FEATURE

A Gap in the Armor: Spearfishing Reduces Biomass of Invasive Suckermouth Armored Catfish

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Suckermouth Armored Catfish spearfished from the San Marcos River.
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Introduced Suckermouth Armored Catfish (SAC; family Loricariidae) have invaded freshwater ecosystems globally. In the San Marcos River, Texas, control of invasive SAC includes spearfishing through public tournaments and contracted spearfishing, yet the effectiveness of these control efforts is unquantified. We used a recently developed length-based Bayesian biomass estimation method to assess spearfishing mortality relative to natural mortality and existing biomass relative to an unexploited population. During 2014–2018, 6,046 SAC were removed and measured (total length, cm) from the San Marcos River through spearfishing. Using the length-based Bayesian biomass, we found fishing pressure increased mortality 1.50- to 1.75-fold relative to natural mortality, and that relative biomass during 2016–2018 was significantly below the threshold at which stock depletion occurs. Our application of fishery stock assessment provides quantitative benchmarks for invasive species control and can be applied to other invaded systems where control methods are unassessed but length data from removed individuals are available.

INTRODUCTION

Human introduction of non-native species threatens aquatic biodiversity (Dudgeon et al. 2006), especially when non-native populations invade aquatic ecosystems inhabited by imperiled species (Havel et al. 2015). Non-native species invasions (i.e., population establishments that results in negative effects) into aquatic ecosystems are mediated by human activities, including movement in ballast water, intentional establishment for recreational purposes, escape from aquaculture facilities, and the aquaria and ornamental trades (Naylor et al. 2001; Padilla and Williams 2004). Species introductions tend to occur near human population centers or areas where human activities alter ecosystems (Johnson et al. 2008). In altered and invaded ecosystems, human activities aimed at controlling invasive populations (e.g., population suppression) stand the best chance of reducing negative ecological consequences (Ricciardi et al. 2011). However, the nature and application of control efforts vary according to the identity of the species and ecosystems involved with invasion (Koehn and MacKenzie 2004). For ecosystems inhabited by multiple imperiled species and where control of invasive species is desired, the utility and efficacy of control methods should be assessed (e.g., Barbour et al. 2011).

Non-native and invasive freshwater fish population control programs would benefit from broader application of new quantitative tools. Prevention of introductions is the best method for avoiding non-native invasions, and statistical models exist for prioritizing preventative measures (Kolar and Lodge 2002). Where populations are already introduced but are not yet established, eradication is possible when removal efforts effectively and efficiently remove individuals from the population (Kolar et al. 2010), and statistical models exist for quantifying eradication (Rout et al. 2009). More frequently, the consequences of invasive fishes are not fully recognized until population sizes have grown beyond the level at which eradication is possible. In these instances, control methods (e.g., chemical applications, physical removal of invasive species) are the most viable option for minimizing the effects of invasive fishes on native ecosystems (Meronek et al. 1996). Yet measuring the efficacy of a control method can be challenging because of limited amounts of information on population size, biomass, or reproductive rate (Simberloff 2003). Fishery stock assessment models have been applied to invasive fish control programs, and these protocols provide valuable insight into the efficacy of control efforts (e.g., Pennock et al. 2018). Moreover, recent advances in fishery stock assessment methods that require minimal information (e.g., Froese et al. 2018) have opened new avenues for evaluating invasive fish control efforts in freshwaters.

Suckermouth Armored Catfish (SAC; Siluriformes: Loricariidae) have invaded freshwater ecosystems on a global scale, facilitated by interactions between the aquarium trade, intentional and accidental releases, and ecological traits that make the species successful invaders (Orfinger and Goodding 2018). The global distribution of SAC is an artifact of exports from South America, stimulated by the aquarium trade, because the species efficiently remove algae from aquaria (Hoover et al. 2004). When individuals grow beyond the capacity to keep them in captivity, they are often intentionally released into aquatic systems where traits such as armor plating, facultative air breathing, and low trophic level allow survival in a range of ecosystems (Pound et al. 2011; Scott et al. 2017). Introduced populations often grow at exponential rates, resulting in high densities of individuals that disrupt native aquatic food chains, compete with native herbivore species, alter aquatic plant communities, and cause bank erosion and other socioeconomic impacts (Hoover et al. 2004; Hussan et al. 2019). Suckermouth Catfish *Hypostomus plecostomus* and the group generally known as Sailfin Catfish *Pterygoplichthys* spp. are among the most widely introduced SAC on a global scale (Figure 1A). Because the native range of SAC is tropical, non-native populations often invade ecosystems that are relatively thermally stable, such as sub-tropical waterbodies, power plant cooling waterbodies, and groundwater springs and rivers (Orfinger and Goodding 2018). In these thermally stable systems, SAC reproduce successfully, encounter few predators, and experience high survival rates (Barron 1964; Nico and Martin 2001; Cook-Hildreth et al. 2016). In response to these invasions, attempts to eradicate or at least control populations of invasive SAC are emerging in freshwater ecosystems (Nico and Walsh 2011), including groundwater-fed spring systems in the United States (Hill and Sowards 2015).

The San Marcos River in Texas represents a typical spring system invaded by SAC. All countries in North America have experienced SAC invasions, and within the United States, the states of Texas and Florida have experienced the most widespread introductions of SAC (Figure 1B). In Texas, multiple waterbodies in the south-central region of the state have experienced SAC introductions (Figure 1C). Introductions in the state of Texas are known from at least the 1960s (Nico and Martin 2001), and SAC were reported in the San Marcos River in the 1990s (Pound et al. 2011). Invasion of the San Marcos River (Figure 1D) is problematic because of the potential negative effects on the ecosystem and endemic species that are Threatened or Endangered (Perkin and Bonner 2011). Some examples include diet overlap with native herbivore fishes (Pound et al. 2011), competition with macroinvertebrates (Scott et al. 2012), and suppression of periphyton biomass (Datri et al. 2015). Because of these and other threats to the spring ecosystem, the Edwards Aquifer Authority, along with the City of San Marcos created the Edwards Aquifer Habitat Conservation Plan (EAHCP) in 2013. The EAHCP was designed to restore the San Marcos River to its native state, including recommended removal of non-native and invasive

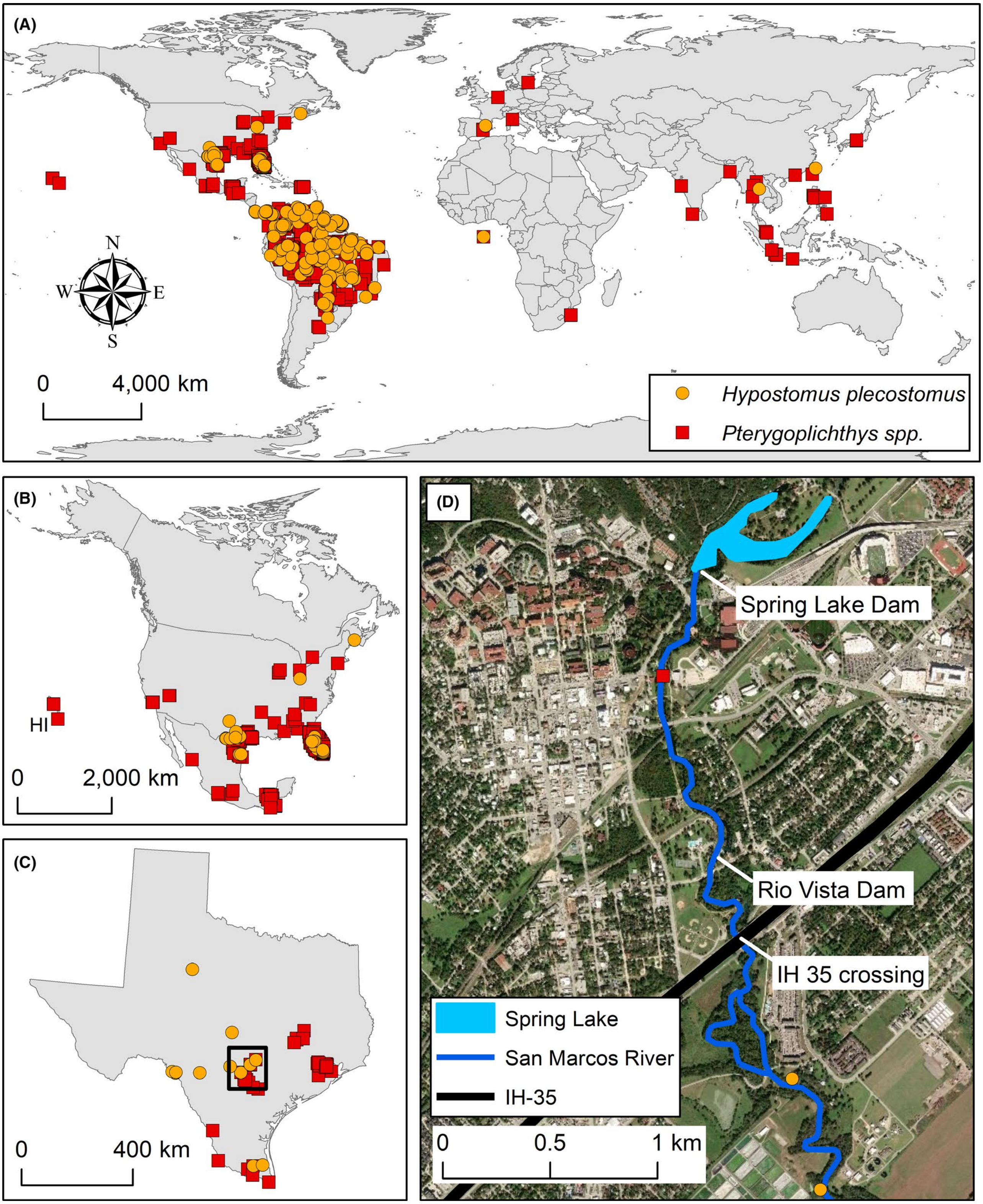

Figure 1. Map of Suckermouth Armored Catfish occurrences at multiple spatial extents according to the Global Biodiversity Information Facility. Occurrence records for Suckermouth Catfish *Hypostomus plecostomus* (orange circles) and *Pterygoplichthys* spp. (red squares) downloaded from the Global Biodiversity Information Facility are shown for **(A)** all countries, **(B)** countries in North America, **(C)** the State of Texas, and **(D)** in the San Marcos River, Texas. The portion of the San Marcos River included in this study extended from Spring Lake Dam to the Interstate Highway (IH) 35 crossing. Note that both species now occur throughout the segment of stream between Spring Lake Dam and IH 35.

animal and plant species. Removals sanctioned under the EAHCP have been conducted since 2013 through contracted spearfishing and public tournaments aimed at removal and composting of invasive SAC, tilapia *Oreochromis* spp., nutria *Myocastor coypus*, red-rim melania *Melonoides tuberculate,* and ramshorn snails *Phanorbarius corneus*. Public involvement and tournament-based participation represent application of emerging methods in invasive species control such as harvest incentives (Pasko and Goldberg 2014) and biocontrol by humans (Bajer et al. 2019). However, the effectiveness of the EAHCP program at reducing biomass of invasive SAC is not currently assessed.

The goal of this paper was to determine the effect of organized spearfishing on the mortality rate and biomass of SAC in the upper San Marcos River. To achieve this goal, we developed three objectives. Our first objective was to review the global distribution of SAC to document the extensiveness of invasions and the geographic areas where improved quantitative assessments of removal efforts might be applied. Our second objective was to assess temporal patterns in catch per tournament participant during 2015–2018. Our third objective was to use a newly developed statistical model known as the length-based Bayesian biomass (LBB) estimation method (Froese et al. 2018) to assess changes in the length–frequency of SAC harvested from the San Marcos River with spearfishing during 2014–2018. We hypothesized that spearfishing would increase mortality relative to natural levels and that this increased mortality would contribute to a reduction in biomass relative to an unmanaged scenario. Although no management goals specific to SAC mortality rate and relative biomass currently exist, the quantitative values identified through our retrospective analysis can be used to identify management goals for the future. Our approach represents the application of a new fisheries stock assessment tool to the problem of invasive fish management and can be applied to other invasive species control programs to quantify control efficacy where length data from removed individuals are available.

METHODS

Study Area

We documented the global distribution of SAC and assessed the efficiency of spearfishing removals in the upper 2 km of the San Marcos River, Texas. Global distribution data were downloaded using the Global Biodiversity Information Facility (GBIF; available: https://www.gbif.org/). We searched the GBIF database for "*Pteryoplichthys* spp." (GBIF 2019a) and "*Hypostomus plecostomus*" (GBIF 2019b) because these classifications were most common in literature reviewing invasions by SAC (Orfinger and Goodding 2018). All GBIF occurrences that were georeferenced were plotted at three scales, including global, North America, and Texas (with focus on the San Marcos River). The San Marcos River originates from the Edwards Aquifer at a series of artesian springs in San Marcos, Texas. The headwaters are impounded by Spring Lake Dam, and Spring Lake is the most upstream known distribution of SAC in the San Marcos system. Water quality in the San Marcos River includes year-round 23°C water temperature, slightly basic pH, and low turbidity during base flows outside of flood events (Groeger et al. 1997). The upstream reaches of the San Marcos River are entirely surrounded by urban land uses (Perkin et al. 2012), yet many imperiled species have persisted despite the urbanized landscapes (Perkin and Bonner 2011; Kollaus et al. 2015). Five Threatened or Endangered species inhabit the upper San Marcos River, including Fountain Darter *Etheostoma fonticola*, San Marcos Gambusia *Gambusia georgei*, San Marcos salamander *Eurycea nana*, Texas blind salamander *E. rathbuni*, and Texas wild rice *Zizania texana*. For this study, SAC that were removed from the San Marcos River between Spring Lake Dam and the Interstate Highway (IH) 35 crossing were included in analyses, though occurrences of SAC do extend further downstream (Figure 1D).

Tournament and Spearfishing Efforts

Atlas Environmental organizes and conducts biannual spearfishing tournaments lasting 3–4 weeks during fall (November) and spring (February–March). During tournaments, SAC, tilapia, snails, and trash are removed by tournament participants via snorkeling and pole-spears. Tournament participants are given three, 5-hour time slots to remove invasive species within their delineated reach (i.e., Spring Lake Dam to Rio Vista Dam, or Rio Vista Dam to the IH 35 crossing) and only two participants are allowed within each reach per time slot. All speared SAC and tilapia are retained and later measured for total length (cm). Outside of these tournaments, Atlas Environmental conducts two-person, year-round efforts of spearing twice a month from October to April and twice a week from May to September. Combined, tournaments and year-round spearfish result in a nearly continuous removal of SAC, but the largest number of SAC at one time are removed during tournaments. For our study, we used length data from SAC speared during tournaments and year-round spearfishing efforts.

Statistical Analysis

We estimated relationships between the number of SAC speared by tournament participants and time during 2015–2018 using a negative binomial generalized additive model (GAM). We combined all SAC speared by tournament participants across time slots to estimate the number of SAC removed by each participant during each season of each year. A value of zero was assumed when no SAC were retained or submitted by the tournament participant at the end of the time slot. Fall 2014 tournament data did not include SAC removal numbers for each participant per time slot and was excluded from the analysis. We fit a GAM in which number of SAC speared was the response (dependent) variable and time in days since the initial tournament with sufficient data (i.e., spring 2015) was used as a predictor variable with a smoothing function. The smoothing function allowed us to test for a significant change in the number of fish speared through time. We employed a negative binomial error distribution because many tournament participants reported zero fish and the data were overdispersed (Cameron and Trevedi 1998). This resulted in the distribution of SAC speared being heavily skewed towards zero with values ranging up to 43 fish per participant. We fit the GAM using the "gam" function from the "mgcv" package (Wood 2017) with family = "nb" in the R statistical environment (R Core Team 2018). The "mgcv" function includes a significance test of the smoothing function (in our case time) based on a Chi-square test, which allowed us to determine if the number of fish speared during tournaments differed through time.

We applied the LBB estimation method of Froese et al. (2018) to assess the influence of spearfishing on SAC mortality and biomass using data from both the tournament and contracted spearfishing. The LBB method relies only on length–frequency data as input, and from these data computes a series of standard fisheries equations to derive estimates of relative fishing mortality and approximate current exploited biomass relative to unexploited biomass. The LBB method first uses length–frequency data to fit the Von Bertalanffy (1938) growth equation as described by Beverton and Holt (1957). From this equation, estimates of growth rate (K), asymptotic length (L_{inf}), and the length where 50% of individuals are retained by the gear, otherwise known as the length of first capture (L_c), are derived. The LBB then estimates ratios of natural mortality (M) to K (i.e., M/K) and fishing mortality (F) to K (i.e., F/K). These parameter estimates allow for estimating biomass depletion or the ratio of current stock size (B) relative to unexploited stock size (B_0) as a measure of relative biomass (B/B_0). Moreover, the LBB approach provides an estimate of optimal L_c (L_{c_opt}) that represents the highest catch and biomass for a respective fishing mortality that minimizes impact on size structure (Froese et al. 2016), as well as the length of highest biomass (L_{opt}). For each of these estimates, the LBB provides posterior distributions with 95% confidence intervals based on a Bayesian analysis assuming a Dirichlet-multinomial distribution (Thorson et al. 2017a). Priors for L_{inf} are derived by pooling data across all years and fitting a nonlinear least squares estimator function as described in detail by Froese et al. (2018).

The LBB is appropriate when applied to fish species that grow throughout their lifetime, length data are representative of lengths within the exploited size range, and populations do not experience strong recruitment pulses (Froese et al. 2018). Suckermouth Armored Catfish continue to grow throughout their lifetime, and often outgrow aquaria during later life stages, after which intentional releases into natural ecosystems often occur (Hoover et al. 2004; Pound et al. 2011). Because the data we used for analyses were collected from fish that were speared, and because adequate sample sizes were obtained, the size ranges included in this study are reflective of lengths within the exploited size range. Reproductive ecology of SAC in the San Marcos River varies seasonally with photoperiod, as it does in the native range of South America, and there is no evidence that spawning or recruitment is subject to pulse events (Cook-Hildreth et al. 2016). Hordyk et al. (2019) provided an alternative equation to Froese et al. (2018) for estimating length distributions and suggested that the assumed default $M/K = 1.5$ might not apply to all fishes. We assess the relationship between M and K for *Hypostomus* spp. using the "FishLife" package described by Thorson et al. (2017b) and found predicted values of M (0.35) and K (0.15) that give a ratio (i.e., 2.3) higher than the default of 1.5 (Froese et al. 2018). Given this finding, we proceeded with fitting LBB model using supplementary R code from Froese et al. (2018), but modified the default M/K ration from 1.5 to 2.3 as suggested by Hordyk et al. (2019). We provide supplemental material illustrating results obtained from the default M/K ratio of 1.5 (Appendix S1) but focus on results obtained from the M/K ratio of 2.3 in the manuscript. We conducted all analyses in R version 3.6.1 (R Core Team 2018).

RESULTS

A total of 6,046 SAC were removed from the upper San Marcos River through spearfishing during 2014–2018 (Figure 2). Spearfishing occurred from Spring Lake Dam down to the IH 35 crossings and resulted in annual removals during 2014 (n = 1,168), 2015 (n = 1,277), 2016 (n = 1,011),

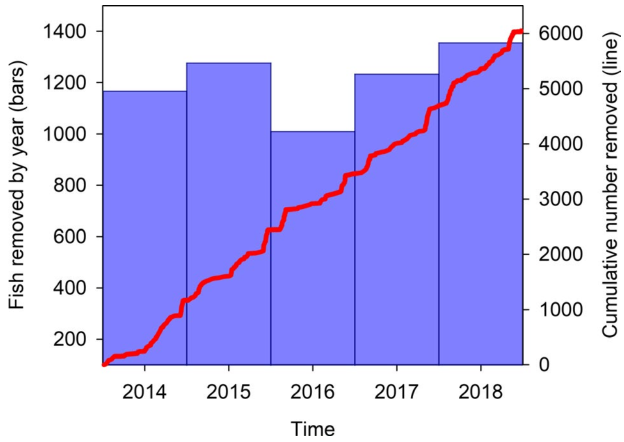

Figure 2. Annual number of Suckermouth Armored Catfish removed from the San Marcos River using spearfishing (blue bars) and the cumulative number removed through time (red line) during 2014–2018. These data include tournament removals plus contracted spearfishing removals.

2017 (n = 1,234), and 2018 (n = 1,356). Among the 6,046 fishes, 19 were Sailfin Catfish (length range = 21.6–62.2 cm) and 6,027 were Suckermouth Catfish (TL range = 10.2–59.7 cm). We focused on Suckermouth Catfish for the catch and LBB analyses given their dominance in the Upper San Marcos River.

In total, 307 participants provided tournament data for 2015–2018. Tournament participation varied between 20 (spring 2016) and 52 (fall 2018) with more spearfishers generally participating in the fall tournaments. Overall, tournament participants accounted for 2,784 (46%) of the SAC removed, with the remaining fishes taken through contracted spearfishing. Fish removed during an individual tournament event ranged from 170 to 400, and there was no significant relationship between the number of tournament participants and total number fish removed ($F_{1,7} = 1.586$, $P = 0.248$, $r^2 = 0.185$). Speared SAC per participant ranged 0 to 43, with distributions heavily skewed towards zero (Figure 3A). The GAM explained only 1.5% of deviance, equivalent to an adjusted r-square of 0.02, but the intercept parameter estimate (1.11) differed significantly from zero ($Z = 13$, $P < 0.01$) and the smoothing term for time was significant ($X^2 = 8.89$, $P = 0.026$). Fitted values for mean catch per tournament participant during events ranged 1.9 (fall 2018) to 3.9 (fall 2016), and there was a general decline in average number of SAC speared by tournament participants during fall 2016 through fall 2018 (Figure 3B).

Annual length estimates for all fish speared (tournament and contracted spearfishing) during 2014–2018 ranged 28.4–30.1 cm for mean total length, 22.4–25.7 cm for length at first capture, and 57.3–59.9 cm for asymptotic length (Figure 4). Mean length and length at first capture both increased during 2015–2018, though neither parameter reached the respective lengths that would maximize catch and individual fish biomass (Figure 5A). Relative fishing pressure was 1.11 (95% confidence interval = 0.91–1.43) during 2014 and declined to 1.00 (CI = 0.81–1.22) during 2015 before steadily rising across 2016 (1.42, 1.13–1.73), 2017 (1.72, 1.40–2.10), and 2018 (1.76, 1.39–2.31). Across all years, relative fishing pressure was 1.00 to 1.76 times higher than natural mortality (Figure 5B). Relative biomass was 0.29 (95% CI = 0.21–0.39) during 2014 and peaked at 0.30 (95% CI = 0.23–0.39) during 2015 before

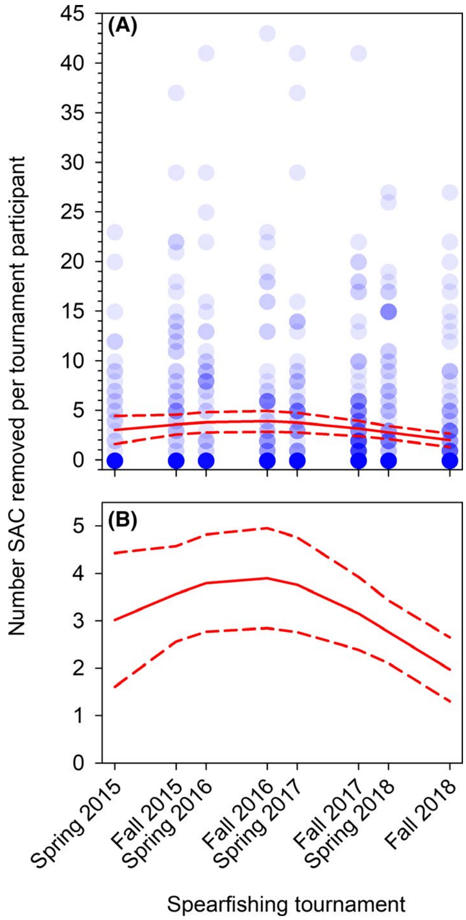

Figure 3. Number of Suckermouth Armored Catfish (SAC) removed by participants in the bi-annual spearfishing tournament during 2015–2018. **(A)** Blue circles represent the number of SAC removed by a single participant and darker symbols represent higher densities of data points. The solid red line is the fit (dashed lines +/- 95% confidence intervals) from a generalized additive model summarizing the number of SAC speared by individual tournament participants. **(B)** A zoomed-in view of the generalized additive model illustrating a recent decline in the number of SAC speared by the average tournament participant.

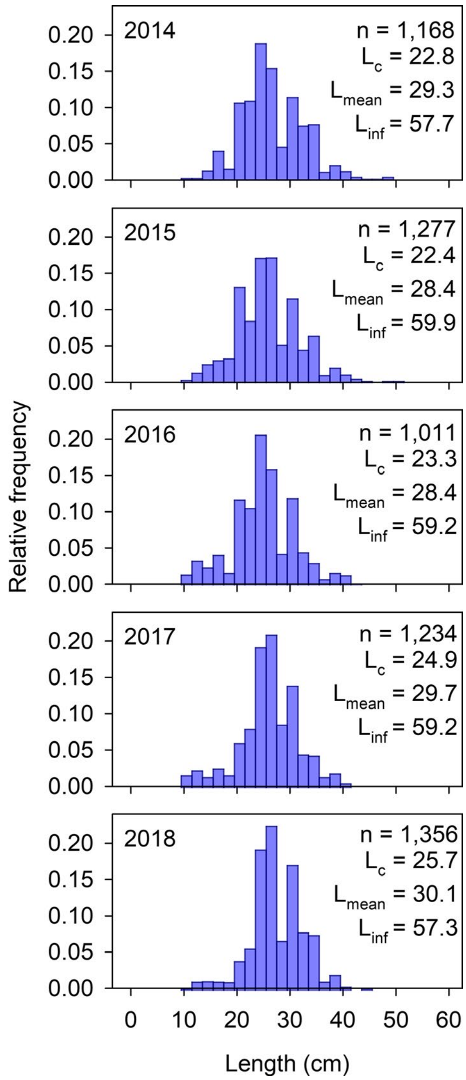

Figure 4. Annual relative length frequencies (2-cm bins) for Suckermouth Armored Catfish spearfished from the San Marcos River during 2014–2018. Relative length frequency data (n = sample size) were analyzed using a length-based Bayesian biomass estimation method to derive the length at first capture (L_c), mean length of spearfished individuals (L_{mean}), and the estimated asymptotic length (L_{inf}) for each year.

declining across 2016 (0.23, 0.17–0.30), 2017 (0.21, 0.15–0.26), and 2018 (0.20, 0.14–0.28). During 2016–2018, relative biomass was suppressed significantly below maximum sustainable yield with lower confidence intervals that overlapped the precautionary threshold at which fishery-induced stock depletion occurs (Figure 5C). Using the default M/K ratio of 1.5 did not change temporal trends, but did influence the magnitudes of estimates and thresholds (Appendix S1). Using the default ratio increased length thresholds for L_{opt} and L_{c_opt} (Appendix S1A), uniformly increased relative fishing pressure (Appendix S1B), and uniformly decreased relative biomass (Appendix S1C) estimates across all years.

DISCUSSION

Our work provides a case study for the application of fishery stock assessment tools to the problem of invasive SAC. Invasive SAC are well-established in the San Marcos River and previous qualitative estimates suggest they dominated fish biomass prior to control efforts (Pound et al. 2011). This dominance, paired with the occurrence of multiple endangered species that SAC likely negatively affect, means that controlling SAC populations is beneficial to the San Marcos River (Pound et al. 2011; Scott et al. 2012; Datri et al. 2015). However, the efficacy of control has not been evaluated, in part because of limited data on population size and natural mortality. Our application of the LBB provided inference on relative fishing mortality and relative biomass using only length–frequency data collected from speared fish. Results revealed spearfishing control efforts increases mortality 1.5- to 1.75-times beyond natural background mortality, and that biomass was 20–30% of what it would be without control. These values provide quantitative estimates of invasive population control and can be used as benchmarks for comparison with future efforts in the San Marcos River or in other invaded ecosystems where length data are collected from individuals as they are removed from populations.

Invasive species control efforts that operate efficiently might be expected to increase mortality and reduce biomass, but quantifying these effects can be challenging. At least one example of eradication of invasive SAC occurred as the result of spearfishing in a spring ecosystem in Florida. The Rainbow River, Florida is a spring run system like the San Marcos River and was invaded by SAC circa 2002. In the Rainbow River, early detection and removal of SAC through spearfishing before evidence of recruitment resulted in successful eradication (Hill and Sowards 2015). Elsewhere in the United States, attempts to eradicate SAC from freshwater systems have failed, including portions of Hawaii (Nico and Walsh 2011), Puerto Rico (Bunkley-Williams et al. 1994), and Nevada (Courtenay and Deacon 1982). Though eradication is rare, previous works have shown that control of invasive fishes, even in the absence of eradication as the end point, can be beneficial (Britton et al. 2011). However, other studies have found that recolonization by invasive species into control areas can negate control efforts and result in little to no net benefit (Propst et al. 2015). Consequently, quantitative evaluation of control efforts is necessary to measure benefits against the sometimes high cost of removal. For example, Pennock et al. (2018) used fishery stock assessment tools to estimate the level of effort required to suppress introduced Channel Catfish *Ictalurus punctatus* in the San Juan River, New Mexico, USA. The authors found that although current levels of effort were suppressing abundance and biomass, increased effort would be necessary to cause fishing-induced stock depletion. In the case of SAC in the San Marcos River, recolonization from outside the control area could offset control efforts if fish move from downstream areas not spearfished, or if new individuals are continually introduced through recruitment and aquaria releases. Some invasive species exhibit compensatory recruitment that acts to offset adult mortality caused by control efforts (Zipkin et al. 2009), though this remains to be confirmed for SAC in the San Macros River. Our results suggest levels of effort applied during 2014–2018 resulted in an upward trend in relative fishing mortality and a non-significant downward trend in relative biomass. These trends were apparent in the LBB analysis despite consistent total removal during 2014–2018 (Figure 2) and an apparent decline in fish speared during tournaments in recent years (Figure 3). This pattern matches the theme highlighted by Allan et al. (2005), in which mean length and biomass of captured fish decline while fishing landings remain stable as exploitation continues. Over a long enough exploitation timeline, catch by weight and mean maximum length both begin decline if overfishing occurs (Allan et al. 2005). Indeed, we may have observed the start of such a pattern in our data, as catch per tournament participant appeared to decline from spring 2016 through fall 2018. Additional monitoring could indicate whether the system has reached the point where catch is declining due to control efforts. As spearfishing efforts continue in the San Marcos River, the baseline and time series data presented here will provide quantitative information for measuring trade-offs in the costs versus benefits of the San Marcos River SAC control program.

Caveats and limitations to the approach applied here should be considered in future applications. First, several factors likely contributed to the variability observed in tournament catch during this study. During each time slot, individuals had the option of removing other non-native

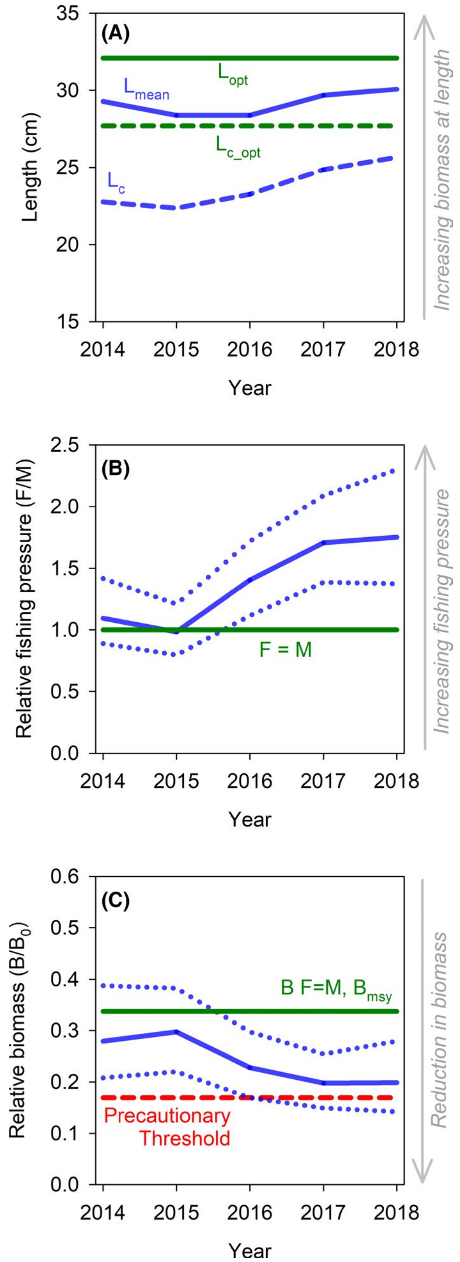

Figure 5. Results from length-based Bayesian biomass estimation method assuming an *M/K* ratio of 2.3 fit to length data from Suckermouth Armored Catfish (SAC) spearfished from the San Marcos River during 2014–2018. **(A)** Shows a time series for annual mean length (L_{mean}) of fish removed relative to the length at which fish reach their maximum biomass (L_{opt}) and the annual length at first capture (L_c) relative to the length at first capture that maximizes catch and biomass (L_{c_opt}). **(B)** Shows a time series of fit (solid blue line) and 95% confidence intervals (dotted blue lines) for estimated relative fishing pressure on SAC, displayed as fishing mortality (*F*) relative to natural mortality (*M*), including a reference where fishing mortality is equal to natural morality (*F=M*; green line). **(C)** Shows a time series of fit (solid blue line) and 95% confidence intervals (dotted blue lines) for estimated relative biomass of SAC, displayed as current biomass (*B*) relative to unexploited biomass (B_0). The reference lines in (C) show relative biomass that can support maximum sustainable yield (green line) and the precautionary relative biomass threshold below which overfishing occurs (dashed red line).

species (i.e., tilapia and nonnative snails) or collecting trash. Consequently, calculating catch by presuming constant and equal effort through time may not be a true representation of the time each tournament participant actively pursued spearing SAC. Additionally, spearfishing ability and experience may also explain some of the variability in catch among tournament participants (Malpica-Cruz et al. 2016). For future tournaments, noting how many times a participant has previously competed could help minimize variation in tournament catch data. Second, we found evidence that the ratio of natural mortality to growth rate (i.e., *M*/*K*) has considerable influence on conclusions drawn from the LBB. When we adjusted the default *M*/*K* ratio to a larger value identified through the FishLife package (Thorson et al. 2017b), we found the estimated level of relative fishing pressure decreased and the estimated relative biomass values increased. This finding supports the suggestion of Hordyk et al. (2019) that users of the LBB consider values other than the defaults when additional data are available. Finally, Froese et al. (2018) suggested *F*/*M* estimates are not recommended as absolute proxies for current fishing pressure, but that LBB estimates of depletion (Figure 5C) are suitable for guiding management of data-poor fisheries. This means the actual ratio of fishing mortality to natural mortality might differ from our model estimates for SAC in the San Marcos River, but the associated pattern of stock depletion (especially after 2015) is likely an accurate representation of change through time. Managing invasive species requires quantitative goals as well as metrics that can be used to track progress towards these goals (Hobbs 2007; Britton et al. 2011). The LBB metrics presented here can serve as a method for tracking progress towards goals ultimately set by managers at the Edwards Aquifer Authority and stakeholders involved with the upper San Marcos River (Hussan et al. 2019).

Invasive species control programs with public activities that promote awareness, coupled with removal efforts stand a better chance at managing invasive species and achieving program goals (Giddens et al. 2014; Bajer et al. 2019). In the San Marcos River, tournament participants contributed to approximately 46% of speared SAC during the first 5 years of the removal program. Continued efforts to expand public involvement might come through public activities such as future SAC tournaments and invasive fish fry cookouts, or by disseminating knowledge through the local river foundation that promotes river stewardship (i.e., San Marcos River Foundation; https://sanmarcosriver.org/). Such effort could broaden public awareness and ultimately increase the number of active participants and effectiveness of the overall invasive species removal program. For example, widespread removal efforts of Indo-Pacific Lionfish *Pterois volitans*/*miles* in the western Atlantic have found public lionfish tournaments and derbies to be an effective tool to locally suppress lionfish densities, and at the same time, raise community participation in an invasive management program (Green et al. 2017). Volunteer-based roundups for the invasive Peacock Hind *Cephalopholis argus* in Hawaii have shown potential for controlling hind populations at a larger scale. For example, one community-wide hind removal effort involving 21 volunteer spearers removed 253 individuals in a 2-day period (Giddens et al. 2014). As part of an extensive Asian carp removal program in the eastern United States, the state of Kentucky held a Carp Madness Bowfishing event in 2018, offering cash incentives for top hauls that resulted in the removal of 20,000 pounds (9,072 kg) of Asian carp from local lakes (KDFWR 2019). Each of these programs presents an opportunity to collect length data on the removed individuals, and the LBB provides a quantitative method for tracking the efficacy of these programs if length data are collected as a part of programs in the future.

Non-native and invasive species represent a primary threat to freshwater biodiversity and successful conservation of imperiled species requires controlling invasions (Dudgeon et al. 2006). For invasions such as SAC in the San Marcos River, population establishment means that control, rather than eradication, is the most effective approach for avoiding negative effects on the ecosystem (Kolar et al. 2010). However, control programs are costly and require evidence of success to justify program persistence (Epanchin-Niell 2017), and this evidence can come from demonstrated declines in invasive species abundance or by positive responses by native species (Havel et al. 2015). Furthermore, control programs are typically designed with clear goals in mind and there is an implicit requirement to achieve said goals (Hobbs 2007). Quantitative assessments of progress towards program goals are therefore critical for successful invasive species control programs, and fishery stock assessment tools provide a means for conducting such assessments (Pennock et al. 2018). Yet stock assessments generally must be applied to situations with limited data (Froese 2004). New quantitative advances such as the LBB (Froese et al. 2018) and associated improvements (Hordyk et al. 2019) provide an approachable tool for stock assessment with limited data. These length-based stock assessment methods provide much-needed quantitative tools that can be used to evaluate, refine, and ultimately improve invasive species management programs.

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