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ORIGINAL PAPER

Movement and mortality of invasive suckermouth armored catfish during a spearfishing control experiment

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Abstract Control of non-native, invasive species in groundwater-dependent ecosystems that are also inhabited by regionally endemic or at-risk species represents a key challenge in aquatic invasive species management. Non-native suckermouth armored catfish (SAC; family Loricariidae) have invaded freshwater ecosystems on a global scale, including the groundwater-dependent upper San Marcos River in Texas, USA. We used passive integrated transponder tags to follow the movements and fates of 65 fish in a 1.6 km spring-fed reach of the upper San Macros River to assess the efficacy of a community-based spearfishing bounty hunt for controlling SAC. We found the weekly probability of SAC survival was negatively correlated with the number of fish removed as a part of the bounty hunt each week ($P=0.003$, $R^2=0.86$), while the probability of SAC being speared and reported was positively correlated with the number of fish removed ($P=0.011$, $R^2=0.53$). The majority of SAC used < 25 m^2 of river over a nine-week tracking period, but the area of river fish used correlated positively with the number of relocations ($P<0.001$, $R^2=0.36$) as might be expected for a population that disperses through diffusive spread. These findings collectively suggest local-scale suppression of the SAC population is possible through community engagement in spearfishing, but over longer time periods immigration might offset some of the removal success. This conclusion provides an explanation for the pattern in which long-term spearfishing tournaments have reduced biomass but ultimately not resulted in eradication of the population.

Keywords Efficacy of population suppression · Movement ecology · Mark–recapture · Telemetry · Survival analysis

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Introduction

Non-native species introduction and population establishment is common among thermally stable ecosystems such as groundwater-dependent ecosystems and power plant cooling reservoirs (Orfinger

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and Goodding 2018; Blanton et al. 2020). These thermally-stable ecosystems serve as warm water refugia from cold winter temperatures among higher latitudes, making them invasion hotspots for temperature-limited species that often originate from subtropical and tropical regions (Hill and Sowards 2015). Groundwater-dependent ecosystems located within urban areas are particularly vulnerable to thermally-limited species invasions (Bowles and Bowles 2015; Nielson et al. 2019). This is, in part, because water access through parks and greenspace increases species introduction occurrences via aquaria dumping and recreational fishing (Copp et al. 2007). Additionally, instream modifications associated with urban development can provide ideal habitats for introduced species to become established populations (Bowles and Bowles 2015). Due to their relatively consistent water quality and quantity, these same groundwater-dependent ecosystems typically support high species richness and endemic taxa that may be federally listed (Bowles and Arsuffi 1993; Hubbs 1995; Craig and Bonner 2021). The negative effects of non-native species are a key threat to some federally listed species and the effects of non-native invasions are documented as the second-most common cause for species extinction in North America (Clavero and García-Berthou 2005). Consequently, establishing management programs that control the spread of non-native species is a critical component to maintain native biodiversity among groundwater-dependent and other freshwater ecosystems (Cartwright et al. 2020).

Preventing the introduction of non-native species is the most effective method for managing invasions, but control of invasive species is necessary for aquatic ecosystems that are already invaded (Kolar et al. 2010). Havel et al. (2015) pointed out that eradication efforts in freshwater ecosystems are generally only successful when invasive species can be isolated and the ecosystem drained or dried. When and where these approaches are not possible, control (e.g., population suppression) of invasive species population size might be the only viable solution to minimizing the effects of invasive species on aquatic ecosystems. For high priority locations, some management frameworks target *functional eradication*, or the suppression of invasive species populations below levels that cause deleterious effects (Green and Grosholz 2021). Functional eradication strategies will only be possible in situations where suppression methods reduce invader populations at a rate that exceeds recolonization (Beric and Maclsaac 2015). Thus, a critical step in controlling invasive species populations is determining the efficacy of suppression methods (e.g., Pennock et al. 2018), particularly with respect to recolonization rates from locations outside of the control area (Moody et al. 2021).

Suckermouth armored catfish (SAC, Siluriformes: Loricariidae) represent a thermally-limited group of fishes that have invaded freshwater ecosystems on a global scale. These fishes are popular in the aquarium trade as algae control agents, but commonly outgrow aquaria and are subsequently released into the wild (Hoover et al. 2004). Within invaded ecosystems, SAC have demonstrated negative effects, including bank erosion and increased sedimentation caused by burrowing behavior (Nico et al. 2009), diet competition with native herbivores (Pound et al. 2011), space competition with native macroinvertebrates (Scott et al. 2012), and reduction of periphyton biomass (Datri et al. 2015). It is also speculated that SAC lead to declines in native fish by consuming or destroying eggs (Hoover et al. 2014). Given these impacts, control efforts targeting SAC suppression or eradication have been established in regions such as tropical Pacific Islands (Nico and Walsch 2011), the US (Hill and Sowards 2015), and India (Hussan et al. 2021). Control efforts for SAC include spearing, targeted seine netting, and dewatering, each of which have shown variable success in effectively suppressing or eradicating SAC. As such, a critical component of any species control program targeting an invasive species such as SAC should be determining the efficacy of the method and whether modifications or improvements are necessary (Blanton et al. 2020).

The goal of this study was to estimate movement and mortality of SAC during a spearfishing removal experiment within an urban, groundwater-dependent ecosystem. Since 2013, community spearfishing tournaments have been used in conjunction with contracted spearfishing to suppress SAC populations within the upper San Marcos River, Texas in the US. Blanton et al. (2020) applied fishery stock assessment models to SAC removal data and found that spearfishing tournaments effectively suppress SAC biomass; however, additional research is needed to determine movement of SAC and the number of fish that must be removed to contribute to population suppression. In particular, whether or not and to what extent

movement by SAC into areas where control efforts are concentrated is of interest (Blanton et al. 2020; Moody et al. 2021). We tagged SAC with external and internal tags, released these fish where they were captured within four locations in the upper San Marcos River, and tracked their movements and survival during a community-based spearfishing bounty hunt. We fit a tag return model using data from fish removed during the bounty hunt to estimate probability of survival and probability that SAC were speared and reported during the spearfishing bounty hunt. We hypothesized that the area used by SAC would be restricted but positively correlated with the amount of time fish were tracked. This hypothesis is consistent with the ideas of restricted movement and diffusive spread by stream fishes as previously demonstrated for multiple species (Skalski and Gilliam 2000; Radinger and Wolter 2014), including one species of SAC (De Fries et al. 2021). We also hypothesized that the probability of SAC survival would be negatively correlated with the number of fish removed during each week of the bounty hunt, while the probability of SAC being speared and reported would be positively correlated with the total number of fish removed during each week of the bounty hunt. This hypothesis is based on the notion that increasing control effort should result in greater mortality of the target population if recolonization from outside the control area is limited and a large enough number of fish are removed relative to total population size (Glen et al. 2013).

Methods

Study area

We studied the movement and survival of non-native SAC in the San Marcos River, Texas. Introduction of two genera of fishes belonging to the family Loricariidae, *Hypostomus* sp. and *Pterygoplichthys* sp., are reported in the San Marcos River (Blanton et al. 2020) with aquarium dumping as the suspected source (Perkin and Bonner 2011; Pound et al. 2011). Both genera are present in the system; however, *Hypostomus* sp. (SAC hereafter) is the most abundant form in the San Marcos River and is the focus of this study. We use SAC as a more general nomenclature because the species historically listed from the system was *Hypostomus plecostomus* (e.g., catalogue numbers 15799.01 and 15800.01 in Texas A&M University Biodiversity Research and Teaching Collections), but new evidence suggests it is more likely *Hypostomus* cf. *niceforoi* (Jonathan Armbruster, Auburn University, *Professional Communication*), a species widely reported as introduced from the aquarium trade (Matamoros et al. 2016). The upper 8 km of the San Marcos River, originating from groundwater sources of the Edwards Aquifer and providing year-round warm water temperatures (~22–23 °C), serves as an aquarium-like oasis that allows for high survival and recruitment for SAC (Cook-Hildreth et al. 2016). Demonstrated impacts of SAC on the San Marcos River in particular include competition with native species and reduction of periphyton biomass (Pound et al. 2011; Scott et al. 2012; Datri et al. 2015). Previous research suggests that spearfishing tournaments conducted twice annually in the upper San Marcos River are contributing to the suppression of SAC biomass (Blanton et al. 2020), thus we concentrated our study on the same segment of river defined by the tournament boundaries. Specifically, we focused on a 1.6 km long segment (wetted area = 50,655 m^2) of the San Marcos River from the outflow of Spring Lake downstream to a series of artificial falls and shoots at Rio Vista Park (Fig. 1). Although this stretch of river is surrounded by urban land use (Perkin et al. 2012), it still maintains clear water with nearly constant water quality and abundant aquatic vegetation, including algae that is consumed by SAC (Groeger et al. 1997; Pound et al. 2011). We focused our tagging and tracking efforts among sites with highly altered banks, generally in the form of concrete or rock bulkheads that have partially eroded and therefore provide crevices that are inhabited by SAC.

Fish tagging

Tagging was primarily done at four sites within the study area, including Spring Lake Dam, Sewell Park, City Park, and Rio Vista Park (Fig. 1). Snorkelers and self-contained underwater breathing apparatus (SCUBA) divers captured fish using dip nets or their hands by swimming near the bottom of the stream or bank and quickly grabbing fish resting on the bottom or walls. Search areas were broken down into smaller zones so that fish could be released in the same location in which they were captured

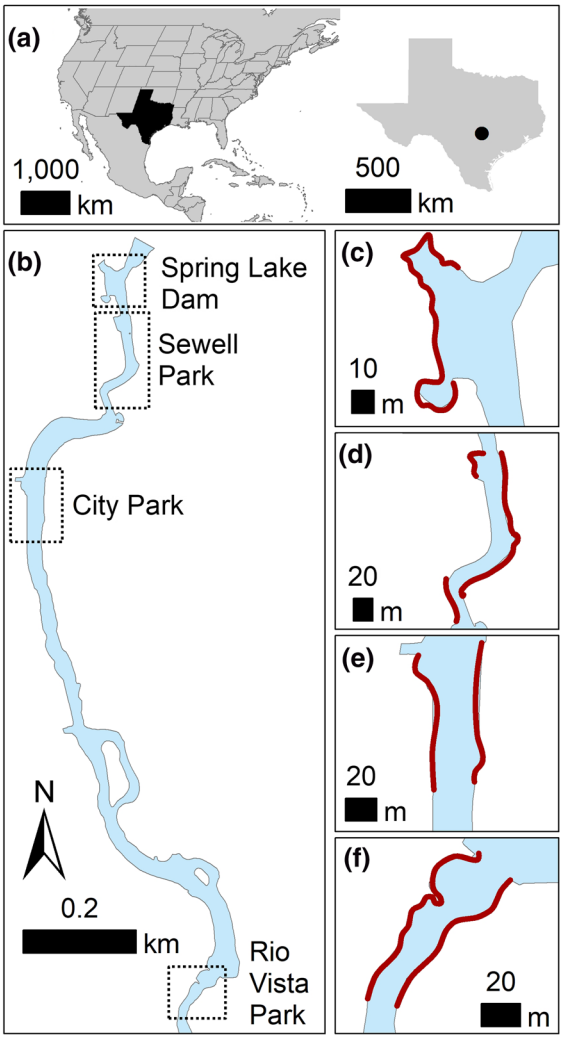

Fig. 1 Study area map illustrating **a** the location of the San Marcos River in the US and Texas, **b** the upper San Marcos River with four scanning locations where searches for tagged fish occurred, including **c** Spring Lake Dam, **d** Sewell Park, **e** City Park, and **f** Rio Vista Park. Red lines in **c–f** represent the banks that were scanned for suckermouth armored catfish during nine relocation attempts

(Fig. 1c–f). Captured SAC were placed in wire-top mesh dive bags and transferred to the bank for a tagging crew to process. On the bank, SAC were measured for total length (mm) and weight (g) and held in buckets containing river water until they were tagged. SAC were tagged externally with anchor tags on their dorsal surface at the insertion of the dorsal fin and internally with BioMark 32-mm and 12-mm passive integrated transponder (PIT) tags. Larger PIT tags were reserved for SAC 120 mm total length or longer and the smaller PIT tags for SAC shorter than this length. The tags came pre-loaded in syringes and were injected into the abdominal cavity on the ventral side of the fish just in front of the origin of the pelvic fins. SAC were held for up to one hour after tagging to ensure tag retention before being released back to the site of capture (Wells et al. 2017). Fish tagging occurred on four sequential weekly events during June 2020, including June 6 ($n=25$ tagged), June 11 ($n=20$), June 17 ($n=56$) and June 24 ($n=14$) for a total of 115 tagged individuals. These 115 individuals were distributed across sites at Spring Lake Dam ($n=63$), Sewell Park ($n=5$), City Park ($n=17$), and Rio Vista Park ($n=30$).

Fish tracking

The movements of tagged SAC were tracked using underwater scanning with a mobile antenna system. This method allowed for determining fish locations without the need to recapture fish (i.e., generating relocations rather than recaptures). A BioMark HPR-Plus scanner with global positioning system (GPS) capabilities was mounted to a floating inner tube on the water surface and connected to a 45-cm circular antenna by a 6-m cable. The same SCUBA divers that performed the captures oversaw the scanning to ensure all areas providing potential SAC habitat were scanned. As SCUBA divers moved the circular antenna along the bottom of the river, a crew of two individuals moved the inner tube on the surface so that time-stamped reads of PIT tags had associated GPS coordinates as close to the SAC location as possible. For particularly steep banks, the HPR-Plus reader was held by a person on the bank of the river near the area where the divers were working. This resulted in some GPS locations appearing on the bank, but they represented fish in the water. The antenna was passed over all man-made structures containing any crevices and holes too small for the antenna to be inserted. The antenna was also placed as deep as possible into larger cavities and undercuts. All previous SAC capture sites were scanned each time along with any surrounding areas containing similar structures and habitat. Scanning began at Spring Lake Dam and the Sessom Creek outflow, covering 120 linear m (Fig. 1c), followed by Sewell Park (215 m; Fig. 1d), City Park (150 m; Fig. 1e), and Rio

Vista (200 m; Fig. 1f). The scanning crew covered areas along the banks/walls and large habitat features in each of the tagging sites. Scanning events occurred during the day when SAC tended to stay closer to cover, requiring less open area to be scanned, apart from the final scan occurring after dark to assess whether stationary tags within cover represented live fish or shed tags. We searched for tags that were relocated in the open or did not show any sign of movement across repeated scans and excluded those from the analysis. This resulted in 65 tagged fish being retained for analysis. Five consecutive weekly tracking events were conducted prior to the initiation of the fall spearfishing bounty hunt, including July 23, July 30, August 6, August 13, and August 20, 2020. Weekly scanning resumed after the initiation of the spearfishing bounty hunt, including November 20, December 2, December 9, and December 17, 2020.

Bounty hunt

Because of the COVID-19 pandemic and a moratorium on gatherings of large groups of people, the bi-annual spearfishing tournament typically held in the San Marcos River (see Blanton et al. 2020) was suspended for fall 2020. In lieu of the tournament, a bounty hunt was conducted during September through December 2020 with rewards offered for the return of tagged SAC. Participants were given access to the river between Spring Lake Dam and Rio Vista Park. Spearing was limited to pole-mounted spears (i.e., no spearguns or Hawaiian slings) and only two spear fishers at a time were given access to the river. All spearing participants were limited to snorkeling only, no SCUBA equipment was permitted. All speared SAC, tagged or untagged, were submitted by participants each week after being weighed and measured. All SAC submitted as a part of the bounty hunt were checked for PIT tags using a BioMark HPR-Lite reader. Reward T-shirts were offered for spearing at least 50 fish or a fish with a tag. The identities of returned tags and the total number of SAC speared during each week of the bounty hunt were tracked by the bounty hunt organizers, who also maintain special permits from the Texas Parks and Wildlife Department for conducting spearfishing (coauthors NM and JW). As with other invasive species control methods, spearfishing bounty hunts require ethical considerations of the perceived benefits and costs from both social and ecological perspectives (Simberloff 2003; Carballo-Cárdenas 2015).

Statistical analyses

We analyzed movement and space use by SAC using underwater relocation data. All relocation data were downloaded from the HPR reader and uploaded into ArcMap 10.7.1 (ESRI, Redlands California). The area (m^2) of minimum convex hull polygons placed around all relocations for each SAC was then calculated in ArcMap to estimate space use. We developed a frequency histogram of areas used by 65 fish with at least one relocation during tracking events. We tested skewness and kurtosis of the distribution of area used with the *agostino.test* and *anscombe.test* functions from the *moments* package (Komsta and Novomestky 2015) in R version 4.0.4 (R Core Team 2020). We tested for differences in the size distributions for all tagged fish ($n = 115$) versus those that were relocated at least once ($n = 65$) using a two-sample t-test implemented with the *t.test* function from the *stats* package (R Core Team 2020). We tested our first hypothesis that the area used by SAC would increase as the number of relocations increased using generalized linear multiple regression. Specifically, we fit a regression model with the number of relocations and size of fish (total length, mm) as independent variables, total area used across all relocations as the dependent variable, and used a quasi-Poisson error distribution to account for non-linearity, non-homogeneity of variances, and overdispersion of the data. We fit the model using the *glm* function and assessed significance of the relationships using the *summary* function from the *stats* package in R version 4.0.4 (R Core Team 2020). We tested for multicollinearity among the independent variables (i.e., number of relocations, fish size) by calculating the variance inflation factor using the 'vif' function from the 'car' package (Fox and Weisberg 2019). We also calculated the coefficient of determination using the *rsq* function from the *rsq* package (Zhang 2021).

We used the tag return model described by Brownie et al. (1985) and Tuckey et al. (2017) for analysis to estimate probability of survival (S) and probability of being speared and reported by bounty hunters (f) for weekly time steps between June 6 and December 27, 2020 (i.e., 30 weeks). We created capture histories for each tagged SAC, including the week in which fish were tagged and the week in which

speared fish were returned with tags. These data were used to fit the Brownie model using the *mark* function from the *RMark* package (Laake 2013). We tested our hypothesis that greater spearfishing effort would result in greater mortality for SAC using a generalized linear model. We first fit a model with the probability of SAC surviving each week (S) as the dependent variable, the corresponding total number of SAC removed by bounty hunters for that same week as the independent variable, and used a quasibinomial error distribution to account for the bound (i.e., between 0 and 1) yet continuous distribution of S values. We then fit a second model using the probability of SAC being speared and reported during the bounty hunt (f) as the dependent variable, total fish removed as the independent variable, and used a quasibinomial error distribution. We tested the significance of the models using the *glm* function from the *stats* package and calculated the default coefficient of determination using the *rsq* function from the *rsq* package (Zhang 2021).

Results

Movement ecology

Underwater tracking relocated 65 SAC (253 total relocations across individuals) within the study area between July 23 and December 17, 2020. Relocations were highly concentrated around artificial structures near Spring Lake Dam, the Sessom Creek outflow, retention walls in Sewell Park, retention walls in City Park, and the artificial rapid structures at Rio Vista (Fig. 2). The average size of all tagged fish was 263 mm (range = 120–401 mm), the average size of relocated fish was 257 mm (range = 120–390 mm), and the distributions of tagged versus relocated fish did not differ ($t = 0.61$, d.f. = 95, $P = 0.547$; Fig. 3a). The distribution of area used by the 65 SAC was strongly positively skewed (skew = 2.31, $Z = 5.55$, $n = 65$, $P < 0.001$) and leptokurtic (kurtosis = 7.91, $Z = 3.84$, $n = 65$, $P < 0.001$). The majority (42 of 65) of SAC used < 25 m^2 of river while a minority (23 of 65) used 30–250 m^2 of river during the tracking study (Fig. 3b). The multiple regression model revealed a significant positive relationship between the number of relocations per fish and the area used by SAC ($t_{1,62} = 5.57$, $n = 64$, $P < 0.001$) but no relationship between fish size and area used ($t_{1,61} = 0.48$, $n = 64$, $P = 0.634$). Variance inflation factor scores were small for the number of relocations (1.03) and fish size (1.03), indicating the model was unaffected by multicollinearity. The model explained 36% of variation in area used (adjusted $R^2 = 0.36$) and because the parameter for fish size was not significant, we interpreted only the effect of number of relocations on area used (Fig. 3c).

Bounty hunt

Twenty-four individuals participated in the bounty hunt and removed a total of 322 SAC during the 14-week period between the beginning of September and end of November 2020. The weekly number of fish removed from the river between Spring Lake Dam and Rio Vista Park ranged from 0 to 56. Individual participants removed between 0 and 26 SAC within a given week, with an average of nine SAC removed per participant per week. Nine bounty hunt participants reported spearing or observing up to two tagged SAC per spearfishing time slot with 15 participants observing zero tagged individuals. The number of tagged SAC returned ranged from 0 to 4 during each week of the bounty hunt.

Survival analysis

Weekly time step estimates of probability of survival (S) and probability of being speared and reported during the bounty hunt (f) varied through time during the bounty hunt. Estimates of S ranged 0.48–0.99 and estimates of f ranged 0.00–0.98. There was a negative correlation between the weekly number of SAC removed during the bounty hunt and the probability that SAC would survive the week ($t = -3.627$, $P = 0.003$, $R^2 = 0.86$). Estimated survival remained high until approximately 25 SAC were removed, and as the number of SAC removed increased to the maximum of 56, the probability of survival declined to 0.54 (Fig. 4a). There was a positive correlation between the weekly number of SAC removed and the probability that SAC would be speared and reported as a part of the bounty hunt ($t = 3.001$, $P = 0.011$, $R^2 = 0.53$). The probability of being speared and reported remained low until approximately 25 SAC were removed, and as the number of SAC removed during the bounty hunt increased to the maximum

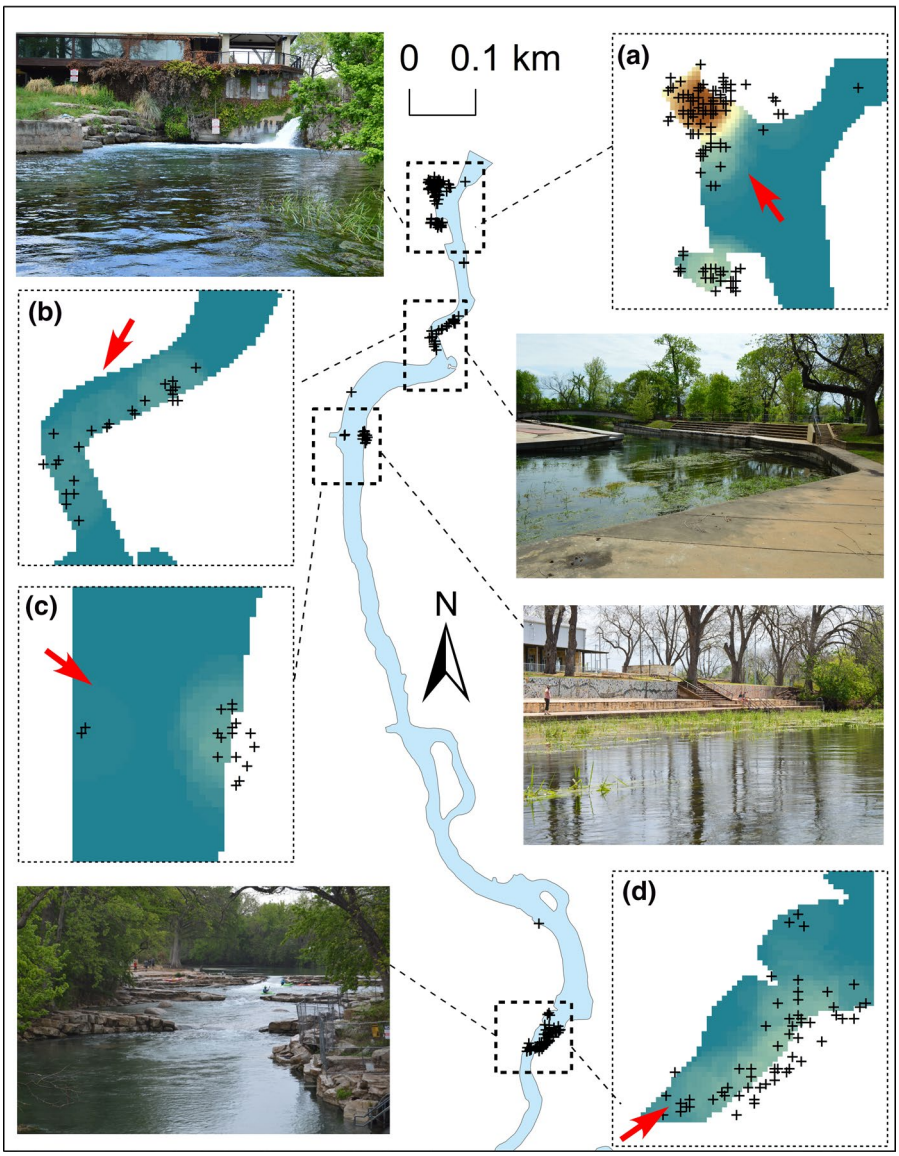

Fig. 2 Underwater tracking relocations of tagged suckermouth armored catfish in the San Marcos River, Texas, USA. Focal sampling sites from upstream to downstream include **a** Spring Lake Dam, **b** Sewell Park, **c** City Park, and **d** Rio Vista Park. Relocations are shown as cross symbols (+) and the relative density of relocations is shown as a heat map ranging from high (red) to low (blue) densities of points. Some points fall outside the polygon of the river but represent locations of fish within the water. Photographs of bank alterations at focal sampling sites are shown from the perspective of the red arrows in the heat maps (photographs by AAH)

of 56, the predicted probability of being speared and reported increased to 0.73 (Fig. 4b).

Discussion

Our study provides empirical evidence that spearfishing suppresses the non-native population of SAC in the upper San Marcos River. Previous research based on fisheries-dependent data (i.e., length of fish removed through spearfishing tournaments) demonstrated a reduction in SAC biomass relative to an unexploited population and estimated that fishing mortality was approximately 1.6-times higher than natural mortality in the upper San Marcos River (Blanton et al., 2020). Our work advances these findings by illustrating the level of effort needed (i.e., number of fish removed) over weekly time periods to achieve a detectable increase in mortality associated with spearfishing. We found support for our hypothesis that the probability of SAC survival would be negatively correlated with the number of fish removed by bounty hunt spearfishing efforts. This hypothesis might not have been supported if the levels of effort were insufficient relative to SAC total population size (MacNamara et al. 2016). Instead, we found

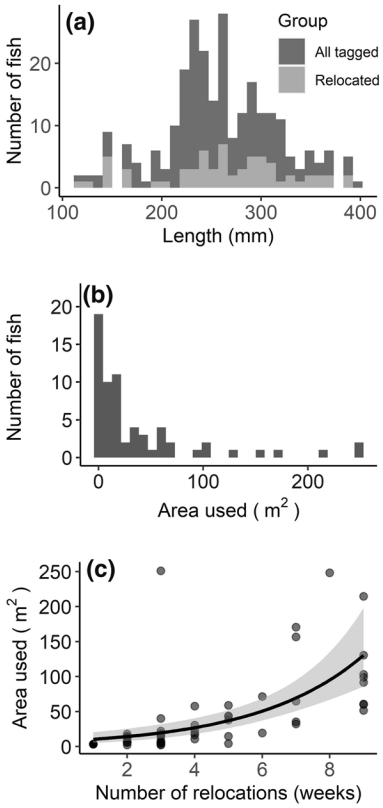

Fig. 3 **a** Frequency histogram comparison for sizes of all fish tagged (dark gray, $n = 115$) and fish relocated at least once (light gray, $n = 65$), **b** frequency histogram of the area used (m^2) by the 65 relocated fish, and **c** relationship between number of relocations and area used by the 65 relocated fish tracked in the upper San Marcos River, Texas, USA. The relationship in panel **c** is summarized with a generalized linear regression model (black line) and 95% confidence interval (gray shaded area)

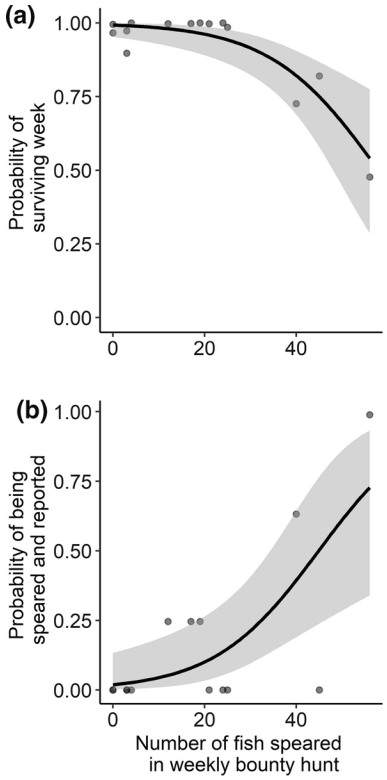

Fig. 4 Relationship between the number of fish speared during weekly bounty hunt periods versus **a** the probability that a fish survived a given week and **b** the probability that a fish was speared and reported based on the tag recovery model by Brownie et al. (1985). Points represent weekly time points between August 30, 2020 and December 5, 2020, black lines are fitted values from a generalized linear model, and gray shaded areas represent 95% confidence intervals

that for the upper San Marcos River, when > 25 fish were removed weekly, SAC survival declined and the likelihood of a member of the population being speared increased. Under lower levels of effort, it is possible that spearfishing mortality is not measurably higher than natural mortality, which is estimated to be 0.35 for SAC according to Thorson et al. (2017). This means the annual survival probability for SAC is estimated to be 0.65 (i.e., 1.00–0.35) under no fishing pressure (Thorson et al. 2017). Our data reveal that the highest levels of fish removal during the spearfishing bounty hunt reduced the weekly survival rate to a value lower than the estimated annual survival rate under no fishing pressure (i.e., 0.54). Over a longer timeline (e.g., multi-week tournaments twice a year) and with sufficient removal of fish (e.g., > 25 fish/week), data suggest organized spearfishing is an effective method for increasing fishing mortality beyond natural background mortality. Removal of adult fish through spearfishing may also contribute to control of the population through demographic collapse caused by the removal of adults before they have the opportunity to spawn (Blanton et al. 2020).

We also found support for the hypothesis that SAC movement is restricted but increases with time. The idea that most members of a population are stationary and do not move long distances has a long history in stream fish movement ecology (e.g., Funk 1957). More recently, quantification of stream fish movements led to development of the "restricted movement

paradigm" (Gowan et al. 1994), which posits that fish are composed of heterogeneous mixes of a large number of stationary fish and a small number of mobile fish (Skalski and Gilliam 2000; Rodríguez 2002). But the distances moved by fishes are not static through time and the distances moved by both stationary and mobile components follow a pattern of diffusive spread (Skalksi and Gilliam 2000; Radinger and Wolter 2014; Wells et al. 2017). The tell-tale signal of this population-level pattern in movement is the existence of leptokurtic movement distributions among individuals characterized by a taller peak and longer tails compared to a normal distribution (Radinger and Wolter 2014). Our results revealed a leptokurtic distribution of area used by SAC as well as an increase in area used with time. We interpret these results as evidence of heterogeneous movements within the population in which most fish are stationary, but a few are mobile. Furthermore, we found that the area used by fish increased with time (here, number of weekly relocations), supporting the notion that diffusive spread is likely operating within the population. This evidence might explain why long-term spearfishing tournaments (Blanton et al. 2020) and focal bounty hunts (this study) are successful at suppressing fish numbers but do not ultimately result in eradication of the population. Moreover, recent research on movement by *Rineloricaria aequalicuspis*, a SAC species native to southern Brazil, found that movement was generally greater than expected under the restricted movement paradigm (De Fries et al. 2021). Thus, it is likely that movement into the control area over longer time periods works in concert with population growth to repopulate the control area. This was the case for Northern Pike (*Esox lucius*) control efforts in the upper Colorado River Basin where removal efforts were offset by recruitment within, and immigration to, the control area (Zelasko et al. 2016). An advantage in the upper San Marcos River is the finite space over which SAC occur, and a greater understanding of fish recruitment locations and movement behaviors could further optimize removal-based control efforts (Januchowski-Hartley et al. 2018).

Emerging evidence suggests control of invasive species is most successful when spatial variation in control efforts match spatial patterns in invasive species abundance. For example, Baker (2017) developed a model that highlighted how spatial alignment between high densities of invasive species and high levels of control effort produced the optimal approach to population suppression. In our study, we found that densities of SAC relocations were highest in areas with failing infrastructure. In fact, these artificial modifications might allow for introduced species such as SAC to become established because of the refuge and potential spawning habitats they provide (Bowles and Bowles 2015). We also observed that these locations often had higher current velocities and increased depths relative to the remainder of the river, including the outfall from the Spring Lake Dam and the pools at Rio Vista Park. Areas such as these are challenging to access using snorkel gear due to a combination of water depth, high turbidity, increased water velocity, and sporadic water movement that collectively create logistical challenges for novice snorkelers to remove fish using pole spears. An advantage to the long-term control efforts in the upper San Marcos River is that contracted spearfishing by professional divers that use SCUBA and spear guns is used to supplement the biannual spearfishing tournaments and boost removal of fish in hard-to-reach areas (Blanton et al. 2020). Still, other areas of high SAC abundance might exist outside the areas of the spearfishing tournament. For example, Scott et al. (2012) used snorkel transect surveys to estimate density of SAC at Sewell Park and Rio Vista Park and found higher densities upstream at Sewell; whereas, Warner (2018) used the same snorkel transect method and random sites between Spring Lake Dam and the Interstate Highway 35 crossing (0.5 km downstream of Rio Vista Falls) and found limited evidence for an increase in SAC density with greater distance downstream from Spring Lake Dam. If higher abundances occur downstream and outside of the control area, then the model of Baker (2017) predicts that optimal control might not be reached. Extrapolation of the relationship between number of weekly relocations and area used documented in this study reveals that SAC could cover the extent of the control area (50,655 m^2) over the course of 28 weeks (i.e., predicted area used = 51,925 m^2). This means that current spearfishing tournaments held every six months (24 weeks; Blanton et al. 2020) approximately match the estimated time of SAC recolonization, and a larger spatial extent of control might be needed. Consequently, as of spring 2021, control efforts were extended another 1.5 km downstream past Rio Vista Park to Stokes Park as a means of targeting a larger area of the river. Extending the control

area down another 4 km, to the confluence with the Blanco River, could cover the entire functional range of SAC that is limited by increased temperature variations within the Blanco River. However, this leads to other limitations associated with decreased water clarity, restricted river access, and necessity for a greater number of tournament participants that would make it challenging to afford equivalent efforts compared to further upstream. Ultimately, more information on the longitudinal distribution of SAC is needed in order to understand where the highest densities of fish are located on the riverscape.

This project is not without limitations and caveats that could be explored in the future. One potential limitation is the presence of *ghost tags*, or tags that were expelled, shed, or left after fish mortality that could potentially be interpreted as tagged fish (Šmejkal et al. 2020). To combat the potential effects of ghost tags, we made note of individuals that remained entirely stationary across multiple tracking events and removed those individuals from the analysis. We also retrieved shed tags from the river as suggested by Šmejkal et al. (2020). A second limitation is that the scope of our study only included relocation events near the site of tagging, which likely biased movement and space use towards stationary fish that used little space (Gowan et al. 1994). This means our estimates of movement should be interpreted as conservative estimates. Use of technologies beyond PIT tags, such as ultrasonic transmitters, could address this limitation in the future and ultimately extend movement inference across broader spatial scales. Still, our documented movements provide baseline information on which hypotheses regarding movement can be built, including the distribution of submersible receivers to monitor fish movement behavior (e.g., Bacheler et al. 2015). A third limitation is that the extent of our study was limited to the area between Spring Lake Dam and Rio Vista Falls. Even though we obtained novel information on the movement of SAC, consideration of a broader spatial extent is likely necessary given what we learned during this study (Januchowski-Hartley et al. 2018). We did not document movement of SAC between the four tagging locations, but movement to and from other areas remains untested. Lastly, this study only encompassed a maximum of nine weekly time steps in observed movement, but movement and survival over longer time periods should be assessed as pandemic conditions improve, research group sizes are allowed to increase, and river access reopens.

Invasions into groundwater-dependent ecosystems, especially those like the San Marcos River with high levels of public access, are likely to increase as human dependence on water sources and threats from climate change cause further alterations (Moyle and Light 1996; Kløve et al. 2014; Alley and Alley 2017). Because of the prevalence of regionally endemic and listed species, these ecosystems cannot be drained or dried completely despite this being the most effective measure to eradicate invasive species (Havel et al. 2015). Instead, control methods focused on population suppression are the most useful strategies for moving toward eradication (Nico and Walsh 2011; Hill and Sowards 2015). However, some programs targeting invasive fish have found little evidence that existing levels of control were sufficient to affect targeted populations, including lamprey in the Great Lakes (Holbrook et al. 2016), Asian carp in Australia, even after 11 years of implemented control efforts (Stuart and Conallin 2018), Bigheaded carp in the Illinois river (MacNamara et al. 2016), and Northern pike in the Colorado River (Zelasko et al. 2016). In other systems, including SAC in the San Marcos River, although control efforts successfully suppress populations, there appears to be a limit to suppression under existing programs (Pennock et al. 2018; Blanton et al. 2020). For ecosystems in which suppression has reached a limit, enhanced suppression will likely come from either increased effort, though it cannot be increased indefinitely (Pepin et al. 2020), or by applying complementary methods that could be used in concert with the existing methods. One promising approach for ecosystems that cannot be dried is the use of *Trojan genes*, or phenotypically sex-reversed carriers of Y chromosomes for fishes with XY sex determination (Cotton and Wedekin 2007). However, additional information is first needed regarding the estimated total population size and the ratio of males to females to determine the feasibility of strongly biasing a population towards males (Schill et al. 2017). Reaching functional eradication is perhaps a more achievable management goal compared with complete eradication (Green and Grosholz 2021), though this is only possible if removal methods sufficiently cause increased mortality beyond natural background mortality. Our work represents a case study demonstrating that community-based control

efforts in which members of the public are invited to serve as citizen scientists can achieve population suppression under the appropriate settings (e.g., public river access, limited range of invasive species). Given the sometimes-high cost and challenge of funding control programs in perpetuity, community engagement and involvement in tournaments or bounty hunts represents a tractable approach to achieving management goals (Wallace et al. 2021).

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Data availability All data used in this study are available from the corresponding author with reasonable request.

Code availability All code used in this study is available in the Supplementary Material.

Declarations

Conflict of interest The authors have no conflicts of interest to report.

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