CPUE data and used to back-calculate expected CPUE at age 0. A lifetime reproductive output index (ROI),

TABLE 1—Larval sampling dates and catch data, Site 2 (Fig. 1), for 2 species of *Catostomus* in New Mexico.

Date	Water temperature	<i>C. commersoni</i>	<i>C. plebeius</i>
7–8 May 2001	8–10°C	0	0
15–16 May 2001	9–12°C	0	0
23–24 May 2001	8–11°C	0	0
29–30 May 2001	11–16°C	0	0
14–15 June 2001	13.5–19°C	34	8
28–29 June 2001	18–20°C	0	10

in relative number of offspring, was estimated for each species using the discontinuous form of the Euler-Lotka equation as:

$$ROI = \sum_x^{\omega} l(x)m(x)$$

where α is the age at maturity and ω is the last age observed for females. I also estimated relative intrinsic rate of reproduction (r) by setting the Euler-Lotka to unity and solving numerically for r (Stearns, 1992). It is important to note that I did not have data on survival from fertilization to the early juvenile stage. Therefore, survival to age 1 was overestimated, and resulting reproductive output values were much greater than 2. Thus, although ROI and r were expressed in units of expected number of offspring per individual, they could not be used for predictions about absolute population size.

RESULTS—Genetic markers revealed no hybridization and allowed unambiguous assignment of

species identity to each individual (for more discussion see McPhee and Turner, 2004). Although larval sampling spanned an 8-week period in 2001, larval catostomids only occurred in the drift 14–15 June and 28–29 June (Table 1). Significantly more *C. commersoni* larvae were captured on the earlier date than were *C. plebeius* larvae ($P < 0.0001$, $n = 52$). *Catostomus commersoni* larvae were significantly longer than were *C. plebeius* larvae (mean total length was 11.9 mm for *C. commersoni* and 10.6 mm for *C. plebeius* larvae, $P = 0.0001$, $n = 52$).

Length-frequency histograms of all individuals collected by electrofishing were plotted, and examination of individuals <70 mm SL indicated that 50 mm marked the approximate cutoff point for young-of-year suckers (Fig. 2). Although the Rio Vallecitos was sampled periodically from September 1999 through November 2001, fish density was low, so statistical comparisons of young-of-year size focused on 3 major collections: September 1999, July 2000, and November 2001. After accounting for the effects of season (“month” in ANOVA model), mean standard length of young-of-year fishes did not differ significantly between the 2 species (*C. commersoni*, 27.8 mm; *C. plebeius*, 28.1 mm; $P = 0.75$, $n = 223$). Conversely, *C. plebeius* had, on average, a significantly larger condition factor (*C. commersoni*, 0.14; *C. plebeius* 0.18; $P < 0.0001$, $n = 245$; Table 2).

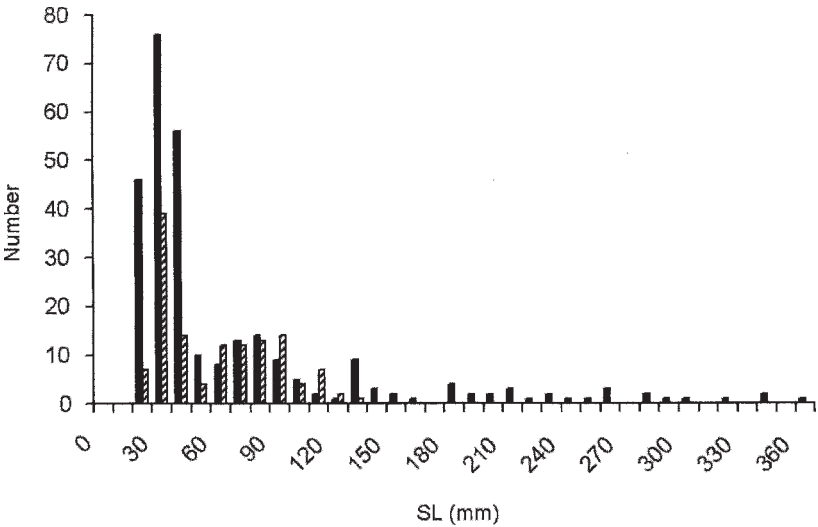


FIG. 2—Length-frequency histograms used for determination of maximum size of young-of-year fish from New Mexico. Solid bars, *Catostomus commersoni*; open bars, *C. plebeius*.

TABLE 2—Analysis of variance of young-of-year length and condition factor for *Catostomus plebeius* and *C. commersoni* from New Mexico. Values considered significant after Bonferroni correction are marked with an asterisk.

Source	df	SS	MS	F	P
Standard length					
Site	3	7700.894	2566.965	157.01	0.0001*
Species	3	2344.617	781.539	47.80	0.0001*
Date	1	4.993	4.993	0.31	0.5810
Month × Site	4	<0.0001	<0.0001	<0.001	1.0000
Month × Species	3	869.191	289.730	17.72	0.0001*
Site × Species	2	725.153	362.577	22.18	0.0001*
Condition factor					
Site	3	0.088	0.029	30.82	0.0001*
Species	3	0.053	0.018	18.62	0.0001*
Date	1	0.045	0.045	46.72	0.0001*
Month × Site	4	<0.0001	<0.0001	<0.001	1.0000
Month × Species	3	<0.0001	<0.0001	<0.001	1.0000
Site × Species	2	<0.0001	<0.0001	<0.001	1.0000

Large differences in the body size of individuals older than a year were observed between the 2 species (Fig. 3a). The largest *C. commersoni* captured was 356 mm SL and the largest *C. plebeius* was 129 mm SL. The oldest *C. plebeius* individuals captured were age 3. *Catostomus commersoni* continued to grow substantially beyond age 3, and the oldest individuals captured were age 7. Growth increment plots indicated that after age 1, *C. commersoni* apparently grew faster than did *C. plebeius* (Fig. 3b); however, the slopes and intercepts of these plots did not differ statistically (slopes, $P = 0.20$; intercepts, $P = 0.66$, $n = 9$).

Sexual maturity was observed in age-2 individuals of both species, but the proportion of age-2 individuals that were mature was significantly greater for *C. plebeius* (0.61 versus 0.11 for *C. commersoni*; $P < 0.0001$, $n = 44$). Of age-2 individuals, mature male and female *C. plebeius* were observed, but only mature male *C. commersoni* were found. By age 3, all individuals of both species were sexually mature. Minimum size at maturity was smaller for *C. plebeius*, and males matured at smaller sizes than did females for both species. The smallest mature male was 60 mm SL for *C. plebeius* and 77 mm SL for *C. commersoni*, and the smallest mature female was 91 mm SL for *C. plebeius* and 126 mm SL for *C. commersoni*.

For both species, fecundity was a function of body size. ANCOVA indicated that slopes and intercepts of the relationship between fecundity and body size did not differ between the 2

species (slopes, $P = 0.62$; intercepts, $P = 0.67$, $n = 15$). Thus, the data were pooled to estimate the linear relationship between fecundity and length ($R^2 = 0.88$, $P < 0.0001$, $n = 15$). The resulting equation, $\ln m = 2.11(\ln sl_x) - 2.5$, was used to calculate $m(x)$ for each species based on mean length at age x (sl_x). Among *C. plebeius* individuals, fecundity ranged from 1,100 to 2,900 eggs per female, and for *C. commersoni* ranged from 2,600 to 19,400 eggs per female.

Plotting average CPUE per age class versus species indicated that the 2 species experienced different mortality rates (Fig. 4). CPUE of age 5 *C. commersoni* was greater than any other age class above age 2. Thus, to estimate meaningful mortality rates for *C. commersoni*, an exponential curve was fitted to the CPUE data from age 2 to 7, and the values predicted by this function were used for $l(x)$ for $x > 2$. For *C. plebeius*, $l(x)$ was estimated directly from the CPUE data, but an exponential curve was fitted to back-calculate CPUE for age-0 fish to estimate probability of survival to age 1. The same procedure was used for *C. commersoni*, but I used a curve fitted to CPUE data, including age-1 fish, to decrease the downward bias caused by the large drop in mortality rates after age 1. Calculation of ROI revealed that relative expected reproductive output for *C. commersoni* was more than twice that of *C. plebeius* (ROI = 509 versus 238, respectively, Table 3). Relative intrinsic rate of increase (r) was estimated as 2.78 for *C. plebeius* and 1.67 for *C. commersoni*.

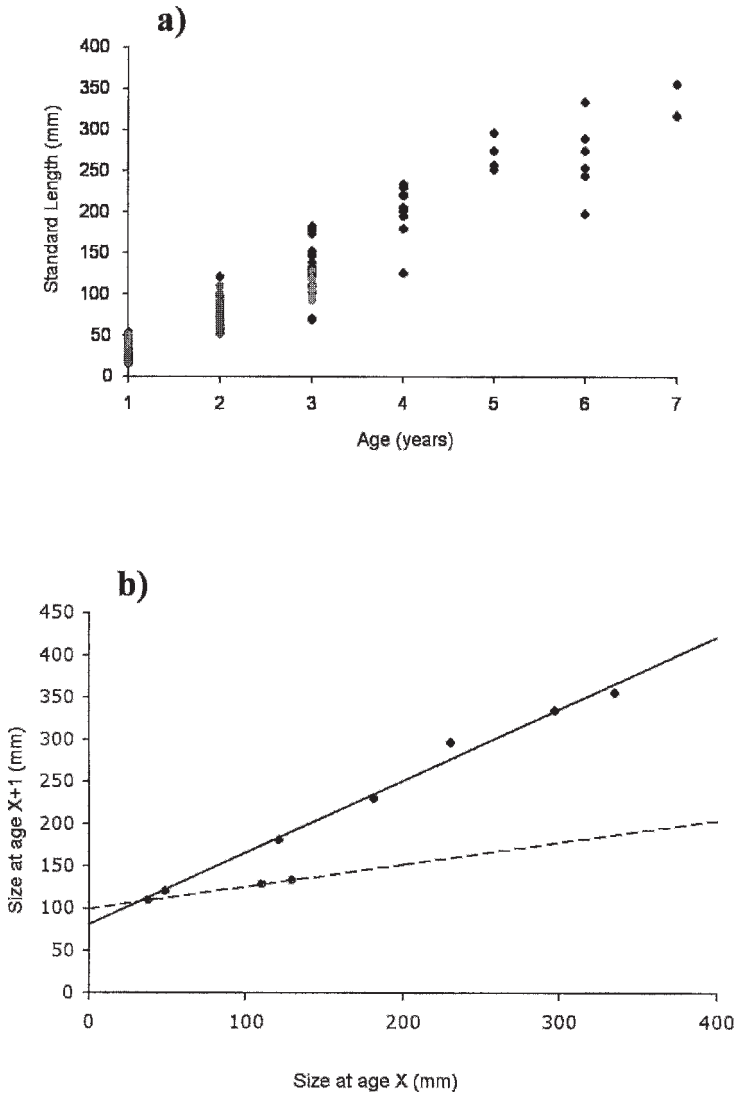


FIG. 3—Size at age for all sites and dates pooled: a) black diamonds, *Catostomus commersoni*; gray circles, *C. plebeius*, b) growth increment plots for *C. commersoni* (solid line) and *C. plebeius* (dashed line).

DISCUSSION—Considering that mortality of fishes in the first year of life is often size-dependent (Post and Evans, 1989), one way that *C. commersoni* could achieve numerical dominance would be by growing faster and reaching a larger size in the first year of life. Instead, the data suggested that the 2 species attained similar lengths by mid summer and into autumn. However, this result was difficult to interpret because individuals were assigned to age-class 1 by an upper bound on body length. In contrast, condition factor was independent of body size

beyond approximately 25 mm, regardless of species (data not shown), so it was more appropriate for comparing growth between the 2 species in the first year of life. Young-of-year *C. plebeius* had, on average, a higher condition factor than did young-of-year *C. commersoni*. This difference could be important biologically, because, on average, a *C. plebeius* of 28 mm would be 0.09 g heavier than a *C. commersoni* of the same size. Furthermore, *C. plebeius* entered the drift slightly smaller and later than did *C. commersoni*, suggesting that *C. commersoni* might

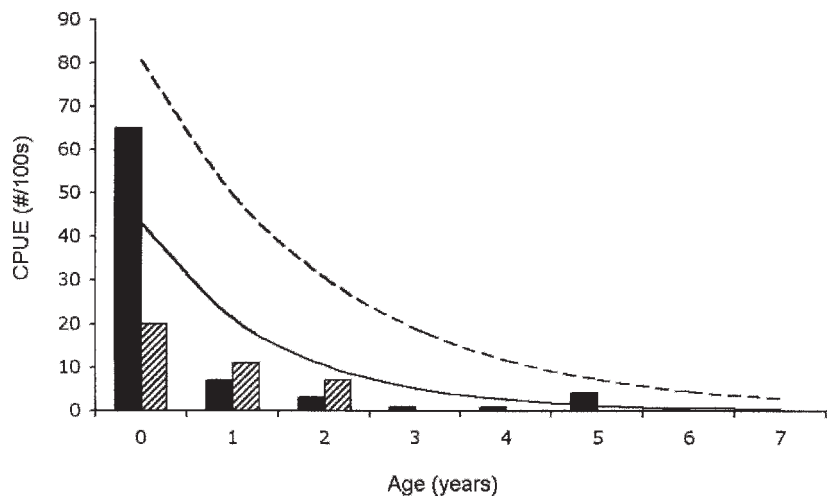


FIG. 4—Catch per unit effort (number of individuals per 100 shocking seconds) by age class. Solid bars, *Catostomus commersoni*; open bars, *C. plebeius*. Dashed line used to estimate mortality for *C. commersoni* younger than age 2; solid line used to estimate mortality for *C. commersoni* > 2 y old.

have had an earlier start on the growing season. Thus, it is possible that *C. plebeius* actually grew better than *C. commersoni* in the first year of life in the Rio Vallecitos. More intensive larval sampling, over more than one reproductive season, could determine whether the observed differences in size and timing of larval drift has biological significance for subsequent growth and survival.

In contrast to young-of-year size, the difference in adult body size of the 2 species was substantial. Based on the empirically derived relationship between size and fecundity, a female *C. plebeius* that lived to age 3 had a lifetime fecundity of

approximately 3,800 eggs versus 59,000 eggs for a female *C. commersoni* that lived to age 7. This 15-fold difference in maximum fecundity was reduced to a 2-fold difference in ROI, however, because *C. plebeius* females matured one year earlier and experienced lower juvenile mortality in the first 2 y of life. This ROI comparison was robust to potential uncertainty associated with the aging of young-of-year individuals; a reanalysis using 60 mm as the age-1 cutoff gave reproductive output values of 258 and 509 for *C. plebeius* and *C. commersoni*, respectively.

Estimation of mortality based on electrofishing CPUE might have been biased by differences

TABLE 3—Comparison of mean standard length (SL), mortality (l), fecundity (m), and reproductive output index (ROI) between *Catostomus plebeius* and *C. commersoni* from New Mexico.

Species	Age (years)	Mean (SL) (mm)	l(x)	m(x)	l(x)m(x)
<i>C. plebeius</i>	1	28	0.59	0	0
	2	75	0.32	703	228
	3	110	0.006	1,582	10
				ROI = 238 eggs	
<i>C. commersoni</i>	1	28	0.62	0	0
	2	74	0.10	0	0
	3	135	0.05	2,432	120
	4	202	0.02	5,689	138
	5	281	0.01	11,425	137
	6	277	0.01	11,029	65
	7	337	0.003	16,683	49
				ROI = 509 eggs	

in catchability of different size classes. Although large fishes are more vulnerable to the effects of electric current, they might also avoid capture by escaping more quickly or remaining in deep, swift parts of rivers that are inaccessible to wading samplers (Reynolds, 1983). The Rio Vallecitos is a small creek and can be crossed on foot during most flow conditions. Throughout the study period, it could be sampled in its entirety at each sampling location. Smaller fishes might have more readily avoided detection by dip-netters, but there is no reason to suspect that this bias would differ between species among individuals of the same size class. Mortality estimates could also be influenced by dispersal, and it seems unlikely that these 2 species have the same tendency to disperse. Therefore, the results of the Leslie matrix analysis should be viewed as rough estimates. However, the salient conclusions, that *C. commersoni* achieves much greater lifetime fecundity but that the effect on comparative reproductive output is reduced by the earlier maturity of *C. plebeius*, are less sensitive to mortality rates.

It could be argued that the intrinsic rate of increase (r) is a more appropriate life history variable for comparing 2 potentially competing species. This would be the case if the Rio Vallecitos was not at carrying capacity for suckers, and thus, the rate of reproduction would be more important than net reproductive output. However, I found a higher r for *C. plebeius*, suggesting that if the 2 species compete for newly available resources (a non-equilibrium situation), *C. commersoni* should not be able to displace *C. plebeius* based on life history alone.

Why is *C. plebeius* declining while *C. commersoni* has become so abundant in the system? Factors not directly related to life history probably also contribute to the ongoing dominance of *C. commersoni*. Habitat degradation or loss is usually to blame, in part, for the decline of freshwater fish species (Miller et al., 1989; Allan and Flecker, 1993), and introduced predators, such as brown trout (*Salmo trutta*), might be influencing *C. plebeius* populations disproportionately. That *C. plebeius* showed better apparent growth during the first year of life suggests that, at the local scale, direct competition for food might not play a significant role in the interaction between these 2 species. More detailed studies, including controlled and replicated field experiments, would be needed to demonstrate a precise role

for direct competition with *C. commersoni* in the decline of *C. plebeius* (e.g., Peterson and Fausch, 2003). However, given the dramatic fecundity effects of the large body size achieved by adult *C. commersoni* demonstrated in this study, efforts to eradicate or exclude large-bodied *C. commersoni* from streams occupied by *C. plebeius* could be an effective conservation tool.

There is considerable confusion in the natural history literature regarding the maximum body size of *C. plebeius*. For example, Koster (1957:46) wrote that adults "may reach a foot in length," while Sublette et al. (1990) reported a maximum body size for *C. plebeius* of 260 mm SL. Neither museum records nor locality data were reported for these values, making assessment of their validity difficult. Furthermore, in his extensive analysis of the subgenus *Pantosteus*, Smith (1966) reported an approximate size of 160 mm SL. More recent reports from the upper Rio Grande indicate a maximum total length of 200 to 209 mm (Calamusso, 1996; Swift, 1996), or approximately 170 to 178 mm SL (M. McPhee, unpubl. conversion). If earlier reports of larger body size are accurate and reflect historical sizes of upper Rio Grande populations, this raises the possibility that the presence of *C. commersoni* depresses maximum size of *C. plebeius*. However, recent collections of *C. plebeius* from the uninvaded Rio Guadalupe (a Jemez River tributary) do not support this hypothesis, because maximum sizes are <175 mm SL (unpubl. records, Museum of Southwestern Biology, University of New Mexico, Albuquerque).

Earlier studies of age and growth of *C. plebeius* in the upper Rio Grande reported that maximum lifespan was 6 to 7 y (Raush, 1963). If individuals this old remain in the Rio Vallecitos but went uncaptured in this study, this suggests that they are rare and, thus, contribute little to the population growth rate. Alternatively, it is possible that interactions with *C. commersoni* have lead to a decreased lifespan of *C. plebeius*, which would then have important implications for the coexistence of the 2 species. Unfortunately, testing this hypothesis was beyond the scope of this study, but future comparisons of *C. plebeius* life histories between invaded and uninvaded populations at similar latitudes could address this hypothesis.

Koster (1957) also reported a second spawning of *C. plebeius* in the fall, but I did not find evidence for this in Rio Vallecitos in November, and Rinne

(1995) did not observe autumn spawning in the Rio de las Vacas (Jemez River drainage). However, Swift-Miller et al. (1999) noted milt-producing individuals in November in Hot Creek, one of the few populations of *C. plebeius* remaining in Colorado. A second spawning in Hot Creek would double the ROI for *C. plebeius* and, assuming body-size distribution and maturity and mortality schedules similar to what I found for Rio Vallecitos, would make it comparable to the ROI estimated for *C. commersoni* in my study, lending support for the role of life history in outcome of co-occurrence of these 2 species.

Ultimately, this study produced more hypotheses about the interactions between *C. plebeius* and *C. commersoni* than it was able to answer. In many ways, the status of *C. plebeius* in the upper Rio Grande parallels that of the Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*), where populations are able to persist primarily in isolated areas free of nonnative congeners (Calamusso and Rinne, 2004). In this case, the invader (*C. commersoni*) attained approximately a 2-fold advantage in net reproductive output over the native congener (*C. plebeius*) by living longer, growing larger, and attaining much greater fecundity, which likely contributes to its dominance in main-stem reaches of the upper Rio Grande. Although many factors influence the interactions between native and invasive species, this study demonstrated that life history is an important component of such interactions and deserves a prominent role in future studies and conservation efforts of our native fishes.

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APPENDIX I—Electrofishing sample dates, effort, and catch of 2 species of *Catostomus*. Sites shown on Fig. 1. Samples from 22 September 1999 were excluded from mortality estimates due to lack of effort data, but were included in comparisons of young-of-year body size.

Date	Site	Shocking (sec)	<i>C. commersoni</i>	<i>C. plebeius</i>
22 September 1999	1	–	6	7
	2	–	29	22
	3	–	29	0
19 February 2000	1	356	1	1
	3	1,148	5	0
9 May 2000	1	734	3	0
	3	839	6	11
	4	2,688	26	0
25 May 2000	2	481	3	1
	3	1,167	14	1
	4	388	6	0
6 June 2000	1	215	8	7
	3	235	2	1
	4	1,110	2	0
19 July 2000	1	382	7	13
	3	458	50	16
	4	175	37	0
12 April 2001	3	775	7	0
	4	903	10	0
6 June 2001	2	1,746	4	4
	4	1,127	9	1
1 November 2001	2	1,492	25	22
	3	492	27	17
	4	637	19	0