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Research article

Rapid species replacements between fishes of the North American plains: a case history from the Pecos River

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Abstract

A non-native population of plains minnow *Hybognathus placitus* in the Pecos River, New Mexico, USA, replaced the endemic, ecologically similar Rio Grande silvery minnow *Hybognathus amarus* in less than 10 years. Competitive exclusion is hypothesized as a mechanism of replacement. The following evidence was examined for potential support: (1) the historical population trend of *H. amarus* versus *H. placitus*; (2) relative suitability of the modified flow regime for *H. amarus* versus *H. placitus*; (3) potential for habitat overlap; and (4) spawning periodicity and body length in the non-native population of *H. placitus*. Historical data indicate *H. amarus* did not decline until *H. placitus* was present, after which it disappeared rapidly and *H. placitus* proliferated. The natural flow regime of the Pecos River was changed via base-flow reductions and capture of spring-snowmelt runoff, making it similar to flow regimes associated with likely source populations of non-native *H. placitus*. Spring runoff is an important spawning cue for *H. amarus*, but not *H. placitus* and *H. placitus* appears to be naturally more tolerant of diminished streamflow. Extant *H. placitus* were associated with a relatively pristine river reach that was most likely the stronghold for the replaced *H. amarus* population. Given high ecological similarity, habitat overlap was likely high during the period of replacement. *Hybognathus placitus* in the Pecos River had a protracted spawning season (April through September), whereas extant *H. amarus* in the Rio Grande had a short spawning season (a few days in May or June during snowmelt runoff). Most *H. amarus* die after their first spawning season and few exceed 60 mm standard length (SL), whereas quite a few *H. placitus* survive at least until their second spawning season and exceed 60 mm SL. Co-occurrence of multiple spawning cohorts may stabilize annual reproductive output of *H. placitus* and larger individuals may be more fecund and produce larger eggs that survive better. Spawning flexibility, greater size, and higher environmental tolerance likely gave *H. placitus* a reproductive and survival advantage over *H. amarus*, consistent with a deterministic pattern of rapid species replacements in the plains, in which tolerant, competitive species from the Red River drainage or Gulf of Mexico coast rapidly replace more sensitive, endemic congeners in disturbed, remnant habitats.

Key words: competitive exclusion, natural flow regime, taxonomic homogenization, *Hybognathus placitus*, *Hybognathus amarus*, Canadian River, Red River

Introduction

Non-native fish invasions threaten native fish faunas (Moyle 1986). Once established, non-natives may assimilate into a fauna without concurrent extirpations or their invasion may facilitate concurrent disappearance of natives (Olden and Poff 2003). Concurrent extirpations are uncommon, but dramatic (Rahel 2002). If fishes from certain sources are better suited for modern stream environments of a broader region, regional invasions may combine with concurrent extirpations to cause taxonomic homogenization (McKinney 2005; Leprieur et al. 2007). For example, taxa from waters with conditions naturally similar to disturbed areas nearby may have a competitive advantage (Bunn and Arthington 2002; Olden et al. 2006), which could lead to invasion of multiple relatively tolerant taxa and concurrent extirpation of multiple less tolerant, native taxa. If this pattern were repeated among drainages, fish faunas would become increasingly similar.

This paper is a study of factors contributing to replacement of native Rio Grande silvery minnow *Hybognathus amarus* (Girard, 1856) by non-native plains minnow *Hybognathus placitus* Girard, 1856 in the Pecos River, New Mexico, USA, which occurred in less than 10 years (1964-1973; Bestgen and Propst 1996). Hybridization was initially hypothesized to be the mechanism of replacement (Bestgen and Platania 1991; Cook et al. 1992; Bestgen and Propst 1996), but recent analysis indicated little if any hybridization and a concurrent Lotka-Volterra analysis suggested a slight inhibitory affect could have allowed *H. placitus* to competitively exclude *H. amarus* in 10 to 15 years (Moyer et al. 2005). High morphological similarity (Hlohowskyj et al. 1989; Schmidt 1994; Bestgen and Propst 1996;) and similar reproductive ecology (Platania and Altenbach 1998) support the hypothesis of competitive exclusion.

Both species belong to an ecological guild of small-bodied cyprinids that use fluvial, open-water habitats of sand-bed streams in the plains of North America (hereafter: sand-bed guild; Matthews and Hill 1980; Bestgen and Platania 1991). Members are declining due to dewatering (Cross and Moss 1987; Bonner and Wilde 2000), stream fragmentation (Winston et al. 1991; Luttrell et al. 1999), sediment deprivation (Anderson et al. 1983; Quist et al. 2004), stream channel modification (Hoagstrom et al. 2008a), flow regime stabilization (Hoagstrom et al. 2007), and non-native species invasions (Cross et al. 1983). *Hybognathus amarus* is endangered and only remains in one portion of the Rio Grande, New Mexico (U.S. Fish and Wildlife Service 1999), but an ongoing effort may establish a population in Texas (U.S. Fish and Wildlife Service 2008). *Hybognathus placitus* also has declined, but because of its much broader natural distribution, it remains more widespread. Relict populations persist in less-degraded river reaches (e.g., Eberle et al. 1997; Quist et al. 2004; Hoagstrom et al. 2006b).

Hybognathus placitus has been introduced widely in the Pecos River drainage but there is only one established population (Sublette et al. 1990; Hoagstrom 2003). It inhabits a unique river reach that is a stronghold for fishes of the sand-bed guild due to its low level of degradation (Dudley and Platania 2007; Hoagstrom et al. 2008a). Adults of other sand-bed guild fishes are restricted to a 158-km reach where they inhabit a relatively wide, sand-bed river channel that contains a dynamic habitat mosaic, but juveniles are distributed more broadly due to downstream displacement of pelagic eggs and larvae (Hoagstrom and Brooks 2005; Hoagstrom et al. 2008b).

Hybognathus placitus has environmental tolerances and behaviors suited for harsh flow regimes characterized by frequent periods of low streamflow punctuated with flash floods. It tolerates relatively high temperatures and salinities (Echelle et al. 1972; Matthews and Maness 1979; Ostrand and Wilde 2001; Higgins and Wilde 2005) and tracks habitat suitability across dynamic riverscapes (Matthews and Hill 1980; Bryan et al. 1984; Yu and Peters 2003). It is widespread among western tributaries of the Mississippi River and inhabits portions of the Brazos and Colorado river drainages in Texas (Al-Rawi and Cross 1964). *Hybognathus placitus* has an extended spawning season (April to September) and spawning sometimes coincides with flash floods (Lehtinen and Layzer 1988; Taylor and Miller 1990; Durham and Wilde 2005, 2006). Individuals as small as 43 mm standard length (SL) may be sexually mature but longer-lived adults often exceed 60 mm SL (Lehtinen and Layzer 1988; Taylor and Miller 1990; Hoagstrom et al. 2006a). These individuals are in their second spawning season (age 2) and typically die after spawning. As *H. placitus* grow, they can produce more, larger eggs, so larger individuals may contribute disproportionately to reproductive success (Taylor and Miller 1990; Durham and Wilde 2005).

Tolerances of *H. amarus* are unstudied, but their smaller historical distribution suggests lower tolerance than *H. placitus* (sensu Matthews 1987). The natural distribution of *H. amarus* was limited to larger rivers with mountainous head-waters (Bestgen and Platania 1991) in which a spring-snowmelt pulse characterized the natural flow regime (Poff and Ward 1989; Poff 1996). Regularity of snowmelt runoff can result in life-history specializations in native biota (Poff and Allan 1995; Lytle and Poff 2004). Extant *H. amarus* have specialized spawning periodicity associated with annual snowmelt. The primary spawning period begins at the onset of the snowmelt pulse (usually in late May or early June) and typically lasts a few days (U.S. Fish and Wildlife Service 1999; Osborne et al. 2005). *Hybognathus amarus* is short-lived. Adults typically die after their first spawning season and rarely exceed 60 mm SL (Bestgen and Propst 1996; U.S. Fish and Wildlife Service 1999).

This case history explores factors that potentially gave *H. placitus* a competitive advantage over *H. amarus* in the Pecos River. The following evidence was considered: (1) the historical population trend of *H. amarus* versus *H. placitus*; (2) relative suitability of the modified flow regime for *H. amarus* versus *H. placitus*; (3) potential habitat overlap between species; and (4) expression of competitive traits (i.e. flexible spawning periodicity, greater body length) in the extant, non-native population of *H. placitus*. This analysis should provide insight into rapid species replacements of all sorts.

Methods

Study area

The Pecos River is a major tributary to the Rio Grande. Headwaters lie in mountains of New Mexico and western Texas, but most of the drainage is in the plains to the east. *Hybognathus placitus* colonized 333km of the Pecos River (Fort Sumner Irrigation District Diversion Dam (FSID Dam) to Brantley Reservoir) in south-eastern New Mexico (Figure 1). Habitat between the Taiban Creek and Rio Hondo confluences was relatively natural, whereas it was increasingly degraded downstream (Hoagstrom et al. 2008a). Natural inflows are presently captured in upstream reservoirs or diverted onto croplands and excessive withdrawals have diminished groundwater inflows, so base-flow is now derived from irrigation return flow, relictual groundwater seepage, and sewage effluent (USNRPB 1942; Thomas 1959; Mower et al. 1964).

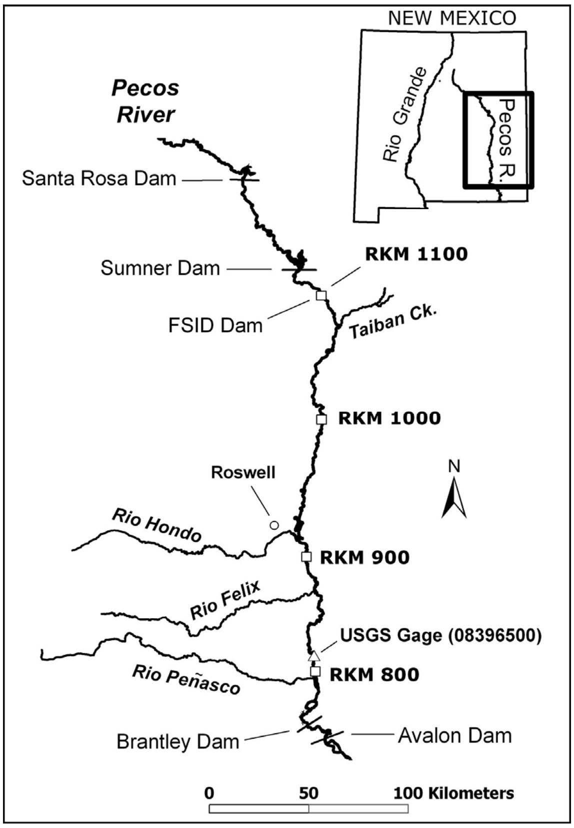

Figure 1. Middle section of the Pecos River drainage showing major dams, the study reach (FSID dam to Brantley dam), river kilometers (RKMs), and the U.S. Geological Survey (USGS) gaging station near Artesia, New Mexico, USA.

Hybognathus amarus extirpation

Historical collection data (up to 1985) were provided by the Museum of Southwestern Biology, University of New Mexico, Albuquerque (A.M. Snyder, pers. comm.). Data from repeated samples that pre-dated *H. amarus* extirpation were available for two sampling locations (U.S. Highway 70 bridge, river km 946; U.S. Highway 380 bridge, river km 919). Sampling effort was not reported, so dominance (percent abundance) of *H. amarus* and *H. placitus* within each collection was plotted over time for each location.

Flow regime comparisons

The pre-impoundment (water years 1905-1936) flow regime of the Pecos River was compared to the period-of-plains-minnow-occupation (water years 1968-2006; Bestgen and Propst 1996) flow regime. The pre-impoundment record did not pre-date all human modifications but did predate major upstream impoundments and excessive groundwater withdrawal (USNRPB 1942; Thomas 1959). Data were gathered from the U.S. Geological Survey (USGS) gaging station near Artesia, New Mexico (08396500), which has the longest period of record. The pre-impoundment flow regime was also compared to flow regimes of likely source rivers (Moyer et al. 2005): the Canadian River near Amarillo, Texas (07227500; water years 1954-1996) and Salt Fork Red River at Mangum, Oklahoma (07300500; water years 1937-1987). Periods of record used corresponded with documented presence of nearby *H. placitus* populations (Hubbs and Ortenburger 1929; Echelle et al. 1972; Winston et al. 1991; Bonner and Wilde 2000). Indicators of Hydrologic Alteration (IHA) software (The Nature Conservancy 2007) was used to compare: mean annual discharge, minimum mean discharge for a 1-day period, minimum mean discharge for a 90-day period, maximum mean discharge for a 1-day period, and maximum mean discharge for a 90-day period, among flow regimes. Three-year hydrographs for each flow regime were plotted for visual comparison. Descriptors of the historical Pecos River flow regime: mean discharge for the *H. amarus* spawning period (May-June), median discharge for the irrigation season (March-October); and median discharge for the non-irrigation season (November-February), were plotted to illustrate historical trends.

Field collections

A 3.2-mmmesh seine, 3.0 m long and 1.2 m deep was used to capture fishes. Sampling locations were selected in an exploratory manner to assess fish distributions at a landscape scale (Fausch et al. 2002). Individual seine hauls were completed in discrete, visually determined mesohabitats, sampled in proportion to their frequency of presence (Vadas and Orth 1998). Normally, between 10 and 20 seine hauls per location were conducted each visit. Length of each seine haul to the nearest meter was measured and multiplied by seine width to determine area sampled. Fishes were preserved in 10% formalin and later transferred to 70% ethanol. Specimens were identified to species, enumerated, and measured to the nearest 0.01 mm SL. All specimens were accessioned to the Museum of Southwestern Biology.

Hybognathus placitus habitat association

The distribution of adult and juvenile *H. placitus* was analyzed to see if it was similar to co-occurring members of the sand-bed guild (Hoagstrom and Brooks 2005; Hoagstrom et al. 2008b). *Hybognathus placitus* 43 mm SL or greater were classified as adults and smaller individuals were classified as juveniles (Lehtinen and Layzer 1988; Taylor and Miller 1990). Box plots of longitudinal position (river kilometer) were prepared for each class and paired with bar graphs of density (fish collected per square meter seined) per two-month periods (Jan.-Feb., Mar.-Apr., etc.). Density by two-month period was also plotted for juveniles and adults upstream of the Rio Hondo confluence.

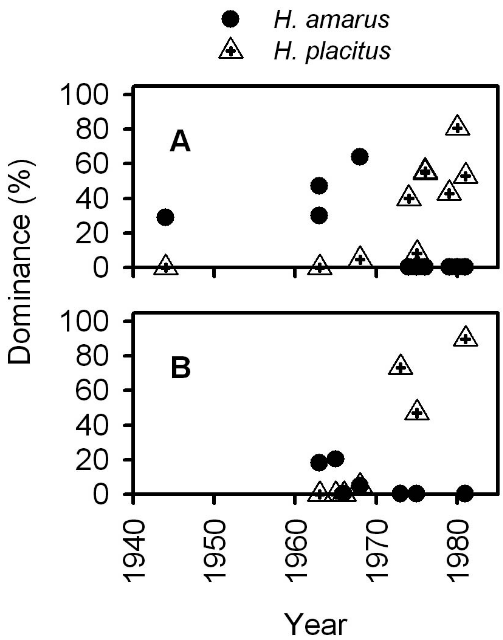

Figure 2. Historical dominance (percent abundance) of *Hybognathus amarus* and *Hybognathus placitus* within historical (pre-1985) collections from the Pecos River at two locations: U.S. Highway 70 bridge crossing (river km 946, A) and U.S. Highway 380 bridge crossing (river km 919, B).

Hybognathus placitus population structure and spawning periodicity

Histograms of *H. placitus* density for 3-mm SL length groups were prepared for two-month periods based on all samples combined. Modes were used to distinguish putative age classes. Histograms were compared with others representing native *H. placitus* populations (Lehtinen and Layzer 1988; Taylor and Miller 1990) and the extant *H. amarus* population (U.S. Fish and Wildlife Service 1999). Monthly mean density of *H. placitus* < 20 mm SL was plotted to assess spawning periodicity. Months with higher densities were assumed to be within the spawning season. Onset of spawning was estimated via back calculation using the smallest *H. placitus* collected in the first month of the approximate spawning season. Growth rate was assumed to be between 0.22 and 1.00 mm/day (Durham and Wilde 2005). Termination of spawning was estimated via back calculation using the smallest individual captured in the last month of the approximate spawning season.

Results

Hybognathus amarus extirpation

Hybognathus amarus dominance in historical collections from the U.S. Highway 70 Bridge exceeded 20% prior to 1970, after which the species was absent (Figure 2). It was present in 3 of 4 historical collections from the U.S. Highway 380 bridge and less dominant than upstream (Figure 2). At both sites, the last collection of *H. amarus* was also the first collection of *H. placitus*. In subsequent collections, *H. placitus* dominance equaled or exceeded prior dominance of *H. amarus* (Figure 2).

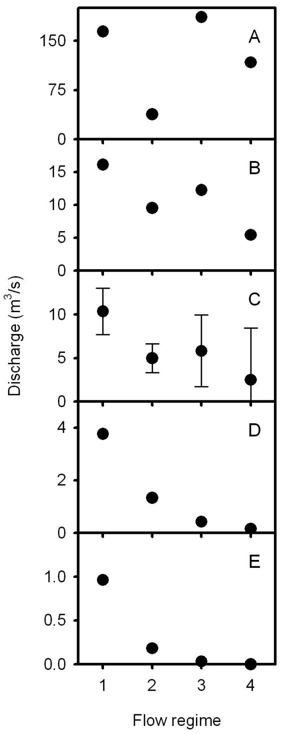

Figure 3. Indicators of Hydrologic Alteration (A = maximum mean discharge for a 1-day period; B = maximum mean discharge for a 90-day period; C = mean discharge with coefficient of variation; D = minimum mean discharge for a 90-day period; and E = minimum mean discharge for a 1-day period) for four flow regimes associated with non-native *Hybognathus placitus* in the Pecos River, New Mexico: (1) the pre-impoundment (and pre-introduction) Pecos River near Artesia, New Mexico (U.S. Geological Survey [USGS] gaging station 08396500; water years 1905-1936), (2) the period-of-occupation (and post-impoundment) Pecos River near Artesia, New Mexico (water years 1968-2006), (3) the likely source population Canadian River near Amarillo, Texas (USGS gaging station 07227500; water years 1954-1996), and (4) the likely source population Salt Fork Red River at Mangum, Oklahoma (USGS gaging station 07300500; 1937-1987).

Flow regime comparisons

With the exception of mean maximum discharge for a 1-day period (Canadian River mean maximum discharge for a 1-day period was higher than all other gages and most similar to the pre-development Pecos River), IHA parameters were more similar among period-of-occupation Pecos River, Canadian River, and Salt Fork Red River flow regimes versus the pre-impoundment Pecos River flow regime (Figure 3). Minimum discharge was notably higher in the pre-impoundment Pecos River. Period-of-occupation Pecos River and source-population hydrographs had lengthy periods of low base flow, typically in winter and spring (Figure 4). In summer, periods of higher discharge alternated with shorter low-flow periods (Figure 4). Flow variability was lowest in the period-of-occupation Pecos River. Diminution of spring runoff and base flow within the Pecos River was most severe in the 1960s (Figure 5).

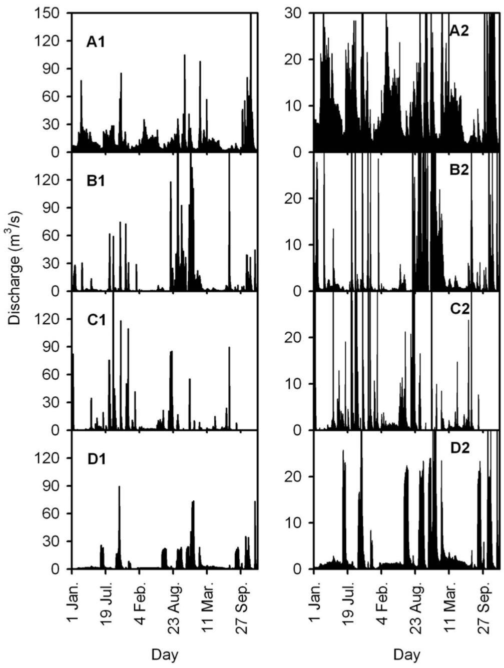

Figure 4. Example hydrographs for the Pecos River near Artesia, New Mexico (U.S. Geological Survey [USGS] gaging station 08396500) pre- (water years 1906-1908, A) and post-impoundment (water years 1968-1970, D) versus the Canadian River near Amarillo, Texas (USGS gaging station 07227500, water years 1968-1970, B) and Salt Fork Red River at Mangum, Oklahoma (USGS gaging station 07300500, water years 1968-1970, C). Right and left columns present the same data at different y-axis scales for different resolution. The Canadian River and Red River drainages in the vicinity of the presented gaging stations were likely the source of *H. placitus* introduced to the Pecos River drainage.

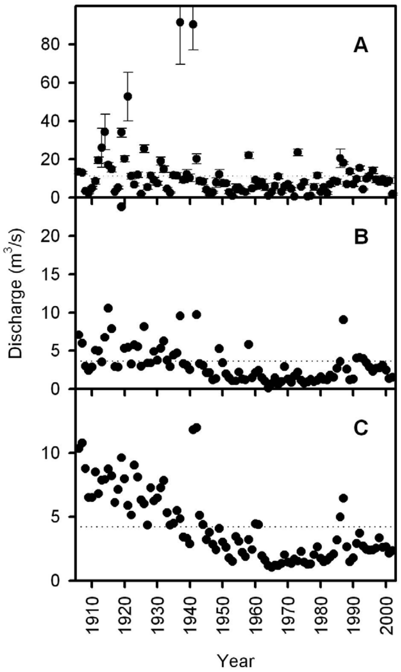

Figure 5. Historical trend in Pecos River discharge near Artesia, New Mexico (U.S. Geological Survey gaging station 08396500). Mean discharge with standard error (base flow and flood flow) is given for the *Hybognathus amarus* spawning season (May-June; A). Median discharge (base flow) is given for the irrigation season (March-October; B) and non-irrigation season (November – February; C). The dotted line in each graph indicates the average of all measurements (for reference).

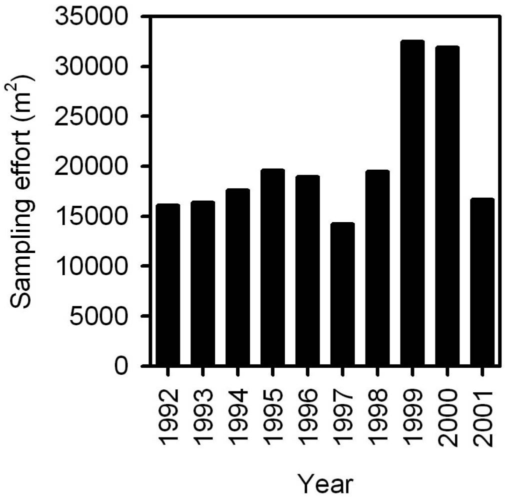

Figure 6. Annual sampling effort (m^2 seined) in the Pecos River between FSID Dam and Brantley Reservoir.

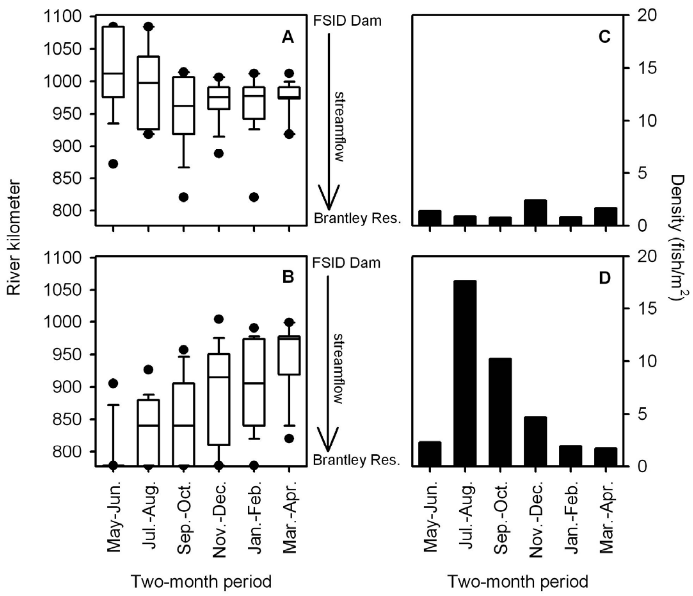

Figure 7. Percent longitudinal distribution (river km) of *Hybognathus placitus* in the Pecos River, New Mexico by two-month periods for all individuals collected between 1992 and 2001 (709 collections). Adult individuals (A, individuals > 43 mm standard length, n = 2,335) and juvenile individuals (B, n = 14,167) are plotted separately. The Y-axes for graphs A and B represent the entire length of the study area from the Fort Sumner Irrigation District (FSID) Dam to Brantley Reservoir. Box plots indicate median km (middle line), 25^{th} and 75^{th} percentiles (top and bottom of box), 10^{th} and 90^{th} percentiles (upper and lower whiskers), and 5^{th} and 95^{th} percentiles (upper and lower dots). Density (fish/m^2) of adult (C) and juvenile (D) *H. placitus* is also shown for each two-month period.

Field collections

A total of 709 collections was made from 1992 through 2001 at a total of 49 sites. Between 4 and 8 sampling trips were made per year and 8 to 14 sites were sampled each trip. Individual sites were visited 14.5 ± 15.68 SD times. A total of 16,502 *H. placitus* was collected. Sampling effort was similar among years, except for being more extensive in 1999 and 2000 (Figure 6).

Hybognathus placitus habitat association

Greater than 75% of adult *H. placitus* were collected upstream of the Rio Hondo confluence year-round with greater than 90% collected there in all two-month periods except September-October and adult density was relatively stable (Figure 7). In contrast, greater than 90% of juveniles were collected downstream from the Rio Hondo confluence from May through August and juvenile density peaked in July-August (Figure 7). The center of juvenile distribution shifted upstream in subsequent two-month periods while the density of juveniles declined (Figure 7). By March-April, greater than 75% of juveniles were upstream of the Rio Hondo confluence. However, juveniles were present upstream of the Rio Hondo confluence in all two-month periods and outnumbered adults from July through February, but peak annual abundance (Figure 8) lagged behind the river-wide peak (Figure 7).

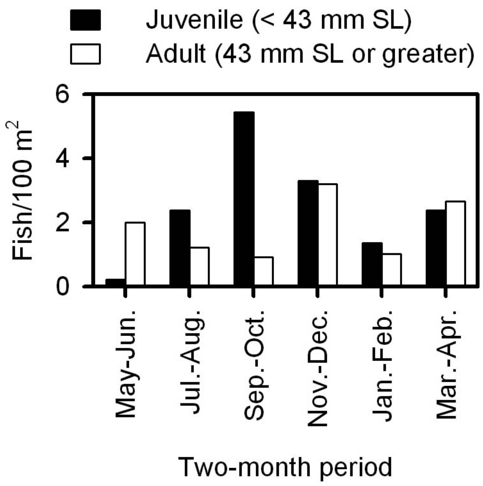

Figure 8. Density of juvenile (*n* = 3,592) and adult (*n* = 2,185) *Hybognathus placitus* in 461 collections upstream of Pecos River kilometer 900 by two-month period. Collections were made from 1992 through 2001.

Hybognathus placitus population structure and spawning periodicity

Hybognathus placitus ranged from 8.0 to 112.5 mm SL (mean = 28.6 ± 14.59 SD mm). Three modes were visible in the May-June SL histogram (Figure 9), indicating three age classes: (1) age 0 (< 33 mm SL), (2) age 1 (36 to 60 mm SL), and (3) age 2+ (> 63 mm SL). Homologous modes were visible in subsequent two-month periods, but age 2+ was rare or missing from September through December. Larger individuals (> 90 mm SL; possibly representing age 3) were present between November and August. Juveniles numerically dominated the population except during March-April (Figure 9). Adults comprised only 16.8% of all individuals collected (Figure 9). Of 1,514

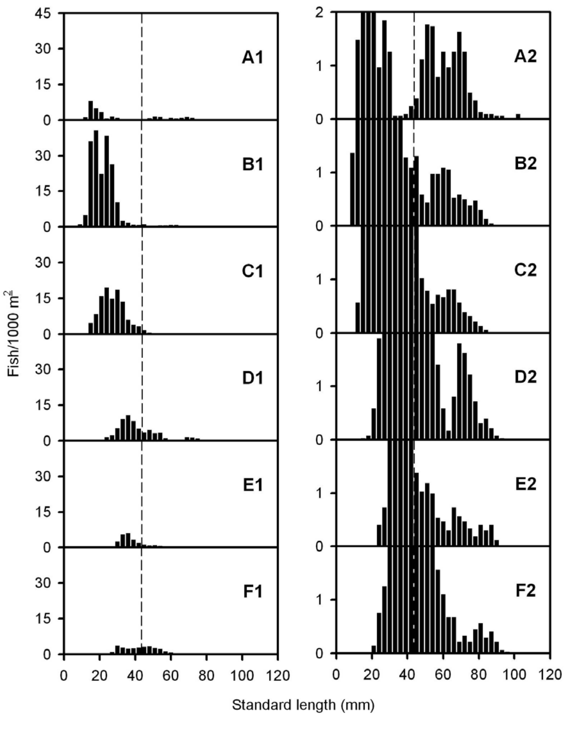

Figure 9. *Hybognathus placitus* standard length histograms from the Pecos River between the FSID Dam and Brantley Reservoir collected from 1992 through 2001. Right and left columns present the same data at different y-axis scales for different resolution. Data are presented for two-month periods: May-June (A1 and A2, *n* = 1,025), July-August (B1 and B2, *n* = 7,097), September-October (C1 and C2, *n* = 4,859), November-December (D1 and D2, *n* = 1,553), January-February (E1 and E2, *n* = 980), and March-April (F1 and F2, *n* = 988). The dashed line at 43 mm SL indicates the division between juveniles and adults. Bars represent 3-mm length groups.

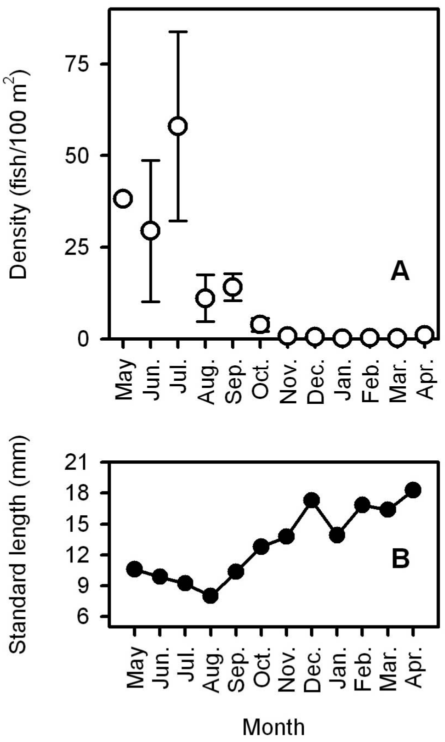

Figure 10. Monthly mean density (± standard error) of *Hybognathus placitus* < 20 mm standard length (SL; A) and SL of the smallest *H. placitus* collected each month (B) from the Pecos River between FSID Dam and Brantley Reservoir (1992 through 2001).

adults, 34.9% exceeded 60 mm SL. *Hybognathus placitus* < 20 mm SL were rare from November through April (Figure 10). Juveniles of all sizes were rare downstream of the Rio Hondo confluence during the same period (Figure 7). Smallest individuals were collected between May and September with relatively high density from May through July (Figure 10). The estimated potential spawning period was 12 April to 26 September because the smallest *H. placitus* captured in May (29 May 1996) was 10.6 mm SL (likely spawned between 12 April and 19 May) and the smallest captured in October (8 October 1996) was a 12.8 mm SL (likely spawned between 12 August and 26 September).

Discussion

It appears *H. amarus* was abundant in the study area until *H. placitus* became established, after which disappearance of *H. amarus* was rapid and *H. placitus* became abundant. Extirpation of *H. amarus* contrasts with other members of the sand-bed guild. All other native guild members (three species) persist and two non-natives (including *H. placitus*) have colonized the reach (Sublette et al. 1990; Hoagstrom and Brooks 2005; Hoagstrom et al. 2008b). The exceptional disappearance of *H. amarus* could be due to competition with *H. placitus*. It is not possible retrospectively to directly assess the nature of historical species interactions, but rapid replacement supports the hypothesis of Moyer et al. (2005) that the *H. placitus* invasion was a critical event in extirpation of *H. amarus*.

The distributional pattern of *H. placitus* indicated habitat needs consistent with other members of the sand-bed guild (Hoagstrom and Brooks 2005; Hoagstrom et al. 2008b). Adults were concentrated between the Taiban Creek and the Rio Hondo confluences even though juveniles were seasonally abundant downstream via displacement of eggs and larvae. Rapid seasonal declines in juvenile density indicated that most displaced *H. placitus* perished downstream, consistent with low daily survival rates in native populations (Wilde and Durham 2008). Similar population dynamics suggest high spatiotemporal overlap of larvae among species of the sand-bed guild. Addition of *H. placitus* to the Pecos River fauna could have exacerbated interspecific interactions in nursery habitats, particularly if space or forage were limited (Pease et al. 2006; Durham and Wilde 2009). Such interactions would have presumably been most intense between *H. amarus* and *H. placitus* because of their ecological similarity.

Association of adult *H. placitus* with less-degraded habitat indicates specific habitat needs. The *H. amarus* population of the Pecos River was never studied, but evidence from the extant population in the Rio Grande (Bestgen and Platania 1991; Platania and Altenbach 1998; Turner et al. 2006) and higher historical dominance in the Pecos River at the U.S. Highway 70 bridge versus the U.S. Highway 380 bridge suggest it exhibited similar distributional patterns to other members of the sand-bed guild, in which case adult *H. amarus* were also likely concentrated between the Taiban Creek and Rio Hondo confluences at the time of the *H placitus* invasion.

Mechanisms that sustain upstream populations of adults in spite of downstream displacement of eggs and larvae are poorly understood. Juvenile *H. placitus* outnumbered adults upstream of the Rio Hondo confluence throughout the spawning period, so retained eggs and larvae may have helped sustain the adult population, perhaps because survival and growth were higher in better habitats upstream, where larval densities were lower. However, peak abundance of juveniles occurred later upstream of the Rio Hondo confluence than overall, suggesting a small proportion of displaced individuals dispersed upstream. If juvenile *H. placitus* had higher growth and survival upstream of the Rio Hondo confluence or were superior upstream dispersers as juveniles, adult *H. placitus* may have rapidly outnumbered adult *H. amarus*.

Modifications to the flow regime of the Pecos River likely facilitated competitive dominance of *H. placitus* over *H. amarus*. Although dewatering has led to declines of native *H. placitus* populations (Cross and Moss 1987; Bonner and Wilde 2000; Hoagstrom et al. 2007), base-flow in the Pecos River still exceeds that of rivers where native *H. placitus* persist (e.g. Durham and Wilde 2008). Relatively high environmental tolerance may explain how *H. placitus* sometimes withstands dewatering and drought severe enough to eliminate other members of the sand-bed guild (Cross and Moss 1987; Kelsch 1994). *Hybognathus amarus* appears to be more sensitive to streamflow intermittence (Propst 1999), so *H. placitus* could have out-lived or out-competed *H. amarus* during low-flow periods. Historical lows in streamflow occurred in the 1960s, which presumably would have been a stressful period for *H. amarus* under any circumstances. Presence of more tolerant *H. placitus* likely exacerbated drought-related stress and decreased *H. amarus* survival in refugial habitats.

Reduced variability of the modern Pecos River flow regime did not preclude *H. placitus* colonization, even though variable flow regimes are important for reproduction (Lehtinen and Layzer 1988; Taylor and Miller 1990; Durham and Wilde 2006) and invariable flow regimes are associated with population declines (Bonner and Wilde 2000; Hoagstrom et al. 2007). Persistence in the Pecos River for at least 40 years indicates remaining flow regime variability was adequate. The estimated *H. placitus* spawning period was consistent with studies elsewhere (Lehtinen and Layzer 1988; Taylor and Miller 1990; Durham and Wilde 2005, 2006) and suggests the species benefitted from flexibility in spawning periodicity. Duration and timing of spawning activity may have varied from year to year, depending on the annual flow regime. For instance, the 1996 spawning season appeared to be the longest during this study. Lower density of individuals < 20 mm SL after July suggests spawning effort and recruitment declined in late summer (at least in some years), perhaps because age 2+ individuals suffered post-spawn mortality in early summer (reducing spawning effort) or interspecific competition and predation were fiercer in late summer (reducing recruitment).

Loss of spring-snowmelt runoff was likely more detrimental to *H. amarus* than *H. placitus*. Natural flow regimes in the Red River drainage, where native *H. placitus* persist, lack spring-snowmelt pulses (Poff and Ward 1989; Poff 1996). Native *H. placitus* also persist in the Canadian River where dams eliminated spring-snowmelt runoff (Bonner and Wilde 2000; Durham and Wilde 2005, 2008). The protracted spawning season of *H. placitus* increases potential for successful recruitment despite variable flow regimes and multiple adult age classes likely stabilize inter-annual reproductive output (Starrett 1951; Durham and Wilde 2008). Larger adults can produce larger larvae that may exhibit better growth or survival (Miller et al. 1988; Rosenfield et al. 2004). Shorter-lived species, such as *H. amarus* in the Rio Grande (Bestgen and Propst 1996; U.S. Fish and Wildlife Service 1999), are more prone to dramatic population fluctuations, which may exacerbate competitive disadvantages and facilitate extirpation (Propst et al. 2008). Indeed, rapid replacement of native fishes by non-natives has been documented several times in the North American plains, all replacements involved closely related congeners, and all replacing species can reach greater maximum lengths than species they replaced (Table 1). This suggests replacing non-natives rapidly outnumbered ecologically similar natives via disproportionate reproductive success that exacerbated competitive interactions and, in some cases, facilitated hybridization (Kodric-Brown and Rosenfield 2004). Longer fishes may have also accumulated greater mass and grown more rapidly, giving them an advantage in aggressive encounters, mate selection, time to maturation, and dispersal ability (Rosenfield and Kodric-Brown 2003; Rosenfield et al. 2004). Thus, greater size and longer life appear to have repeatedly combined with a modified natural flow regime to facilitate rapid species replacements in the plains.

Examples from the plains (Table 1) suggest rapid species replacements are regional phenomena facilitated by synergy of evolutionary

Table 1. Rapid species replacements[1] in fish faunas of the plains of North America with source drainages of each species (non-native replacers, native species replaced) and maximum lengths for comparison.

Species pair		Source river drainage (tributary drainages)		Maximum length[2] (mm)	
Replacer	Replaced	Replacer	Replaced	Replacer	Replaced
Hybognathus placitus Girard, 1856	*H. amarus* (Girard, 1856)	Mississippi (Arkansas, Red)	Rio Grande	127	89
Notropis bairdi Hubbs and Ortenburger, 1929	*N. girardi* Hubbs and Ortenburger, 1929	Mississippi (Red)	Mississippi (Arkansas)	83	51
Fundulus grandis Baird and Girard, 1853	*F. zebrinus* Jordan and Gilbert, 1883	Gulf of Mexico coast	Rio Grande (Pecos)	152	102
Cyprinodon variegatus Lacépède, 1893	*C. bovinus* Baird and Girard, 1853	Gulf of Mexico coast	Rio Grande (Pecos)	76	58
Cyprinodon variegatus	*C. pecosensis* Echelle and Echelle, 1978	Gulf of Mexico coast	Rio Grande (Pecos)	76	46

[1]References: Felley and Cothran (1981); Cross et al. (1983); Childs et al. (1996); Bestgen and Propst (1996); Echelle and Echelle (1997); Hoagstrom (2003)
[2] Length data are from Lee et al. (1980); Miller and Robison (2004), and Thomas et al. (2007)

history and human disturbance. There were three commonalities among all rapid species replacements: (1) all replacing species grow to be larger than species they replaced (discussed above), (2) all invaded habitats were modified (Hubbs 1980; Cross et al. 1983; Hoagstrom et al. 2008a; Hoagstrom 2009), and (3) all replacements involved plains endemics being replaced by closely related taxa from waters that were naturally similar to disturbed conditions. Main sources of replacing species (Red River drainage, Gulf of Mexico coast) had relatively harsh natural environments (Gunter 1947; Simpson and Gunter 1956; Echelle et al. 1972; Poff and Ward 1989). Invading species were tolerant of environmental fluctuations and noted for aggressiveness (Baughman 1950; Simpson and Gunter 1956; Bennett and Beitinger 1997; Rosenfield and Kodric-Brown 2003). Other invasions from these sources have occurred (Sublette et al. 1990; Miller and Robison 2004; Thomas et al. 2007), yet reciprocal introductions have failed (Cross 1970; Pigg 1991; Miller and Robison 2004). The Red River drainage has experienced relatively few invasions overall (Gido et al. 2004) and there are no cases of plains endemics invading the Gulf of Mexico estuary. The Gulf of Mexico coast and Red River drainage are regional sources for invasive fishes that have potential to homogenize disturbed faunas of the plains by rapidly replacing endemic species. Conservation of natural stream sediment and stream flow regimes is critical for conservation of endemics and could reduce the risk of rapid species replacements (Walters et al. 2003; Poff et al. 2007; Rahel 2007), but eliminating transport of fishes among river drainages is the only way to prohibit them. Endemic species that persist in modified habitats are perpetually at risk of competitive exclusion from closely related, non-native taxa that are naturally tolerant of modified conditions.

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