

TRIBUTARY STREAMS PROVIDE MIGRATORY FISH WITH ACCESS TO FLOODPLAIN

HABITATS IN A REGULATED RIVER: EVIDENCE FROM ALLIGATOR GAR

(Atractosteus spatula)

A Thesis

by

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ABSTRACT

Fishes that migrate within freshwater and exhibit periodic life history traits are broadly distributed and particularly sensitive to the effects of river regulation. However, persistence of migratory fishes in highly regulated rivers may be related to tributaries providing necessary spawning and early life stage habitats. To explore this, I studied the movement of Alligator gar, *Atractosteus spatula*, and hydrology, in a highly regulated North American river, the Brazos River. I hypothesized that: 1) mainstem flood pulses would be much more limited than tributaries due to historical river regulation and 2) fish movements into tributaries would be best predicted by higher flows and temperatures. My analysis revealed that flood pulses were drastically reduced on the mainstem, but not a tributary, and tributary occurrence was highest above mean temperatures (i.e., 25°C) and when flows exceeded a 3 pulse per season (i.e., 300 cms) frequency. These results provide a framework for advancing the conservation of migratory fishes in regulated rivers and further highlight the use of tributaries in buffering mainstem populations against the effects of river regulation.

DEDICATION

I would like to dedicate this thesis to my parents and grandparents. Through exposure early in my life these individuals introduced me to the wonders of the natural world. These experiences have substantially influenced the decisions I have made for a career in fisheries. I'm forever thankful and would not have it any other way.

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Contributors

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All other work conducted for the thesis was completed by the student independently.

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INTRODUCTION

Humans rely on rivers for water supplies, irrigation, transportation, power generation, fisheries, and recreation (Karr and Chu 2000; Grill et al. 2019). As a consequence, nearly all of the world's rivers have been modified, often extensively. Lehner et al. (2011) estimated there are >50,000 large dams (height over 15 m) storing approximately one-sixth of global annual river discharge into oceans. The combination of water consumption and impoundments has left only 23% of the world's longest rivers (>1000 km) still flowing unimpeded (Grill et al. 2019). Further, the number of dams and consequent storage of water is predicted to increase as additional hydropower dams are completed (Zarfl et al. 2014). Freshwater rivers are hotspots for biodiversity, yet their inhabitants face a disproportionate threat of extinction due to the large ratio between species richness and area of habitat (Dudgeon et al. 2006). Surface freshwater habitats constitute approximately 0.01% of the world's water by volume but contain nearly one third of all vertebrate species (Dudgeon et al. 2006). Ultimately, conservation of the world's rivers and their biota is critical to maintaining both human water security and global biodiversity (Vörösmarty et al. 2010).

Among freshwater ecosystems, river-floodplains (i.e., riverscapes) are among the most biodiverse ecosystems in the world. Natural disturbances within riverscapes, such as flooding and channel migration create and maintain habitat heterogeneity that supports high biodiversity (Ward 1998). However, anthropogenic river fragmentation and regulation alter the dynamics of river-floodplain ecosystems resulting in biodiversity loss (Dynesius and Nilsson, 1994). Floodplain connectivity is essential for the population persistence of many freshwater organisms (Ward 1998; Lewis et al. 2001). The Flood Pulse Concept (FPC) stresses the importance of

periodic floodplain inundation for the productivity and biodiversity of rivers (Junk et al. 1989). Floodplains available during higher flows provide a wide range of benefits for fishes including habitat for spawning, recruitment, foraging, and refuge (Junk et al. 1989). Consequently, fishes have emerged as model organisms and ecological indicators for riverscape connectivity yet there is still limited understanding of fish migration into floodplains (Lasne et al. 2007; Castello et al. 2008). This information is critical as fish species that rely on floodplains are among the most imperiled (Tockner and Stanford 2002).

Among freshwater fishes, migration for reproduction is strongly associated with life history. Winemiller and Rose (1992) defined three life history strategies (i.e., periodic, opportunistic, and equilibrium) defined by trade-offs in demographic traits (e.g., age of maturity, fecundity, juvenile survivorship) and gradients of environmental variation at various scales that select for these strategies. This concept has received considerable attention in the context of flow regimes filtering life history strategies on a global scale, but work has focused primarily on community ecology (Perkin et al. 2017). Periodic strategists, characterized by relatively late maturation, large size, and high fecundity are able to exploit large-scale variation in environmental conditions occurring spatiotemporally. Migration is common among periodic strategists presumably because movement into favorable habitats during appropriate periods has fitness benefits in terms of spawning success and subsequent early life stage survival (Winemiller and Rose 1992). Unfortunately, river fragmentation and regulation negatively effect migrations both longitudinally (i.e., upstream-downstream) and laterally (i.e., channel-floodplain). This is problematic because migratory fishes with periodic life history strategies (hereafter called migratory fishes) play critical ecological and economical roles, as they are often keystone species, subsidize biogeochemical cycles, and support popular recreational and

commercial fisheries (Flecker et al. 1996; Aprahamian et al. 2010; Dugan et al. 2010). Migratory fishes make up a \$2.5 billion fishery comprising 70% of total fisheries yield in the largest inland fishery, the Mekong River, while certain migratory species (e.g., sturgeon and salmon) in recreational fisheries significantly contribute to a \$4.3 billion economic impact in the United States (Barlow et al. 2008; Hughes 2015). Unfortunately, there is high spatial overlap between the distribution of migratory fishes and regulated rivers leading to an emerging conservation crisis for these species (Grill et al. 2019; He et al. 2019; Aló et al. 2021).

Despite global river regulation and habitat fragmentation, some migratory fish populations persist (Agostino et al. 2004; Esguicero et al. 2010). One reason for this may be the existence of unobstructed tributaries that provide ecosystem services (e.g., floodplain connectivity) which promote this persistence (Pracheil et al. 2013). Migratory fishes are known to use unregulated stretches of tributaries for important aspects of their life history such as reproduction and recruitment (Pracheil et al. 2009). Additionally, migrations to tributary streams by the threatened Humpback chub, *Gila cypha*, and Colorado pikeminnow, *Ptychocheilus lucius* fulfill population processes that no longer occur in the highly regulated mainstem Colorado River of North America (Gorman and Stone 1999; Irving and Modde 2000). These observations suggest that tributaries might be essential for the conservation of migratory fishes (Starcevich et al. 2012).

In North America, the Alligator gar, *Atractosteus spatula*, represents a periodic life history strategist known to migrate between mainstem and tributary habitats (Kluender et al. 2017). The Alligator gar is considered an apex predator and popularity of trophy angling of this species has increased substantially in recent decades (Smith et al. 2020a). Alligator gar rely on seasonal connectivity to inundated floodplains (Figure 1b) and backwater habitats for

reproduction and successful recruitment (Buckmeier et al. 2017; Kluender et al. 2017; Smith et al. 2020b). Populations of Alligator gar have declined in the Mississippi River basin and many coastal rivers draining into the Gulf of Mexico due to a loss of floodplain connectivity (Figure 1c) as well as historical eradication efforts, and overharvest (Kluender et al. 2017, Lochmann et al. 2021). There is a general lack of knowledge regarding movements and habitat use by Alligator gar across the range of the species (Buckmeier et al. 2013, Smith et al. 2020a). A few recent studies have investigated these topics, but the majority of this work has focused on longitudinal distribution of Alligator gar in mainstem systems with minimal consideration of the importance of lateral movement (Buckmeier et al. 2013; Kluender et al. 2017, Wegener et al. 2017). Current populations of Alligator gar are stable in Texas and Louisiana, yet mainstem rivers in these regions are just as fragmented as other portions of Alligator gar range where declines have occurred (Smith et al. 2020a). Therefore, understanding persistence of Alligator gar populations within portions of their remaining distribution may be related to use of less regulated tributaries and associated floodplain habitat for reproduction (Figure 1d). This strategy highlights the importance of using tributaries and their floodplains during seasonal flood pulses where mainstem connections no longer exist. Thus, understanding the extent, duration, and predictors of movement of Alligator gar into tributaries is essential for their conservation and management.

The goal of this study was to test the prediction that Alligator gars use tributaries to access floodplain habitats during the spawning season. First, I performed a hydrological analysis of the lower Brazos River and a tributary, the Navasota River, to determine the frequency of flood pulses within mainstem and tributary reaches. Due to the high degree of fragmentation on the mainstem portion of the study area, I hypothesized that the frequency of flood pulses would

be higher in the less modified tributary compared to the regulated mainstem. Second, using a combination of stationary and mobile acoustic telemetry, I assessed predictors of Alligator gar occurrence in mainstem and tributary reaches. I hypothesized that occurrence of Alligator gar would increase in tributaries during flood pulses that occurred when water temperatures met requirements for reproduction (Buckmeier et al. 2017). My work provides insight into how regulated rivers might be managed to benefit Alligator gar populations throughout their range, and by extension, declining populations in other river systems where migratory fishes persist.

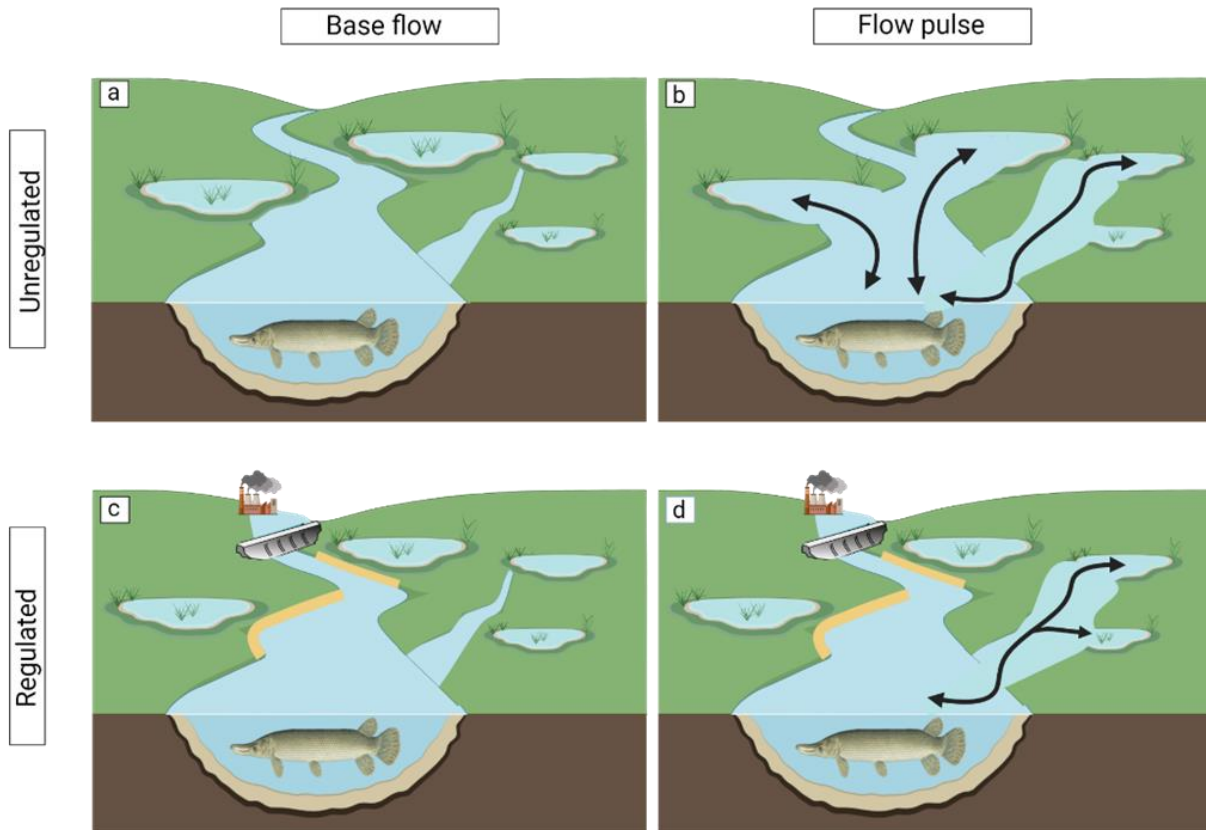


Figure 1. Conceptual diagram demonstrating: (a) isolation of floodplain habitats during base flows in a unregulated river; (b) high pulse flows and resulting lateral connectivity that provides migration pathways (double arrows) between mainstem rivers and floodplains; (c) a regulated mainstem river with reservoirs and levees at base flows; and (d) a high pulse flow in a regulated river where the effects of dams and levees prevent mainstem-floodplain connectivity, but tributaries still provide corridors of connectivity to floodplains for freshwater migratory fishes such as Alligator gar. Figure created with BioRender (<https://biorender.com>) using Alligator gar image by Rick Hill (used with permission).

METHODS

Study area

The Brazos River is 2,060 kilometers (km) long and originates near the border of New Mexico and Texas flowing southeast to the western Gulf of Mexico (Kammerer, 1987). The basin is highly regulated and includes large reservoirs in the system such as Possum Kingdom Lake, Lake Granbury, and Lake Whitney arranged along the middle Brazos River. Downstream of these reservoirs, the lower Brazos River is a meandering, lowland river that primarily drains nutrient rich forested and agricultural land (Winemiller et al. 2000). I tracked movements of Alligator gar along 200 km of the Brazos River centralized around College Station, TX (Figure 2). I also tracked movements in 162 km of the lower sections of three major tributaries until their confluences with the mainstem, including 58 km of the Little River, 56 km of the Navasota River, and 33 km of Yegua Creek upstream to the dam at Somerville Lake (Figure 2). The remaining 16 km composed of minor tributaries (e.g., Beason creek; Figure 2) only accessible during higher flows. Average stream width of mainstem habitat was 70 m during base flows, and substrate was predominantly sand with intermittent limestone outcroppings and gravel bars. Average stream width of tributary habitat was 24 m during base flows and more commonly interrupted by riffle habitats. Substrate in tributaries was sand and silt except for the Little River where limestone outcroppings, gravel and boulders were more frequent.

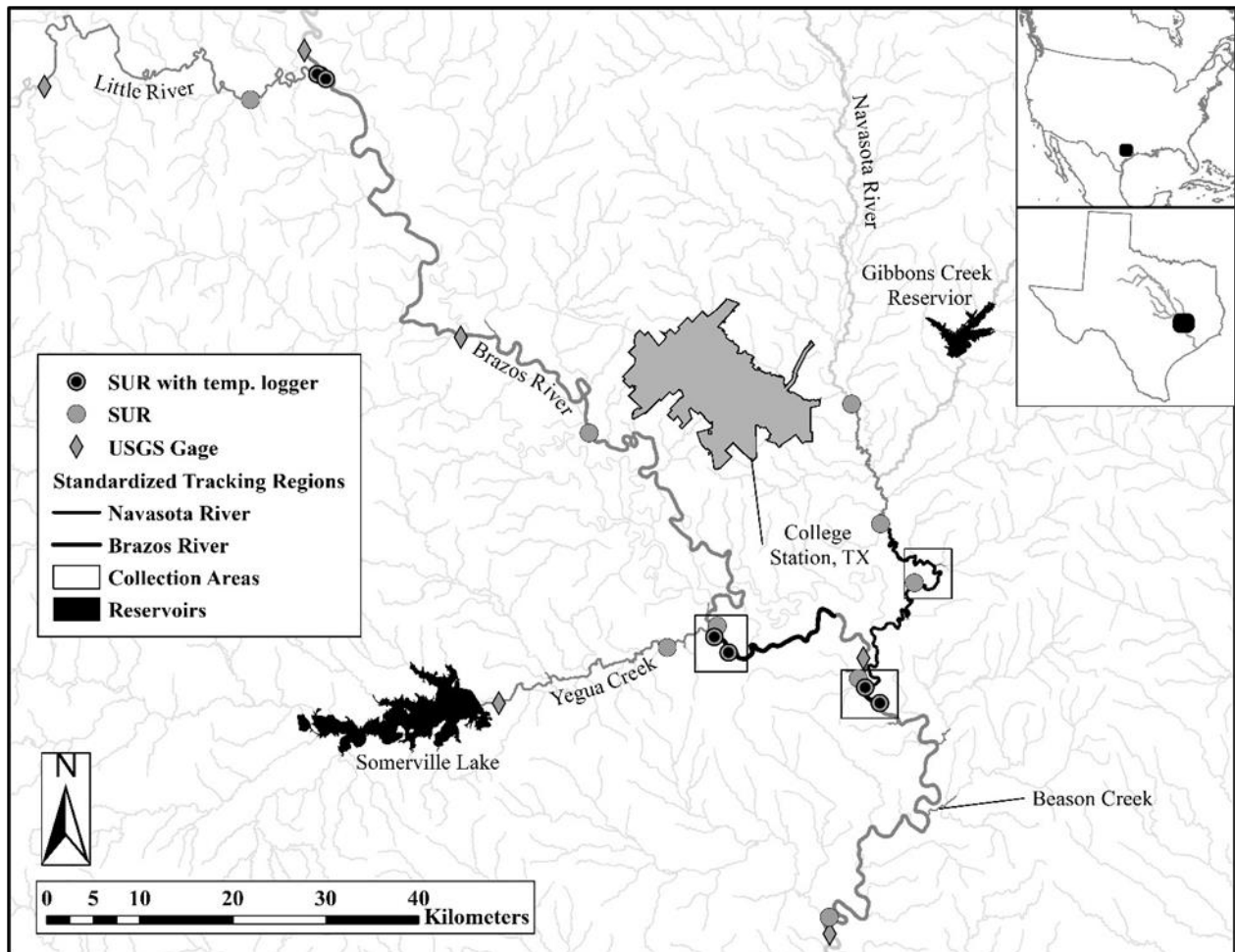


Figure 2. Map of study area along the lower Brazos River basin centralized around College Station, TX. Dark grey lines represent where the study was carried out, light gray lines are un-surveyed regions of the Brazos River basin. Black lines are standardized tracking regions conducted during each tracking event. Grey circles are SUR locations without temperature loggers, grey and black circles are SUR locations with a temperature logger, grey diamonds are locations of USGS gages, boxes are general regions of the study area where Alligator gar were tagged.

Fish Collection and Tagging

Alligator gar were captured primarily from three collection areas (Figure 2) across five tagging events from April 2020 to March 2021 (Table 1). Tagging was distributed throughout

the study area in low-velocity pool habitats within the mainstem, tributaries, and tributary confluences. I used large mesh experimental gill nets (76-127-mm mesh size, 61 m net length, 3 m net depth) as described by Bodine et al. (2015) and Schlechte et al. (2016). This included short-term net sets (≤ 1 hr set time) in areas where Alligator gar activity was observed on the surface or by locating fish using side scan sonar (Humminbird Helix 10 chirp GPS G2N sonar unit) as described by Fleming et al. (2018). Once a fish was captured, I collected morphological variables from each fish to predict sex as described by McDonald et al. (2018). I triple-tagged each captured fish using a passive integrated transponder (PIT) tag, a T-bar anchor tag inserted in soft tissue directly posterior to the dorsal fin, and one of two transmitter types inserted into the peritoneal cavity. Transmitters were either an ultrasonic transmitter with a 14-month battery lifespan (Model CT-82-2-I; Sonotronics, Tuscon, Arizona) or a combined acoustic and radio transmitter (CART) with a 26-month acoustic and 13-month radio battery lifespan (Model MM-RC-16-25, Lotek, Ontario, Canada). Transmitters were surgically inserted with a single incision along the soft tissue directly posterior to the right pelvic fin following methods developed by the U.S. Fish and Wildlife Service, Baton Rouge Fish and Wildlife Conservation Office (K. Kimmel, *personal communication*). During tagging, fish were kept in a plexiglass cradle reinforced with an aluminum frame to reduce the risk of thrashing and increase stability during the surgical procedure. Following tagging and recovery, fish were released within 100 meters of the capture location.

Table 1. Summary of the five tagging events conducted for the duration of the study including the date the tagging event begun, ended, and the number of Alligator gar collected for each tagging event.

Tagging Event	Date (Start)	Date (End)	Number Tagged
1	4/14/2020	4/30/2020	15
2	5/19/2020	5/27/2020	8
3	7/20/2020	7/23/2020	4
4	12/16/2020	12/17/2020	5
5	3/15/2021	3/17/2021	13

Telemetry

I monitored Alligator gar movement using both stationary and mobile telemetry. For stationary telemetry, a total of 16 submersible underwater receivers (SURs; Sonotronics SUR-3BT) were deployed (Figure 2). I continuously monitored the movement exchange of individual fish across mainstem-tributary ecotones using a three-grid array of SURs deployed at each of the three major tributaries, including one SUR in the mainstem upstream of the confluence, one SUR in the mainstem downstream of the confluence, and one SUR in the tributary upstream of its confluence. I separated SURs within the tributary confluence arrays by a minimum of 1200 m to ensure no overlap in detections were possible and that detections represented fish locations firmly within either mainstem or tributary habitats. Additional SURs were deployed well within each of the major tributaries (≥ 6000 m) and throughout the Brazos River (Figure 2). I attached temperature loggers (Onset HOBO® UTBI-001 Tidbit temperature data logger, Onset Computer Corp., Bourne, Massachusetts) to the SURs in the confluence of each of the major tributaries and to the SURs downstream of each confluence in the Brazos River to record hourly water temperatures. Three SURs were lost during a high-water event towards the end of the study period in May 2021, resulting in an approximately 90-day gap in Brazos River receiver coverage

at those locations. However, given the limited data collected on these SURs prior their loss and that the receivers were lost towards the end of the study period, I consider their loss minimal. Otherwise, SURs were maintained such that they continuously listened for transmitters. Because of the dynamic nature of flows and stream widths, it's unlikely that SURs maintained total coverage of stream channels during high flow events (Casto-Yerty and Bettoli 2009). However, I emphasize that the SUR arrays generally acted as a series of grids to detect large-scale movements (e.g., migrations into tributaries) consistent with previous studies of Alligator gar movement (Buckmeier et al. 2013).

I used mobile telemetry to determine whether Alligator gar occupied either mainstem or tributary habitats in regions outside of the fixed ranges of the SURs, as well as in minor tributaries where I had no coverage of stationary receivers. Thirteen tracking events were conducted monthly from May 2020 to August 2021 (Table 2) by driving a boat downstream (≤ 8 km/h) using a Sonotronics USR-14 ultrasonic tracking receiver and a towable Sonotronics TH-2 omnidirectional hydrophone towed just below the water surface. Once a transmitter was detected, a Sonotronics DH-4 directional hydrophone was used to determine fish location as accurately as possible before a global positioning system (GPS) was used to georeference fish relocations. The size and navigability of the study area made it impractical to survey entirely for any given tracking event. Therefore, standardized tracking reaches (Figure 2) were searched during each tracking event encompassing the majority of tagged fish each month. Additional tracking was conducted outside of the standardized tracking regions when: (1) detections were low in the standardized reaches, (2) flow stages were high or, (3) the occurrence of both situations. Higher water stages allowed for better navigability in the mainstem, major tributaries, floodplains, and minor tributaries.

Data processing and subsetting

Stationary detections from SURs were processed using Sonotronics SURsoft Stand Alone Data Processing Center (SURsoft version 1.0.6) as described by Buckmeier et al. (2013).

SURsoft records a confidence field for each recorded detection as an integer value ranging from 2 to 5, where 2 is low confidence that the detection was not background noise and 5 is maximum confidence that a detection was an actual transmitter. I only analyzed detections with the highest confidence values of 4 and 5 for analysis to avoid uncertainty regarding noise versus fish detection. Raw stationary detection data were sorted by receiver, Fish ID, and date and time. Raw detection data was then aggregated to a sum of detections on a given day and receiver for each individual to prepare for further analysis. Fish available for detection varied by tracking event due to the length of the tagging period and loss of fish due to suspected tag loss, harvest, emigration, or tag failure (Table 2). I considered a fish undetectable if the individual was not detected on any of the stationary receivers or relocated with mobile telemetry for two consecutive tracking events.

Table 2. Total count of tagged Alligator gar, Alligator gar available for detection, and proportion of relocated Alligator gar across each mobile tracking event. Numbers of tagged fish varied through time due to the duration of study, and suspected mortality, tag failure, and emigration. Beginning and end of each tracking event are defined as the first and last days I scanned for Alligator gar.

Tracking Event	Date (start)	Date (end)	Total Tagged	Tags Available	Proportion Relocated
1	5/11/2020	5/14/2020	15	15	0.73
2	6/2/2020	6/12/2020	23	22	0.91
3	9/10/2020	9/26/2020	27	18	1
4	10/7/2020	10/16/2020	27	18	0.89
5	11/4/2020	11/12/2020	27	18	0.89
6	1/13/2021	1/20/2021	32	19	1
7	2/22/2021	3/3/2021	32	19	0.84
8	3/24/2021	4/2/2021	45	31	0.97
9	4/21/2021	5/3/2021	45	31	0.87
10	5/26/2021	6/3/2021	45	29	0.48
11	6/23/2021	7/2/2021	45	27	0.85
12	7/22/2021	7/24/2021	45	24	0.92
13	8/23/2021	8/26/2021	45	21	0.81

To account for variation in available fish for detection, both stationary and mobile telemetry datasets were subsetted using data filtering techniques. I filtered observations in two steps, duration and transition, to test my hypotheses. My duration filter retained individuals for further analysis that I was able to continuously monitor until the end of the study period. This allowed me to look at individuals with the highest amount of seasonal variation in environmental conditions (i.e., temperatures and flows) which best represented population level tributary use. Of these individuals filtered for duration, I only looked at fish that made transitions (i.e., transition filter) from the mainstem Brazos River into the major tributaries (stationary telemetry) or major and minor tributaries (mobile telemetry).

Statistical Analysis

Flow Pulses

I performed hydrological analyses on two gages to test the hypothesis of reduced flow pulses in the mainstem relative to a tributary. My analysis employed daily flow data from the Brazos River gage in Waco, TX (USGS Gage ID; 08096500), and the Navasota River Gage (USGS Gage ID; 08110800) near Easterly, TX. These gages were selected because they were: 1) the only local gages that had hydrology data prior to river regulation, 2) are currently still in operation, and 3) had no significant gaps in gage data. I quantified the frequency (i.e., number per year) of flow pulse magnitudes with ecological relevance as determined by the Brazos River Basin and Bay Expert Science Team (BBEST; Gooch et al. 2012). Specifically, the frequency of overbank events (average one pulse per 5 years; one pulse per 2 years) and high flow pulses (average one pulse per year) were estimated for the two gages (hereafter referred to as 5-year, 2-year, and 1-year pulses). The discharge thresholds for these recommended pulses included 971 cms (1-year), 1206 cms (2-year), and 1583 cms (5-year) in the Brazos River, and 345 cms (1-year), 453 cms (2-year), and 852 cms (5-year) in the Navasota River (Gooch et al. 2012). I analyzed a continuous time series of flows including unregulated (pre-impact) and regulated (post impact) time periods and noted the timing of impoundment construction along each river modeled. Statistical relationships were developed by fitting generalized additive models (GAMs) where flow pulse count (response variable) was fit as a function of time (explanatory variable) for each of the flood pulse category independently (i.e., 5-year, 2-year, and 1-year pulses). I elected to use a generalized model structure with a negative-binomial error distribution because the response variable was bound by zero, variance was greater than the mean, and used an additive model structure because the relationship between pulses and time was non-linear

(Wood, 2017). Specifically, I fit smoothing functions to time (years) that varied by my factor variable, gage identity (i.e., Brazos vs. Navasota River) to look at the interaction between this factor and time with the hypothesis that mainstem and tributary flood pulses differed temporally and were more common in the Navasota River. Models were fit and summary statistics and parameter estimates were obtained using the ‘gam’ function from the ‘mgvc’ package (Wood, 2017) in R.

Stationary Telemetry

I modelled detections of fish across SURs to test the hypothesis that movement into tributaries correlated with higher flows and warmer temperatures. Occurrence was modeled only on days when Alligator gar were detected by at least one of the SURs, and other calendar days were excluded from this analysis. Daily detection data were then transformed to binary such that detections on tributary SURs were assigned a “1” and detections among mainstream SURs were assigned a “0”. I used generalized linear mixed effects regression (GLMER) to model probability of fish occurrence in tributaries. This generalized model structure allowed me to use logistic regression to encompass the binomial nature of the response variable (i.e., binomial error distribution). Mixed effects allowed me to account for non-independence of repeated observations of the same fish by using fish ID as a random term in the model. I allowed the intercept and slope of the relationships to vary by the random terms specific to each model (Harrison et al. 2018). I included four explanatory variables in this analysis, including daily discharge (cms) measured on the Brazos River at the Highway 21 crossing near Bryan, TX (USGS gage ID 08108700), daily temperature (°C) of the mainstem measured using a TidBit deployed immediately downstream of the Navasota River confluence (Figure 2), fish total length

(cm), and fish sex (see McDonald et al. 2018). I considered all possible subsets and combinations of variables and used Akaike's Information Criterion corrected for small sample size (AICc) to compare candidate models, including interaction terms for discharge and temperature and considered models competing when $\Delta\text{AICc} < 2$. After model selection, I plotted the marginal effects of my top model. Prior to modelling, temperature, discharge, and fish total length (TL) were transformed using the 'BestNormalize' package in R to best approximate Gaussian distributions (Peterson, 2021). Parameter estimates were assessed using transformed predictor variables and plotted using back-transformed values for interpretability. I assessed model fit using adjusted McFaddens pseudo- R^2 values for logistic regression. According to McFadden (1977), the scale of these pseudo- R^2 values is considerably lower than R^2 values using ordinary least squares regression, where pseudo- R^2 values ranging from 0.2 to 0.4 are considered excellent fit. I fit GLMER models using the 'glmer' function from the 'lme4' package (Bates et al. 2015) and developed and assessed candidate models using the 'dredge' function from the 'MuMIn' package (Barton, 2009) in R.

Mobile Telemetry:

I modelled detections of fish across mainstem and tributary relocations during mobile telemetry as an additional method for testing my hypothesis of tributary occurrence. For this analysis I used the same: (1) subsetting criteria, (2) set of predictor variables, (3) data transformation routine, (4) candidate model formation approach, and (5) metric to assess model fit as the stationary telemetry analysis. I classified the 'state' of each fish location on a given tracking event using GPS coordinates. This resulted in three mutually exclusive states, where each fish was located in either the mainstem, a tributary, or not detected (i.e., 'mainstem',

‘tributary’, or ‘not detected’ states) for each tracking event. I then used multinomial logistic regression (MLR) to model the relationship between fish state and the explanatory variables. Estimation of coefficients in MLR requires setting a reference factor and I elected to use the mainstem state as the reference condition. I used the results of the AICc selection procedure to identify the best-fit model among the candidate models and then used cross-validation and estimates of parameter significance to explore the best-fit model. Validation of the top model was conducted by splitting the original dataset into testing and training sets (i.e., 40% testing, 60% training) and used as input for a confusion matrix to determine the degree of misclassification of my top model. I calculated the statistical significance of parameter estimates for tributary and not detected states relative to the baseline mainstem state and then exponentiated coefficients to estimate relative risk (RR) for each parameter. These steps give the probability of Alligator gar being observed in each state where marginal effects plots from my top model were interpreted as with the GLMER results. I fit MLR models using the ‘multinom’ function from the ‘nnet’ package in R (Venables and Ripley, 2002). All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

RESULTS

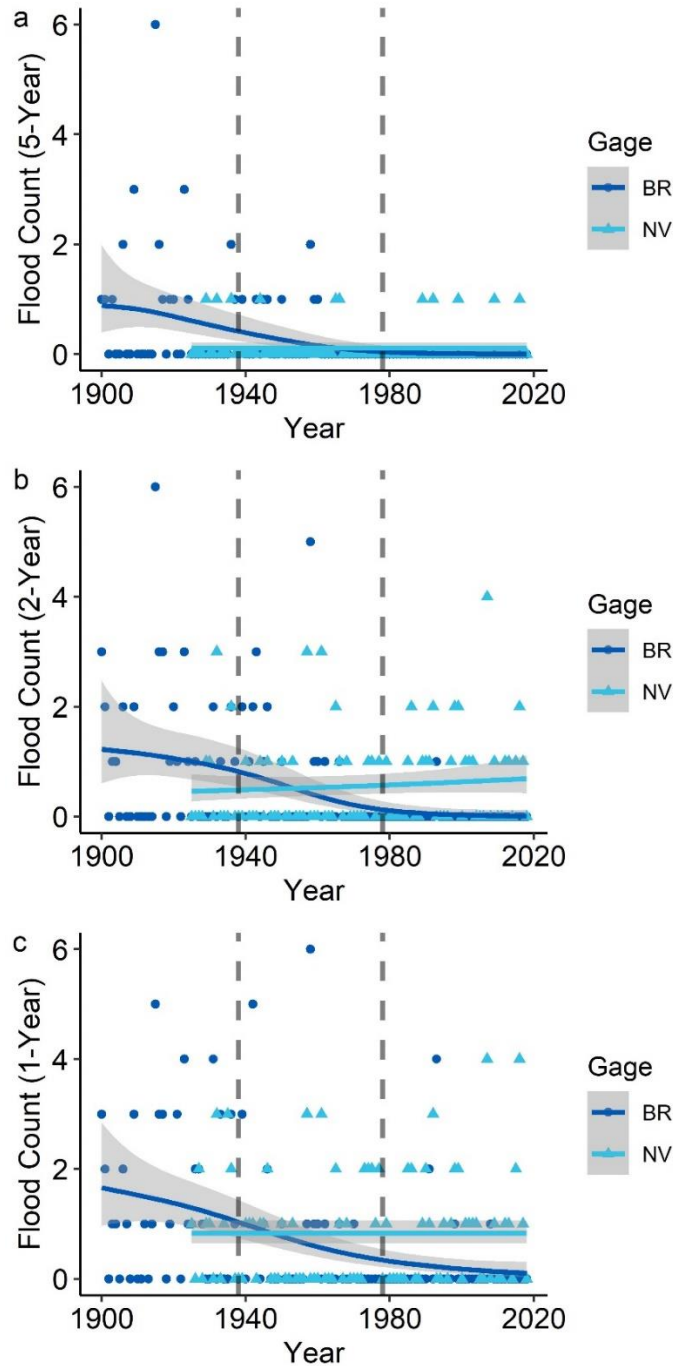
Flow Pulses

The Brazos River gage in Waco, TX had 119 years of flow data (1900-2018), whereas the Navasota River gage near Easterly, TX had 94 years (1925-2018). For the Brazos River there were significant reductions in pulse frequencies for the Brazos River at the 5-year ($\chi^2 = 10.96$, $p=0.04$), 2-year ($\chi^2=24.23$, $p<0.01$), and 1-year ($\chi^2=35.80$, $p<0.01$) pulse thresholds, but no significant changes in the Navasota River temporally (Table 3). Pulse frequencies at all thresholds declined the most in the mainstem Brazos River between 1940 and 1970 during the period of impoundment (Figure 3). The decline of 5-year pulses in the Brazos River resulted in flow pulse frequencies that matched the Navasota River after 1970 (Figure 3a), but pulse frequencies in the mainstem dropped below frequencies in the Navasota after 1970 for the 2-year (Figure 3b) and 1-year (Figure 3c) thresholds.

Table 3. Summary of parameter estimates and smoothing functions for generalize additive models (GAMs) fit to the relationship between time and frequency of 5-year, 2-year, and 1-year flood pulses in the Brazos and Navasota Rivers. Parameter estimates represent the coefficients for intercept, standard error (SE), test-statistic (Z), and the p-value for each term in the model. Smoothing functions represent the effective degrees of freedom (edf), reference degrees of freedom (df), test-statistic (Chi. Sq), and p-values for the smoothing functions derived from the gage locations.

Flood Frequency	Parameter Estimates					Smoothing Functions				
	Parameter	Estimate	SE	Z	p-value	Parameter	edf	df	Chi.sq	p-value
5-Year	Intercept	-4.00	1.87	-2.14	0.03	GageBrazos	3.92	4.78	10.96	0.04
	GageNavasota	1.86	1.9	0.98	0.33	GageNavasota	1.00	1.00	0.01	0.92
2-Year	Intercept	-1.69	0.34	-5.00	<0.01	GageBrazos	2.25	2.84	24.23	<0.01
	GageNavasota	1.03	0.38	2.75	<0.01	GageNavasota	1.00	1.00	2.255	0.13
1-Year	Intercept	-0.72	0.18	-4.00	<0.01	GageBrazos	3.09	3.86	35.80	<0.01
	GageNavasota	0.51	0.23	2.26	0.02	GageNavasota	1.06	1.12	0.39	0.54

Figure 3. Generalized additive model (GAM) fits from an analysis of mainstem versus tributary high pulse frequencies for the: (a) 5-year; (b) 2-year; and (c) 1-year recurrence intervals. Dark blue lines represent the smoothing function for the Brazos River models (dark blue circles) and light blue lines represent the smoothing function for the Navasota River model (light blue triangles) across time (years) for the flood count at each recurrence interval. Light grey shading are the 95% confidence intervals. Dashed lines represent the period of reservoir construction (1940-1970) for the rivers I modeled.



Telemetry Summary

Forty-five Alligator gar (118–238 cm TL) were tagged during this study. Of these fish, two individuals were not tracked due to a suspected tag loss and confirmed death. The remaining 43 individuals were monitored between one and 15 months (\bar{x} =7.5 months, sd = 4.6). All but one SUR (i.e., upstream-most SUR on the Navasota River; Figure 2) recorded detections resulting in 132,546 stationary receiver detections. The number of detections varied by individual (range = 5–38,822, \bar{x} =3,682, sd =8,557 detections). Thirty-six of the 43 individuals were detected on stationary receivers. After filtering for duration, 24 of the 36 individuals were tracked until the end of the study period. Of these 24, I analyzed the 14 individuals that made transitions which comprised of 80% of the original dataset while the remaining 10 individuals were only detected in tributaries. For mobile telemetry, I was able to relocate all 43 fish at least once. This resulted in a total of 259 relocations, which varied across individuals (range =1-12 relocations, \bar{x} = 6, sd =3.12). After filtering the data for duration, 29 of the 43 individuals were monitored until the end of the study period. Of these 29, I analyzed the 18 individuals that made transitions which comprised of 54% of the original dataset. Ten of the 11 remaining individuals were only found in tributaries while only one individual was detected exclusively in the mainstem. It should be noted that my filtering process removed some transitioning individuals from both datasets, however, these individuals had much more limited coverage of days compared to the other transitioning individuals and therefore were considered unreliable to make inferences on movement behavior.

Stationary Telemetry

I assessed 20 candidate GLMER models to test my hypothesis of tributary occurrence. The top model consisted of a two-way interaction term for temperature and discharge. Support

for this model was strong as it contained the lowest AICc value, the highest relative likelihood, had a high adjusted psuedo- R^2 of 28%, and there were no competing models (Table 4). Within this model, the discharge term was statistically significant ($Z=5.40$, $p<0.01$), but the main effect of temperature and the interaction term for discharge and temperature were not (Table 5). The marginal effect plot of discharge showed an increase in probability of Alligator gar occurrence in tributary streams as discharge increased (Figure 4a). The probability of tributary occurrence was above 90% at one standard deviation above mean discharge values (i.e., 368 cms). There was strong agreement among individual fish observations at the random effect level, except for one individual that was predicted to be present in tributaries regardless of discharge (Figure 4b). For temperature, the marginal effects plot exceeded a 50% probability of Alligator gar occurrence in tributaries at mean temperatures (i.e., 25 °C, Figure 4c), but term was not statistically significant because several individuals showed an opposing trend of declining probability of occurrence in tributaries compared with other fish included in the model (Figure 4d).

Table 4. Akaike information criterion for small sample size (AICc) ranking the top five GLMER models predicting tributary probability (TP) for the stationary telemetry dataset (top-panel) and top five MLR models for predicting state probability (SP) for the mobile telemetry dataset (bottom-panel). Candidate model structure include predictions as a function of discharge (D), water temperature (T), fish total length (TL), estimated fish sex (S), and various subsets of those parameters with additive (+) or interactive (*) terms. The number of parameters (k), AICc score, Δ AICc (i.e., difference in AICc values from model with lowest AICc score), relative likelihood (ω), and McFaddens R^2 demonstrates model fit but not on the same scale as the traditional coefficient of determination.

Dataset	Model Structure	k	AICc	Δ AICc	ω	Adjusted Psuedo- R^2
Stationary	TP(D*T)	4	945.8	0	0.59	0.28
	TP(D+S+T)	4	948.6	2.8	0.14	0.28
	TP(D*T+S)	5	949.7	3.8	0.09	0.29
	TP(D+T)	3	949.7	3.9	0.09	0.27
	TP(D+T+TL)	4	950.6	4.8	0.05	0.28
Mobile	SP(D*T+TL)	5	264.1	0	0.73	0.19
	SP(D*T+S+TL)	6	267.4	3.3	0.14	0.19
	SP(D*T)	4	267.9	3.9	0.11	0.14
	SP(D*T+S)	5	271.4	7.3	0.02	0.12
	SP(D+T+TL)	4	273.9	9.8	<0.01	0.14

Table 5. Summary of parameter estimates from the top candidate generalized linear mixed effects regression (GLMER) model fit to the stationary telemetry dataset. The model has two states, including mainstem (0) and tributary (1), and the parameters present the probability of tributary occurrence. Parameters include the intercept, main effect of discharge, water temperature, and the interaction of discharge and water temperature. For each parameter, I report the estimate, standard error (SE), test-statistic (Z), and the p-value.

Response State	Parameter	Estimate	SE	Z	p-value
	Intercept	-0.25	0.42	-0.60	0.55
Tributary	Discharge	1.86	0.34	5.40	<0.01
	Temperature	0.14	0.33	0.42	0.68
	Discharge:Temperature	0.56	0.34	1.63	0.10

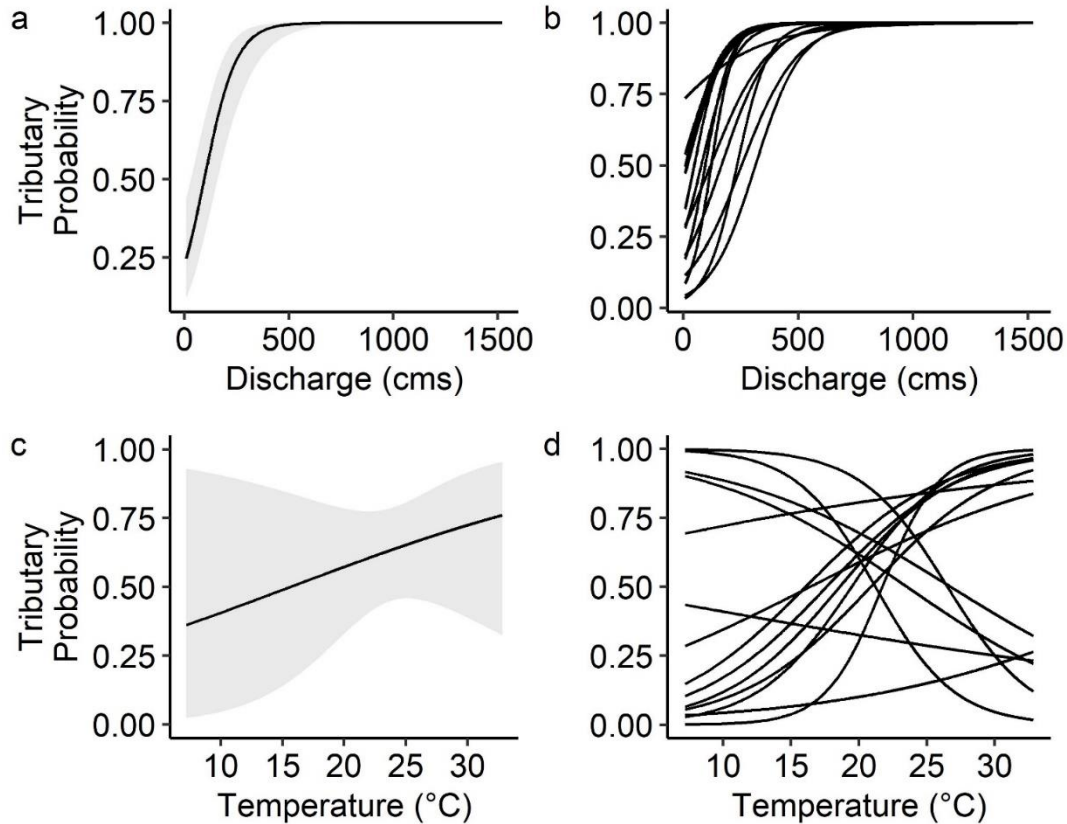


Figure 4. Marginal responses from the top GLMER model out of my candidate models in the stationary telemetry dataset including: (a) the population-level response to mainstem discharge (cms); (b) the random individual-level response to mainstem discharge (cms); (c) the population-level response to temperature (°C) and; (d) the random-individual response to temperature (°C). Dark lines are the fitted response for each parameter at the population (single line) and individual (line for each fish modeled) levels. Shaded grey regions are the 95% confidence intervals for the population-level models.

Mobile Telemetry

Using the same candidate models for mobile telemetry, the top model consisted of a two-way interaction term for temperature and discharge, along with the main effect of fish TL. This model also had the lowest AICc value, the highest relative likelihood, had a high adjusted pseudo- R^2 of 19%, and had no competing models (Table 4). Partitioning of the data and subsequent cross-validation revealed that the model had a misclassification rate of 39%.

Parameters in the not-detected state were significant for discharge ($Z=3.61$, $p<0.01$) and temperature ($Z= 2.02$, $p=0.04$) estimates (Table 6). The parameter estimate for discharge was

Table 6. Summary of parameter estimates from the top candidate multinomial logistic regression (MLR) model fit to the mobile telemetry dataset. The model has three states including mainstem (the baseline), tributary, and not detected, and parameters shown here represent the probability of not being detected or being detected in tributaries. Parameters include the intercept, main effects of discharge water temperature, fish total length, and the interaction effect of discharge and water temperature. For each parameter, I report the estimate, standard error (SE), test-statistic (Z), relative risk (RR), and the p-value.

Response State	Parameter	Estimate	SE	Z	RR	p-value
Not Detected	Intercept	-1.74	0.35	-4.93	0.17	<0.01
	Discharge	1.40	0.39	3.61	4.07	<0.01
	Temperature	0.61	0.30	2.02	1.84	0.04
	TL	0.36	0.30	1.20	1.43	0.23
	Discharge:Temperature	-0.63	0.66	-0.95	0.53	0.34
Tributary	Intercept	-0.93	0.26	-3.57	0.39	<0.01
	Discharge	0.95	0.26	3.73	2.59	<0.01
	Temperature	0.44	0.25	1.79	1.55	0.07
	TL	0.62	0.22	2.77	1.86	<0.01
	Discharge:Temperature	1.32	0.42	3.14	3.75	<0.01

positive, revealing that undetected occurrence was more likely as discharge increased. For the tributary state, the main effects of fish TL ($Z=2.77$, $p<0.01$), discharge ($Z=3.75$, $p<0.01$) and the interaction term discharge and temperature ($Z=3.14$, $p<0.01$) were significant (Table 6). As temperature values increased, there was an decrease in the probability of fish being in the mainstem state and concordant increase in probability of being undetected or in a tributary (Figure 5a) although this effect was not significant. For fish TL, there were similar state occurrence patterns with a significant increase in fish TL with increases in tributary occurrence and decline in the mainstem for the largest fish tagged (fish $TL \geq 200\text{cm}$; Figure 5b). For the

interaction parameter, the marginal effects plot for discharge when temperature was held at one SD below mean values, (i.e., 16 °C) showed a reversal of high probabilities between mainstem and undetected states with increases in discharge while simultaneously tributary probability decreased under these “cool” conditions (Figure 5c). At mean temperatures (i.e., 23°C), the probability of mainstem and not-detected states followed a similar pattern, however tributary state probability increased and approached a 50% probability at values over 400 cms (Figure 5d). At one SD above the mean temperatures (i.e., 29° C), fish transitioned from mainstem to tributary states along a gradient of discharge magnitudes. Under these “warm” conditions there was a reversal in states such that fish were predominantly in the mainstem at lower discharges, but at one SD above mean discharge (i.e., 468 cms) highly likely to be in tributaries (i.e., > 75 % probability).

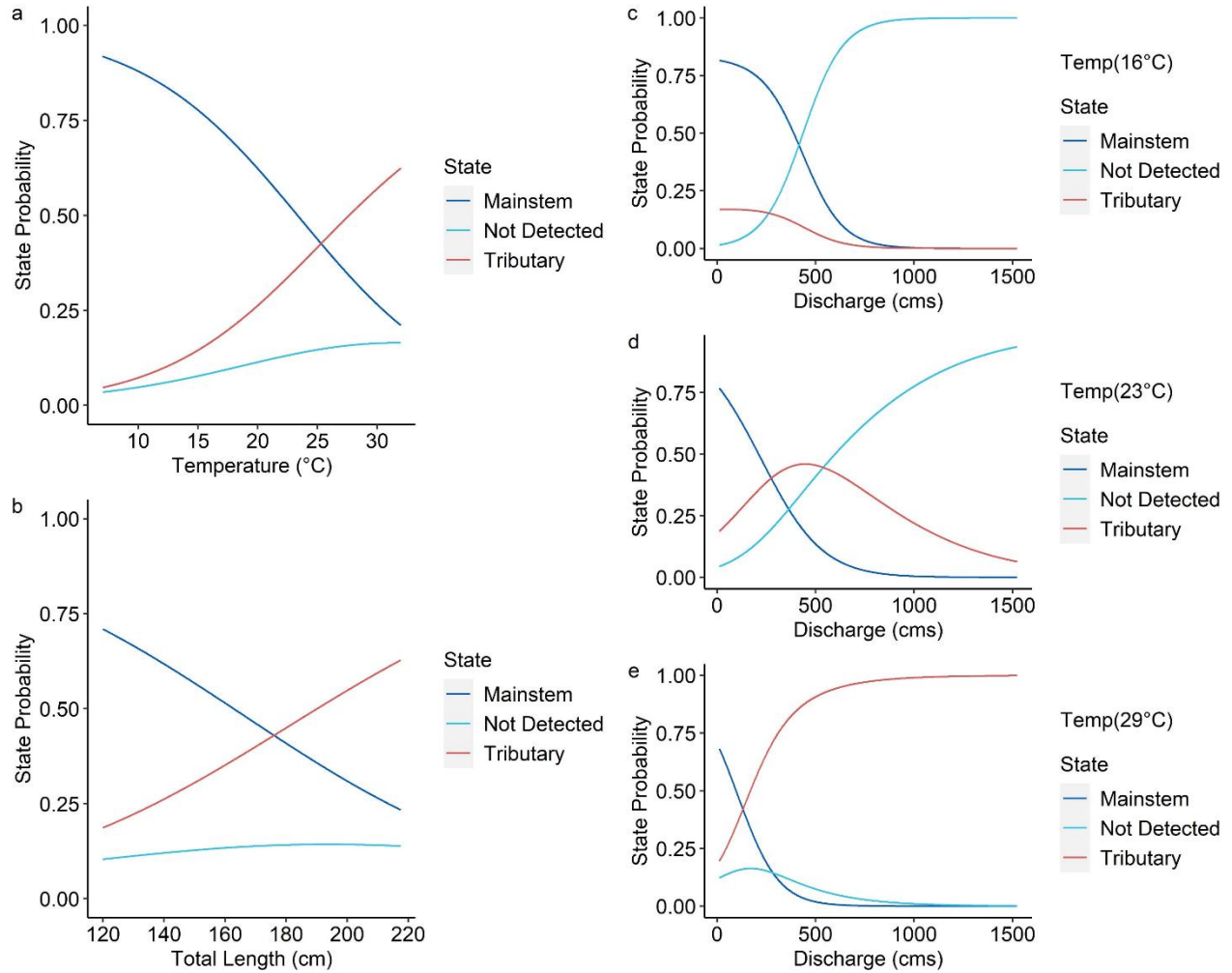


Figure 5. Marginal responses from the top MLR model out of my candidate models in the mobile telemetry dataset including: (a) temperature (°C); (b) fish total length (cm); and (c-e) the interaction between temperature and discharge for predicting probability of occurrence in the three mutually exclusive states, mainstem (dark blue line), not detected (light blue line), and tributary (red line). For (c-e) the effect of discharge is shown held at: (c) “cool” conditions 1 SD below mean temperature (16°C); (d) “average” conditions at the mean temperature (23°C); and (e) “warm” conditions at 1 SD above mean temperature (29°C).

SUMMARY

This study provides insight into the use of tributary habitats by a migratory fish inhabiting a regulated river. The Brazos River provides a microcosm for the global changes occurring in regulated rivers (Lehner et al. 2011), generally characterized by the removal of large flood pulses that historically provided mainstem river-floodplain connectivity. I found a clear reduction in the 5-year, 2-year, and 1-year flood frequencies along the Brazos River, but no detectable changes occurring in the Navasota River tributary. These changes collectively created a reversal of pulse conditions such that although the mainstem historically had a greater frequency of out-of-bank pulses, under current regulated conditions, the tributary now has greater pulse frequencies. Similar patterns in regulated rivers have led to the realization that tributary streams are essential in buffering the effects of riverscape alteration on large river biota in general, and fishes in particular (Pracheil et al. 2009; Pracheil et al. 2013).

The movements of Alligator gar into and out of tributary streams, as quantified here, suggests transitions across the mainstem-tributary ecotone are predictable based on combined conditions of discharge magnitude and water temperature. Previous studies have suggested that inundation of floodplain habitat characterized by high flow pulses during periods of warm water temperatures are critical for successful recruitment of Alligator gar (Robertson et al. 2018; Smith et al. 2020b). However, the inundation of mainstem floodplains requires higher pulse magnitudes compared to tributary streams, and these magnitudes might not be possible in some mainstem rivers under regulated and non-stationary hydrologic conditions (Poff, 2018). My work provides empirical evidence that high flow pulses elicit a movement response among Alligator gar, particularly when pulses occur during warmer water temperatures. These results provide

quantitative guidance on management of flows to benefit populations of Alligator gar in the Brazos River (Gooch et al. 2012), but more broadly, I elucidate ecological patterns that might be critical for the conservation of other migratory fishes inhabiting regulated rivers.

The Brazos River has received increasing attention regarding management of flows to sustain ecological conditions and functions since the creation of the Texas Instream Flows Program (TIFP) in 2007 (Opdyke et al. 2014). Previous research established ecological links between seasonal flow pulses and occurrence or recruitment of small-bodied, opportunistic strategist fishes in the Brazos River such as Shoal chub, *Macrhybopsis hyostoma*, Plains minnow *Hybognathus placitus*, Smalleye shiner *Notropis buccula*, and Sharpnose shiner *N. oxythrynychus* (Rodger et al., 2016; Nguyen et al. 2021). My work broadens the understanding of flow-ecology relationships in the Brazos River by including a periodic life history strategist. I found that movement of Alligator gar into tributary habitats during the spawning season was strongest when discharge exceeded 300 cms, particularly when temperatures were near 29 °C. This provides critical information pertaining to the ecological benefits of larger, rarer flow events less likely to occur within the life span of the average opportunistic species (Stewart-Koster et al. 2014). These large and rare flood events present unique challenges within contemporary riverscapes because their magnitudes might exceed the capacity of controlling structures or availability of upstream water currently or in the future (Poff, 2018). However, Konrad et al. (2011) suggested that reservoir releases might be timed with natural high flow periods to achieve larger magnitude releases in regulated rivers. Given the rise of large-scale flow experiments, my study provides information that might be used to generate new hypotheses to be tested during such experiments (Olden et al. 2014). These hypotheses might focus on: 1) identification of minimal discharge thresholds to elicit movement into tributaries, 2) use of temperature-sensing transmitters to refine

the role of temperature in stimulating tributary migration, or 3) distribution of stationary receivers in flood-prone areas to refine exact spawning locations or pathways into floodplains. Koster et al. (2021) suggested movement of migratory fishes might be used to inform flow regime regulation in Australian rivers, and my work suggests the same for Alligator gar in North America. The broad spatial overlap between regulated rivers and migratory fish distribution suggests other opportunities for linkages between flow variability and ecological attributes that could be used to guide management of regulated flow regimes.

The coupled effects of habitat fragmentation and flow alteration broadly affect stream fish assemblages, but these effects might be offset by tributary connections. Within freshwater ecosystems, the importance of suitable river temperature and discharge conditions for fish migrations is well documented (Albanese et al. 2000; Taylor and Cook 2012). The migratory behavior fishes is often considered an adaptation to the dynamism in the environmental conditions under the natural flow regime (NFR) within lotic systems (Poff et al. 1997). I found that the historical magnitude of floods in the lower Brazos River mainstem was much higher than under current conditions, and this pattern is widely reported among regulated rivers (Magillan et al. 2003). Previous studies have documented the consequences of fragmentation and flow alteration among fishes with different migratory adaptations (Haro et al. 2000; Pelicice et al. 2015). However, persistence of migratory fishes within regulated rivers may be explained by their plasticity and use of alternative migratory routes, such as tributaries, in the presence of impoundments on mainstem rivers (Antonio et al. 2007). Historically, flooding likely occurred in mainstem rivers and tributaries alike, leading to an adaptation to multiple migratory reproductive routes among migratory fishes (Koster et al. 2021). However, given many large mainstem rivers are fragmented today, selection towards migratory routes in tributaries that are more prone to

flooding would be more advantageous for migratory fishes than use of floodplains constrained to more limited mainstem inundation (Dunn et al. 2018). Tributaries can also provide other ecosystem services, such as supplying organic matter, nutrients, and sediment that can be limiting in fragmented mainstem rivers with disrupted energy flows (Sabo et al. 2018). These ecosystem services are known to positively influence the growth and survival of migratory fishes across life history stages (Ebersole et al. 2006; Spuregon et al. 2006). Therefore, tributaries that maintain certain aspects of the NFR provide a fitness advantage for migratory fishes that use these habitats for recruitment and reproduction (Pracheil et al. 2009; Pracheil et al. 2013). My work extends the known benefits of tributaries to migratory fishes such as Alligator gar by revealing common use of these habitats during the spawning season in a highly regulated river.

Although this study has elucidated predictors of tributary use for Alligator gar, there are caveats and limitations that need to be acknowledged. My study investigates the tributary ecology of one migratory species in one system among many migratory species of fishes distributed worldwide. However, given the degree of river regulation is distributed globally, it's possible that other species are facing similar ecological challenges (e.g., Koster et al. 2021). Further research investigating the tributary use of other migratory species fishes inhabiting different regulated rivers will address the generality of this paradigm. Another limitation of my study is that I was unable to relocate every individual fish during each tracking occasion. This is likely due to two factors, signal attenuation and the exponential increase in search area. Signal attenuation caused by increased water depth is well known for radio transmitters, and therefore I relied on ultrasonic transmitters or CART tags in my study design. However, interference from high velocities during higher flows cannot be ruled out as contributing to my inability to find some individuals (Cooke et al. 2013). This might explain why the probability of fish assigned to

mainstem state in my top MLR model suddenly transitioned to the undetected state as discharge increased during cooler seasons (i.e., 16 °C). As modelled water temperature increased to 29 °C, increased discharge correlated with a greater number of undetected fish. I hypothesize this was related to fish moving into expansive floodplains where logistics prevented comprehensive searches and shallower water likely reduced ranges of ultrasonic transmitters (Kluender et al. 2017). Further, there were differences in fish retained for my analyses across stationary and mobile telemetry techniques, due to differences in my ability to quantify tributary use between both methods. I observed less mainstem-tributary transitioning fish using stationary telemetry because the fixed locations of these receivers could not account for the network of additional tributary streams within the study area. However, when flows allowed, manual telemetry allowed me to determine additional tributaries Alligator gar were using during high flows that my stationary grid was unable to detect. Therefore, I suspect that my analyses represent a conservative estimate of transitions and that a greater number of transitioning individuals likely occurred. Both stationary and mobile telemetry methods have advantageous and disadvantages (Cook et al. 2013) and my analysis of both techniques, as others have done (Acolas et al. 2004; Buckmeier et al. 2013), gave consistent inference regarding tributary occurrence of Alligator gar.

Conclusion

Large rivers are regulated on a global scale (Grill et al. 2019) and declines among riverine fishes are commonly attributed to this alteration (Haro et al. 2000; Pelicie et al. 2015). Migratory fishes in particular are sensitive to the effects of flow alteration and fragmented lateral connectivity (Pracheil et al. 2009). Despite this sensitivity, migratory fishes persist in regulated riverscapes, perhaps because tributary inflows and access corridors to floodplain habitats provide buffering capacity for populations of fishes that are sensitive to flow alterations. I used the

Brazos River of Texas and its population of Alligator gar as a case study for the emerging paradigm that tributaries provide avenues to floodplains. I showed that 1) flood pulses in the mainstem are infrequent in contemporary flows and that pulses within at least one tributary stream now provide the dominant source of out-of-bank pulses, 2) Alligator gar transition from mainstem to tributary habitats, and 3) these transitions are driven primarily by discharge and water temperature such that high flow pulses during warm seasons are most likely to trigger movement. These data can be used to develop more optimal management of Alligator gar, further refine environmental flow standards, and act as a baseline for future studies investigating the tributary use of migratory fishes inhabiting regulated rivers elsewhere.

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