Reproductive Ecology of Alligator Gar: Identification of Environmental Drivers of Recruitment Success

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Abstract: Alligator gar (*Atractosteus spatula*) exhibit many characteristics of a periodic life-history strategy, including extended longevity, late maturity, high fecundity, and variable recruitment success. Observations of alligator gar spawning events indicate that recruitment in inland waters may be linked to spring and summer flood pulses and the availability of floodplain spawning habitats. However, because data have mostly come from observation and not formal experimentation, it is unknown whether these data represent true requirements or if they simply reflect conditions that were easily observed. Therefore, we reviewed existing data regarding alligator gar spawning and early development to draft habitat suitability criteria related to recruitment success and then tested these criteria against historic annual recruitment variability (i.e., year-class strength) in the Trinity River and Choke Canyon Reservoir, Texas. Habitat suitability criteria were proposed for water temperature (20 to 30 °C, coinciding with spring and summer), hydrology (inundation of floodplain habitats to a depth of at least 1 m for a minimum of 5 days), and spawning habitat characteristics (open canopy with herbaceous or small woody vegetation within 0.5 m of the water surface where there is little or no flow). In both the Trinity River and Choke Canyon Reservoir, we found that historic annual recruitment of alligator gar generally corresponded closely with the availability of suitable hydrologic conditions during spring and summer. Alligator gar recruitment was highly variable in both systems with above expected recruitment only occurring in about 30% of the years. The strongest two year classes comprised about half of the population in each system and were produced in years with large, long duration flood pulses during June and July. While additional research is needed to refine the proposed habitat suitability criteria, our study verifies a link between alligator gar recruitment success and the availability of floodplain spawning habitats during the spring and summer in inland waters.

Key words: Atractosteus spatula, year-class strength, spawning habitat suitability, age structure

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Alligator gar (*Atractosteus spatula*) exhibit many characteristics of a periodic life-history strategy as defined by Winemiller and Rose (1992). This species' longevity is >50 years, females generally mature between 5 and 10 years with a fecundity of >4000 eggs kg^{-1} body weight, and populations can have highly variable recruitment (Ferrara 2001, Buckmeier et al. 2012, Buckmeier et al. 2015). As a result of these characteristics, stock densities can fluctuate greatly over time, driven by environmental variables that regulate interannual recruitment variability (Winemiller 2005). Periodic life-history strategists can also experience significant population declines resulting from anthropogenic changes to the environment and overfishing (Parent and Schrimi 1995, Boreman 1997, Winemiller 2005). The listing of alligator gar as "vulnerable" by the American Fisheries Society (AFS; Jelks et al. 2008) provides impetus to closely monitor and carefully manage remaining populations. In Texas and coastal portions of Louisiana, alligator gar populations appear to have sufficient recruitment to support existing fisheries (Ferrara 2001, DiBenedetto 2009, Binion et al. 2014, Felterman 2015, Buckmeier et al. 2015); however, increasing demands on water supplies and fishing pressure pose future threats. Reduced floodplain connectivity is suspected to limit recruitment and subsequently has caused significant population declines in Lake Pontchartrain, Louisiana (O'Connell et al. 2007), and the Mobile River, Alabama (Pringle et al. 2000). Consequently, data regarding alligator gar recruitment dynamics, including knowledge of environmental drivers that regulate recruitment success, are needed to inform future decisions regarding harvest regulations and recommendations for water management.

The reproductive ecology and early-life history of alligator gar are poorly understood because these topics have received little formal study. What is known is largely the result of observations of spawning events in the wild and from culture of the species in hatcheries (e.g., Aguilera et al. 2002, Mendoza et al. 2002). Therefore, it is unknown whether these observations represent true requirements or if they simply reflect conditions that were easily detected. Based on these data, alligator gar recruitment success in inland waters appears to be linked to the availability of floodplain spawning habitats during spring and summer flood pulses (Inebnit 2009, Allen et al. 2014, Kimmel et al. 2014, Kluender et al. 2016); however, the exact nature of this relationship has not been quantified. To determine if these observations reflect actual requirements, we first reviewed existing data regarding alligator gar spawning and early development to identify common elements. We then developed habitat suitability criteria for common variables likely related to recruitment success and quantified their historic availability in the Trinity River and Choke Canyon Reservoir in Texas. Finally, we compared historic availability data with past recruitment variability (i.e., year-class strength) to validate these environmental variables as drivers of recruitment success for inland populations of alligator gar.

Methods

Review of Alligator Gar Spawning and Early Development

Using existing data from observations of alligator gar spawning events and published data from culture of the species in hatcheries, we identified and summarized common environmental variables that appeared to be related to recruitment success. Data were gathered from published literature, agency reports, and personal communications with members of the Alligator Gar Technical Committee of the Southern Division of the AFS (i.e., expert observations). Accounts of alligator gar spawning were predominantly acquired through personal communications and from agency reports and student theses (Table 1). In contrast, the majority of data describing early development of eggs and larvae were found in published papers describing culture techniques for the species (Table 2). Sum-

Table 1. Summary information associated with anecdotal observations of alligator gar spawning events.

Location	Date	Water temperature	Hydrologic characteristics	Spawning habitat characteristics	Source
Fourche LaFave River, Arkansas	mid May–mid June 2007, 2008	25–30 °C	during ascending limb or peak of flood pulse, Fourche LaFave and back flooded from Arkansas River	inundated floodplain of tributaries (West Fork Mill and Lawson Creeks), mean depth = 0.5 m, spawning substrate = herbaceous vegetation, woody shrubs, and floating woody debris, eggs were in upper half of water column	Inebnit 2009
Fourche LaFave River, Arkansas	late May 2010	not available	peak of flood pulse, Fourche LaFave back flooded from Arkansas River	inundated floodplain of tributary (West Fork Mill Creek)	Kluender et al. 2016
Heart of the Hills Fisheries Science Center, Mountain Home, Texas	1–2 June 2010	28–29 °C	rising water level in research pond	1-ha research pond, depth ≤0.5 m, spawning substrate = flooded shoreline vegetation, no canopy	Sakaris et al. 2014, TPWD unpublished data
Lake Texoma, Oklahoma	late May (estimated)	not available	not available	collected 103- and 117-mm alligator gar on 15 July 1965 and 93-mm fish on 22 July 1965	May and Echelle 1968
Lake Texoma, Oklahoma	11 May 2008	not available	flood that inundated wetland area	flooded wetland, mean depth = 0.3 m, spawning substrate = Spikerush (*Eleocharis* spp.), no canopy	Brinkman 2008
Mississippi River backwater	not available	not available	not available	mean depth ≤0.6 m, fish spawned over rough cocklebur (*Xanthium strumarium*) and primrose (*Ludwigia* spp.)	Richard Campbell, USFWS, personal communication
Mississippi River, Mississippi	25 April 2013	not available	not available	inundated floodplain adjacent to shrub and forested area, spawning substrate = submerged woody thin vegetation, no canopy	Allen et al. 2014
Mississippi River, Mississippi	22 April 2014	23 °C	during flood	flooded ditch about 19 km from main river, depth ≤1.2 m, spawning substrate = herbaceous vegetation and woody shrubs, no canopy	Kimmel et al. 2014
Pointe Aux Chenes Wildlife Management Area, Louisiana	25 April 2003	not available	salinity = 7 ppt	mean depth ≤0.6 m, fish spawned over saltmeadow cordgrass (*Spartina patens*)	Q. Fontenot, Nicholls State University, personal communication
Robert S. Kerr Lock and Dam (below), Oklahoma	16 June 1993	not available	not available	larvae 15- to 21-mm total length in large, shallow floodwater area	Pigg and Gibbs 1996
Tampico, Tamaulipas, Mexico	31 May 1998	30 °C	not available	20 x 30 m hatchery pond, mean depth = 0.95 m, spawning substrate = ironwood (*Casaurina* spp.), dissolved oxygen = 2.9 mg L^{-1}	Aguilera et al. 2002
Trinity River, Texas	29 April 2015	20 °C	cresting flood pulse, ~1 m above minor flood stage	ditch associated with wetland impoundments, mean depth = 0.6 m, spawning substrate = flooded terrestrial vegetation, no canopy	M. Symmank, TPWD, personal communication

Table 2. Sources and summary information associated with early development of eggs and larval alligator gar. Measurements are reported for total length in terms of days after hatch (DAH) or as mean size by a given month.

Incubation period	Exogenous feeding/yolk-sac absorption	Growth	Miscellaneous	Source
48 h at 31.0 C	mostly absorbed 5 DAH, began exogenous feeding, suctorial disk disappeared	at hatch, mean = 6.6–8.8 mm; 14.2–19.2 mm at 5 DAH, 23–32 mm at 10–12 DAH; 34.8–50 mm at 15 DAH	unfed larvae stopped growing at 8 DAH; averaged 19.6 mm, all died by 15 DAH	Aguilera et al. 2002
50 h at 28 C	at 5 DAH, yolk sac mostly absorbed, began exogenous feeding, detached from vegetation; yolk sac completely absorbed at 8 DAH	mean of 7.2 m at hatch, 18 mm at 5 DAH, 23 mm at 10 DAH, nearly 50 mm at 15 DAH; growth rate 1.5 mm day^{-1} to 10 DAH, 5 mm day^{-1} after	digestive track developed by 5 DAH	Mendoza et al. 2002
not applicable	not applicable	mean = 15.4 mm at 5 DAH, 18.9–23.6 mm at 10 DAH, 19.7–34.1 mm at 15 DAH, 30.5–46.1 mm at 20 DAH	starved larvae died by 15 DAH	Mendoza et al. 2008
48–72 h at 27.5–30.0 C	assumed 5–7 DAH	mean of 8.6–11.0 mm at hatch (2–3 days post spawn), mean of 446–492 mm by end of summer	at hatch, yolk-sac larvae would swim to adjacent resting site when disturbed	Inebnit 2009
about 72 h at 28 C	exogenous feeding began 3 DAH, yolk sac mostly absorbed	11–17 mm at 3 DAH, 18–45 mm at 13 DAH, 95–129 mm at 30 DAH, 356–452 mm at 104 DAH	not applicable	Sakaris et al. 2014, TPWD unpublished data

marized data associated with spawning and early development included time of year, corresponding water temperature, water level and flood stage, flood duration, physical habitat characteristics at spawning sites (e.g., depth, vegetation type, flow), egg incubation period, time to important developmental stages (e.g., initiation of exogenous feeding), and growth rates.

Alligator gar spawning was typically observed during flood pulses occurring from April through June when water temperatures at spawning sites were 20–30 °C (Table 1). When hydrologic conditions were reported, spawning always coincided with the ascending limb or peak of a flood pulse in rivers or when water levels in reservoirs increased sufficiently to flood terrestrial vegetation (Table 1). In addition, Kluender et al. (2016) documented radio-tagged alligator gar moving from staging areas in the main channel to spawning habitats in upstream reaches of tributaries and spawning during a flood pulse. These observations suggest alligator gar recruitment may be limited in years without flooding. While there is limited information regarding the magnitude of flooding required for successful alligator gar spawning, observed spawning events were linked to water-level increases that inundated substantial floodplain habitat. Furthermore, the duration of these flood pulses had to be sufficient for eggs to hatch and larvae to be capable of responding to receding flood waters (3–5 days; Table 2). Inebnit (2009) and Kluender (2011) documented egg desiccation when flood waters receded before hatching occurred.

Most sources generally agreed that alligator gar spawned in these flooded areas over terrestrial or wetland vegetation (Table 1). Use of herbaceous vegetation was most common, but small woody shrubs and woody debris were also used. Documented spawning sites were located in floodplain habitats in open canopy areas where waters were backed up with little or no flow. These sites were typically less than 1 m deep and eggs were deposited on vegetation within 0.5 m of the water surface. In hatcheries, alligator gar were successfully spawned when these conditions were replicated in ponds (Aguilera et al. 2002, Mendoza et al. 2002, Texas Parks and Wildlife Department [TPWD], unpublished data).

Alligator gar eggs required 48–72 h of incubation to hatch at water temperatures between 27–31 °C (Table 2). At hatching, yolk-sac larvae were about 7–9 mm total length (TL) and adhered to vegetation using an adhesive suctorial disc (Aguilera et al. 2002, Mendoza et al. 2002). Yolk-sac larvae are mobile, but typically only release from vegetation to move between resting locations (Inebnit 2009). At 3–5 days after hatch (DAH), alligator gar larvae were 11–19 mm TL, had mostly absorbed their yolk sacs, and began exogenous feeding (Table 2). At this stage, the suctorial disc disappears and the digestive tract is completely formed (Mendoza et al. 2002).

Larval alligator gar grow very quickly and have been collected from a variety of habitats including inundated floodplains, backwaters, tributaries, and along the margins of main channel rivers (Table 2). Free-swimming larvae (>15 mm TL) often lie nearly motionless near the water surface in areas with little or no flow and can be found camouflaged among sticks, debris, roots, and vegetation (Inebnit 2009, TPWD, unpublished data). During early development, young can grow an average of 1.5 mm day^{-1} and attain 19–32 mm TL within 10 d of hatching. Growth rates can continue to increase and exceed 5.0 mm day^{-1} in older larvae; fish nearly 50 mm TL have been reported by 15 DAH (Aguilera et al. 2002, Mendoza et al. 2002).

Proposed Habitat Suitability Criteria and Assessment of Historic Availability

The many similarities among environmental data and conditions associated with alligator gar spawning events and early development of eggs and larvae suggest that these data may reflect actual spawning requirements. Using the range of values observed for these variables, we drafted habitat suitability criteria (USFWS 1981) for season and corresponding water temperature, hydrology, and spawning habitat characteristics. For each of these categories, we assigned a suitability value of 1 for conditions where successful spawning was observed and a value of 0 for conditions where there was no evidence of spawning. Because historic spawning habitat characteristics (e.g., vegetation type, flow, and canopy) could not be directly estimated in the Trinity River and Choke Canyon Reservoir, Texas, historic availability was quantified based solely on water temperature and hydrologic regime.

Relating Historic Availability of Suitable Conditions with Annual Recruitment

To verify that our proposed habitat suitability criteria reflect true requirements for alligator gar recruitment success, we associated characteristics of past environmental conditions with estimates of annual recruitment variability of two Texas populations. Relative year-class strength was assessed using adult age data collected from the Trinity River ($n=120$; Buckmeier et al. 2015) and Choke Canyon Reservoir ($n=99$; Binion et al. 2014). For both populations, sagittal otoliths were opportunistically collected from harvested alligator gar; samples were predominantly collected from anglers, bow fishing tournaments, taxidermists, and other research projects using 7.6- to 15.2-cm mesh gill nets. While sampling size biases were unknown, we believe that opportunistically-collected samples were adequate for categorizing year-class strength as above or below expected because both populations exhibited highly variable growth (Binion et al. 2014, Buckmeier et al. 2015). Variable growth reduces the effects of size bias because fish of a given size can represent many year classes (Schlechte et al. 2016). For example, a 150-cm alligator gar ranged from age 4 to 28 in the Trinity River (Buckmeier et al. 2015) and from age 5 to 15 in Choke Canyon Reservoir (Binion et al. 2014).

Year-class strength was calculated by comparing the number of fish observed in a given year with the number of fish that would be expected if recruitment and survival were constant across years. This approach is analogous to the use of residuals from a catch curve (Maceina 1997); however, we used an independent estimate of survival instead of calculating it by regressing catch against age (Ricker 1975). Years examined were limited to a 25-yr period (1986–2010) for both populations because older age estimates were less accurate (Buckmeier et al. 2012), and because low sample size limited our ability to identify anything other than very strong year classes among age groups >25 years. Expected values for each year class were calculated by iteratively adjusting the $n_1 =$ (number of fish expected for the most recent year class; i.e., 2010) until the following conditions were met:

$$1)\ n_{i+1} = n_i \times S$$

and

$$2)\ \Sigma\, n_i = N$$

where $S =$ an annual survival rate of 0.915 (Buckmeier et al. 2015) and $N =$ the total number of fish collected with ages corresponding to the 25-yr period (i.e., $n=98$ and 96 fish for Choke Canyon and the Trinity River, respectively). Recruitment in a given year was considered strong when the observed number of fish in that year was greater than expected and weak when the observed value was less than expected.

Proposed habitat suitability criteria were verified by comparing the historic availability of suitable water temperatures and hydrologic conditions with their corresponding recruitment estimate in the Trinity River and Choke Canyon Reservoir. If our criteria adequately reflected spawning requirements, then years with suitable conditions should also be characterized by strong alligator gar recruitment. To test this relation, we used a chi-square test of independence ($\alpha=0.05$) because our assessments of suitability and recruitment were limited to binary values (i.e., a year was suitable or unsuitable and recruitment was either above or below expected). We tested the null hypothesis that recruitment success was independent of the availability of suitable conditions based on our criteria for each system. Because sample sizes were relatively small in each system ($n=25$ years), we also tested this hypothesis on the pooled data set to increase statistical power.

Results

Proposed Habitat Suitability Criteria and Assessment of Historic Availability

Based on similarities among environmental data and conditions associated with alligator gar spawning events, a suitability value of 1 was assigned when water temperatures at spawning sites range from 20–30 °C during the spring and summer. Suitable hydrologic conditions were defined as water-level increases that inundate floodplain habitats to a depth of ≥1 m for a period ≥5 days. These definitions were based on observations that spawning sites were typically 0.5–1.0 m deep (Table 1) and the amount of time needed for eggs to hatch and larvae to become mobile enough to respond to receding waters (i.e., 2–3 DAH; Table 2). Commonalities in spawning habitat characteristics among the ob-

Table 3. Alligator gar year-class data collected from the Trinity River, Texas (1986–2010). Variables reported for each year class include the number of fish collected (Obs), the number expected (Exp) assuming constant recruitment and a constant annual survival rate of 91.5%, deviation from expected, and the relative contribution of a given year class (Obs/Exp). Hydrologic data for the period of 1 April–31 July include the number of days habitat suitability (HS) equaled 1 summed for 3 gages, number of gages (gages) with at least one minor flood, and number of floods (floods) that occurred. Data in bold reflect years when recruitment was greater than expected.

Year	Obs	Exp	Deviation	Obs/Exp	HS = 1 (d)	Gages	Floods	Hydrologic comments (*n* gages, duration)
1986	**2**	**1.09**	**0.91**	**1.84**	**11**	**1**	**1**	**June (1, 11 days)**
1987	**2**	**1.19**	**0.81**	**1.69**	**0**	**0**	**0**	
1988	0	1.30	−1.30	0	0	0	0	
1989	**10**	**1.42**	**8.58**	**7.06**	**70**	**3**	**2**	**May (3, 8–15 days), June (3, 7–15 days)**
1990	**6**	**1.55**	**4.45**	**3.87**	**91**	**3**	**2**	**early April (1, 7 days), May (3, 19–40 days)**
1991	**6**	**1.69**	**4.31**	**3.54**	**0**	**0**	**0**	
1992	1	1.85	−0.85	0.54	0	0	0	
1993	1	2.02	−1.02	0.49	0	0	0	
1994	**3**	**2.21**	**0.79**	**1.36**	**8**	**1**	**1**	**late May (1, 8 days)**
1995	0	2.41	−2.41	0	46	3	3	mid April (1, 6 days), early May (1, 7 days), May (3, 8–17) days) gages)
1996	1	2.64	−1.64	0.38	0	0	0	
1997	0	2.88	−2.88	0	32	2	2	April (2, 7–12 days), early May (2, 5–8 days)
1998	1	3.15	−2.15	0.32	0	0	0	
1999	0	3.45	−3.45	0	0	0	0	
2000	1	3.77	−2.77	0.27	0	0	0	
2001	0	4.11	−4.11	0	9	1	1	early April (1, 9 days)
2002	1	4.50	−3.50	0.22	13	1	1	mid April (1, 13 days)
2003	0	4.91	−4.91	0	0	0	0	
2004	2	5.37	−3.37	0.37	5	1	1	early May (1, 5 days)
2005	0	5.87	−5.87	0	0	0	0	
2006	5	6.42	−1.42	0.78	0	0	0	
2007	**43**	**7.01**	**35.99**	**6.13**	**61**	**3**	**3**	**April (1, 7 days), June (1, 10 days), June–July (3, 13–31 days)**
2008	5	7.66	−2.66	0.65	0	0	0	
2009	5	8.37	−3.37	0.60	0	0	0	
2010	1	9.15	−8.15	0.11	0	0	0	

served spawning events included vegetation type, location of inundated vegetation in the water column, flow, and canopy cover (Table 1). Based on the observed data, we recommend a suitability value of 1 for vegetation types that include herbaceous vegetation (e.g., grasses, crops, and wetlands) and small woody shrubs when their location in water column is 0–0.5 m from the water surface, and these habitats are in open canopy areas with little or no flow. Suitability criteria for water temperature, hydrology, and spawning habitat characteristics should not be considered independent. Thus, for spawning habitat to receive a suitability value of one, it must contain herbaceous or small woody vegetation within 0.5 m of the water surface, and occur in an area with little or no flow and an open canopy. In addition, this area must have a water temperature between 20 and 30 °C and be inundated during a water-level increase sufficient to flood the habitat to a depth of ≥1 m for at least 5 days. For any conditions outside these bounds we used a suitability value of 0.

Spawning season for the Trinity River and Choke Canyon Reservoir was defined as 1 April through 31 July because water temperatures between 20 and 30 °C generally occur during this period based on available data from U.S. Geological Survey (USGS) gages in the region. Dates outside this window were considered unsuitable. This standard spawning period was used for all years because daily water temperature data were not available for either system for the entire period of interest. For each day from 1 April through 31 July we assigned a suitability value of 0 or 1 based on hydrologic conditions (i.e., water elevation). However, application of the hydrology criteria differed somewhat because one system was a river and the other was a reservoir. In the Trinity River, water elevation data were available from three USGS gages (i.e., Trinidad, Oakwood, and Crockett). At each of these gages, we used the National Weather Service (NWS) classification of "minor flood" to represent conditions that approximated our criteria (i.e., inundate floodplain habitats to a depth of at least 1 m) based on field observations. A suitability value of 1 was assigned when a flood pulse exceeded the minor flood classification for a minimum of 5 days. For each year, the total number of days hydrologic suitability criteria were met were then summed across the three gages (Table 3). In Choke Can-

Table 4. Alligator gar year class data collected from Choke Canyon Reservoir, Texas (1986–2010). Variables reported for each year class include the number of fish collected (Obs), the number expected (Exp) assuming constant recruitment and a constant annual survival rate of 91.5%, deviation from expected, and the relative contribution of a given year class (Obs/Exp). Hydrologic data for the period of 1 April–31 July include the number of days habitat suitability (HS) equaled 1, change (Δ) in water level (m), and mean water elevation above sea level (67 m = full pool). Data in bold reflect years when recruitment was greater than expected.

Year	Obs	Exp	Deviation	Obs/Exp	HS = 1 (d)	Δ Level	Elevation	Hydrologic comments
1986	0	1.11	−1.11	0	49	0.9	58.9	1.3 m rise, 26 days in June, through 31 July
1987	1	1.21	−0.21	0.83	56	5.2	64.2	5.4 m rise, 25 days in late May–June, through 31 July
1988	**2**	**1.32**	**0.68**	**1.51**	**0**	**0.0**	**67.0**	
1989	0	1.45	−1.45	0	0	−1.7	65.2	
1990	1	1.58	−0.58	0.63	12	2.0	62.1	1.9 m rise, 12 days in late July, through 31 July
1991	0	1.73	−1.73	0	0	−0.8	63.1	
1992	0	1.89	−1.89	0	0	0.5	67.1	
1993	0	2.06	−2.06	0	0	0.0	66.9	
1994	0	2.26	−2.26	0	0	−0.5	65.6	
1995	0	2.47	−2.47	0	0	−1.5	63.1	
1996	**3**	**2.69**	**0.31**	**1.11**	**0**	**−1.7**	**59.2**	
1997	**13**	**2.94**	**10.06**	**4.42**	**35**	**4.0**	**59.1**	**3.7 m rise, 21 days in late June–July, through 31 July**
1998	**9**	**3.22**	**5.78**	**2.80**	**0**	**−1.0**	**60.5**	
1999	**4**	**3.52**	**0.48**	**1.14**	**0**	**−0.4**	**62.5**	
2000	0	3.84	−3.84	0	0	−0.5	61.0	
2001	1	4.20	−3.20	0.24	0	−0.7	60.4	
2002	**28**	**4.59**	**23.41**	**6.10**	**29**	**6.4**	**62.0**	**7.3 m rise, 20 days in late June–July, through 31 July**
2003	5	5.02	−0.02	1.00	0	0.0	67.2	
2004	3	5.48	−2.48	0.55	0	0.0	67.2	
2005	2	5.99	−3.99	0.33	0	−0.2	67.1	
2006	0	6.55	−6.55	0	0	−0.6	65.8	
2007	**8**	**7.16**	**0.84**	**1.18**	**40**	**2.1**	**66.0**	**1.8 m rise, 22 days in late June–July, through 31 July**
2008	0	7.82	−7.82	0	0	−0.5	66.6	
2009	1	8.55	−7.55	0.12	0	−0.7	65.0	
2010	**17**	**9.34**	**7.66**	**1.82**	**106**	**1.7**	**65.9**	**1.9 m rise, 41 days in mid April–May, through 31 July**

yon Reservoir, we examined daily elevation data from a USGS gage located at the dam and assigned a suitability value of one starting on the day when the water elevation rose by a minimum of 1 m from preceding conditions; subsequent days continued to receive a value of 1 until water elevation dropped more than 0.5 m or until 31 July. We then summed the total number of days the hydrologic suitability criteria were met each year (Table 4).

Relating Historic Availability of Suitable Conditions with Annual Recruitment

Year-class strength of alligator gar was highly variable for the period examined in both the Trinity River and Choke Canyon Reservoir (Tables 3 and 4). From 1986 to 2010, we identified 7 year classes (28% of years) in the Trinity River (Table 3) and 8 year classes (32% of years) in Choke Canyon Reservoir (Table 4) that had positive deviations from expected values, indicating recruitment was greater than expected under a constant recruitment scenario. Although strong recruitment occurred in less than one third of the years, these year classes comprised 75% and 86% of the age samples from 1986–2010 in the Trinity River and Choke Canyon Reservoir, respectively. In addition, the two strongest year classes in each system comprised about half of the age sample (1989 and 2007 = 55% in the Trinity River; 1997 and 2002 = 42% in Choke Canyon Reservoir). Subsequently, the relative contribution of these dominant year classes was 4 to 7 times that of an expected year class assuming constant recruitment and survival (Tables 3 and 4).

In general, strong recruitment corresponded with years when suitability criteria were met and weak recruitment corresponded with years when conditions were deemed unsuitable (Table 3 and 4; Figure 1). Although we could not reject our null hypothesis that recruitment of alligator gar was independent of the availability of suitable conditions in Choke Canyon Reservoir ($\chi^2 = 2.824$; df = 1; $P = 0.093$), we found that above average recruitment was linked to the availability of suitable conditions in the Trinity River ($\chi^2 = 4.001$; df = 1; $P = 0.045$) and for the pooled data ($\chi^2 = 6.455$; df = 1; $P = 0.011$). In the Trinity River, the exceptionally strong 1989 and 2007 year classes occurred in years when large flood pulses inundated floodplain habitats throughout the study area (i.e., all 3 gages exceeded

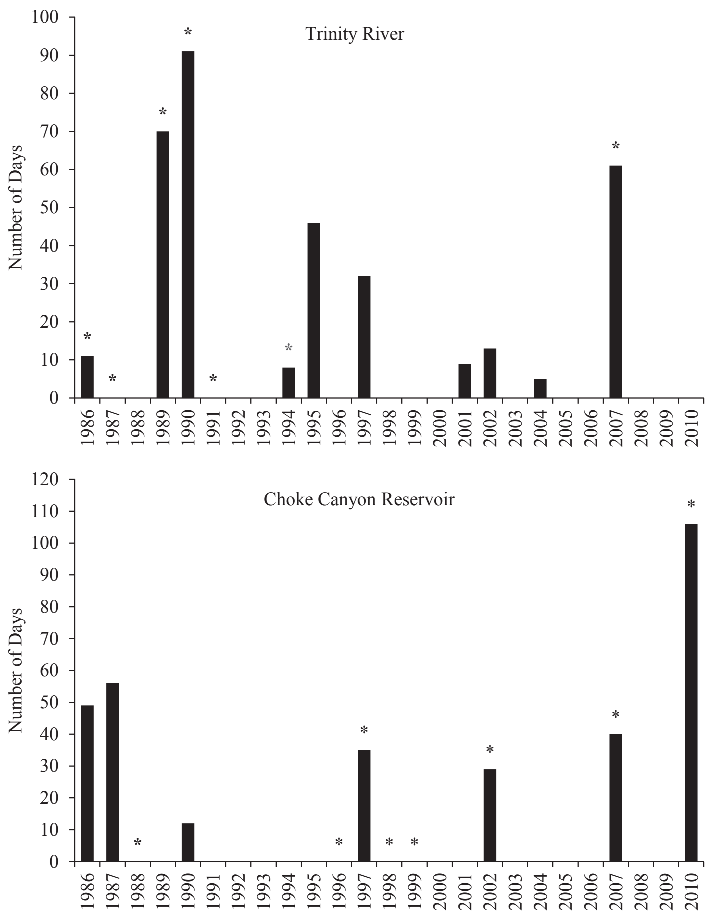

Figure 1. Cumulative number of days each year that habitat suitability equaled 1 for the Trinity River (top) and Choke Canyon Reservoir (bottom) based on hydrologic data for the period of 1 April–31 July. Years with above expected recruitment are noted with an asterisk (*).

minor flood classification) for extended periods in June and July (Table 3; Figure 1). Similarly, the strong year classes of 1997 and 2002 in Choke Canyon Reservoir corresponded with water level rises of 4–7 m in July (Table 4; Figure 1). Years without suitable conditions were common (60%–72%) in both systems and typically corresponded with poor recruitment. Of the 15 years without suitable flood pulses in the Trinity River, only two (13%; 1987 and 1991) corresponded with years of above expected recruitment (Table 3; Figure 1). Similarly, in Choke Canyon Reservoir, of the 18 years without suitable water level increases, above expected recruitment was only observed in 4 (22%; 1988, 1996, 1998, and 1999). With the exception of the 1996-year class, these strong year classes occurred in years where reservoir water levels remained high following a year when suitability criteria were met (Table 3 and 4; Figure 1).

Discussion

Our analysis of alligator gar year-class strength data from the Trinity River and Choke Canyon Reservoir indicated that recruitment success was highly variable and coincided with the availability of suitable conditions based on our proposed habitat suitability criteria. In both systems, the two strongest year classes corresponded with years where large, long duration flood pulses occurred in June and July, inundating floodplain spawning habitats. With few exceptions, years without suitable environmental conditions coincided with weak recruitment. While this initial evaluation of the proposed habitat suitability criteria is insufficient to develop predictive models of recruitment success based on environmental variables, it does validate a relationship between water temperature, hydrology, and recruitment for alligator gar in inland waters.

Out of a combined 33 years characterized as having unsuitable conditions for alligator gar recruitment in our study systems, only six corresponded with above expected year-class strengths. In the Trinity River, strong year classes in 1987 and 1991 (when conditions were deemed unsuitable) followed years with strong recruitment and suitable conditions. This was also true for the 1988 and 1998 year classes in Choke Canyon Reservoir. One probable explanation is that age estimation error may have inflated the number of fish in these year classes, given that age estimation of alligator gar can be difficult (Buckmeier et al. 2012). However, the above expected recruitment reported in 1988, 1998, and 1999 in Choke Canyon Reservoir may also reflect actual strong recruitment and indicate a need to revise hydrologic suitability criteria for reservoirs. While no water-level increase occurred during the defined spawning season in these years in Choke Canyon Reservoir, in all instances high water levels persisted following a previous rise. A similar scenario occurred in 2003 when we observed expected recruitment in a year of stable high water that followed a water level increase of 7 m in 2002. Prior to these significant water-level increases, low water levels likely resulted in the growth of substantial terrestrial vegetation in the exposed reservoir bottom. As the reservoir filled and these areas became inundated, the decaying vegetation may have continued to provide spawning habitat in subsequent years.

While recruitment success of alligator gar typically related well with the historic availability of suitable conditions based on our proposed suitability criteria, we recognize that further validation of these criteria is needed. In addition, some criteria may need refinement to develop models that can predict recruitment success in rivers with varying levels of regulation and geology. For instance, spawning season should be defined by water temperatures and will likely vary with latitude and geomorphology. Although we are unaware of any direct observations of alligator gar spawning in the late summer or fall, gonadosomatic index values suggest such spawns may occur (Garcia De Leon et al. 2001). Furthermore, Aguilera et al. (2002) documented fall spawning in tropical gar (*Atractosteus tropicus*), a congener of alligator gar. Suitability values within the range of observed temperatures likely occur along a gradient from zero to one because incubation times for eggs may be longer and growth of larvae may be reduced at cooler temperatures. Data from the Trinity River and Choke Canyon Reservoir support the idea that flood pulses occurring during warmer months may produce stronger year classes. In both systems, we observed that the strongest year classes coincided with years when June and July flood pulses provided suitable environmental conditions. In contrast, years where suitable floods occurred from April to early May were associated with weak recruitment in the Trinity River. Allen et al. (2014) also suggested that telemetered alligator gar selected floodplain habitats with the highest available temperatures and Inebnit (2009) and Kimmel et al. (2014) found that water temperatures at spawning sites were several degrees warmer than in the main channel.

Suitability values for the magnitude and duration of a flood pulse occurring during the spawning season almost certainly occur along a gradient from 0 to 1. Suitability likely increases from 0 when the floodplain is first inundated to a value of 1 when access to spawning habitat is no longer limiting. Similarly, suitability likely increases from zero for floods inundating floodplain habitats for <5 days to one for floods lasting ≥15 days because extended floods may provide additional opportunities to spawn and increase survival of developing larvae (Inebnit 2009). At 15 days, 12–13 DAH alligator gar will be large and highly mobile so additional duration is unlikely to further increase suitability. Our data also provide support for assigning values between 0 and 1 for these variables. In the Trinity River, exceptionally strong year classes in 1989 and 2007 coincided with floods classified as "moderate" and "major" according to the NWS criteria. These floods inundated floodplain habitats from 7–31 days in late June and July throughout the river reach. In Choke Canyon Reservoir, exceptionally strong year classes in 1997 and 2002 coincided with 4–7 m rises in late June and July that inundated floodplain habitats for ≥20 days. While smaller, shorter duration rises occurring earlier in the year often coincided with recruitment of alligator gar, these strong year classes suggest that large, long duration flood pulses occurring late in the spawning season when water temperatures are high may be ideal.

Future efforts to refine the proposed habitat suitability criteria for alligator gar recruitment should also include quantitative approaches to assessing spawning habitat characteristics and the relation between hydrology and spawning habitat availability. We assumed spawning habitat availability was positively related with water elevation but lacked the data needed to vet our criteria and quantify these relations. We suspect that, in general, larger floods will provide greater access to spawning habitats, but the shape of this relation will vary with local geography. For example, a 1-m rise in a reservoir may be sufficient to inundate significant floodplain habitat when a reservoir is near full pool but may inundate minimal spawning habitat when the water level is low and the reservoir is largely contained within the original river channel. Similarly, the magnitude of a rise needed to inundate floodplain spawning habitats in large rivers that are entrenched will typically be greater than those that are not. As a result, our initial evaluation likely incorporated additional error. If possible, future efforts should attempt to directly estimate spawning habitat availability and correlate this variable with recruitment. An approach similar to that developed by Allen (2015) to identify the extent of floodplain inundation and used by Allen et al. (2014) to identify potential spawning locations for alligator gar in the lower Mississippi River could be used to quantify historic spawning habitat availability by correlating habitat availability with river stage.

In addition to refining suitability criteria to improve relations with historic recruitment success, more detailed study of conditions associated with successful spawning events is needed. Data in this study were predominantly based on direct observations of alligator gar spawning events. While such observations were critical to the development of the proposed habitat suitability criteria, it can be difficult to find and directly observe spawning alligator gar. In addition, this approach can be biased (e.g., the inability to directly observe fish spawning below the water surface). The recent validation of daily age and subsequent hatch-date estimates by Sakaris et al. (2014) may offer a feasible approach to quantifying detailed information about the environmental conditions associated with spawning. When local hydrologic and other environmental data are available, hatch date estimates can provide high resolution data regarding the conditions immediately preceding and during spawning events. In addition, hatch-date distributions in the fall can provide insight regarding variables that regulate survival of individual cohorts (e.g., Mion et al. 1998, Durham and Wilde 2005). Using such data, researchers may be able to assign intermediate values (i.e., between 0 and 1) to variables such as water temperature, flood magnitude, and flood duration.

While our current assessment was insufficient to fully validate the proposed habitat suitability criteria for recruitment of alligator gar in inland waters, successful recruitment does appear to be closely linked with water temperature, hydrology, and access to spawning habitats. In general, our findings corroborated an earlier hypothesis proposed by Inebnit (2009) relating alligator gar recruitment success with flood pulse characteristics and support the conclusions that population declines may be the result of reduced floodplain connectivity (Pringle et al. 2000, O'Connell et al. 2007). As a species with many characteristics of a periodic life-history strategist, it is not surprising that alligator gar populations in this study exhibited highly variable recruitment and were dominated by only a few strong year classes. Because of the longevity and high fecundity of alligator gar, populations should remain viable when strong year classes occur periodically (e.g., every 5–10 years). However, because strong recruitment can be infrequent, stocks must be managed cautiously and managers should monitor recruitment dynamics and subsequent abundance fluctuations to ensure that strong year classes are not over exploited. As such, the ability to develop predictive models to project recruitment success based on habitat suitability criteria could provide an important tool. Such models could also be used to inform water management decisions and efforts to improve connectivity to and quality of spawning habitats.

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