

Long-term Declines in Two Apex Predators, Bull Sharks (*Carcharhinus leucas*) and Alligator Gar (*Atractosteus spatula*), in Lake Pontchartrain, an Oligohaline Estuary in Southeastern Louisiana

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ABSTRACT: We analyzed historic and current fishery independent data to determine if the abundance of two apex predators, bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*), in Lake Pontchartrain had changed significantly over the last half century. Lake Pontchartrain is an environmentally degraded oligohaline estuary in southeastern Louisiana that has experienced considerable changes in fish assemblage composition over this interval. Using gillnet, beach seine, and trawl data collected during three time periods (1953–1955, 1977–1978, and 1996–2005), we analyzed trends in abundance for *C. leucas* and *A. spatula* using generalized linear models with a negative binomial error structure and a log link. Lake Pontchartrain data were divided into four spatial locations (northwest, northeast, southwest, southeast) since each region represents a unique combination of anthropogenic and natural influences that could affect catches. For each species and gear type, we produced log-likelihood profiles for the instantaneous rate of change in relative abundance through time. Raw catches were generally lower for both species in the later surveys. *C. leucas* were not captured in beach seines since the 1950s and *A. spatula* were rarely captured in trawls or seines since the 1970s. Likelihood profiles of changes in abundance for *C. leucas* and *A. spatula* showed very large declines in both species since 1953. *C. leucas* declined by 98.6% (95% CI: 73.4–99.9%) in gillnets and became functionally extirpated in beach seines with a decline of 99.9% (95% CI: 23–99.9%). Among all gears, *C. leucas* declined by the same rate as in gillnets. The decline in *A. spatula* was also large with a decrease of 98.6% (95% CI: 73.4–99.9%) in beach seines and a decline of 99.2% (95% CI: 54.8–99.9%) in trawls since 1953. Catches of *A. spatula* in gillnets did not show a significant change over the study period. The continued decline of these two apex predators could seriously affect efforts to restore this degraded estuarine ecosystem.

Introduction

The role of bottom-up versus top-down effects in estuaries has been extensively studied (Armitage and Fong 2004; Hughes et al. 2004; Posey et al. 2006) but often without regard to the role of top apex predators, despite evidence that they play a key role in determining estuarine trophic structure (Power 1990; Jackson et al. 2001; Lotze et al. 2006; Myers et al. 2007). The removal of apex predators can lead to system effects that may cascade down through multiple trophic levels, fundamentally changing ecosystem structure (Power 1990; Terborgh et al. 2001). In aquatic ecosystems, the presence or absence of an apex predator can alter foraging behavior (Gilliam and Fraser 1987) and movement patterns (Fraser et al. 2006) of those

organisms that are potential prey. Such alteration of trophic structure can be especially disastrous in highly productive ecosystems, such as estuaries where primary producers can respond quickly to ecological imbalances (e.g., algal blooms).

Lake Pontchartrain is an oligohaline estuary in southeastern Louisiana that has been subject to numerous negative effects such as urban and agricultural runoff, shell dredging, overfishing, artificial saltwater and freshwater inputs, shoreline alteration, and industrial discharges (Penland et al. 2002; O'Connell et al. 2004, 2006). These influences have altered the local ecosystem, and fish assemblages in Lake Pontchartrain have undergone marked change since the 1950s (O'Connell et al. 2004). More specifically, the two most numerous Lake Pontchartrain fish species, bay anchovy (*Anchoa mitchilli*) and Atlantic croaker (*Micropogonias undulatus*), responded differently to a half century of effects. Between 1954 and 2000, the percent

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composition of *A. mitchilli* in trawl collections increased significantly whereas the percent composition of *M. undulatus* decreased significantly (O'Connell et al. 2004). While the decline of *M. undulatus* (a benthic member of the drum family) is understandable in light of the extensive alteration of mid-lake demersal habitat by widespread shell dredging between 1933 and 1990 (Francis and Poirrier 1999), the relative increase in *A. mitchilli* (a small, schooling, pelagic species) is less easily explained by such habitat destruction. Similar increases in such r -selected species is instead usually associated with a loss of top-down predation pressure (Power 1990). A decline or loss of apex predators within Lake Pontchartrain over the last half century could be a factor in the observed fish assemblage changes.

To test for possible declines in predators in Lake Pontchartrain since the 1950s, we used historic and recent fishery-independent data to assess changes in the abundance of two apex predators, bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*). In southeastern Louisiana *C. leucas* is a coastal marine species that enters oligohaline estuaries mostly as juveniles, although adults will also occur in these habitats during warmer months. *A. spatula* is primarily a freshwater species though it is tolerant of and occurs in the brackish conditions of coastal marshes (Douglas 1974). Fishing pressure, habitat alteration, and active management to remove all gar species as nuisance fishes has reduced *A. spatula* populations throughout its range, including Oklahoma, Texas, Alabama, Mississippi, and Florida (Gilbert 1992; Scarnecchia 1992; Ross et al. 2001; Aguilera et al. 2002). Regardless of their preferred habitats, both species occur in Lake Pontchartrain and are known to prey on estuarine species such as striped mullet (*Mugil cephalus*), hardhead catfish (*Ariopsis felis*), and blue crab (*Callinectes sapidus*; Lambou 1952; Darnell 1962; Goodyear 1967; Compagno 1984). Here we examine the longest survey conducted in an estuary that we are aware of that consistently targeted and captured apex predators using multiple gear types. Our goal was to determine if the abundances of these two apex predators declined significantly in Lake Pontchartrain over the last half century. By analyzing data collected from multiple gears (gillnets, beach seines, and trawls), we hoped to better determine habitat-specific trends.

Materials and Methods

We used data on *C. leucas* and *A. spatula* abundance obtained from historic and current gillnet, beach seine, and trawl surveys conducted in Lake Pontchartrain (Fig. 1). These surveys were conducted during three time periods since the

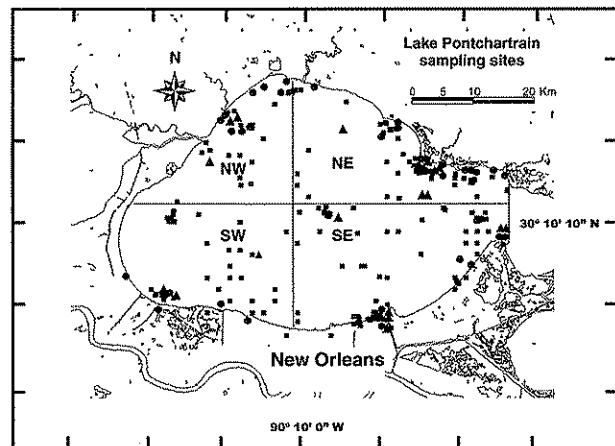


Fig. 1. Map of the Lake Pontchartrain area showing locations sampled by gillnets (triangles), beach seines (circles), and trawls (squares) during fishery-independent surveys from 1953 to 2005.

1950s: 1953–1955, 1977–1978, and 1996–2005 (Table 1). Sampling during the 1950s and 1970s was conducted monthly at both fixed stations and random sites throughout Lake Pontchartrain (Suttus et al. 1954; Thompson and Fitzhugh 1985). Recent sampling (1990–2005) was carried out quarterly at 15 fixed stations until June 2000 when monthly sampling was implemented at the same locations (O'Connell et al. 2004). Over the entire period, there were 269, 532, and 984 samples taken within Lake Pontchartrain with gillnets, beach seines, and trawls, respectively (Table 1). For these analyses we divided the Lake into four spatial locations (Fig. 1; northwest [NW], northeast [NE], southwest [SW], southeast [SE]) since these areas represent unique combinations of anthropogenic and natural influences (O'Connell et al. 2004), which could affect catches.

Trends in abundance of *C. leucas* and *A. spatula* were analyzed using generalized linear models. Generalized linear models relax many of the assumptions associated with traditional linear models such as analysis of variance or linear regression by allowing the mean of a population to depend on a linear predictor through a nonlinear link function, such as a power function, log function, or logit function, among others (McCullagh and Nelder 1989). The distribution of the response variable can be any member of the exponential family of distributions (e.g., Poisson, binomial, gamma) rather than just the normal distribution. The use of such models is common when estimating long-term trends in population abundance or estimating environmental effects on species status (Myers et al. 2007). In this instance, temporal trends in abundance of *C. leucas* and *A. spatula* were estimated

TABLE 1. Summary of Lake Pontchartrain sampling effort and number of bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*) collected for each gear type from 1953 to 2005. Sampling effort is the number of collections made in a particular year (#). No gillnet data were collected in 1953–1955 and 1996–1997.

Year	Gillnet			#	Beach seine		#	Trawl	
	#	<i>C. leucas</i>	<i>A. spatula</i>		<i>C. leucas</i>	<i>A. spatula</i>		<i>C. leucas</i>	<i>A. spatula</i>
1953	0			36	1	5	52	0	0
1954	0			34	2	5	118	0	1
1955	0			1	0	0	29	0	1
1977	0			6	0	4	6	0	0
1978	46	21	5	71	0	0	135	0	4
1996	0			1	0	0	3	0	0
1997	0			33	0	0	56	0	0
1998	8	4	2	17	0	0	32	0	0
1999	1	0	0	12	0	0	10	0	0
2000	30	0	0	54	0	0	97	0	0
2001	65	4	0	96	0	0	183	0	0
2002	61	6	3	94	0	1	144	0	0
2003	27	3	0	45	0	0	61	0	0
2004	13	0	1	13	0	0	24	0	0
2005	18	0	0	19	0	0	34	0	0

using generalized linear models with a negative binomial error structure and a log link.

The probability of catching C_i individuals of a given species in survey set i was assumed to follow a negative binomial distribution with the mean μ_i ,

$$p(C_i; k; \mu_i) = \frac{\Gamma(C_i + \frac{1}{k})}{\Gamma(C_i + 1)\Gamma(\frac{1}{k})} \frac{(k\mu_i)^k}{(1 + k\mu_i)^{C_i + (\frac{1}{k})}}$$

for $C_i = 0, 1, 2, \dots$

there Γ is the gamma function and k is the negative binomial dispersion parameter. The expected mean catch of a given species is then

$$\log(\mu_i) = \beta_y y_i + \beta_s s_i + \beta_m m_{i,j} + \beta_z g_{i,j} + \log(O_i)$$

where y_i is the year in which set i occurred, s_i is salinity, and O_i is the size of the fishing gear, treated as an offset term. The term $m_{i,j}$ is an indicator variable for the month in which the set occurred such that $m_{i,j} = 1$ if set i was in the j^{th} month or otherwise $m_{i,j} = 0$. Likewise, $g_{i,j}$ is an indicator variable for gear type such that $g_{i,j} = 1$ if gear type j was used in set i , otherwise $g_{i,j} = 0$. The generalized linear models allow estimation of the instantaneous rate of change in abundance, β_y , and symmetrical errors. We took the approach of examining the log-likelihood profiles of β_y that allows for nonsymmetrical errors and estimation of trends in cases with few data points. For each species and gear type, we produced log-likelihood profiles for the instantaneous rate of change in relative abundance through time, and displayed them as raindrop plots (Barrowman and Myers 2003). Interpreting raindrop plots is

a straightforward process whereby the horizontal limits represent the upper and lower 95% confidence limit of the estimated parameter (abundance) and the maximum likelihood estimate for the parameter is where the plot is thickest, as it is proportional to the log-likelihood.

Results

In 50 years of intermittent sampling, 38 *C. leucas* were captured in gillnets and three were captured in beach seines in all nearshore areas of Lake Pontchartrain except the SE (Fig. 2 and Table 1). During these sampling efforts *C. leucas* was never collected by trawls or in any offshore areas of the

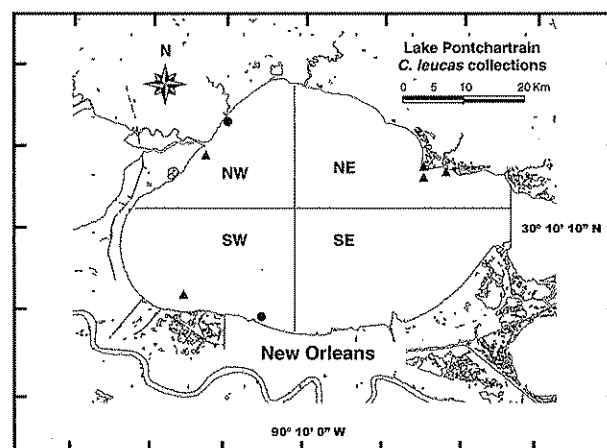


Fig. 2. Map of the Lake Pontchartrain area showing locations of bull shark (*Carcharhinus leucas*) collections made during fishery-independent surveys from 1953 to 2005 relative to all sampling locations used. Gillnet (triangles) and beach seine (circles) collections are shown. No bull sharks were collected in trawls.

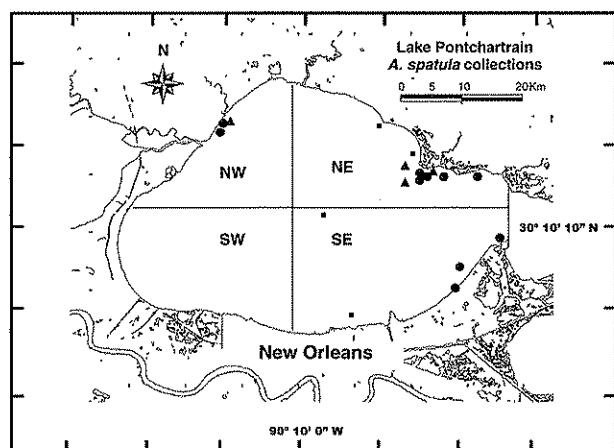


Fig. 3. Map of the Lake Pontchartrain area showing locations of alligator gar (*Atractosteus spatula*) collections made during fishery-independent surveys from 1953 to 2005. Alligator gar were collected by gillnets (triangles), beach seines (circles), and trawls (squares).

Lake (Fig. 2). Over the same period, 11 *A. spatula* were captured in gillnets, 15 were captured in beach seines, and six were captured in trawls in all areas of the Lake except the SW (Fig. 3 and Table 1). As well as being captured in nearshore areas, *A. spatula* was also captured in more open waters of Lake Pontchartrain (Fig. 3).

Raw catches and model estimates were generally lower for both species in later observations (Fig. 4 and Table 1). *C. leucas* has not been collected in beach seines since the 1950s. *A. spatula* has rarely occurred in beach seine or trawl collections since the 1970s. Both species continue to be collected in small numbers in later gillnet sampling efforts (Table 1).

Likelihood profiles of changes in abundance for *C. leucas* and *A. spatula* showed significant declines in both species since 1953 (Fig. 5). Instantaneous rates of decline can be converted to absolute declines by employing the formula: $1 - \exp(-\beta_y X \pm 1.96(\text{s.e.})X)$, using the assumption that the decline is constant over the period X and s.e. is the standard error of the instantaneous rate of decline in abundance (β_y). *C. leucas* declined by 98.6% (95% confidence interval [CI]: 73.4–99.9%) in gillnets and became functionally extinct in beach seines with a decline of 99.9% (95% CI: 23–99.9%).

The decline in *A. spatula* was also large with a decrease of 98.6% (95% CI: 73.4–99.9%) in beach seines and a decline of 99.2% (95% CI: 54.8–99.9%) in trawls since 1953. Collections of *A. spatula* in gillnets exhibited no significant change over the study period. Among all gears, *A. spatula* declined by 98.1% (95% CI: 88.0–99.8%). The raindrop plots allow an easy comparison among all gear types; the

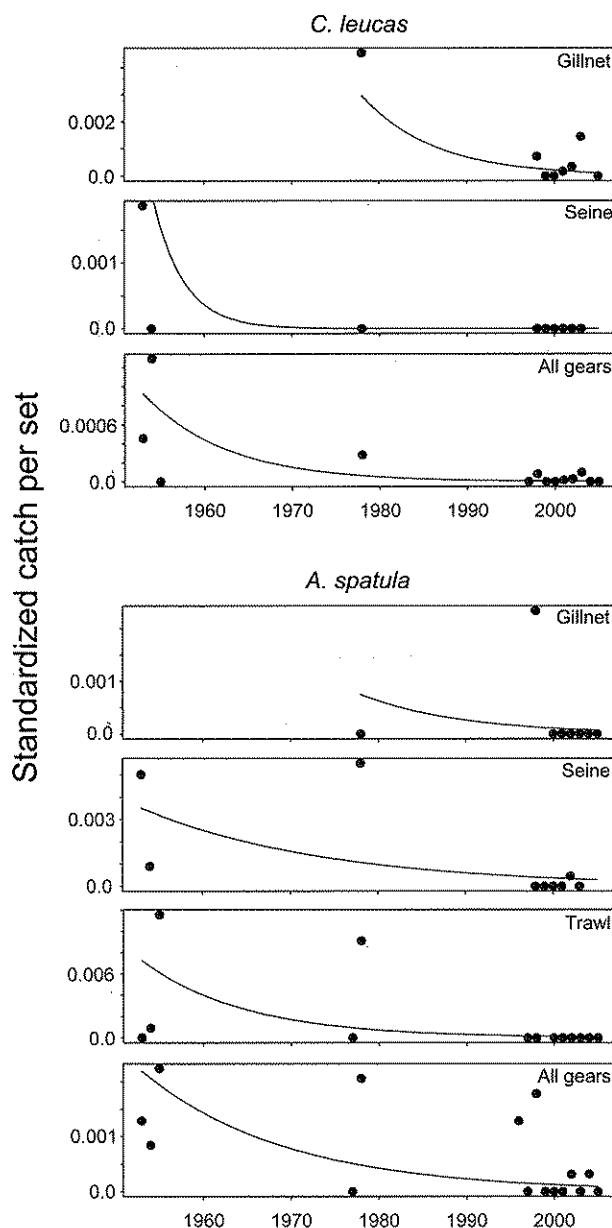


Fig. 4. Generalized linear model estimates of standardized catch rates per set of bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*) captured in gillnets, beach seines, trawls, and all gears combined during sampling of Lake Pontchartrain from 1953 to 2005. Circles represent estimates for a particular year while smooth lines represent long-term trends in abundance. Within each gear type, catch rates were adjusted to a standard of a 91-m gillnet, 15-m beach seine, or 5-m trawl.

rates of decline are consistent among all gear types as shown by the overlapping raindrops.

Discussion

The significant decline of *C. leucas* and *A. spatula* in Lake Pontchartrain mirrors a worldwide trend of

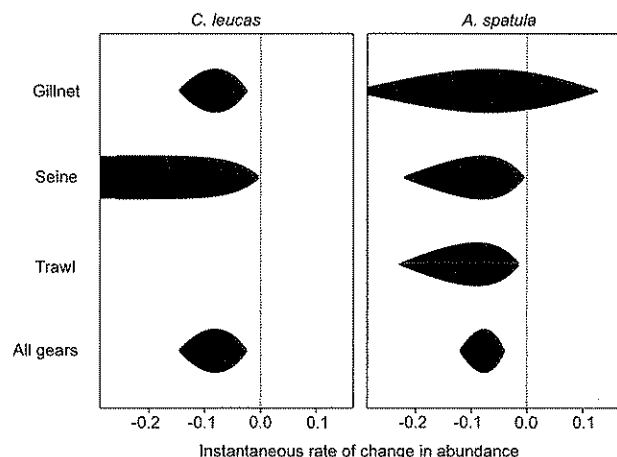


Fig. 5. Rates of change in abundance in bull sharks (*Carcharhinus leucas*) and alligator gar (*Atractosteus spatula*) captured in gillnets, beach seines, trawls, and all three gears combined during sampling of Lake Pontchartrain from 1953 to 2005. Estimates were derived from generalized linear models using a negative binomial error structure and a log-link. Plots (raindrop plots) are generated from likelihood profiles of the instantaneous rate of change in abundance. The thickest portions of the raindrop plots correspond to estimated instantaneous rates of change, while the limits of the plots represent the lower and upper 95% confidence limits.

apex predators becoming rare in estuarine and marine environments (Baum et al. 2003; Baum and Myers 2004; Ward and Myers 2005). Species at the top of coastal food webs are the most vulnerable to the multiple effects associated with human development of shorelines. Direct fishing mortality, either through overharvesting or bycatch, is higher for apex predators in easily accessible nearshore habitats compared to more remote offshore areas (Garcia de Leon et al. 2001). Human development of coastal areas tends to eliminate shallow nearshore habitats used as nurseries or refugia for juvenile stages of these organisms (Peterson et al. 2000). Pollution associated with these high human densities (e.g., heavy metals) is also more likely to affect apex predators rather than lower trophic animals due to the process of bioaccumulation (Mason and Sullivan 1997; Chen et al. 2000). While it is difficult to tease apart the relative damage caused by each of these effects to apex predators, the loss of higher-trophic organisms from aquatic communities is a clear sign of environmental degradation, because these less common and more specialized species are the most vulnerable members of the ecosystem.

The most dramatic decline was that of *C. leucas* in beach seine samples. In Lake Pontchartrain the shallow nearshore habitats sampled by beach seines are considered prime nursery grounds for many estuarine-dependent and marine species, including *C. leucas* (O'Connell et al. 2005). Most *C. leucas*

collected in these habitats by beach seines are pups born the previous spring (Clark and von Schmidt 1965). While this significant decrease of juvenile *C. leucas* over half a century could be attributed to effects occurring outside of the estuary itself (e.g., overharvesting of adults, bycatch), the long-term loss of vegetated shallow-water nursery habitats likely contributed to declines in all local fishes including apex predators (O'Connell et al. 2006). Between 1900 and 1980 as habitats degraded, fisheries production in the Lake declined by 49% (Stone 1980). During the early twentieth century (1920–1930s), extensive portions of the shoreline in the SE region were converted to concrete seawall and riprap with the expansion of suburban New Orleans (O'Connell et al. 2004). Shallow vegetated habitats were converted to deep water habitats with high wave energy and hard-bottom artificial substrates. It is interesting to note that since this habitat change, *C. leucas* have not been collected in the SE region using any gear type in the last half century (Fig. 2). The loss of submersed aquatic vegetation (SAV) from shallow water habitats is a Lake-wide phenomenon with only the NE region retaining extensive beds of vegetation (Cho and Poirrier 2002). As recently as 50 years ago researchers described SAV as being abundant on both the north and south shores of this estuary (Suttkus et al. 1954). The less affected vegetated habitats of the NE region currently support the most stable fish assemblages (O'Connell et al. 2006) and have produced more occurrences of *C. leucas* and *A. spatula* over time than the other three regions of the Lake (Figs. 2 and 3). The long-term decline of juvenile *C. leucas* in Lake Pontchartrain appears closely related to the loss and degradation of these nearshore habitats.

Both adult and juvenile *C. leucas* were collected by gillnets in deeper, more pelagic habitats. As with the beach seine data, gillnet sampling showed a significant decline in this species since the 1950s, though the rate of change in abundance was not as large (Fig. 5). This trend may be more associated with mortality from bycatch and offshore overexploitation than habitat degradation within the estuary, because adult *C. leucas* spend the majority of their lives outside of the Lake in more marine habitats (Thompson and Fitzhugh 1985; Chesney et al. 2000). As with any estuary, discerning exact causes for declines in a species is problematic because of the natural variation associated with these ecosystems and the multiple environmental stressors linked to coastal areas worldwide (O'Connell et al. 2004). While the degradation of Lake Pontchartrain SAV habitats may have reduced the numbers of some potential prey species for adult *C. leucas*, many of the fishes eaten by these sharks have no strong

associations with plants (e.g., *M. cephalus*) and would not be affected by the loss of vegetation. Significant declines recorded by both gear types reiterate the likeliness that *C. leucas* in this coastal system is being affected by multiple stressors. The lack of trawl collections containing *C. leucas* implies that they are very good at avoiding the smaller trawl nets used in these surveys, though they have been caught by larger offshore trawls (Shepherd and Myers 2005).

Significant declines in *A. spatula* were recorded for all three gear types with open-water habitats (i.e., those sampled with gillnets), reflecting the largest instantaneous rates of change in abundance, though also showing the largest variation in these values (Fig. 5). The scarcity of occurrence data for *A. spatula* has given this species nominal conservation status throughout its range based solely on its rarity (Gilbert 1992; Ross et al. 2001; Boschung and Mayden 2004). We offer the first quantitative long-term evidence that *A. spatula* has declined in abundance in Lake Pontchartrain. As with *C. leucas*, multiple factors are likely responsible for the decrease of this apex predator, though habitat loss and overharvesting appear to be the most substantial effects (Gilbert 1992; Etnier and Starnes 1993; Pflieger 1997). Loss of floodplain connectivity (i.e., alteration of freshwater spawning habitats) was linked to population declines of *A. spatula* in the Mobile River Basin of Alabama (Pringle et al. 2000). Floodplain connectivity in many of the streams and bayous that flow into Lake Pontchartrain on its north shore has been altered through urban and suburban development (O'Connell personal observation; Penland et al. 2002). Prior to human expansion into these riparian habitats, Lake Pontchartrain *A. spatula* likely moved onto forested floodplains and swamps to spawn during high flow periods as they do in other parts of their range (Etnier and Starnes 1993; Boschung and Mayden 2004). Loss of SAV habitat within the Lake may have also played a role in the decline of *A. spatula* because this species is also thought to use shallow vegetated backwater areas for spawning (Gilbert 1992; Garcia de Leon et al. 2001). In another Louisiana coastal system, greater amounts of *A. spatula* biomass were found in vegetated habitats versus nonvegetated habitats (Weaver 1969). Habitat degradation in multiple areas has probably affected all life history stages of *A. spatula* from loss of vegetated nursery habitats (juveniles), loss of habitats for prey species (fishes and crabs in Lake Pontchartrain), and loss of floodplain spawning habitat (adults).

Beyond habitat destruction, populations of *A. spatula* have been reduced by recreational and commercial fishing (Garcia de Leon et al. 2001;

Aguilera et al. 2002). Gars as a group have been widely targeted for destruction by management agencies, because they are considered nuisance species in some fisheries (Scarnecchia 1992; Pflieger 1997). Whereas many recreational anglers view gars as direct competitors to preferred game fishes, commercial fishers consider these large fishes as significant threats to their fishing gear. Adult *A. spatula* are known to destroy gillnets and trawls in both estuarine and freshwater habitats (O'Connell personal observation; Cook 1959). Increasing appreciation for biodiversity in recent years has likely helped gar populations as management efforts have changed from attempts to limit or exterminate gar populations to conserving whole aquatic ecosystems (Scarnecchia 1992). Beyond conservation there is also growing interest to manage *A. spatula* as both a game species (e.g., bow hunting in particular; Ross et al. 2001) and a commercial species (Garcia de Leon et al. 2001). There are also some preliminary attempts to examine the possibility of culturing *A. spatula* as an aquaculture species or at least to use hatchery techniques to augment declining natural populations (Aguilera et al. 2002). While this current interest in *A. spatula* may help the overall conservation of the species, it remains to be seen whether populations of this apex predator can recover from the types of significant declines we report here.

Our results emphasize the value of estuarine habitats to nonresident species that may not be recognized as needing protection under typical management or conservation efforts in coastal areas. Besides maintaining or improving the habitat quality within the estuary itself, efforts should be made to retain the connectivity among all aquatic habitats. Without migratory corridors from rivers to estuaries to marine habitats, apex predators such as gars and sharks cannot assert important top-down pressure on the estuarine ecosystems. In Lake Pontchartrain the increase in dominance of *A. mitchilli* (a small, r-adapted species) in trawl collections over the last half century could be in part explained by the decrease in potential predators over this same period (O'Connell et al. 2004). The construction of barriers that impede the movement of both freshwater and marine predator species into estuaries (e.g., dams on rivers, surge-control structures in tidal passes) poses a significant threat to the local trophic structure. Without the biotic control offered by multiple apex predators, the restoration of degraded estuarine ecosystems such as Lake Pontchartrain will continue to be problematic.

ACKNOWLEDGMENTS

This work was funded by the Pew Global Shark Assessment, with additional support provided through grants from the United

States Fish and Wildlife Service, the National Marine Fisheries Service (National Oceanic and Atmospheric Administration Grant # NA96FW0380), and the Freeport-McMoran Foundation. Significant additional support was provided by the Louisiana Department of Wildlife and Fisheries. We are appreciative of the efforts of M. Catallo, H. Finley, K. Foote, D. Norriss, R. Pausina, and M. Schexnayder for sustaining the later and current portions of these sampling efforts. Special acknowledgments are given to R. D. Suttikus and the late B. A. Thompson for making available raw data from their respective comprehensive studies of Lake Pontchartrain and to H. L. Bart for allowing us access to the collection information at the Tulane University Museum of Natural History. J. M. Humphries developed the original database. We thank C. S. Schieble, K. G. Blanke, G. N. Fuentes, and N. E. Rios for their provision and collection of data. We also thank R. C. Cashner, J. M. King, and S. L. Penland for their continued encouragement and support of these endeavors. This manuscript represents publication No. 4 for the Nekton Research Laboratory, Pontchartrain Institute for Environmental Sciences.

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Received, December 7, 2006

Revised, June 7, 2007

Accepted, June 18, 2007