

SPECIAL SECTION: ALLIGATOR GAR

Advances in Conservation and Management of the Alligator Gar: a Synthesis of Current Knowledge and Introduction to a Special Section

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Abstract

Growing appreciation of biodiversity and the role of apex predators, along with the increasing popularity of multi-species and trophy-oriented angling, has elevated the status of gars—in particular, the Alligator Gar *Atractosteus spatula*—among anglers and biologists alike. As a result, considerable effort has been spent in recent years to gain a working knowledge of the biology and ecology of the species in order to advance science-based management. In January 2019, the Alligator Gar Technical Committee of the Southern Division of the American Fisheries Society hosted a symposium entitled “Advances in the Conservation and Management of North American Gars” to showcase the results of research and management efforts conducted throughout the species’ range. Fishery researchers and managers presented a diversity of works, furthering our understanding of population dynamics, stock assessment, genetics, hatchery practices and stocking, habitat use, and angler desires associated with Alligator Gar fisheries. In our

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introduction to this special section, we introduce these works and provide a synthesis of the current state of scientific knowledge regarding the Alligator Gar. We hope that this will provide context to the works presented in the symposium and will serve to guide the development of future research that addresses the remaining knowledge gaps concerning the species and its growing fishery.

Gars...have long been viewed by many anglers and managers as harmful to game fishes and recreational angling. Most investigations of these ancient, piscivorous predators have centered on their dietary habits, not on their broader ecological role in aquatic communities. Most management has involved eradicating these fishes rather than using them constructively. It is suggested that managers should view gars...not merely as nuisances to be destroyed, but as contributors to ecosystem stability and function, to balance predators and prey, and to more successful angling in the long term. [From Scarnecchia 1992.]

Since Scarnecchia's (1992) progressive treatise on gars (Lepisosteidae), perspectives on these ancient holdovers from the age of the dinosaurs have changed (David et al. 2018). Fueled by increased understanding of the importance of native species (e.g., Hooper et al. 2005; Worm et al. 2006) and the critical role of large predators in ecosystems (Power et al. 1985; O'Connell et al. 2007; Sandin et al. 2008; Estes et al. 2011) and by the rising popularity of multispecies and trophy-oriented recreational angling (Ross et al. 2001; Binion et al. 2015; Bohn et al. 2017; McDonald et al. 2018; Smith et al. 2018), management that once focused on eradicating gars now aspires to conserve, rehabilitate, or repatriate populations throughout their range. However, efforts have been hampered by a lack of information. As noted by Scarnecchia (1992), work prior to 2000 focused largely on diet due to long-held beliefs that gars were unequivocally detrimental to game fish populations. As a result, basic information on the life history and ecology of gars has lagged far behind our knowledge of many other fishes (Buckmeier et al. 2013; Binion et al. 2015; David et al. 2015, 2018; Smylie et al. 2015). A greater understanding of these species is critical to the development of effective management strategies (David et al. 2018).

Among the gars found in U.S. waters, the greatest need for information lies with the Alligator Gar *Atractosteus spatula*. The *Lepisosteus* spp. (Longnose Gar *L. osseus*, Shortnose Gar *L. platostomus*, Spotted Gar *L. oculatus*, and Florida Gar *L. platyrhincus*) populations remain stable throughout much of their North American ranges, whereas the Alligator Gar is regarded as vulnerable and in need of management action (Warren et al. 2000; Jelks et al. 2008). Historic removal efforts, chronic overfishing, and habitat loss due to river fragmentation and flow modifications have resulted in the extirpation of populations from many mid-Mississippi drainages (Robinson and Buchanan 1988; Scarnecchia 1992; Etnier and Starnes 1993; Kluender et al. 2016; David et al. 2018). In addition, the status of Alligator Gar stocks

throughout much of the lower Mississippi River and Gulf Coast drainages from Florida to northern Mexico remains unknown (Wegener et al. 2017). Increased angler interest combined with a reduced distribution exerts greater pressure on the remaining stocks and has resulted in the implementation of strict fishery regulations or closures in several states (Buckmeier et al. 2016; Wegener et al. 2017).

Over the last two decades, significant efforts have been undertaken to better understand the biology and ecology of gars, particularly the Alligator Gar. To address knowledge gaps for the species and to foster increased communication among gar researchers, the Alligator Gar Technical Committee was formed in 2008 as part of the Southern Division of the American Fisheries Society (SDAFS). Since that time, several theses and dissertations have been completed, a number of peer-reviewed scientific articles has been published, and multiple symposia have been held. In 2016, a symposium dedicated to the ecology, management, and conservation of gars and the Bowfin *Amia calva* was held at the 146th Annual Meeting of the American Fisheries Society. The full-day symposium resulted in the publication of an additional seven articles on Alligator Gar in *Transactions of the American Fisheries Society* during 2018. However, abstract submissions far exceeded the symposium's capacity. As a result, another symposium that was focused primarily on the Alligator Gar was held at the 2019 Annual Meeting of the SDAFS in Galveston, Texas. Fisheries scientists and managers presented on a diverse array of topics related to continued advances in the science of the family Lepisosteidae. Our intent herein is to introduce the works published in this special section of the *North American Journal of Fisheries Management* as well as to provide the first comprehensive synthesis on the current status of populations and the state of scientific knowledge regarding the Alligator Gar. We hope that this will serve as a launching point for the development of future research that addresses remaining knowledge gaps for the species and evolving fishery.

RANGEWIDE POPULATION STATUS

Considerable changes have occurred in the status of Alligator Gar stocks across their historic range since the Alligator Gar Technical Committee of the SDAFS surveyed state agencies in 2009. Since that time, many

agencies have undertaken efforts to assess or actively manage stocks, including the re-establishment of extirpated populations. We again surveyed representatives from state agencies in 2018 to quantify changes in status; an electronic questionnaire was distributed to representatives of the 13 agencies within the known historic range of Alligator Gar (Figure 1). Representatives were asked to provide an overall trend assessment of Alligator Gar populations, identify changes in management within their state, and define the current status of Alligator Gar populations at the subbasin (i.e., 8-digit hydrologic unit code) level (Figure 1).

Currently, none of the states within the native range of the Alligator Gar considers its populations to be in decline; this is an improvement from 2009, when 5 of the 13 states held that designation (Figure 2). Illinois, Missouri, and Mississippi consider populations to be improving—likely attributed to numerous repatriation stockings in Mississippi River drainages. Ohio and Indiana still consider the Alligator Gar to be extirpated; however, an Alligator Gar was harvested by a bow angler in Indiana's White River during 2017. Examination of this individual's coded wire tag later revealed that it had been stocked in Kentucky. Recent captures in Ohio are also thought to be either aquarium releases or from downstream stocking events. Texas and Louisiana have generally been accepted

as having the largest and most stable populations. However, a number of populations in Louisiana's Gulf coastal drainages appear to be affected by limited reproduction (Figure 1). In general, coastal populations that move between freshwater, brackish water, and salt water (e.g., Daugherty et al. 2017, 2019b) appear to be less stable east of the Texas Gulf coast, which may be a reflection of differences in recreational and commercial fishery regulations among states.

GENETICS

A variety of studies has dealt with the systematics of gar either in the context of broader phylogenetic studies of the Actinopterygii (e.g., Inoue et al. 2003) or a more focused examination of the family Lepisosteidae (e.g., Wright et al. 2012). Inoue et al. (2003) provided a mitogenomic perspective on the basal actinopterygian lineages of “ancient” fishes, including bichirs (Polypteriformes), sturgeons (Acipenseriformes), the Bowfin, and gars. Unlike previous studies of ancient fishes, Inoue et al. (2003) included Alligator Gar as one of the representatives from the family Lepisosteidae. Their phylogenetic analysis confirmed the basal position of the four ancient lineages and the monophyly of teleosts. However, in contrast to previous morphological studies the acipenseriforms, *Amia*, and

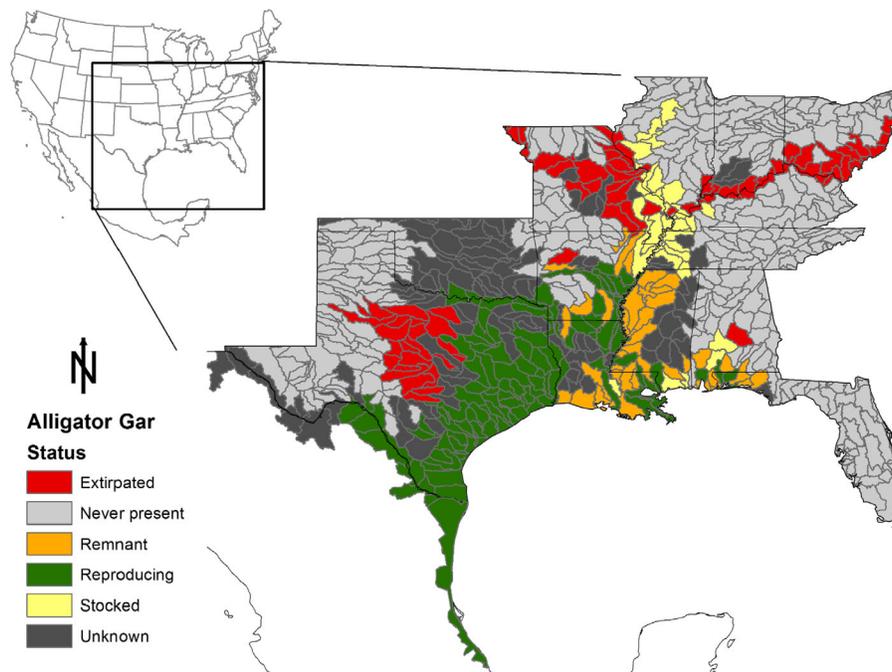


FIGURE 1. Current status of Alligator Gar populations at the 8-digit hydrologic unit code watershed level. Populations for each watershed were assigned one of six status values: never present (gray); unknown (black; no recent records of the species, but habitat conditions would allow them to inhabit the watershed); stocked (yellow; populations are only present as a result of stocking efforts); reproducing (green); remnant (orange; currently present, but no evidence of reproduction has been documented in over 30 years); and extirpated (red).

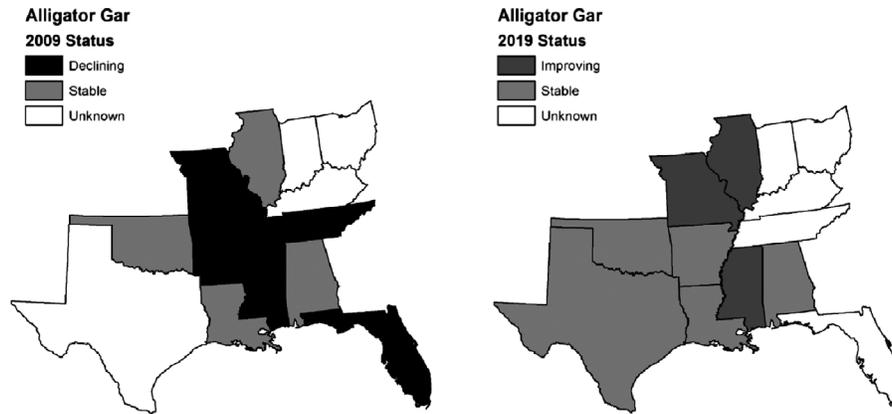


FIGURE 2. Perceptions of state agency representatives regarding statewide Alligator Gar population trends in 2009 and 2018.

lepisosteids were a strongly supported monophyletic group sister to the teleosts. The remaining ancient lineage (Polypteriformes) was the most basal group. Wright et al. (2012) examined the phylogenetic relationships among the seven extant gar species by using sequence data for one mitochondrial gene and seven nuclear genes. Both genera of gars (i.e., *Lepisosteus* and *Atractosteus*) were found to be monophyletic, as was indicated by previous phylogenies produced from morphological data. Within *Atractosteus*, Alligator Gar was sister to Cuban Gar *Atractosteus tristoechus*, while in *Lepisosteus* sister relationships were found between the Spotted Gar and Florida Gar and between the Longnose Gar and Shortnose Gar. The work of Sipiorski (2011) found similar relationships among the species based on his analysis of four mitochondrial genes and one nuclear gene.

Molecular tools have proven useful in detecting hybrids and characterizing patterns of introgression in fishes, although hybridization has only been infrequently documented in ancient lineages. Gibbons and Whitt (1990) were the first to describe an Alligator Gar \times Longnose Gar hybrid individual in the wild on the basis of species-specific allozyme loci. Later, Herrington et al. (2008) documented Alligator Gar \times Longnose Gar hybrids in a captive environment by using one mitochondrial locus, one nuclear gene locus, and one microsatellite locus. The four hybrid offspring were found to be the product of a female Longnose Gar and a male Alligator Gar. Bohn et al. (2017) conducted a more thorough survey of hybridization in wild populations of Alligator Gar. They developed a new set of markers to distinguish among Alligator Gar, Longnose Gar, and Spotted Gar. Seventeen Alligator Gar \times Longnose Gar hybrids were confirmed from sites across Texas; in all of those hybrids, the mitochondrial locus indicated that the Alligator Gar parent was female. Snout morphology proved useful for field identification of hybrids with an 81% success rate (Bohn et al. 2017).

Taylor et al. (2020, this special section) additionally reported one Alligator Gar \times Longnose Gar hybrid from Lake Texoma.

The development of microsatellite loci for Alligator Gar was fundamental to the application of molecular tools to a variety of ecological or management-based questions. Moyer et al. (2009) characterized 17 microsatellite loci that were polymorphic in Alligator Gar. Some of these loci also proved useful in other gars, including Spotted Gar, Longnose Gar, and Tropical Gar *Atractosteus tropicus* (Bohn et al. 2013). An additional six microsatellite loci for Alligator Gar were later developed (Daugherty et al. 2017).

Bohn (2013) provided a broad-range analysis of population genetic structure through the analysis of microsatellite genotypic data for over 600 individuals from 19 sites across the species' range. Populations of Alligator Gar from the Rio Grande River and Choke Canyon Reservoir, Texas, differed from the remainder of the range at the deepest structural level. The next level of genetic structure identified five groups: (1) the Rio Grande River–Choke Canyon group, (2) the Brazos River, (3) the remaining Texas sites, (4) Gulf of Mexico sites from Louisiana to Florida, and (5) sites within the Mississippi River drainage. Numerous researchers have provided additional collections in recent years, resulting in samples from 935 individuals across 26 sites (B.R.K., unpublished data), and recent preliminary analyses have detected finer levels of population genetic structure. Along the Gulf of Mexico, five genetic groups were found among Texas sites; samples from Louisiana to Alabama formed a single group; and the Escambia River, Florida, was genetically distinct. Within the interior portion of the range (i.e., Mississippi River basin), three additional genetic groups were found, with two representing drainages in Arkansas and the third from a collection on the Mississippi River. Work is currently underway that incorporates mitochondrial data

from across the species' range to produce a more thorough representation of rangewide population genetic structure (D. Williford and J. Anderson, Texas Parks and Wildlife Department, unpublished data).

Potential population genetic structure at finer spatial scales has also been examined in two studies. Bohn (2013) tested the hypothesis that individuals in spawning aggregations located across Choke Canyon Reservoir might exhibit site fidelity, potentially producing genetically distinct stocks within the reservoir. However, microsatellite genotype data from 102 individuals sampled at four locations found no evidence of distinct genetic groups, and pairwise genetic differentiation index F_{ST} values were not significant. Daugherty et al. (2017) used otolith microchemistry and genetic data to assess population structure across the freshwater-saltwater interface in the Guadalupe River-San Antonio Bay system (about 300 river kilometers in length). Those authors reported significant F_{ST} values, suggesting that some genetic differentiation existed among four sample locations on a continuum from the upper river to the bay.

Genetic data can also provide insight into reproductive dynamics and recruitment success. Both environmental conditions and aspects of reproductive behavior (e.g., spawning aggregations) can lead to variability in reproductive success among individuals and reduce the effective size (N_e) of a population relative to the actual number of spawning adults. Estimating N_e for long-lived, iteroparous species can be problematic, so an increasing number of studies employ the sibship assignment method of Wang (2009) to estimate the effective number of breeding adults (N_b) that produced a particular cohort of offspring. Kreiser et al. (2020, this special section) used sibship analysis of age-0 fish to determine the effective number of breeding adults at multiple spatial and temporal scales across two Texas systems. At all of the sites, offspring demonstrated low levels of relatedness, with N_b values being similar to the sample sizes obtained at respective sites. As a result, Kreiser et al. (2020) suggested that reproductive success was similar among adults at a given locale instead of those cohorts of age-0 fish being produced by only a few individuals.

A fairly recent innovation in the ecologist's molecular toolbox is environmental DNA (eDNA; Bohmann et al. 2014). This technique provides a means by which to detect the presence of species on the basis of DNA that has been shed into the environment—the water column in the case of fishes. One of the challenges of eDNA is designing species-specific primers to ensure that false positives are not produced through the detection of nontarget species. Farley et al. (2018) were able to design species-specific primers for Shortnose Gar, Longnose Gar, and Tropical Gar, but their Alligator Gar primers also amplified Cuban Gar. Additionally, they tested their methods on water from

tanks with and without gar present located at the Belle Isle Aquarium (Detroit, Michigan). In this proof of concept, Farley et al. (2018) were able to obtain eDNA and correctly identified the gar species that were present in the tank.

REPRODUCTIVE BIOLOGY

The Alligator Gar can be classified as a periodic life history strategist, characterized reproductively by a late age at maturity, polyandry, and large adult body size, which facilitates high fecundity (Winemiller and Rose 1992). The reproductive life history of Alligator Gar has been poorly understood in comparison with that of many other fishes (Buckmeier et al. 2017), largely because obtaining quantitative data requires sacrifice of fish—an undesirable condition for stocks of unknown or remnant status. However, population sampling and field observations of spawning events in recent years, as well as efforts to culture fish in hatcheries, have provided some information (reviewed by Buckmeier et al. 2017).

Ferrara (2001) estimated the onset of reproductive maturity in female Alligator Gar in southeastern U.S. systems at 10 years of age, with reproductive maturity of the population (i.e., the age at which $\geq 50\%$ of individuals are mature) at age 14. However, subsequent estimates from other populations suggest earlier ages. DiBenedetto (2009) reported that Alligator Gar of both sexes in Bayou Dularge, Louisiana, appeared to mature by age 5. Daugherty et al. (2019a) inferred that because reduced somatic growth is commonly associated with reproductive development (Moyle and Cech 2000), the t_{crit} parameters, which represent the pivotal age when growth rates change in the double von Bertalanffy growth model (VBGM; 2.6 years for males and 2.5 years for females, respectively) suggested the onset of reproductive maturity at these ages. Daugherty et al. (2019a) further noted that although these ages may indicate the onset of reproductive maturation, they should not be confused with the age at first reproduction. Patterson et al. (2019) reported the earliest (i.e., youngest) observation of volitional spawning by captive-reared, age-4 Alligator Gar. Collectively, these contemporary results suggest a likely age at maturity that is considerably younger than the age at maturity proposed by Ferrara (2001). For species with life history characteristics similar to those of the Alligator Gar, gonadal development and maturation may take multiple years to complete (Jordan et al. 2016). Thus, both the initiation of gonadal development and the age and size at which Alligator Gar actively reproduce warrant further study.

Fecundity in the Alligator Gar is high. Ferrara (2001) estimated fecundity to be 4.1 eggs/g of maternal body weight, whereas Harried et al. (2020, this special section) reported a value of 7.8 eggs/g for fish in the Trinity River,

Texas. These estimates are far greater than those reported for other lepisosteids, including the Longnose Gar (0.8 eggs/g) and the Spotted Gar (0.1 eggs/g; Ferrara 2001). Harried et al. (2020) found no relationship between absolute fecundity or maternal size characteristics and egg quality based on total egg lipid concentration. Finally, Ferrara (2001) reported that the mean egg diameter of Alligator Gar was about 10–20% smaller than that of both the Spotted Gar and the Longnose Gar. Collectively, these traits indicate a reproductive life history strategy that is focused largely on maximizing fecundity (Winemiller and Rose 1992; Ferrara 2001).

Evidence to date indicates that successful spawning is closely tied to spring and summer (i.e., April–July) over-bank flooding at water temperatures greater than about 20°C (Aguilera et al. 2002; Brinkman 2008; Inebnit 2009; Allen et al. 2014, 2020, this special section; Sakaris et al. 2014; Kluender et al. 2016; Buckmeier et al. 2017; Robertson et al. 2018). Although most observations of spawning have occurred in freshwater systems, Alligator Gar embryos and larvae tolerate salinities up to 8‰ and spawning has been observed in a brackish Louisiana marsh (Suchy 2009; Daugherty et al. 2017). Prespawn fish move onto the floodplain as water levels rise; aggregations of 20 or more individuals can be found in shallow (<1-m water depth) areas associated with inundated terrestrial vegetation (Inebnit 2009; Allen et al. 2014; Kimmel et al. 2014; Sakaris et al. 2014). Individual female Alligator Gar are joined by multiple males, typically numbering from two to eight fish, who compete to fertilize the eggs as they are broadcast over vegetation (Mendoza et al. 2008). Spawning has been observed during both the day (Inebnit 2009) and the night (Aguilera et al. 2002). Males are also believed to remain in floodplain areas longer than females during spawning, presumably in search of prespawn females (Garcia de Leon et al. 2001).

Eggs are pale yellow to olive in color, adhesive, and readily observable attached to vegetation at or near the water surface (Inebnit 2009). The eggs are toxic to crayfishes (Astacoidea) and small rodents (Rodentia; Ostrand et al. 1996), which may serve to counteract their conspicuousness. Incubation is short lived, ranging from about 48 to 72 h at water temperatures of 27.5–31.0°C (Aguilera et al. 2002; Mendoza et al. 2008; Inebnit 2009). After hatch (~7–11 mm TL), larval fish attach to vegetation via a suction disc on the anterior of the snout, often immediately below the water surface (Mendoza et al. 2008; Inebnit 2009; Buckmeier et al. 2017). Larvae generally remain sedentary, endogenously absorbing their yolk-sac reserves. About 5 d after hatch (~15–20 mm TL), both the yolk sac and the suction disc are largely resorbed and fish become free-swimming, feeding exogenously (Aguilera et al. 2002).

YEAR-CLASS STRENGTH AND RECRUITMENT

Given the strong relationships between hydrology and successful reproduction in the Alligator Gar, strong year-classes and subsequent recruitment of age-0 fish to populations are sporadic, largely dependent on the occurrence, timing, and duration of flood events (Buckmeier et al. 2017). Large variation in the production and recruitment of year-classes is common among periodic strategists, attributed to the effects of climate on spawning habitat availability as well as the distribution of larval food and predators (Sissenwine 1984; Fletcher and Deriso 1988; Shepherd and Cushing 1990; Winemiller and Rose 1992). Natural variability in these conditions has been altered by the construction of dams and associated modification of flow regimes, which not only fragment populations and block longitudinal migration but also moderate or minimize the magnitude and duration of flood events (Junk et al. 1989; Ferrara 2001; Brinkman 2008; Mendoza et al. 2008; Inebnit 2009; Kluender 2011; Buckmeier et al. 2013).

Given the reduced abundance of many Alligator Gar populations throughout the species' range in the USA, year-class strength has not been widely assessed. However, age distributions of Alligator Gar in the Trinity River and Choke Canyon Reservoir, Texas, indicated that strong year-classes occurred in those systems about three times per decade (Buckmeier et al. 2017; Smith et al. 2018). Moreover, those year-classes comprised 75% and 86% of the fish sampled in the two systems, further illustrating a high degree of recruitment variability and the importance of a relatively few abundant year-classes for maintaining stocks. Smith et al. (2020, this special section) reported that although spring flooding produced abundant young-of-the-year Alligator Gar during both 2015 (May) and 2016 (June) in the Trinity River, the 2016 cohort was no longer detected by July of that year. Smith et al. (2020) further reported that many age-1 fish (2015 cohort) occupied the same habitats as the 2016 fish. Cannibalism at early life stages is known to be high (Mendoza et al. 2002, 2008; Perschbacher 2011; Porta et al. 2019); thus, the authors attributed the potential loss of the 2016 year-class to cannibalism between year-classes. These results suggest that both abiotic and biotic factors play important roles in determining Alligator Gar year-class strength.

AGE, GROWTH, AND MORTALITY

Ferrara (2001) provided the first quantitative assessments of Alligator Gar population dynamics in Louisiana and Alabama systems. Based on the examination of whole otoliths, Ferrara (2001) reported extended longevity (to 50 years) and slow adult growth (growth coefficient $K = 0.032$). Total annual mortality of adult fish was low and varied among populations (range = 0.04–0.16), attributed

to differences in exploitation among systems. Ferrara (2001) also observed that female Alligator Gar tended to be older and larger than males; however, no formal assessment was conducted.

In subsequent work, DiBenedetto (2009) reported ages of Alligator Gar in Bayou Dularge, Louisiana, to 26 years and reported substantially faster growth ($K=0.32$). Annual mortality was similar between studies (0.20), and the author also reported greater maximum ages (26 versus 16 years) and TLs (2,120 versus 1,495 mm) for females relative to males, respectively. However, DiBenedetto (2009) suggested that comparisons between studies were likely confounded by differences in sampling gears and age estimation techniques. In contrast to the multifilament gill nets and whole otoliths used by Ferrara (2001), DiBenedetto (2009) sampled fish from the commercial jugline fishery and used sectioned otoliths to estimate fish age. The author noted a need for formal evaluation and validation of age estimation techniques and structures for the species.

Buckmeier et al. (2012) assessed aging structures and processing techniques for Alligator Gar. Initial attempts to estimate ages by using whole or sectioned otoliths as described by Ferrara (2001) and DiBenedetto (2009) were deemed unsuccessful; growth marks were evident but were difficult to discern near the otolith edge due to changes in the plane of calcium deposition. However, Buckmeier et al. (2012) found that otoliths ground along the transverse plane provided accurate age estimates through the oldest fish in their study (31 years). The authors also evaluated scales and pectoral fin rays, but annulus formation in these structures was not validated for fish older than age 6. The techniques described by Buckmeier et al. (2012) for processing and interpreting age using sagittal otoliths provided a standardized approach and improved comparability among future studies. Furthering this validation work, Buckmeier and Smith (2020, this special section) examined characteristics of annuli versus subannual growth checks in juvenile Alligator Gar. Additionally, Daugherty et al. (2020, this special section) used bomb radiocarbon analysis to confirm the validity of the age estimation technique developed by Buckmeier et al. (2012) among older age-classes of Alligator Gar (i.e., up to 68 years).

Subsequent to standardization of the aging technique, a few studies have estimated age-based dynamic rates for the Alligator Gar (Table 1). These studies illustrated a progression in the understanding of growth in the species. Binion et al. (2015) modeled growth using a traditional VBGM; they reported that growth was greatest through age 5 and slowed substantially at older ages. Binion et al. (2015) also noted that females appeared to grow faster and reach greater sizes than males; however, sample sizes associated with fish of known sex were limited. Felterman (2015) modeled growth independently for male and female

fish and reported 152- and 411-mm differences in theoretical maximum lengths (L_{∞}) in two Louisiana systems, favoring females (Table 1). Buckmeier et al. (2016) found that a power model provided a marginally better fit than the VBGM for Alligator Gar in the Trinity River, Texas. The authors noted that the power model provided a better fit to the accelerated growth at young ages. Daugherty et al. (2019a) built upon these works by comparing the performance of the VBGM, the power model, and the double VBGM for modeling growth of each sex across Texas Alligator Gar stocks. The authors found that the double VBGM, which accounts for biphasic growth, provided the best fit by parameterizing rapid juvenile growth (i.e., phase 1) independently from slower adult growth (i.e., phase 2) for each sex. Similar to previous studies, female fish grew to substantially greater sizes than males (Table 1). Differences in the maximum observed sizes of male and female Alligator Gar are likely related to differences in longevity. Both Felterman (2015) and Daugherty et al. (2019a) reported 25–40% lower total annual mortality rates for female fish compared to males (Table 1).

Analyses of daily growth increments (Sakaris et al. 2014; Long and Snow 2016) have revealed that early growth is extremely rapid. Sakaris et al. (2019) reported that larval and early juvenile Alligator Gar grew at rates of 4–8-mm/d over the first 3 months of life in the Trinity River. These rates are consistent with the Alligator Gar growth model proposed by Daugherty et al. (2019a), which estimated that both males and females reach an average TL of about 480 mm at 90 d of age—a daily mean of 5.3 mm. Thus, to our knowledge, the Alligator Gar is one of the faster-growing freshwater fishes at early life stages, growing at rates equal to or greater than those of the Dolphinfin *Coryphaena hippurus*—one of the fastest growing pelagic marine species (3.78 mm/d in the first 6 months; Schwenke and Buckel 2008; Sakaris et al. 2019).

HABITAT USE AND MOVEMENT

Although the relationship between habitat loss and observed declines in Alligator Gar populations is widely accepted, information on critical habitat and habitat utilization have historically been limited. Alligator Gar primarily inhabit large, slow-moving rivers; estuaries; and lowland reservoirs (Page and Burr 1991; Etnier and Starves 1993; Ferrara 2001). In recent years, a number of studies have evaluated habitat use and movement of adult and juvenile Alligator Gar (Sakaris et al. 2005; Brinkman 2008; Buckmeier et al. 2013; Solomon et al. 2013; Klueder et al. 2016; Daugherty et al. 2017, 2019b; Wegener et al. 2017).

Alligator Gar habitat use varies seasonally, likely guided by changes in water temperature. During the winter, Alligator Gar tend to congregate in deep, slack-water

TABLE 1. Age-based dynamic rates reported for Alligator Gar populations following the age estimation techniques of Buckmeier et al. (2012; M = total annual mortality; VBGM = von Bertalanffy growth model; t_0 = theoretical age at zero length; t_{crit} = critical age when growth rate changes in double VBGM; K = growth coefficient; L_∞ = theoretical maximum length).

Study	System	M	Growth model	t_0 (years)	K	L_∞ (mm)
Binion et al. 2015	Choke Canyon Reservoir, Texas		VBGM	-2.430	0.143	1,784
Felteman 2015	Terrebonne Estuary, Louisiana	0.194	VBGM _{male}	-2.507	0.209	1,409
	Rockefeller Wildlife Refuge, Louisiana	0.124	VBGM _{female}	-3.229	0.136	1,887
			VBGM _{male}	-10.000	0.076	1,476
Buckmeier et al. 2016	Trinity River, Texas	0.085	VBGM _{female}	-3.364	0.169	1,628
			VBGM ^a	-9.980	0.049	2,295
Daugherty et al. 2019a	Texas populations	Male ^b = 0.24–0.30	Double VBGM _{male}	$t_1 = 0.121$	$K_1 = 0.409$	1,760
				$t_{crit} = 2.600$		
				$t_2 = -10.300$	$K_2 = 0.078$	
		Female ^b = 0.18	Double VBGM _{female}	$t_1 = 0.246$	$K_1 = 0.346$	2,377
				$t_{crit} = 2.500$		
				$t_2 = -12.700$	$K_2 = 0.051$	

^aAuthors also fit the power model, $L_t = -72.6 + 150.6t^{0.17}$, which provided marginally better fit than the VBGM.

^bCalculated independently for the Guadalupe and Trinity rivers, Texas.

habitats (Buckmeier et al. 2013; Kluender et al. 2016) and remain relatively inactive (Brinkman 2008; Wegener et al. 2017). As waters begin to warm in the spring, fish disperse from overwintering areas (Brinkman 2008; Buckmeier et al. 2013; Kluender et al. 2016; Wegener et al. 2017), often moving several kilometers (Buckmeier et al. 2013) to river reaches with potential off-channel spawning habitat (Kluender et al. 2016). Most research indicates that this prespawn period begins when water temperatures reach 12–15°C (Brinkman 2008; Buckmeier et al. 2013; Wegener et al. 2017); however, Kluender et al. (2016) found that the prespawn period began at colder temperatures (i.e., 8°C). Because spawning generally coincides with seasonal (April–July) flooding (Buckmeier et al. 2017), off-channel habitats, such as inundated floodplains, backwaters, tributaries, and large embayments, provide important spawning habitat (Suttkus 1963; Mendoza et al. 2008; Inebnit 2009). Off-channel areas may also provide nursery habitat for juvenile Alligator Gar after hatch (Ferrara 2001; Robertson et al. 2018; Smith et al. 2020). Buckmeier et al. (2013) and Kluender et al. (2016) indicated increased use of off-channel habitats during the spawning season at water temperatures greater than 20°C. Although unable to capture Alligator Gar in their surveys, Schumann et al. (2020, this special section) found a high occurrence of Longnose Gar, Shortnose Gar, and Spotted Gar in lower Mississippi River floodplain lakes. A postspawn period of increased adult activity has been associated with movement back to

main-channel habitats as seasonal floods recede (Buckmeier et al. 2013; Kluender et al. 2016). Finally, juvenile Alligator Gar generally tended to move less and use more off-channel habitats than adults (Sakaris et al. 2005; Buckmeier et al. 2013; Solomon et al. 2013).

Estimated home ranges for Alligator Gar appear quite variable, both among individual fish and among populations. Sakaris et al. (2005) found some of the smallest home ranges (mean = 6.6 km) in the Mobile–Tensaw Delta, Alabama, whereas Wegener et al. (2017) reported much larger home ranges (mean = 41.3 km) in the Escambia River system in nearby Florida. Buckmeier et al. (2013) found that in another coastal river, home ranges varied from 1 to 176 km (mean = 35 km). Finally, Brinkman (2008) reported that linear home range sizes for an inland Alligator Gar population in the Red River system, Oklahoma, ranged from about 6–50 km (mean = 15.3 km). Average home range size also varies seasonally (Buckmeier et al. 2013; Wegener et al. 2017), with larger home ranges being associated with generally increased movement during warmwater periods (>15°C).

Otolith microchemistry has also been used to assess habitat use and movement of Alligator Gar in Gulf coastal rivers (Daugherty et al. 2017, 2019b). In both the Guadalupe River–San Antonio Bay (Daugherty et al. 2017) and Trinity River–Galveston Bay systems (Daugherty et al. 2019b), otolith chemistry suggested the presence of multiple stocks that differed in prevalence on a

longitudinal gradient. River-resident fish spent their life exclusively in freshwater and were most common in upper-river reaches, whereas transient fish that used both river and bay habitats were more commonly found nearest the bay. Bay-resident Alligator Gar that exclusively used the saltwater bay habitat were relatively rare (i.e., about 2% of the fish examined). Alligator Gar are euryhaline (Suttkus 1963; Hoese and Moore 1998), and recent work has quantified salinity tolerances and found the species to be abundant in Gulf Coast bays (Daugherty et al. 2018). Suchy (2009) reported complete survival of larval Alligator Gar (TL ~ 15 mm), and tolerance to higher salinities increased with increasing size and age. Schwarz and Allen (2014) reported 100% survival of age-0 fish up to 400 mm TL in 24‰. These results suggest that Alligator Gar can spawn successfully in low-salinity estuarine environments (Daugherty et al. 2017).

FOOD HABITS AND FEEDING ECOLOGY

Due to long-held beliefs that Alligator Gar selectively prey on desirable sport fish species, such as crappies *Pomoxis* spp. and Largemouth Bass *Micropterus salmoides*, a relatively large body of literature exists on the diet in comparison with other biological attributes. Investigations of Alligator Gar food habits date to the early 1900s, when Hussakof (1914) reported observing a crappie in the stomach of an Alligator Gar. A multitude of studies since (summarized by Scarnecchia 1992) almost universally indicated that Alligator Gar feed opportunistically, thus consuming both game and nongame species in proportion to abundance. Only one study has reported a sport fish species dominating the diet: Garcia de Leon et al. (2001) found Largemouth Bass to be the primary diet item of Alligator Gar in Vicente Guerrero Reservoir, Mexico. However, those authors also reported that the majority of stomachs examined were empty as well as potential biases induced by their sampling design. Haase (1969) found that Longnose Gar are unlikely to negatively impact sport fisheries; rather, they are more likely to improve the fisheries via effective predation. Becker (1983) noted that fishery managers considered the use of gars to restructure stunted panfish populations. Grider (2013) found evidence that reintroduced juvenile Alligator Gar in Illinois selected for Gizzard Shad *Dorosoma cepedianum*. Ianni (2011) evaluated the use of stocked Alligator Gar and Spotted Gar to suppress invasive tilapias *Oreochromis* spp. Recent studies have expanded the understanding of food habits in coastal systems. DiBenedetto (2009) reported mullets (Mugilidae) to be the most common diet item in Terrebonne Estuary, Louisiana, and Felterman (2015) reported similar results for Terrebonne Estuary and Rockefeller Wildlife Refuge. Alligator Gar may play an

(2018) found that Alligator Gar abundances were equivalent to or far exceeded those of the Bull Shark *Carcharhinus leucas*, which is considered the most abundant shark species in Texas bays.

Additional recent work on Alligator Gar diet has focused on prey selection at early life history stages. Butler et al. (2019) documented several functional and behavioral changes in age-0 fish (15–70 mm TL) that facilitated a rapid transition to piscivory. Zooplankton were the primary diet item for fish up to 30 mm TL, whereas piscivory became increasingly more important at larger sizes. Using stable isotope analysis, Snow et al. (2020b, this special section) found that trophic position was positively related to the length of age-0 gars, including Alligator Gar, in Lake Texoma. Fish prey are generally considered to provide higher energetic returns than alternative prey (e.g., zooplankton and invertebrates; Galarowicz and Wahl 2005; Graeb et al. 2006; Butler et al. 2019). Thus, the availability of fish prey likely plays a critical role in supporting the rapid growth and survival of age-0 fish. This rapid transition to piscivory may also explain the high degree of cannibalism observed in the Alligator Gar. Mendoza et al. (2008) noted the importance of maintaining adequate densities of live prey to prevent cannibalism in culture environments.

GAR CULTURE

Gar culture techniques and applications have advanced over the past decade, with a network of researchers freely sharing knowledge and expertise. Of the seven gar species, the Alligator Gar, Tropical Gar, Cuban Gar, and Spotted Gar are the most commonly cultured, with focal species varying across the USA, Mexico, Central America, and Cuba. In the USA, Alligator Gar and Spotted Gar are the most frequently cultured species, with Alligator Gar culture being more widespread. The Alligator Gar and Tropical Gar are cultured in northeast and southern Mexico, and the Tropical Gar is the primary species produced in Central America. The Cuban Gar is the only cultured species of gar in Cuba.

Although gar culture in the USA primarily focuses on Alligator Gar and Spotted Gar, research on the induced spawning of gars began with the Cuban Gar in the 1970s in Havana, Cuba. Alligator Gar culture followed in 1982 (Environment, Natural Resources and Fisheries Ministry of México [Tancol, Tamaulipas] in collaboration with Universidad Autónoma de Nuevo León [UNAL; Monterrey, Mexico]), and Tropical Gar in the late 1980s (Universidad Juárez Autónoma de Tabasco [UJAT; Villahermosa, Tabasco, Mexico]; Amador-del Ángel et al. 2006; Mendoza et al. 2008). Building on techniques developed and shared by colleagues at UJAT and UNAL, A. M. Ferrara developed Spotted Gar culture at Nicholls State

University (Thibodaux, Louisiana) in 2003. The majority of Alligator Gar cultured in the USA are produced by the U.S. Fish and Wildlife Service at the Private John Allen National Fish Hatchery (Tupelo, Mississippi) and the Tishomingo National Fish Hatchery (Tishomingo, Oklahoma).

New research on the aquaculture of gars has led to an improved understanding of gar development (Comabella et al. 2006, 2014), feeding and nutrition (Márquez-Couturier et al. 2006; Clay et al. 2011; Aguilera et al. 2012; Bollfrass 2012; Guerrero-Zárate et al. 2014; Frías-Quintana et al. 2015; Escalera-Vázquez et al. 2018; Huerta-Ortiz et al. 2018; Nájera-Arzola et al. 2018; Saenz de Rodrigáñez et al. 2018), and ultimately production (Mendoza et al. 2008; Bodin 2018). Applications of cultured gars are diverse, including biological and ecological research (Comabella et al. 2010; Ianni 2011; David et al. 2015; Bodin 2018), phylogenetics (Wright et al. 2012), and more recently, functional genomics (Amores et al. 2011; Braasch et al. 2016; Venkatachalam et al. 2018). Cultured Alligator Gar, Tropical Gar, and Cuban Gar have also been used to restore wild populations (Mendoza et al. 2002; Thomas and Hilsabeck 2011; W. Contreras-Sánchez, UJAT, personal communication; Andrés Hurtado, Centro de Reproducción de la Ictiofauna Indígena, Ciénaga de Zapata, Cuba, personal communication).

To culture gars, broodstock may be captive reared or wild caught. Captive broodstock may be wild caught and maintained at an aquaculture facility or may be the adult progeny of natural or induced captive spawns (Comabella et al. 2006; Mendoza et al. 2008; Patterson et al. 2019). Alternatively, adult fish may be collected for each spawn (Mendoza et al. 2008; Castillo et al. 2015; Armstrong and Purcell 2020, this special section). Induced spawns typically occur during the natural spawning season, the timing of which varies by species and latitude (David et al. 2015). Under laboratory conditions, out-of-season spawning of wild-caught Spotted Gar can produce winter cohorts (Bodin 2018). To synchronize gamete maturation and spawning behavior and maximize embryo production, hormone injections or implants of a synthetic analog of a gonadotropin-releasing hormone are typically used, although non-induced spawning may also occur (Mendoza et al. 2002, 2008; Frenette and Snow 2016; Patterson et al. 2019).

Gars are tolerant of poor water quality and can be maintained in high densities, and captive-reared broodstocks of the three *Atractosteus* species have been spawned in captivity (Comabella et al. 2006; Márquez-Couturier et al. 2006; Mendoza et al. 2008). Adult gar accept and can be maintained on pelleted floating feeds, but diets should be supplemented with live or frozen fish or other high-protein and high-lipid items, such as liver or squid, prior to induced spawning (Mendoza et al. 2008; S.R.D., unpublished data; G. Márquez-Couturier, UJAT, unpublished data).

Broodstock sex ratios of 1:3 and 1:4 (female : male) are recommended, although different ratios, single pairs, and gamete stripping have resulted in successful spawns and embryo production (Boudreaux 2006; Márquez-Couturier et al. 2006; Amores et al. 2011; David et al. 2015; Porta et al. 2019). A variety of nonlethal, species-specific morphologic features and vitellogenin assays have been used to assign sex of individual broodstock (Love 2004; Mendoza et al. 2012; McDonald et al. 2013, 2018). Additional work is needed to determine whether the use of morphologic features to identify sex can be applied widely across multiple populations.

Induced and non-induced captive spawns may be conducted in earthen ponds or in indoor or outdoor tanks of various sizes and compositions, including cement, fiberglass, or plastic tanks; plastic kiddie pools; and inflatable or framed recreational pools (Mendoza et al. 2008; Comabella et al. 2010; Bodin 2018; Porta et al. 2019). Greater control and easier observation, recapture, and movement of broodstock and collection of embryos can be accomplished in smaller spawning tanks (Porta et al. 2019). Round tanks are recommended over square or rectangular tanks, with preferred diameters of at least twice the TL of the longest fish (A.M.F., unpublished data). Water temperatures for spawning may range from 15°C to over 30°C depending on species and latitude (Haase 1969; Aguilera et al. 2002; Comabella et al. 2010; Frenette and Snow 2016; Scherrer et al. 2017; Bodin 2018). Long et al. (2020, this special section) found that incubation temperature was correlated with the timing of hatch and survival to the free-swimming stage in Alligator Gar and Spotted Gar, with colder temperatures being associated with delayed hatching and reduced survival.

Natural or artificial spawning substrates are provided and facilitate removal of adhesive embryos from spawning tanks (Mendoza et al. 2008; Frenette and Snow 2016; Bodin 2018; Porta et al. 2019). Substrates can be left in the spawning tank or can be removed with attached embryos. To facilitate collection of embryos, a sodium sulfite solution can be used to de-adhere embryos from spawning substrates (Stone and Ludwig 1993; Bodin 2018). To reduce cannibalism, larvae must be frequently graded by size. Broodstock and larval hormone treatments to reduce cannibalism have also been investigated (Mendoza et al. 2008; Castillo et al. 2015).

FISHERY MANAGEMENT

Over the last decade, much effort has been directed toward learning how to sample Alligator Gar populations both efficiently and with minimal bias. Schlechte et al. (2016) quantitatively assessed the selectivity of various sizes of black-mesh, number-21 twine multifilament experimental gill nets that have become the preferred gear for

sampling adult size-classes of Alligator Gar. The authors found that by weighting relative lengths of mesh panels ranging in size from 88.9 to 139.7 mm (bar measure), greater than 80% retention was achieved for a broad range of adult size-classes. Bodine et al. (2015) found that an aggressive predator strategy, characterized by short (i.e., <30-min) set times and relocation to new sampling sites when catch rates were low, resulted in an eightfold increase in Alligator Gar catch rates and minimized incidental mortality when sampling with multifilament gill nets. Populations are often sampled with gill nets during summer, when higher water temperatures result in increased metabolic and activity levels (Allen et al. 2017). Although typically considered facultative air breathers (Moyle and Cech 2000), gars receive 70–80% of their oxygen from the atmosphere at high (>22°C) temperatures but rely solely on the gills at low (<10°C) temperatures (Rahn et al. 1971). Thus, gars that are entangled in gill nets at increased water temperatures have the potential to effectively drown if unable to reach the water surface. Recent advances in side-scan sonar technology have provided a means of gaining insights into Alligator Gar abundance and distribution without the need to handle fish, which may provide a useful alternative approach to sampling remnant populations (Fleming et al. 2018).

In addition to evaluations of sampling gears for the Alligator Gar, retention of various tags has also been assessed. Buckmeier and Reeves (2012) estimated the retention of PIT tags, T-bar anchor tags (Floy), and coded wire tags in Alligator Gar, Longnose Gar, and Spotted Gar. Retention for all three tag types was high (i.e., ≥97%) through 800 d posttagging across all three species. However, the authors noted that after 500 d, Floy tags became inconspicuous due to extensive algal growth and fading of the identifying information (e.g., phone number or identification number), which could confound mark–recapture and tag reporting assumptions. Snow et al. (2020a, this special section) examined the efficacy of immersion marking for juvenile Alligator Gar and found that otoliths could be effectively marked at concentrations from 500 to 700 mg/L for 4–6 h.

The growing popularity of hook-and-line angling and bowfishing for Alligator Gar has prompted agencies to actively manage existing populations, and a few recent studies have examined these fisheries and potential actions. Bennett and Bonds (2012) and Bennett et al. (2015) characterized bowfishing tournaments and bow angler demographics and attitudes in the Trinity River, Texas, fishery. Smith et al. (2018) modeled the effects of various length-based harvest regulation options for Alligator Gar and concluded that length-based regulations could be used to achieve various fishery management goals.

In addition to surveying state agencies on the status of Alligator Gar in their states, we also asked representatives

to provide information on current management actions (Supplement available in the online version of this article). Three states have developed Alligator Gar management plans to synthesize and focus their state-specific management efforts. Only one state (Missouri) has implemented habitat management efforts directed at Alligator Gar. The most common management actions used are stocking, harvest restrictions, and public education (Figure 3). Six states are stocking to repatriate populations, while three states use stocking to augment remnant stocks. Alabama employs stocking for both purposes.

Both recreational and commercial fishing regulations for Alligator Gar have undergone considerable change over the last decade (Figure 4). Four states have closed specific areas to fishing to protect known spawning locations or to provide refuges for remnant populations. Arkansas, Oklahoma, and Texas are employing seasonal closures during the spawning period to improve spawning success and protect adult fish from harvest during spawning. Florida and Kentucky have closed fishing for the species statewide. Harvest is prohibited in Ohio and Tennessee. Six states limit the number of Alligator Gar that recreational anglers can keep daily, annually, or based on a statewide quota. Arkansas has also imposed a length restriction (914-mm maximum length), and Louisiana limits recreational anglers on what methods they can use to target the species. Indiana and Illinois impose no restrictions on recreational anglers for the harvest of Alligator Gar; however, Indiana considers the species extirpated. Arkansas and Missouri require permits to participate in Alligator Gar fisheries.

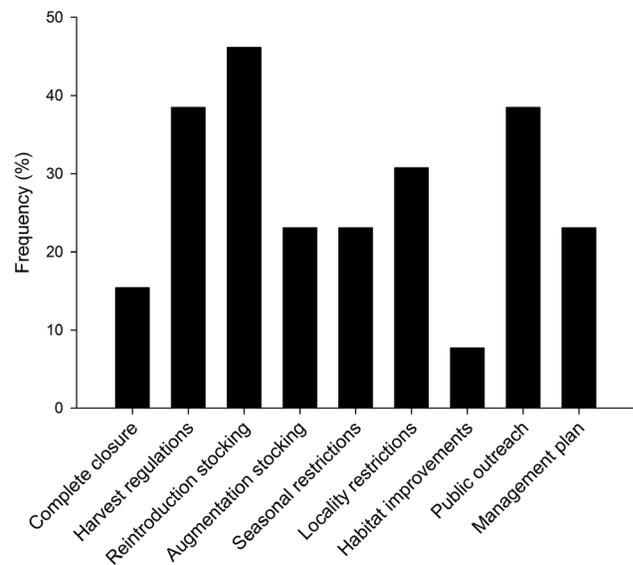


FIGURE 3. Relative use of management actions by 13 state conservation agencies since 2008 to conserve Alligator Gar populations in the species' historic range.

In 2009, no state agencies reported restrictions on commercial harvest of the species. In contrast, seven states have since imposed regulations prohibiting harvest with commercial fishing gears. Alabama and Indiana currently have no commercial restrictions for the species. Texas, Missouri, and Mississippi allow limited commercial harvest but require permits to participate in the fishery. Mississippi has additionally imposed length restrictions on commercial Alligator Gar catch. Commercial fishers are limited to 1 fish/d in Texas, and Louisiana has applied gear restrictions.

State conservation agencies categorize Alligator Gar in a variety of ways. These categories often determine which funding sources can be applied for management and

which staff members, if any, are assigned to oversee agencies' interests regarding the species. In 2018, Indiana and Ohio considered the Alligator Gar to be extirpated. However, with stocking events occurring along the Ohio River in Kentucky, individuals are beginning to migrate back into those states. Over half of the states ($N = 7$) in the species' range designate the Alligator Gar as a "species of greatest conservation need" or similar classification under state wildlife action plans. This classification frequently allows for the funding of conservation efforts and research for nongame species through the U.S. Fish and Wildlife Service's State Wildlife Grants program. Five states classify the Alligator Gar as a "commercial/rough fish," whereas Florida and Louisiana consider the species a "nongame fish." These two categories do not have any particular funding sources tied to them but would likely place the species under the purview of specific agency personnel. Finally, four states identify the species as a "sport fish/game fish." This classification would typically allow for the application of Sport Fish Restoration Program funds (i.e., the primary funding source for fisheries management in most state conservation agencies).

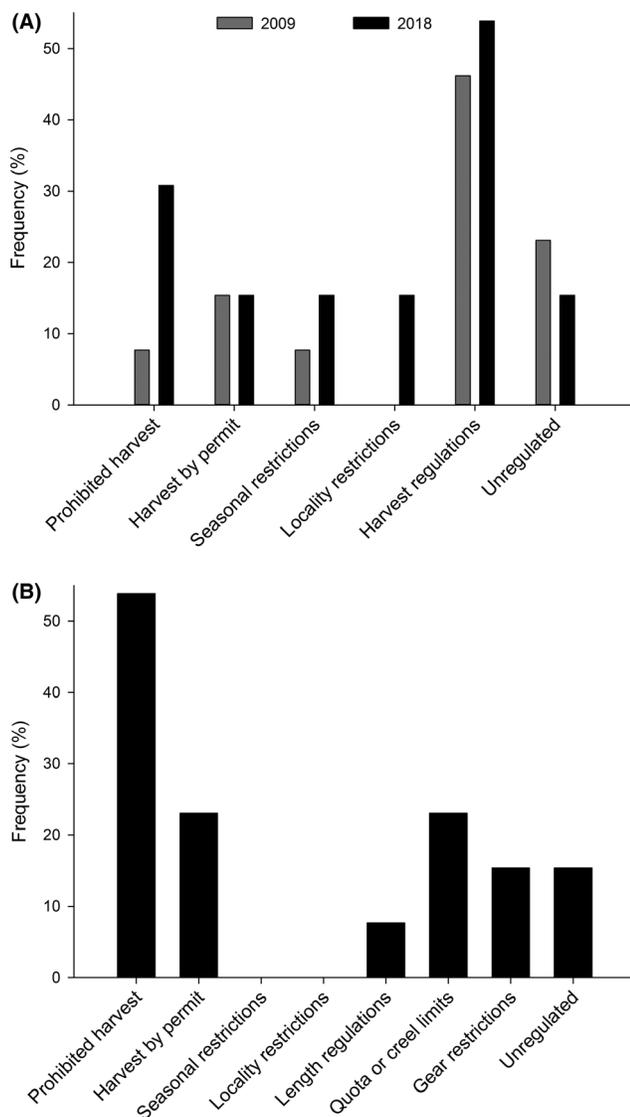


FIGURE 4. Frequency of (A) recreational and (B) commercial harvest restrictions for Alligator Gar in 13 U.S. states.

CONCLUSION

Much progress has been made over the past two decades in advancing the knowledge of Alligator Gar distributions, genetics, life history, culture, and management. However, our depth of understanding still lags far behind what is known of many other recreationally and commercially important fishes. We may have just begun to scratch the surface on potential differences among populations found in our coastal zones, major rivers, and reservoirs. Likewise, there has been little investigation of how population abundance or reproductive status may influence life history characteristics, including growth and the onset of maturity. Culture techniques have been established and stocking efforts have been initiated in many states, but evaluation of these efforts and development of best practices for re-establishing populations are needed. Finally, further research on the effects of recreational and commercial fishery exploitation on populations is similarly needed in addition to research on the efficacy of the various harvest regulations that have been implemented over recent years. The works published in this special section, and others referenced herein, will serve to inform the development of future research that addresses the remaining knowledge gaps concerning the Alligator Gar and growing gar fisheries.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.