

FLOW REGULATION AND FRAGMENTATION IMPERIL PELAGIC-SPAWNING RIVERINE FISHES

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Abstract. Flow regulation and fragmentation of the world's rivers threaten the integrity of freshwater ecosystems and have resulted in the loss or decline of numerous fish species. Pelagic-spawning fishes (pelagophils) are thought to be particularly susceptible to river regulation because their early life stages (ichthyoplankton) drift until becoming free-swimming, although the extent of transport is largely unknown. Transport velocity and distance were determined for passively drifting particles, which mimicked physical properties of ichthyoplankton, in two large, regulated rivers (Rio Grande and Pecos River) of the arid Southwest United States. Particle drift data were incorporated into celerity–discharge equations ($r^2 > 0.90$; $P < 0.001$), and reach-specific transport velocity was modeled as a function of discharge. Transport velocities of particles exceeded 0.7 m/s in all river reaches during typical spawning flows (i.e., reservoir releases or rainstorms) and were greatest in highly incised and narrow channel reaches. Mean transport distance of particles released in the Pecos River during sustained reservoir flows (141.1 km; 95% CI = 117.0–177.5 km) was significantly longer than during declining reservoir flows that mimicked a natural rainstorm (52.4 km; 95% CI = 48.8–56.5 km). Mean transport distance of particles in the Rio Grande during sustained reservoir flows was 138.7 km (95% CI = 131.0–147.2 km). There are 68 dams and 13 reservoirs that fragment habitats and regulate flow in the Rio Grande Basin (Rio Grande and Pecos River) in areas historically occupied by pelagophils. While the basin historically provided 4029 km of free-flowing riverine habitat, reservoir habitat now represents >10% of the longitudinal distance. Only five unfragmented nonreservoir reaches >100 km remain in the Rio Grande, and two remain in the Pecos River. Pelagophils were extirpated from all reservoirs and from nearly all short, fragmented reaches (<100 km) of the Rio Grande Basin, but at least some fraction persisted in all longer reaches (>100 km). The recovery and long-term persistence of pelagophils in regulated rivers, including those in this study, will likely depend on reestablishment and protection of long unfragmented reaches coupled with mimicry of the natural flow regime.

Key words: dams; downstream transport; extinction; extirpation; fish eggs; freshwater fishes; hydraulic geometry; larval fish drift; reproductive guild; Rio Grande basin; river fragmentation and regulation.

INTRODUCTION

Dams fragment and disrupt the natural flow regime of over half of the world's large river systems (Dynesius and Nilsson 1994, Nilsson et al. 2005) and threaten naturally evolved processes in freshwater ecosystems (Naiman and Turner 2000, Jackson et al. 2001, Malmqvist and Rundle 2002). Construction and operation of dams and reservoirs for flood control, hydroelectric power generation, and irrigation have led to global declines in the abundance and diversity of freshwater fauna (Petts 1984, Zwick 1992, Richter et al. 1997, Pringle et al. 2000). Dams and reservoirs block natural migration routes of many freshwater fishes (Leggett 1977, Fausch et al. 2002) and increase the likelihood of extirpation or extinction by fragmenting populations (Jager et al. 2001, Speirs and Gurney 2001,

Morita and Yamamoto 2002). Numerous obligate freshwater fish species may be particularly affected by river regulation because their eggs and larvae (propagules) drift passively downstream with the water current. Drifting propagules require a specific developmental time to become free-swimming individuals capable of seeking nursery habitats. However, river fragmentation and regulation have reduced the available time that propagules can drift prior to being swept into unsuitable downstream environments such as reservoirs or irrigation networks. Knowledge of propagule transport would likely provide insight into patterns of decline, extirpation, and extinction of freshwater fishes in regulated rivers that could aid in the recovery of affected taxa.

The geographic distribution of freshwater fishes with drifting early life history phases is global, with representatives in most large river systems (Breder and Rosen 1966). Drift is a fundamental early life history characteristic of nearly all freshwater fish families (Lowe-McConnell 1987, Pavlov 1994, Pavlov et al.

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1995). Pelagic-spawning riverine fishes (pelagophils) compose a reproductive guild whose propagules drift downstream for several days until they attain a free-swimming phase (Battle and Sprules 1960, Balon 1975, Araujo-Lima 1994, Platania and Altenbach 1998). Riverine pelagophils typically spawn during elevated flows (e.g., spring runoff or summer rainstorms), and drifting early life stages (ichthyoplankton) are transported downstream (Moore 1944, Taylor and Miller 1990, Platania and Altenbach 1998).

River fragmentation and regulation are thought to have contributed either directly or indirectly to the decline or loss of numerous pelagic-spawning fishes throughout the Great Plains and Southwest United States (Cross et al. 1983, Cross and Moss 1987, Winston et al. 1991, Platania and Altenbach 1998, Luttrell et al. 1999, Alò and Turner 2005). Studies of pelagophils in the Pecos River, New Mexico, demonstrated that, following spawning, the highest densities of young occurred in downstream reaches, whereas adults were most abundant in middle and upstream reaches (Hoagstrom and Brooks 2005, Hoagstrom et al., *in press*). Ichthyoplankton are also subject to transport into downstream reservoirs, which sustain nonnative piscivorous fishes and lack appropriate habitat for pelagophils (Winston et al. 1991, Platania and Altenbach 1998). Dams prevent subsequent upstream movement of individuals transported over these instream barriers and out of their natal reach. Further, reduced water temperatures (e.g., downstream of hypolimnetic release dams) and prolonged development to the free-swimming phase are thought to increase mortality risk for ichthyoplankton (Platania and Altenbach 1998).

Geomorphic complexity of the riverine environment is thought to reduce downstream transport of drifting propagules of numerous freshwater species (Reynolds et al. 1991, Lancaster and Hildrew 1993, Winterbottom et al. 1997, Reckendorfer et al. 1999, Bond et al. 2000). However, flow regulation changes the natural biophysical patterns and continuity of rivers, which leads to a reduction in geomorphic heterogeneity (Stanford et al. 1996). The deleterious consequences of downstream transport of reproductive propagules into unsuitable environments, such as reservoirs, are magnified for pelagophils because these short-lived species cannot endure consecutive reproductive failures. Numerous pelagophils in highly regulated river ecosystems are now extirpated from much of their native range, or extinct (e.g., Cross and Moss 1987, Winston et al. 1991, Platania and Altenbach 1998).

Despite the imperiled status of many fishes with drifting early life history stages, few studies have provided quantitative estimates of the rate or magnitude of propagule transport. Several authors have qualitatively estimated probable downstream transport distances of drifting life phases using spawning dates and changes in drift densities between sites (e.g., Nesler et al. 1988, Tyus and Haines 1991, Araujo-Lima and Oliveira

1998, Robinson et al. 1998). Reinert et al. (2004) used drifting particles that mimic properties of ichthyoplankton to estimate sampling efficiency, but did not present data on transport rates. An exception is the work of Crisp (1989), who conducted one of the few quantitative studies of fish propagule transport by using negatively buoyant particles to mimic temporary displacement of salmonid eggs during high flows. However, it is unclear how these results translate to transport processes of passively drifting propagules.

In contrast to the lack of quantitative studies of propagule transport, numerous models have been developed to predict the dispersion and transport of contaminants in rivers (see Beven et al. 1994, Rutherford 1994, Runkel 1998). While these models have been successful in predicting dispersion processes in rivers, attempts to predict downstream transport velocity yielded results that were either not applicable over a wide range of discharges, or were inaccurate at an individual discharge value (e.g., Boning 1974, Graf 1986, Jobson 1997). Jobson (2001) concluded that an empirically based approach, using relationships between wave speed (celerity) and discharge, reduced many of the estimation errors encountered when calculating transport velocity. Models developed from these celerity-discharge equations produced accurate predictions of particle transport velocity when calibrated with empirical contaminant transport data (Jobson 2001).

Additionally, radioactively labeled particles have been used in numerous studies to determine transport distance of drifting organic particles (see Cushing et al. 1993, Thomas et al. 2001, Georgian et al. 2003, Newbold et al. 2005). In those works, particle drift data were combined with transport efficiency equations to generate a model capable of quantifying the proportion of particles retained in transport as a function of distance downstream of the release point. While most particle transport studies have been conducted in small streams (first and second order) and over short distances (<1 km), the underlying concepts and equations should be applicable to higher order rivers (Minshall et al. 1992).

In our study, passively drifting particles that mimicked ichthyoplankton of Rio Grande Basin pelagic-spawning minnows (Platania and Altenbach 1998, Dudley and Platania 1999) were used to calculate transport velocity and distance in two large, regulated rivers (Rio Grande and Pecos River) of the arid Southwest United States. Objectives of this study were (1) to model transport velocity of ichthyoplankton as a function of discharge for different river reaches, (2) to calculate transport distance of ichthyoplankton during typical spawning flows, and (3) to compare fragmented river reach length with extirpation of pelagophils. Our goal in conducting this research was to explore and elucidate factors that could account for the decline and loss of pelagophils from the fragmented and regulated Rio Grande Basin. Increased knowledge of ichthyoplankton transport processes in regulated rivers could

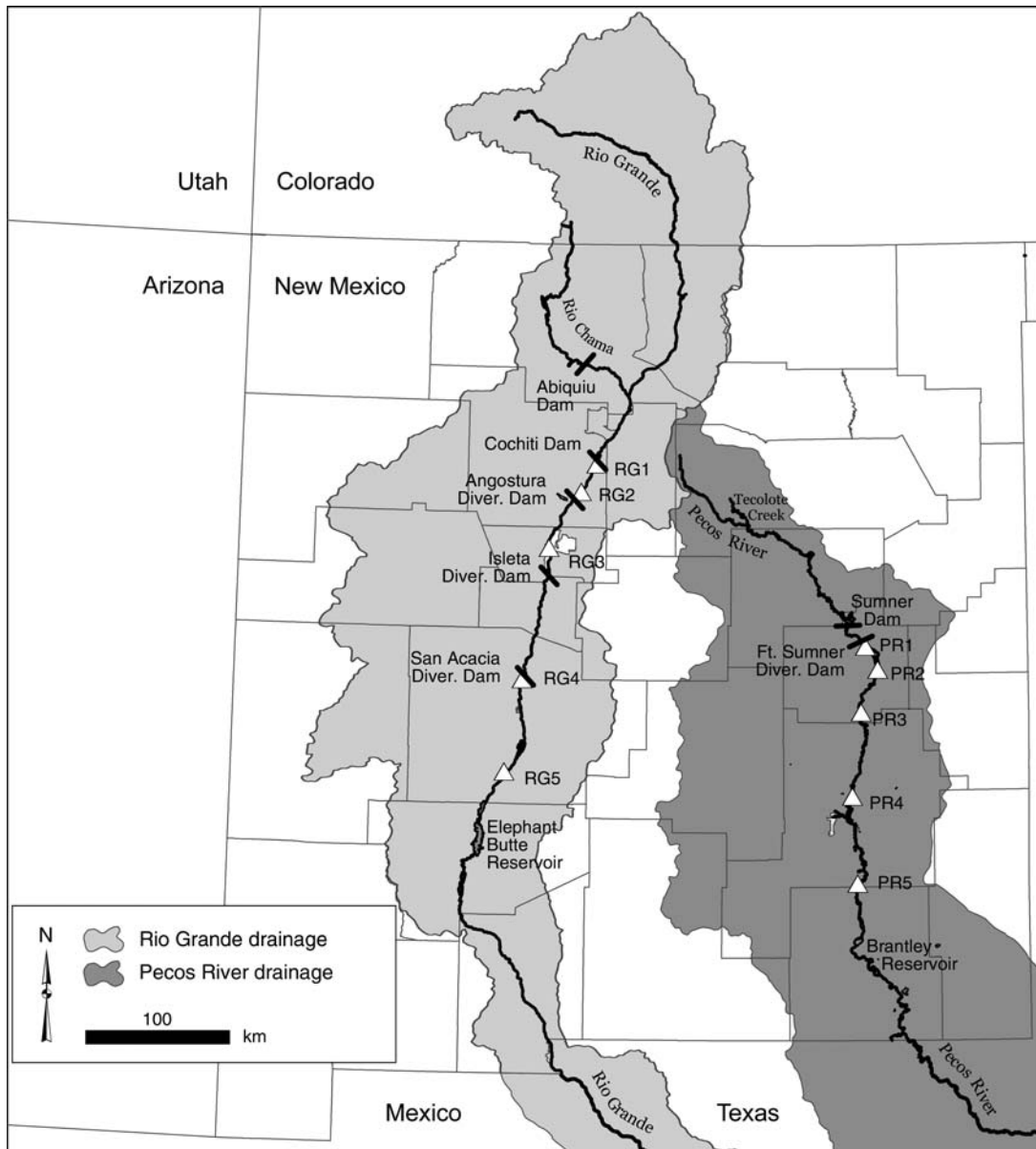


FIG. 1. Map of the upper Rio Grande and Pecos River drainages, illustrating select dams, reservoirs, and gauging stations (triangles) in the study areas.

assist in the development of strategies to curtail future losses of imperiled freshwater fishes in other endangered river ecosystems.

METHODS

Study area

The headwaters of the Rio Grande Basin (Fig. 1) are located in the San Juan Mountains of southern Colorado. The Rio Chama is the only major perennial tributary of the Rio Grande in New Mexico. Spring snowmelt from southern Colorado and northern New Mexico provides the majority of water for the Rio Grande. Cochiti Dam is the primary flood control

structure downstream of the Rio Chama confluence and has caused narrowing and incision of the river channel downstream to Elephant Butte Reservoir (Richard 2001). Additionally, three diversion dams (Angostura, Isleta, and San Acacia) fragment habitats between Cochiti Dam and Elephant Butte Reservoir. While diversion dams do not create reservoirs like large dams, they block upstream movement of fishes, and, via diversion, can greatly reduce flows downstream.

The Pecos River flows from its headwaters in the Sangre de Cristo Mountains of northern New Mexico to its confluence with the Rio Grande in Texas. While operations at Sumner Dam result in periodic episodes of

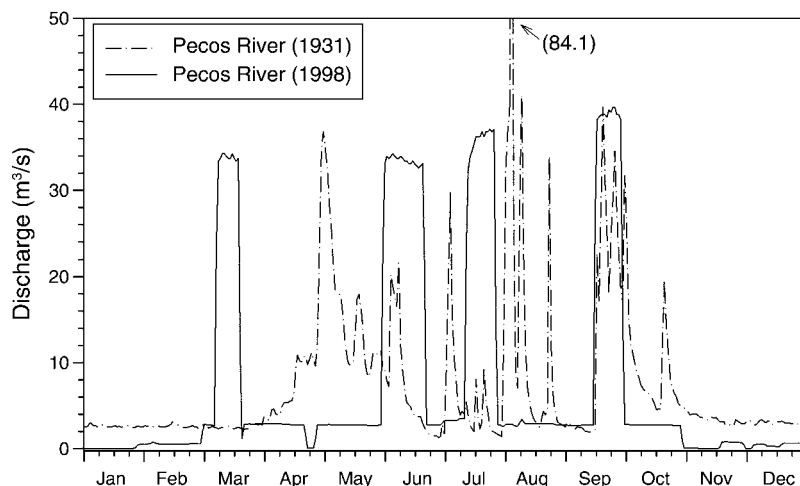


FIG. 2. Mean daily discharge in the Pecos River (USGS Station Number 08384500) in 1931 (pre-dam) and 1998 (post-dam) during similar periods of mean annual discharge (1931 discharge = $7.36 \text{ m}^3/\text{s}$; 1998 discharge = $7.39 \text{ m}^3/\text{s}$). August discharge in 1931 is off the scale ($84.1 \text{ m}^3/\text{s}$).

stable elevated discharge, followed by extended intervals of low discharge, the pre-dam flow regime was much more variable (Fig. 2) and likely contributed to the historically broad river channel. The river channel is now narrow and incised from Sumner Dam to Brantley Reservoir. A single diversion dam (Ft. Sumner) fragments habitats downstream of Sumner Dam.

Upstream dams and downstream reservoirs bounded study areas in the Rio Grande Basin (Pecos River and Rio Grande). Study reaches in the two study areas were demarcated by United States Geological Survey (USGS) gauging stations and generally were <100 km apart. A series of gauging stations were chosen from the Rio Grande (USGS 08317400 [RG1], 08319000 [RG2], 08330000 [RG3], 08354900 [RG4], 08358400 [RG5]), and Pecos River (USGS 08384500 [PR1], 08385522 [PR2], 08385630 [PR3], 08386000 [PR4], 08395500 [PR5]). Reaches were selected because of the availability of 15-minute discharge data at USGS gauging stations, which facilitated model development and allowed for precise measurement of variables used in transport velocity equations.

Particle transport

Passively drifting particles (PDPs) with physical properties that mimicked drifting fish eggs of Rio Grande Basin pelagic-spawning minnows (Platania and Altenbach 1998, Dudley and Platania 1999) were used to generate data regarding drift dynamics. Fish eggs and PDPs had nearly identical values of specific gravity (~ 1.005 [Dudley and Platania 1999]) and remained in suspension at the lowest water velocities generated ($\sim 0.01 \text{ m/s}$) in aquaria. Transport times of drift were determined by releasing PDPs at an upstream location and recording time and rate of capture of the particles at multiple downstream sampling localities (study reaches) within each study river.

In both the Rio Grande and Pecos River, PDPs were released during relatively stable flows to obtain estimates of reach-specific transport velocities and the fraction of PDPs remaining in transport as a function of distance. Additionally, two releases of PDPs were made in the Pecos River downstream of Sumner Dam, using predictable reservoir releases to simulate dynamic hydraulic conditions. One of these trials was conducted just prior to the cessation of a reservoir release (i.e., flow rapidly declined shortly after PDPs were released; referred to hereafter as declining discharge) and simulated propagule transport following a rainstorm. The second trial was initiated one day after the initial arrival of water from a reservoir release, as flow was still increasing, and was to mimic transport during a minor storm surge.

Moore Egg Collectors (Altenbach et al. 2000), equipped with mechanical flow meters to calculate the volume of water sampled, were used to collect PDPs. Continuous sampling was initiated upon capture of the first particle, with data recorded at 15-minute intervals; sampling duration extended for at least 48 hours. Density of PDPs (number of PDPs per volume of water sampled) was calculated for each 15-minute sampling interval.

Travel time T was the interval between release of PDPs and peak density (i.e., maximum capture rate) of particles at a site, following the method described by Jobson (2001). Mean cross-sectional area A for each river reach was calculated as

$$A = \frac{Q \times T}{X} = \frac{Q}{V} \quad (1)$$

where Q = discharge, X = distance, and V = velocity.

Transport velocity

Models of ichthyoplankton transport velocity developed during this study were derived from relationships

among wave speed, discharge, and mean cross-sectional area in rivers (Wilkinson 1945, Chow 1959, Jobson 2001). Jobson (2001) demonstrated that differentiation and inversion of the classic area–discharge relationship (Leopold and Maddock 1953) allowed for a direct relationship of wave speed (celerity = C) to discharge and area by

$$C = \frac{\Delta X}{\Delta t} = \frac{dQ}{dA} = \frac{Q^{(1-\alpha_2)}}{\alpha_1 \times \alpha_2} \quad (2)$$

where ΔX = the distance moved by the wave in time Δt , α_1 = the hydraulic-geometry coefficient, and α_2 = an exponent for area. In our study, celerity was calculated as the time from the midpoint of the rise in discharge between an upstream and downstream gauging station (X meters apart). Least-squares linear regression of log-transformed celerity and discharge produces

$$C = y \times Q^z \quad (3)$$

where y is a constant and z defines nonlinear changes in discharge Q . Values of α_1 and α_2 were computed based on the relationship between Eq. 2 and Eq. 3. The transport velocity between two gauging stations for any discharge can be solved using

$$A = A_0 + \alpha_1 \times Q^{z_2} \quad (4a)$$

$$V = \frac{Q}{A_0 + \alpha_1 \times Q^{z_2}} \quad (4b)$$

in which A_0 = the mean cross-sectional area of the river channel with negligible water velocity, and where Eq. 1 is used to determine the empirical value of A . Modeled relationships of mean cross-sectional area as a function of discharge were calibrated using empirical transport velocity data from PDPs.

A sensitivity analysis was conducted to assess the relative impact of different errors in the estimation of the hydraulic parameters (A_0 , α_1 , and α_2) on the model results. The area–discharge relationships for the Cochiti Reach (RG1–RG2) of the Rio Grande, New Mexico were used for the sensitivity analysis. This reach was chosen because of its relatively short distance and stable flows.

Transport distance and time

The fraction of PDPs remaining in suspension at each sampling locality was computed by integrating and comparing the areas under each time–density curve. The longitudinal loss coefficient of particles (k_p) and initial density ($F_{(0)}$) were determined with an exponential decay model as

$$F_{(X)} = F_{(0)} \exp(-k_p X) \quad (5)$$

where $F_{(X)}$ = the fraction of particles remaining in suspension at each downstream distance X (Newbold et al. 1981). Mean transport distance (S_p) of particles was calculated as the inverse of k_p . To permit comparisons

between particle releases, the $F_{(0)}$ for each release was set equal to 100% and values of $F_{(X)}$ were calculated as a percentage of $F_{(0)}$. Linear ANCOVA was used to detect differences in k_p between particle releases, using natural log-transformed $F_{(X)}$ and untransformed X (Georgian et al. 2003).

The time taken for particles to travel the mean transport distance was calculated as S_p divided by the transport velocity V (Eq. 4b). Mean discharge during the particle release was used to calculate V . In cases where particles traveled through multiple reaches, total transport time was calculated as the sum of the transport times within each reach.

Fragmentation of the Rio Grande Basin

Fragmentation of the Rio Grande Basin was quantified by using digital raster graphics (DRGs) of USGS topographic maps and digital orthophoto quadrangles (DOQs) from New Mexico and Texas. Several thousand images were used to create a highly detailed mosaic of the river system. ArcView GIS software (version 3.2; ESRI, Redlands, California, USA) was used to mark the location of dams and to determine the geographic extent of reservoirs (i.e., from dam to headwaters of reservoir). Irrigation diversion dams that fragmented the Rio Grande Basin were also included in this study, but these structures did not have associated reservoirs. Distances between USGS gauging stations, dams, and reservoirs were determined by measuring along the centerline of the river channel.

Distribution of native pelagophils

Historical (pre-1980) distributions of Rio Grande Basin fishes were compiled using data from surveys performed in the latter half of the 19th century and early part of the 20th century (Lee et al. 1980). Recent (post-1980) distributions of fishes were compiled from a variety of sources (Chernoff et al. 1982, Smith and Miller 1986, Bestgen and Platania 1990, 1991, Edwards and Contreras-Balderas 1991, Platania 1991, Hoagstrom 2003; Museum of Southwestern Biology, University of New Mexico, unpublished data). Platania and Altenbach (1998) identified a reproductive guild of four extant native Rio Grande Basin cyprinids (Rio Grande silvery minnow, *Hybognathus amarus*, speckled chub, *Macrhybopsis aestivalis*, Rio Grande shiner, *Notropis jemezianus*, and Pecos bluntnose shiner, *Notropis simus pecosensis*) that spawn drifting eggs; they provided information that strongly suggests two extinct forms, phantom shiner (*Notropis orca*) and Rio Grande bluntnose shiner (*Notropis simus simus*) were also pelagophils. The aforementioned six fish taxa comprised the pelagophil community used in the extirpation analysis portion of this study. The length of each fragmented study reach was plotted against the percentage of species of pelagic-spawning fishes that had been extirpated in that reach.

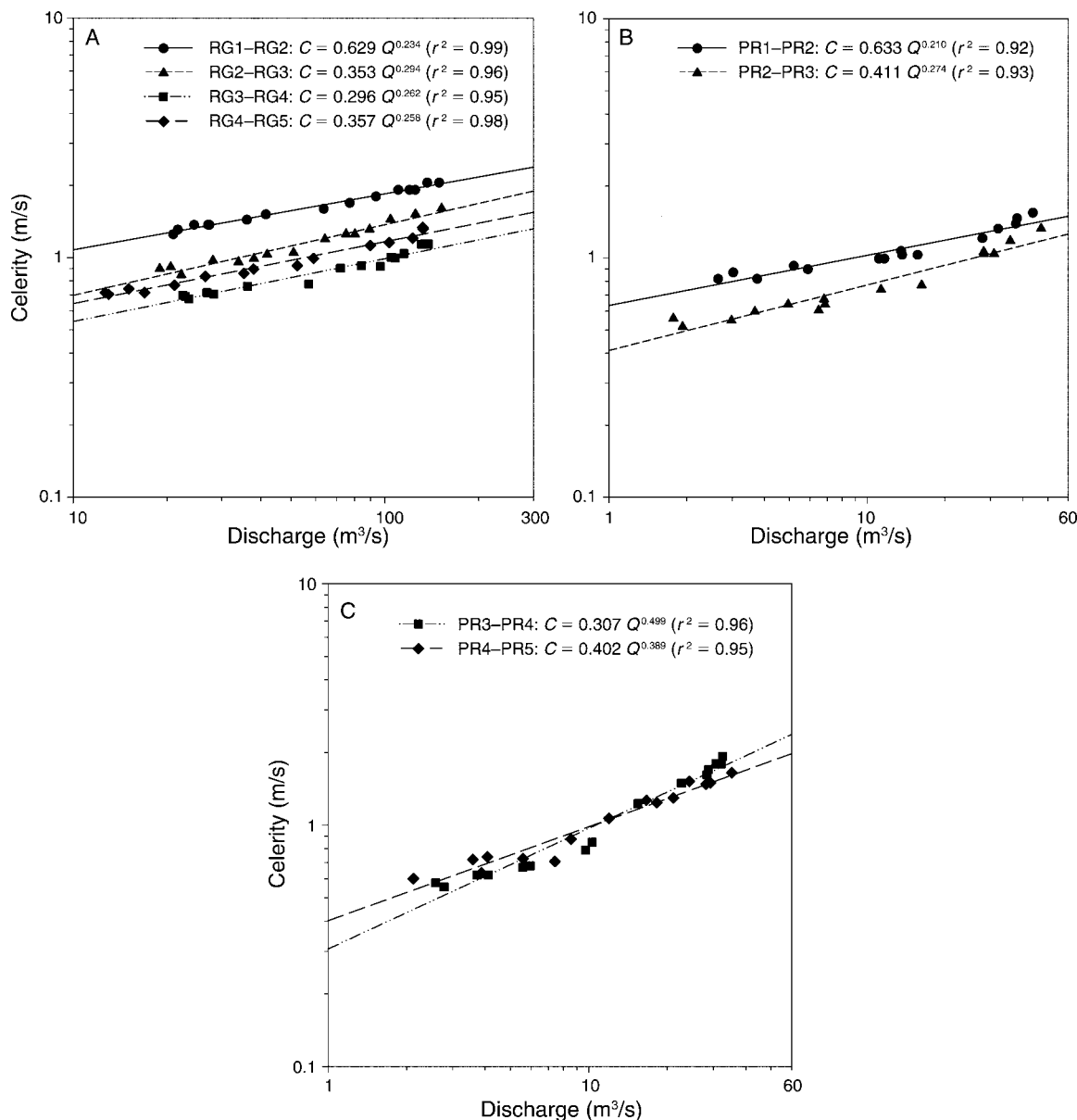


FIG. 3. Relationship between celerity (C) and discharge (Q) for different reaches in (A) the Rio Grande (RG), and (B and C) the Pecos River (PR). Note the logarithmic scale on both axes in all panels.

RESULTS

Celerity–discharge relationships

There were significant relationships ($r^2 > 0.90$; $P < 0.001$) between celerity and discharge for all study reaches of the Rio Grande and Pecos River. Values of y (see Eq. 3) in the Rio Grande ranged from 0.296 to 0.629, but values of z were similar (range = 0.234–0.294) and indicated that celerity in the Rio Grande scaled predictably with discharge as a simple power function (Fig. 3A). Wave celerity was positively correlated with discharge in the Pecos River ($P < 0.001$ for all reaches; Fig. 3B, C) and r^2 values (range = 0.92 to 0.96) were

similar to those of the Rio Grande. However, reach-specific values of z were much more variable (range = 0.210 to 0.499) for the Pecos River than the Rio Grande.

Transport velocities of PDPs

Calculated transport velocities in the Rio Grande ranged between 0.0 and 1.4 m/s, depending on discharge (0.0 to 120.0 m³/s) and river reach (Appendix A). For discharges exceeding 8.0 m³/s, transport velocity in the upper reach (RG1–RG2) was the highest of any Rio Grande reach. For the three downstream-most Rio Grande reaches, particle transport velocities increased rapidly up to a discharge of ~20 m³/s, followed by a

modest increase in velocity (~ 0.5 – 1.0 m/s) from 20.0 to 120.0 m^3/s . In the Pecos River, the PR1–PR2 reach had the highest velocity (~ 1.0 m/s) across the highest discharges modeled (30.0 – 35.0 m^3/s), while the PR2–PR3 reach had the lowest velocities (~ 0.8 m/s). Transport velocities increased most rapidly as a function of discharge in the PR3–PR4 and PR4–PR5 reaches.

Sensitivity analysis of hydraulic parameters

Errors that ranged from 0 to +20%, in 5% increments, were included in a sensitivity analysis of hydraulic parameters (A_0 , α_1 , and α_2) to determine the impact of errors on model results (Appendix B). The relationship between area and discharge was least affected by changes in A_0 and most affected by changes in α_2 . However, estimated errors calculated from celerity–discharge linear least-squares regression analyses were relatively small for both α_1 ($x = 6.6\% \pm 1.9\%$, mean \pm SD) and α_2 ($x = 2.9\% \pm 1.2\%$), indicating that model results were quite accurate for all river reaches.

Transport distance and time

During a stable release of reservoir water ($x = 34.2 \pm 1.5$ m^3/s), mean PDP transport distance (S_p) in the Pecos River (Fig. 4) was 141.1 km (95% CI = 117.0 to 177.5 km) and transport time was 45.4 h. In contrast, $S_p = 52.4$ km (95% CI = 48.8 to 56.5 km) and transport time was 27.9 h during the rapidly declining flows (30.2 m^3/s [0 h], 13.5 m^3/s [4 h], 5.0 m^3/s [12 h], and 3.2 m^3/s [24 h; hours after peak flow in brackets]) at the cessation of a reservoir water release. There was a significant difference ($F = 47.4$, $df = 3, 4$, $P < 0.005$) between loss coefficients (k_p) from the stable discharge vs. declining discharge trials. Data from the PR4–PR5 reach were not included in the comparison, as they were only available during the stable discharge trial. However, nearly all (92.5%) particles passing PR4 were transported to PR5 during the stable discharge trial.

Particles released in the Pecos River one day after the initial arrival of a reservoir water release, as flow was increasing ($x = 30.5 \pm 0.5$ m^3/s ; range = 29.2 – 31.4 m^3/s), were transported a mean distance of 153.6 km (95% CI = 142.3 to 166.8 km) in 51.4 h. The longitudinal loss coefficient ($k_p = 6.51 \times 10^{-6}$ m^{-1}) for the increasing discharge release was well supported ($r^2 = 0.998$, $P < 0.05$). However, there was no significant difference ($F < 0.01$, $df = 3, 3$, $P > 0.05$) in loss coefficients (k_p) between the stable and increasing discharge trials in the Pecos River.

The longitudinal loss curve for the Rio Grande was calculated from data collected during a period of stable discharge ($x = 102.0 \pm 2.5$ m^3/s). Mean transport distance ($S_p = 138.7$ km, 95% CI = 131.0 to 147.2 km) and transport time (44.4 h) in the Rio Grande were similar to values calculated during the stable discharge release in the Pecos River. The Rio Grande longitudinal loss coefficient ($k_p = 7.21 \times 10^{-6}$ m^{-1}) was also well supported ($r^2 = 0.999$, $P < 0.05$).

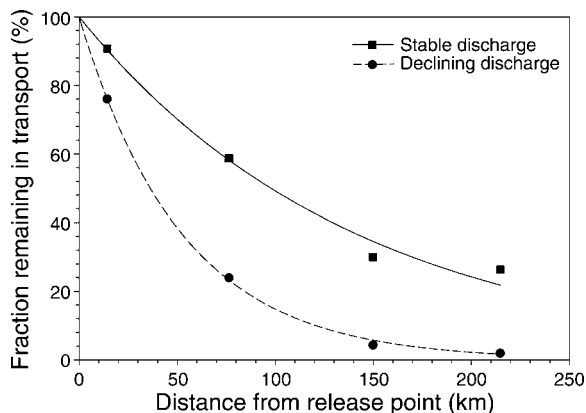


FIG. 4. Transport of PDPs (passively drifting particles), as a percentage of input, at multiple downstream locations in the Pecos River. Stable discharge longitudinal loss coefficient: $k_p = 7.09 \times 10^{-6}$ m^{-1} , $r^2 = 0.985$, $P < 0.01$. Declining discharge longitudinal loss coefficient: $k_p = 1.91 \times 10^{-5}$ m^{-1} , $r^2 = 0.999$, $P < 0.001$.

Transport times in the Rio Grande (RG1 to RG5 = 260.3 km; Fig. 5A) ranged between 82.0 h at 120.0 m^3/s and 137.2 h at 20.0 m^3/s . The difference in overall transport time (RG1 to RG5) was greatest between 20.0 and 40.0 m^3/s (25.5 h) and least between 100.0 and 120.0 m^3/s (4.2 h). Transport times in the Pecos River (PR1–PR5 = 263.8 km; Fig. 5B) ranged between 79.6 h at 35.0 m^3/s and 171.8 h at 5.0 m^3/s . The overall transport times in the Pecos River were similar to those calculated in the Rio Grande despite large differences in the range of modeled discharges between the two study areas.

River fragmentation and extirpation of native pelagophils

A total of 36 dams and five reservoirs fragment the Rio Grande from its confluence with the Rio Chama to its terminus at the Gulf of Mexico (Fig. 6A). Historically, this free-flowing length was 2651 km, but now only five free-flowing reaches remain that exceed 100 km. The lower section of the Rio Chama (downstream of Abiquiu Dam) that historically supported pelagophils is also highly fragmented by dams. The Pecos River from its confluence with Tecolote Creek to its confluence with the Rio Grande (1378 km) is fragmented by 22 dams and eight reservoirs (Fig. 6B). While there are two free-flowing river reaches >300 km in this section of the Pecos River, all other reaches are <65 km. Reservoir habitat now represents 13.6% and 10.8% of the longitudinal distance in the Rio Grande and Pecos River study areas, respectively.

A high percentage of native pelagophilic species that formerly occupied much of the Rio Grande Basin have been extirpated (Fig. 7). Nearly all reaches <100 km no longer retained any pelagic-spawning freshwater fishes. River reaches >100 km retained at least some percentage of native pelagophils that historically occupied these areas. However, populations of native pelagophils have

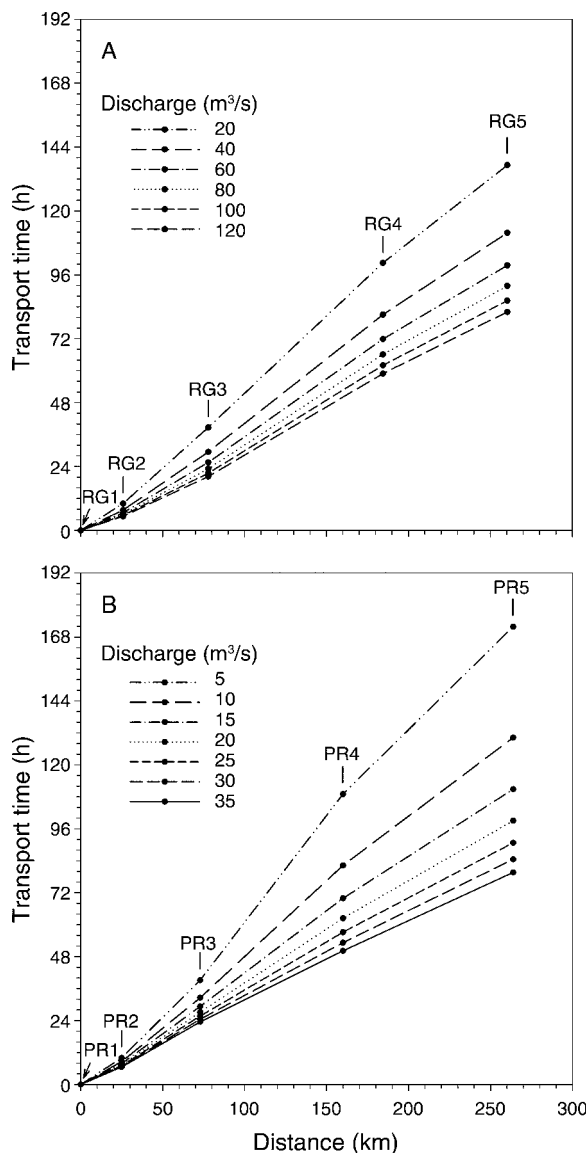


FIG. 5. Relationship between transport time and distance for different discharges and reaches (delineated by solid dots) in the two study rivers: (A) Rio Grande and (B) Pecos River.

been extirpated from all river reaches that now provide only reservoir habitat.

DISCUSSION

Ichthyoplankton transport velocities and distances

Although deleterious effects of river fragmentation and regulation have been documented for a variety of freshwater fishes, causal mechanisms are often difficult to identify and even more difficult to quantify. In this study, a quantitative approach was used to calculate the transport velocity and distance of drifting early life stages of fishes in regulated rivers. Velocity–discharge relationships varied among reaches of the Rio Grande and Pecos River and appeared to be related to river

channel morphology. Transport velocities were highest in reaches immediately downstream of dams where channel narrowing and incision were most pronounced. Increased mean cross-sectional area in wider and more braided downstream channel reaches resulted in reduced water velocities. Slower transport rates in wider and less incised channel reaches allowed more time for eggs and larval fish to develop to a free-swimming stage and move into nursery habitats.

Flow regulation causes increased channelization, decreased geomorphic complexity, loss of connectivity between rivers and floodplains, and thus decreased habitat heterogeneity (Ward and Stanford 1995, Kondolf 1997). Direct river channelization, dredging, rock dikes (groynes), and shoreline revetment also increase flow velocity and redirect flow toward the thalweg. Levee construction for flood control reduces channel area during flow pulses, further increasing velocity (Stanford et al. 1996). These collective effects of river regulation likely increase the downstream transport of ichthyoplankton into unsuitable downstream environments such as reservoirs or irrigation networks.

Transport velocities and distances recorded during this study were likely higher than historical values because of channel narrowing and incision caused by flow regulation. There has been a reduction in the frequency and magnitude of peak flows, resulting in a more stable flow regime since the construction and operation of dams in the Rio Grande Basin (Richard 2001). The reduced variability of the recent flow regime has resulted in a relatively static channel compared to historical conditions when high flows from snowmelt or seasonal rains periodically reshaped the channel and facilitated over-bank flooding. Stabilization of banks by invasive woody vegetation, which thrives under non-flooding flow regimes, has further contributed to the narrowing and habitat homogenization of these regulated rivers.

While runoff and rainstorms historically prompted spawning by pelagophils, releases of reservoir water now often provide this spawning stimulus (Platania and Altenbach 1998). Unlike reservoir releases that result in extended stable flows, runoff and rainstorms are more variable and often of a shorter duration. The results of this study indicated that the mean transport distance of propagules was greatly reduced during rapid drops in flow (e.g., following rainstorms) compared to stable elevated flows characteristic of reservoir releases. Increased habitat heterogeneity during declining flows likely resulted in higher retention rates of ichthyoplankton in pools, backwaters, and other low-velocity nursery habitats. It is likely that over-bank flooding from runoff or rainstorms historically provided similar habitats suitable for rapid development of larval fishes. In contrast, high-volume releases of reservoir water remain primarily within the narrow banks of the river channel and result in a preponderance of homogeneous high-velocity runs.

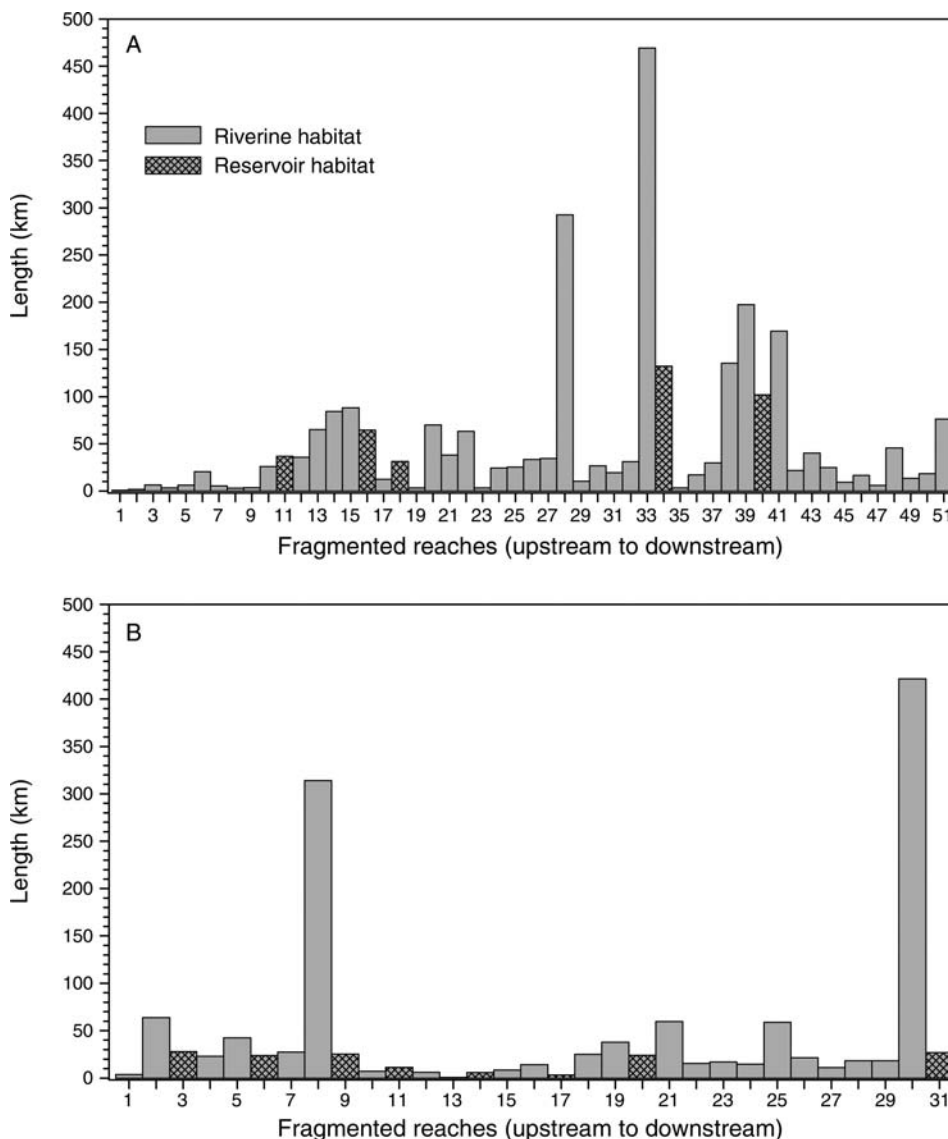


FIG. 6. Lengths of fragmented reaches (shown by reach number) (A) in the Rio Chama below Abiquiu Dam (Reaches 1–9) and in the Rio Grande from its confluence with the Rio Chama to the Gulf of Mexico (Reaches 10–51), and (B) in the Pecos River from its confluence with Tecolote Creek to its confluence with the Rio Grande.

The effects of downstream transport of ichthyoplankton are also dependent on the developmental rate from a drifting to a free-swimming phase. Development of the gas bladder is associated with free-swimming ability (i.e., transition from the “free embryo” to larval stage) and initiation of exogenous feeding in pelagophils (Sliger 1967, Platania and Altenbach 1998). This period of larval development occurred about four days post-spawning at 25°C for plains minnow, *Hybognathus placitus* (Flittner 1964), emerald shiner, *Notropis atherinoides* (Sliger 1967), and Rio Grande silvery minnow, *Hybognathus amarus* (S. P. Platania, unpublished data). However, free swimming was not achieved until about 7 and 10 days post-spawning at cooler water temperatures (20°C and 15°C, respectively) for Rio Grande silvery

minnow, *Hybognathus amarus* (S. P. Platania, unpublished data).

Transport distance of ichthyoplankton in the Rio Grande and Pecos River was dependent on water temperature, discharge, and channel morphology. When calculated transport times during high-volume reservoir releases were combined with ichthyoplankton developmental rates at 25°C, we found that propagules were likely to be swept long distances downstream prior to reaching a free-swimming phase. In contrast, declining and lower discharges resulted in reduced transport velocities and magnitudes, which would allow a sufficient developmental period at 25°C for substantially more free-swimming larvae to be retained upstream.

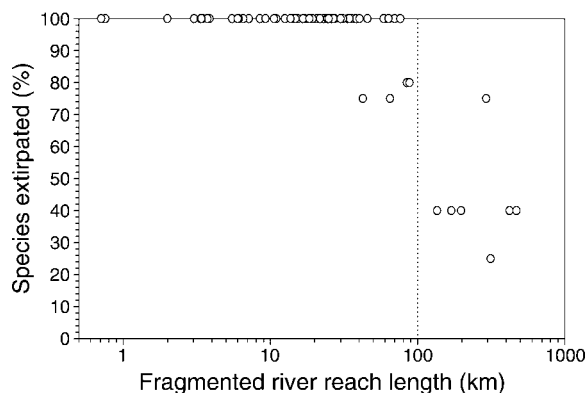


FIG. 7. The relationship between the percentage of Rio Grande Basin pelagophilic fish species extirpated and fragmented river reach length (note logarithmic scale). The dotted line represents the minimum reach length possibly required to sustain long-term viable populations of Rio Grande Basin pelagophils under present conditions.

Implications for conservation of pelagophilic fishes

The Rio Grande Basin historically supported at least six pelagophils in three genera (Platania and Altenbach 1998). Several of these species have declined dramatically throughout their range, resulting in federal protection for Pecos bluntnose shiner, *Notropis simus pecosensis*, (threatened) and Rio Grande silvery minnow, *Hybognathus amarus*, (endangered). Two additional taxa, phantom shiner, *Notropis orca*, and Rio Grande bluntnose shiner, *Notropis simus simus*, declined in abundance during the 1950s and 1960s and are now extinct (Bestgen and Platania 1990). The conservation status of other fish species with drifting embryonic phases, in the Rio Grande Basin and other river basins of the Great Plains, is tenuous and has resulted in recent federal protection of the Arkansas River shiner, *Notropis girardi*. Additional protection may be necessary for other pelagophils within the region in the near future.

Fragmentation and regulation of most of the world's rivers, including those in this study, have resulted in environments vastly different from those in which their fishes evolved. River channelization and habitat degradation now result in the rapid and efficient downstream transport of young over long distances. The small percentage of drifting fish eggs and free embryos retained in reaches <100 km under present conditions makes long-term persistence of self-sustaining populations in these areas unlikely. However, few free-flowing river reaches >100 km remain in the contiguous United States, particularly in arid regions (Stanford and Ward 1979, Benke 1990).

Early life history stages of native fishes transported into or spawned in reservoirs of the Southwest United States are subject to high mortality because these artificial lentic environments harbor nonnative piscivorous fishes (Minckley 1983). Furthermore, eggs and free

embryos fall out of suspension in standing water, where they are possibly subject to hypoxic conditions and vulnerable to suffocation in bottom sediments. Diversion dams reduce upstream populations of pelagophils by preventing the return of any spawned fish that were transported over these instream barriers as propagules. Additional threats to ichthyoplankton imposed by diversion structures include entrainment in irrigation canals and drying of downstream reaches during low-flow periods.

While downstream transport of ichthyoplankton appears to be a pivotal factor in the decline and loss of pelagophilic freshwater fishes, river fragmentation and regulation have also resulted in habitat changes that frequently favor nonnative fishes. The transformation of naturally flooding rivers in the Southwest United States into controlled low-disturbance systems has allowed the invasion of nonnative fishes that compete with and prey on various life stages of native fishes (Minckley and Meffe 1987). Numerous invasive fishes now occupy lentic and lotic environments within the Rio Grande Basin, especially in reservoirs and in the cold and clear waters released downstream of dams. Nonnative fishes are likely contributing to the decline of pelagophils from highly fragmented and regulated reaches of the Rio Grande Basin. However, it is less certain how much nonnative fishes are negatively impacting pelagophils in longer floodprone reaches where temperature, discharge, and sediment input are more variable.

A combination of short-term and long-term management strategies will likely be required to combat the deleterious effects of river fragmentation and regulation on pelagophils in the Rio Grande Basin. Release of warm epilimnetic water from reservoirs could be implemented in the short term, and would increase developmental rate of ichthyoplankton in reaches downstream of dams, allowing young to reach a free-swimming stage more rapidly. However, careful consideration would have to be given to potential undesirable effects, such as the proliferation of warm-water-adapted nonnative fishes, prior to altering the thermal regime. Another short-term strategy for existing fragmented reaches would be revision of dam operation protocols to allow for a more natural flow regime, including passage of high flows from snowmelt or seasonal rains (Stanford et al. 1996). A more natural flow regime would presumably benefit native fishes by helping to restore some degree of floodplain connectivity, habitat heterogeneity, and river channel complexity. Physical habitat restoration (e.g., removing or relocating levees, destabilizing banks, and reconnecting rivers with floodplains) could be undertaken in concert with a return to the natural flow regime to maximize the effectiveness and long-term efficacy of both approaches. While implementation of the aforementioned strategies would likely decrease the transport distance of ichthyoplankton, further studies will be required to determine how much

drift distance would be reduced as a function of flow or habitat modification.

Neither natural flow regimes nor habitat restoration efforts are likely to result in long-term recovery of pelagophils without also restoring connectivity between fragmented river reaches. It is becoming increasingly apparent that solutions to river fragmentation and regulation need to be conceptualized and implemented at the catchment scale (Pringle 1997, Saunders et al. 2002). River fragmentation is globally pervasive, and arid biomes are particularly sensitive to its deleterious upstream and downstream effects (Nilsson et al. 2005). The few remaining free-flowing river reaches of notable distance (>100 km) in the Rio Grande Basin warrant preservation, while in shorter reaches, efforts should be made to modify or remove existing dams, to allow unimpeded upstream fish passage.

Dam modification or removal efforts should first be directed to structures that pose a safety risk, are old or no longer in use, or whose primary purpose is to divert water for irrigation. The numerous small dams in these categories disrupt the connectivity of riverine systems and their strategic removal could create longer free-flowing river reaches. For example, modification or removal of Isleta and San Acacia diversion dams in the Rio Grande to allow full upstream passage of fishes would create a single, long (~250 km) free-flowing river reach from three short (<100 km) fragmented reaches. Quantifiable risk criteria may be appropriate to assess the possible ecological effects of dam renovations or removal (Pejchar and Warner 2001, Hart et al. 2002, Poff and Hart 2002) and may provide direction for future efforts in the Rio Grande Basin. Large- and small-scale dam renovation and removal projects are being implemented globally, and ecologists can provide guidance toward the goal of restoring riverine ecosystem function (Poff et al. 1997, Galat et al. 1998). The recovery and long-term persistence of pelagophils in regulated rivers, including those in this study, will likely depend on reestablishment and protection of long, unfragmented reaches coupled with mimicry of the natural flow regime.

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APPENDIX A

A figure showing the relationship between velocity and discharge for different reaches in the two study rivers (Rio Grande and Pecos River) (*Ecological Archives* A017-082-A1).

APPENDIX B

A figure showing a sensitivity analysis of the relationship between area and discharge for the Cochiti Reach (RG1–RG2) of the Rio Grande, New Mexico (*Ecological Archives* A017-082-A2).