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Tournament and non-tournament anglers have little effect on a largemouth bass population compared to natural mortality

Andrea Sylvia, Stephen J. Dinsmore, and Michael J. Weber

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Abstract: Popularity of bass (*Micropterus* spp.) catch and release and tournament angling during the past decade has resulted in increased potential for these activities to induce population level effects. Understanding capture rates and mortality sources relative to total population mortality is essential to focus of management. We conducted monthly electrofishing, solicited non-tournament angler tag returns, and censused largemouth bass (*Micropterus salmoides*) tournaments at Brushy Creek Lake, Iowa, USA, from April 2015 to June 2018. We used a multistate mark–recapture model to evaluate the effects of air temperature, water temperature, tournament bass per angler, and tournament initial mortality on non-tournament and tournament angler capture probability and natural, non-tournament angling, and initial and delayed tournament mortality. Average total annual mortality was 0.66 with natural mortality representing the largest mortality source (0.57) followed by delayed tournament mortality (0.06), non-tournament angling mortality (0.02), and initial tournament mortality (0.006). Our results reveal both non-tournament and tournament angling mortality are low compared to natural mortality in some lakes. Therefore, cumulative angling mortality likely has minimal population level effects on some bass populations.

Résumé : La popularité de la pêche avec remise à l'eau et des tournois de pêche à l'achigan (*Micropterus* spp.) au cours de la dernière décennie s'est traduite par un potentiel accru d'effets de ces activités à l'échelle de la population. La compréhension des taux de capture et des sources de mortalité par rapport à la mortalité totale de la population est un aspect central de la gestion. Nous avons réalisé des pêches électroniques mensuelles, sollicité les étiquettes prélevées par des pêcheurs hors tournois et effectué des recensements dans des tournois de pêche à l'achigan à grande bouche (*Micropterus salmoides*) au lac Brushy Creek (Iowa, États-Unis) d'avril 2015 à juin 2018. Nous avons utilisé un modèle multi-états de marquage–recapture pour évaluer les effets de la température de l'air, de la température de l'eau et du nombre d'achigans pêchés par pêcheur et de la mortalité initiale dans le cadre de tournois sur la probabilité de capture par pêcheur dans le cadre de tournois et hors tournois et sur la mortalité naturelle hors tournois et les mortalités initiale et différée associées aux tournois. Le taux de mortalité annuel total moyen était de 0,66, la mortalité annuelle en représentant la plus grande source (0,57), suivie de la mortalité différée des tournois (0,06), de la mortalité par pêche hors tournois (0,02) et de la mortalité initiale des tournois (0,006). Nos résultats révèlent que les taux de mortalité par pêche tant dans le cadre de tournois que hors tournois sont faibles comparativement à la mortalité naturelle dans certains lacs. La mortalité cumulative par pêche a donc probablement des effets limités à l'échelle de la population sur certaines populations d'achigans. [Traduit par la Rédaction]

Introduction

Largemouth bass (*Micropterus salmoides*) represent an example of shifts in angler behaviors and motivations. Historically, overharvest of black bass (*Micropterus* spp.) was common (Holbrook 1975; Redmond 1986; Long et al. 2015). More recently, catch and release can approach nearly 100% in many systems throughout North America (Henry 2003; Isermann et al. 2013), although harvest can still make up a significant portion of mortality in some black bass populations. For example, annual fishing mortality rates of adult largemouth bass in a Connecticut Lake was estimated as 0.42 (Edwards et al. 2004), and harvest rates in a Florida Reservoir were estimated as high as 0.60 (Kerns et al. 2016). Even when anglers release black bass alive, they can still experience mortality because of hooking wounds (Cooke et al. 2003; Fernholz et al. 2018), exhaustion during capture (Schreer et al. 2001), air exposure (Gingerich et al. 2007), warm temperatures (Suski et al. 2003), and handling stress (Williamson and Carmichael 1986). Combined, factors associated with catch and release angling can lead to mortality ranging from 5%–10% at the individual level (Muoneke and Childress 1994; Hayes et al. 1995) but the relative effects of this mortality source for the population remains unexplored.

Black bass fishing tournaments commonly use catch and release angling procedures that can result in mortality. While similarities exist between factors affecting mortality of competitive and recreationally captured black bass (e.g., increased air and water temperature; Cooke et al. 2003, 2004), additional stressors imposed on black bass during tournament events, including live-well and weigh-in bag confinement and increased air exposure during weigh-ins (Kwak and Henry 1995; Weathers and Newman 1997) may further increase mortality. Further, black bass tournament angling events have grown dramatically in number in recent decades (Schramm and Hunt 2007; Driscoll et al. 2013; Long et al. 2015), leading to considerably more fish being captured and subjected to tournament stressors and exacerbating mortality.

Largemouth bass mortality at an individual tournament can be as high as 61% (Wilde 1998; Neal and Lopez-Clayton 2001; Gravel and Cooke 2008; Sylvia and Weber 2019) and is composed of both initial and delayed mortality. Initial mortality, accounting for

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largemouth bass dying before or during weigh-in, can be easy but labor-intensive to determine if all tournaments are censused, as dead fish can be observed and counted given tournament procedures and culling of dead largemouth bass prior to weigh-in can result in disqualification from a tournament. In contrast, delayed mortality occurring post-release is difficult to assess (Schramm et al. 1987; Sylvia and Weber 2019). While relationships between initial and delayed tournament mortality exist (i.e., increased initial mortality can be related to increased delayed mortality; Wilde 1998), delayed mortality can be highly variable as a result of environmental and tournament conditions (e.g., water temperature, prior tournament capture, largemouth bass density in livewell; Schramm et al. 1987; Kwak and Henry 1995; Sylvia and Weber 2019) but often accounts for a significant component of tournament mortality in many instances (exceeding 50%; Steeger et al. 1994; Weathers and Newman 1997; Neal and Lopez-Clayton 2001), making it important to include in assessments. Despite their potential importance, the combined population-level effects of initial and delayed tournament mortality have rarely been assessed.

Understanding population-level importance of harvest, catch and release mortality, and natural mortality is critical. Yet, population-level analyses separating these sources of mortality are rare. Therefore, the objective of this study is to determine largemouth bass capture and mortality probabilities of tournament and non-tournament anglers and assess their effect on a population compared to natural mortality. A mark–recapture approach was used to estimate natural mortality compared to fishing mortality, including both tournament mortality and non-tournament angling mortality. We expand upon prior work that estimated delayed tournament mortality within Brushy Creek Lake (Sylvia and Weber 2019) and estimate additional mortality sources using mark–recapture methods. The effects of various environmental and fishery related factors on capture and mortality probabilities were also modeled. Finally, we estimated abundance of largemouth bass in the lake and applied our model estimates to determine the relative effects of each source. Our results provide new insights into potential population-level effects of tournament and non-tournament anglers on largemouth bass.

Methods

Sampling

Brushy Creek Lake is a 279 ha reservoir in Webster County, Iowa, USA, consisting of 33.8 km of shoreline. The lake has a maximum depth of 22.9 m, mean depth of 8.9 m, and is densely covered in both emerged and submerged vegetation and coarse woody habitat along the perimeter of the lake. Brushy Creek Lake is used extensively by both non-tournament and tournament angler. Recreationally, the system has a continuous season for largemouth bass with a 381 mm (15 inch) minimum length limit and a daily bag limit of three fish. The lake can be accessed by eight jetties and four boat ramps. The system also hosts more than 40 largemouth bass tournaments annually between April and October (mean = 32.3; SE = 18.0 tournament angler hours·ha^{-1}·year^{-1} from 2015–2017). Electrofishing (pulsed DC 300 V and 8 amps) occurred once monthly on Brushy Creek Lake during the open water season (April–November) for 2015, 2016, and 2017 and for April–June 2018, with intensive weekly sampling at the beginning of each season to estimate population abundance. Electrofishing lasted approximately three to five consecutive days (based on weather constraints and sampling efficiency) each month until the entire accessible shoreline had been sampled. As a result of the large amount of course woody habitat throughout the lake, some areas of the shoreline were inaccessible to electrofishing. A single netter captured all encountered largemouth bass and placed them in a livewell with a continuous flow of supplemental oxygen and fish were processed once the live well reached capacity. Electrofishing effort averaged 242 min (SE = 26 min) of shock time per month. All largemouth bass captured during sampling were weighed (g) and measured (mm; TL) and largemouth bass ≥381 mm (15 inches) were tagged on the top left jaw with a metal Monel butt end band (selected due to their high retention for black bass; 0% tag loss after 1 year in smallmouth bass (*Micropterus dolomieui*); MacCrimmon and Robbins 1979; Hanchin et al. 2007).

All largemouth bass tournaments at Brushy Creek Lake were attended and censused from April 2015 through June 2018 (n = 142 tournaments; mean anglers per tournament = 25.65, SE = 1.77). Tournament events began in April and continued until October each year, with a minimum of one tournament weekly (Wednesday evenings) and a maximum of three tournaments per week (two weekend tournaments). Tournament events were not allowed one weekend per month but permitted the remaining weekends. Tournaments were regulated by a 381 mm (15 inch) minimum length limit and a three fish per angler bag limit, until the final season of sampling, when bag limits were increased to a five fish per angler bag limit. Some team tournaments occurred throughout the study that permitted a two-angler team to weigh-in five largemouth bass at an event. Culling was also allowed during tournament angling events and anglers were asked to record culled largemouth bass and report tag information. Weigh-in procedures differed across tournament events but primarily consisted of dry weigh-ins. Number of anglers, number of boats, and number of largemouth bass weighed-in were recorded for each tournament event. Following weigh-in, all largemouth bass were placed in an insulated livewell with lake water and supplemental oxygen. All largemouth bass were weighed (g), measured (mm), and evaluated for jaw tags: all untagged largemouth bass were tagged on the left upper jaw with a metal Monel band and released. To facilitate reporting of tagged fish by non-tournament anglers (considered non-tournament anglers in this context), project e-mail and telephone contact information was placed on signs throughout the lake. Anglers were asked to report capture date and largemouth bass tag number, harvest, length, and weight. To estimate reporting rates, 10% of bass in Brushy Creek Lake were systematically (one of every ten bass received a reward tag) tagged with reward tags ($99; REWARD printed on jaw tag) during each tagging event while the remainder of largemouth bass received non-reward tags.

Model

State definitions

Individual largemouth bass encounter histories were analyzed during 2015–2018 in program MARK (White and Burnham 1999). We used a multistate, live–dead encounter model for maximum-likelihood estimates of survival (S; hereinafter referred to as survival), recapture probability (representing electrofishing capture; p), transition probabilities (representing non-tournament and tournament angler capture probabilities; ψ), and dead recovery (the state of the animal at the time of dead recovery) rate (r; Lebreton et al. 1992; Fig. 1). Multistate models are an extension of the Cormack–Jolly–Seber model that uses capture–recapture data to understand individual movement of animals among a finite number of states (Lebreton et al. 1992). State designation in multistate models can represent physical locations or states such as diseased or breeding and are well established statistical tools in the wildlife literature (White et al. 2006) but our use of this modelling framework represents a novel approach for assessing different sources of fish mortality, as it allows for estimation of both capture probability and survival of a population of fish across an extended time period. Further, it also allows for the use of covariates to describe these parameters. Largemouth bass in our analysis could reside in one of five physical states (Fig. 1): Brushy Creek Lake (B), captured by a non-tournament angler (NT), captured and brought into a fishing tournament (T), a delayed mortality state post-tournament capture (D), and a tag loss state (TL) that was used to correct for negative bias in survival, capture probability, and recapture probability estimates (Nichols and Hines 1993; Pine et al. 2012). Tagged

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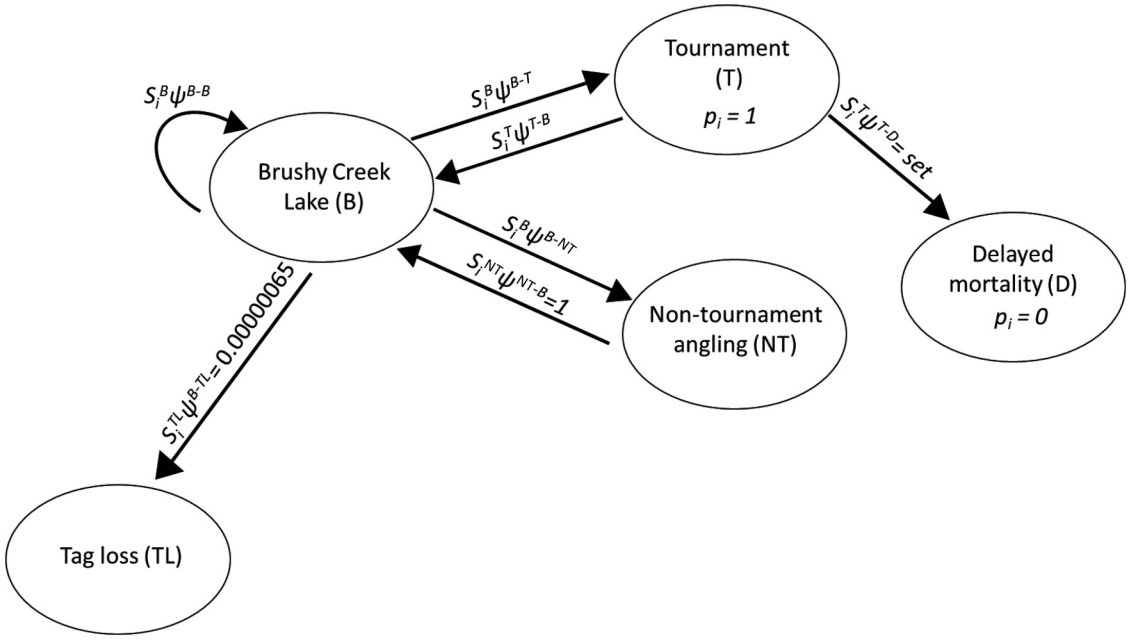
Fig. 1. Conceptual diagram of multistate model design that includes Brushy Creek Lake, tournament and non-tournament angling, delayed mortality, and tag loss of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018. Arrows represent transition probabilities (ψ) between states, p represents recapture probabilities within states, and S represents survival estimates of each state. All remaining parameters not indicated in the figure were set as constants within the model: $\psi^{B\text{-}B} = 1 - (\psi^{B\text{-}T} + \psi^{B\text{-}NT})$.



and recaptured largemouth bass could be observed alive or dead in Brushy Creek Lake, alive or dead at a tournament state, or alive or harvested in the non-tournament angling state; largemouth bass were marked as dead in the non-tournament state if harvested by an angler. Transitions could occur from Brushy Creek Lake to a tournament state if a fish was captured and brought into a tournament event (ψ B to T), from Brushy Creek Lake to a non-tournament angling state (i.e., NT = non-tournament) if a fish was captured and reported by a non-tournament angler (ψ B to NT), from a tournament state back to Brushy Creek Lake after a fish was released from a tournament event (ψ T to B), from a non-tournament angling state back to Brushy Creek Lake when a fish was released from a non-tournament angler (ψ NT to B), from a tournament state to a delayed mortality state if a largemouth bass died after release from a tournament event (ψ T to D), remain in Brushy Creek Lake if a fish was not captured through any fishing event (ψ B to B), and transition to the tag loss state from Brushy Creek Lake at a set rate (ψ B to TL; Fig. 1).

Largemouth bass could not stay in a tournament or non-tournament angling state, move between tournament and non-tournament angling states without first returning to Brushy Creek Lake, move out of the delayed mortality state or tag loss state, or move from non-tournament angling to the delayed mortality state; thus, transition probability between these states were fixed to zero (Fig. 1). No instances of multiple state transitions were observed on a single day (e.g., largemouth bass were not captured by both a non-tournament and tournament angler on the same day).

Transition probabilities from the tournament to delayed mortality state were fixed a priori based on a separate analysis conducted on the Brushy Creek Lake largemouth bass populations. We used daily estimates of delayed mortality directly from Sylvia and Weber (2019) to fix transition probabilities to the delayed mortality tournament state. Because unknown states, such as the delayed mortality state in this model, can be difficult to estimate even with large amounts of mark–recapture data (Kendall and Nichols 2002), we chose to use robust estimates of 3-day delayed mortality rates (Sylvia and Weber 2019) to increase the accuracy of our population model. Sylvia and Weber (2019) used a Cormack–Jolly–Seber mark–recapture model to estimate delayed mortality of tournament captured largemouth bass in Brushy Creek Lake. Both acute (1, 2, 3, 4 days), and chronic (7, 15 and 30 days) trends were assessed to determine the best pattern in post-tournament mortality. Model results showed support for acute mortality effects, but not for chronic mortality. Thus, estimates of delayed mortality from one, two, and three days post-release were multiplied together to obtain a cumulative delayed mortality estimate in the multistate model. Additional details of the delayed mortality model can be found in Sylvia and Weber (2019). Further, a constant daily tag loss rate of 0.0000065 estimated in this project using secondary marking methods outlined in Pine et al. (2012) was set as the transition probability from Brushy Creek Lake to the tag loss state.

Additional constants in the model included recapture probabilities (p) fixed to one for the tournament state, as all largemouth bass captured at a tournament event were censused, whereas recapture probabilities (p) were set to zero in the delayed mortality state as delayed mortalities cannot be observed. Reporting rate and dead recovery rates (λ) of fish captured through non-tournament angling were calculated at 0.32 across years using the formula:

$$(1) \qquad \lambda = \frac{R_s N_r}{R_r N_s}$$

where N_s is the number of standard tags released, N_r is the number of reward tags released, R_s is the number of standard tags returned, R_r is the number of reward tags returned (Henny and Burnham 1976; Conroy and Blandin 1984; Pollock et al. 1991). We assumed 100% reporting of $99 reward tags as prior studies have found that rewards of $100 dollars or greater approached 100% reporting rates (Nichols et al. 1991; Pollock et al. 2001; Meyer et al. 2012). We used the same reporting rate for both live release and harvested largemouth bass, as adjustments for biases in reporting rates are needed as a result of the decision to remove the tag from a fish (Meyer et al. 2012) or when all tags were removed regardless of harvest or

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capture (Smith et al. 2000), both of which were not required in this study.

Model assumptions

Assumptions of multistate models include that every marked animal present in some state immediately following sampling period *i*, where *i* represents an indexing variable of some time period, have the same probability of recapture and every marked animal present in some state immediately following the sampling period *i* have the same probability of surviving until $i + 1$. Moving to another state by period $i + 1$ and state at time $i + 1$ is dependent only on the state at time *i*. Additionally, reporting rates of dead animals depend only on the state of the animal in the immediately preceding live-recapture. Survival in Brushy Creek Lake represents fish that died and those that left the study area due to permanent emigration; however, emigration of largemouth bass from Brushy Creek Lake is minimal, as only two largemouth bass during the study period were found to have emigrated over the spillway; indicated through spillway electrofishing (<0.001% across the entire study period; A. Sylvia, unpublished data). Further, we assumed temporary emigration (i.e., increased water depth leading to decreased vulnerability of capture during electrofishing) was negligible as largemouth bass remained in relatively shallow water (mean depth use = 2.2 m) and were vulnerable to angling across all depths (Sylvia et al. 2020). Although post-capture refractory periods for largemouth bass may exist for short periods following angling (Cline et al. 2012; Sass et al. 2018), black bass resume feeding within 16 hours following an angling event (Siepker et al. 2007). Thus, we assumed that all individuals were equally available for recapture by anglers during consecutive sampling events. Basic notation of the estimation of survival, recapture, transition event, and recovery rate follow probabilities associated with each capture occasion conditional on the fish's first release and whether the fish was found dead, or recaptured alive. Probability functions of the models can be found in White et al. (2006).

Parameter estimation

Survival was estimated for 476 days during the open water seasons. Days with a tournament or electrofishing, days following a tournament or electrofishing or non-tournament angling event, and weekends were included as dates across the three years. Because transitions in multistate models occur on the next consecutive time period, survival rates are estimated across the two time periods and adjusted to a daily rate in Program MARK by exponentiation of the survival rate by the number of days between intervals (Cooch and White 2001). An ice-up survival rate that began after the last electrofishing event in November and ended on the first day of electrofishing the following April was also included in the model. All intervals were adjusted in program MARK and calculated a single daily survival estimate that was constant across the entire winter period.

Capture histories were created for 5143 largemouth bass ≥381 mm (Table 1), where an individual largemouth bass received a letter representing the state they were captured in during the sampling period in a live column (i.e., B, NT, T; Fig. 1) and a 1 in the dead column if they were reported dead in that state. If the fish was not seen during the sampling period, it would receive a 0 in both the live and dead column during that sampling period. An example recapture history of a largemouth bass in the model would be written as: T0 00 R1, indicating a fish was originally captured at a tournament alive, was not seen on the second occasion, and was captured by a recreation angler and died on the third occasion. Time-varying covariates (i.e., covariates that changed on each time interval) were used in the analysis to describe variation in recapture probability, transition probability, and survival probability. These included water temperature (°C), a single daily mean taken across temperature loggers (Onset Corporation HOBO Pendant Temperature/Light 64 K Data Logger, 15 min sampling intervals) sampled continuously from two locations within the lake at 0 and 4.6 m depth, mean daily air temperature (°C; attained from NOAA climate data, https://www.ncdc.noaa.gov/cdo-web/), mean bag per angler calculated by dividing the total number of captured largemouth bass by the total number of anglers for each tournament event, initial mortality of tournament events, daily effort for tournaments (angler hours), and daily effort for electrofishing (s; Table 2).

Table 1. Number of largemouth bass tagged and recaptured by electrofishing and tournaments at Brushy Creek, Iowa, USA, from 2015 to 2018.

		No. recaptured				
Year	No. tagged	2015	2016	2017	2018	Total largemouth bass
Tournament						
2015	1183	260	138	42	4	444
2016	1250	—	128	86	12	226
2017	1460	—	—	243	28	271
2018	0	—	—	—	0	0
Tournament total	3893	260	266	371	49	941
Electrofishing						
2015	353	123	91	18	24	256
2016	364	—	84	44	4	132
2017	269	—	—	55	34	89
2018	264	—	—	—	31	31
Electrofishing total	1250	123	175	117	93	508
Total largemouth bass	5143	383	441	488	142	1454

Using hierarchical model-selection procedures based on Akaike's information criterion, where lower AIC values and higher Akaike weights represent the most parsimonious model (Akaike 1973), we characterized variation in largemouth bass recapture probability in Brushy Creek Lake, transition (or capture) probability, and finally largemouth bass survival across states. Models were established in this order to control for the main sources of variation on recapture probability and capture probability, thus maximizing power to detect patterns in survival. Models were developed for explaining variation in largemouth bass recapture probability in Brushy Creek Lake as the first step of the hierarchical model selection procedure. As a base model to evaluate alternative models for recapture probabilities, we allowed survival and transition probabilities to differ among states but did not include covariates. We evaluated a model with no variation in recapture probability [p (.)], a linear effect of electrofishing effort [p (effort)] and water temperature [p (water T)], a quadratic effect of water temperature [p (waterT + water T^2)], and a linear effect of effort and a quadratic effect of temperature for each group [p (effort + water T + water T^2)]. Similar combinations of models for air temperature [p (effort + air T + air T^2)] were also evaluated (Table 3).

Using the best explanatory model for recapture probability in Brushy Creek Lake, we evaluated variation on angler capture probabilities for largemouth bass within Brushy Creek Lake to non-tournament angling and tournament states. First, we evaluated a model assuming capture probabilities were the same [ψ (B-T = B-NT)] and different [ψ (B-T ≠ B-NT) for largemouth bass from Brushy Creek Lake to both the non-tournament angling and tournament states]. Once the best state capture probability was determined, we evaluated linear and quadratic effects of water temperature and air temperature [ψ (state + water T)], [ψ (state + water T + waterT^2)], [ψ (state + air T)], and [ψ (state + air T+ air T^2)], a linear effect of tournament effort for the tournament states [ψ (B-T + effort)], and a linear effect of effort and a quadratic effect

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Table 2. Mean, standard error (SE), and range of covariates used in multistate models to estimate survival (S), angler capture probability (ψ), and electrofishing recapture probability (p) of jaw tagged largemouth bass in Brushy Creek Lake, Ioaw, USA, from 13 April 2015 through 1 June 2018.

	2015			2016			2017			2018		
	Mean	SE	Min, Max	Mean	SE	Min, Max	Mean	SE	Min, Max	Mean	SE	Min, Max
Mean daily water temperature (°C)	16.1	0.3	6.3, 21.3	17.2	0.4	7.1, 22.9	15.8	0.4	7.6, 19.9	12.4	0.49	4.0, 17.6
Mean daily air temperature (°C)	17.7	0.5	4.0, 28.0	17.7	0.6	1.1, 28.3	17.4	0.7	−2.2, 29.0	17.9	1.1	−3.9, 28.3
Tournament angling effort (h)	223.3	4.1	20.0, 738.0	168.8	2.3	84.0, 512.0	158.2	1.8	51.0, 384.0	135.8	3.1	92.0, 198.0
Tournament CPUE (no.·h^{-1})	0.2	0.0	0.1, 0.5	0.2	0.0	0.0, 0.5	0.3	0.0	0.0, 0.7	0.5	0.0	0.38, 0.76
Electrofishing effort (s)	5271.8	93.1	1305.0, 11 527.0	6318.7	150.2	1374.0, 18 354.0	5652.0	128.7	1532.0, 13 152.0	7526.4	257.0	4000.0, 10 495.0
Average tournament bass per angler	1.4	0.0	0.4, 3.0	1.3	0.0	0.3, 3.0	1.5	0.0	0.1, 3.0	2.2	0.11	0.7, 3.0
Initial tournament mortality (no.)	1.1	0.4	0.0, 27.0	0.1	0.1	0.0, 3.0	0.3	0.1	0.0, 10.0	1.0	0.37	0.0, 11.0

Table 3. Live–dead multistate models used to estimate recapture probability (p) of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, for 377 periods beginning 13 April, 2015 through 1 June 2018.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
p (waterT + waterT^2 + effort)	192 871.91	0.00	0.67	9	192 853.88
p (waterT + effort)	192 873.32	1.41	0.33	8	192 857.30
p (airT + effort)	192 896.98	25.07	0.00	8	192 880.96
p (airT + airT^2 + effort)	192 898.05	26.14	0.00	9	192 880.02
p (effort)	192 958.04	86.13	0.00	7	192 944.02
p (waterT)	193 087.05	215.14	0.00	7	193 073.03
p (waterT + waterT^2)	193 088.60	216.69	0.00	8	193 072.58
p (airT)	193 110.48	238.57	0.00	7	193 096.46
p (airT + airT^2)	193 110.56	238.65	0.00	8	193 094.54
p (.)	193 191.21	319.30	0.00	6	193 177.19

Note: Effects evaluated influencing p include a constant model (.), electrofishing sampling effort (s), linear and quadratic water temperature (°C; waterT; waterT^2), and linear and quadratic air temperature (°C; airT, airT^2). Parameters in the table include AIC_c = sample-sized corrected Akaike's information criterion, ΔAIC_c = relative difference between the particular model and the best model, w_i = Akaike weight, K = number of parameters, Deviance = −2 × log-likelihood of the model less −2 × log-likelihood of the saturated models (same number of parameters and degrees of freedom).

of temperature for Brushy Creek Lake to the tournament state [ψ (B-T + effort + water T + water T^2)], [ψ (B-T + effort + air T + air T^2)]. We also evaluated combinations of models that used tournament CPUE for tournament angling capture probabilities ([ψ (state + CPUE)]; Table 4).

Largemouth bass survival in each state was assessed after both recapture and capture probability models were determined. For largemouth bass survival, first we evaluated models estimating survival in Brushy Creek Lake, non-tournament, and tournament states separately [S (state)], models where survival in the tournament state was equal to the non-tournament state [S (Brushy Creek Lake, Tournament = Non-tournament)], models where survival in all states were equal [S (.)], and models where either tournament [S (Brushy Creek Lake = Tournament, Non-tournament)] or non-tournament [S (Brushy Creek Lake, Non-tournament, Tournament)] survival was equal to survival in Brushy Creek Lake. We then evaluated a linear effect of water temperature on the best combination of survival by states [S (state + water T)], and a quadratic effect of water temperature [S (state + water T + waterT^2)] as well as a linear [S (state + air T)] and quadratic effect of air temperature [S (state + water T+ waterT^2)]. For largemouth bass survival in the tournament state, we also included a linear effect of average bag per angler [S (state + bag/angler)] as well as the number of initial mortalities occurring at each tournament event [S (state + initial mortality)]. Additive combinations of the covariates were also evaluated (Table 5).

Markov chain Monte Carlo (MCMC) simulations were used in the final model to obtain better estimates on error for model parameters that were not estimated well using maximum likelihood estimates in program MARK. We specified uniform (flat) priors for each parameter estimated on the logit scale and original maximum likelihood parameter estimates from the top model were used as starting values. We used twenty chains comprising 4000 tuning iterations, 1000 burn-in iterations, followed by 10 000 iterations used in the final estimates. Parameter convergence was assessed using R^ statistics between duplicate chains (Gelman 1996) and evaluation of trace plots using the coda package (Plummer et al. 2006) in program R. Parameters and their standard errors were estimated by the mean and standard deviations from the MCMC iterations. Convergence diagnostics of the final MCMC model indicated that all R^ parameters were between 0.999 and 1.1, and all trace plots showed low serial correlation. All results are reported as mean parameter values, their standard deviations, and 95% credibility intervals from the simulations.

Population estimation

Annual population abundance and 95% confidence intervals of largemouth bass ≥381 mm in Brushy Creek Lake were estimated for 2015, 2016, and 2017 using Schnabel models calculated by

$$\hat{N} = \frac{\sum_{i=4}^{t} n_i M_i}{\sum_{i=4}^{t} m_i + 1} \quad (2)$$

where t is the number of sampling occasions; n_i is the number of fish caught in the ith sample; m_i is the number of fish caught with marks in the ith sample; and M_i is the number of marked fish present in the population of the ith sample. The variance estimator for the 95% confidence interval was

$$\hat{V}(N) = \hat{N}^2 \left[\frac{\hat{N}}{\sum n_i M_i} + 2 \cdot \frac{\hat{N}^2}{(\sum n_i M_i)^2} + 6 \cdot \frac{\hat{N}^3}{(\sum n_i M_i)^3} \right] \quad (3)$$

(Hayes et al. 2007). Assumptions of the Schnabel model include a closed population, all animals equally likely to be sampled, capture and marks do not influence catchability, marks are not lost, and all marks are recorded and reported (Hayes et al. 2007). Closed period electrofishing events occurring in the beginning of April, followed by four electrofishing events, with each event lasting one to three days to sample the entire lake within the event, in the four following weeks in 2015, 2016, and 2017 were used as sampling periods in the model. We assumed no significant births, deaths, emigration, or immigration occurred during this period, as it was prior to tournament events and high non-tournament angling effort and the period was short enough that tag loss did not influence estimates.

Table 4. Live–dead multistate models used to estimate capture probability (ψ) from non-tournament angling and tournament angling (state) of jaw tagged largemouth bass Brushy Creek Lake, Iowa, USA, for 377 periods beginning 13 April 2015 through 1 June 2018.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
ψ (state + airT + $airT^2$ + Tournament CPUE)	192 669.66	0.00	1	11	192 647.62
ψ (state + airT + Tournament CPUE)	192 779.70	110.04	0	11	192 755.65
ψ (state + waterT + $waterT^2$ + Tournament CPUE + Tournament effort)	192 784.36	114.70	0	13	192 760.31
ψ (state + waterT + Tournament CPUE)	192 789.60	119.94	0	11	192 767.56
ψ (state + Tournament CPUE)	192 812.30	142.64	0	10	192 792.27
ψ (state + airT)	192 832.28	162.62	0	10	192 812.25
ψ (state + waterT + $waterT^2$ + Tournament CPUE)	192 845.72	176.06	0	12	192 821.67
ψ (state + waterT)	192 860.29	190.63	0	10	192 840.26
ψ (state)	192 875.33	205.67	0	9	192 857.30
ψ (B-T = B-NT)	194 067.92	1398.26	0	8	194 051.90

Note: Effects evaluated influencing ψ include tournament angler effort (h), tournament catch-per-unit-effort (no.·h^{-1}; CPUE), linear and quadratic water temperature (°C; waterT; $waterT^2$), and linear and quadratic air temperature (°C; airT, $airT^2$). Parameters in the table include AIC_c = sample-sized corrected Akaike's information criterion, ΔAIC_c = relative difference between the particular model and the best model, w_i = Akaike weight, K = number of parameters, Deviance = −2 × log-likelihood of the model less −2 × log-likelihood of the saturated models (same number of parameters and degrees of freedom).

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Schnabel population estimates provided the number of largemouth bass present in the lake at the beginning of each year to assess the three sources of mortality. While largemouth bass <381 mm recruited to the population throughout the year, these recruits would not affect this assessment. Once population size was determined, we first applied the daily capture probability to determine the number of largemouth bass that were captured at individual tournament events for each year. We then applied the initial survival rate to the number of largemouth bass captured at tournaments to estimate initial mortality. Of the remaining surviving tournament largemouth bass, we applied the transition probability from the tournament to the delayed mortality state to determine the number of largemouth bass lost to delayed tournament mortality. We summed the total number of largemouth bass captured, lost to initial mortality, and lost to delayed mortality divided by the total number of fish in the population to find the proportion of largemouth bass captured and lost to cumulative tournament mortality. We repeated the steps for non-tournament angling capture probabilities and survival rates. However, because estimates were adjusted to single days in program MARK, we extrapolated estimates to account for the number of days between time period estimates. We then summed total number of largemouth bass captured through non-tournament angling and mortality due to non-tournament angling. Finally, we applied extrapolated daily survival estimates to the largemouth bass population in Brushy Creek Lake to determine population level natural mortality.

Results

A total of 3893 largemouth bass ≥381 mm were captured at 142 largemouth bass tournaments and an additional 1250 largemouth bass were captured during 139 hours of electrofishing at Brushy Creek Lake from April 2015 – June 2018. A total of 1950 largemouth bass were recaptured during the sampling period, of which 1407 (27.4%) recaptured once, 330 (6.4%) recaptured twice, 140 (2.7%) recaptured three times, and 73 (1.4%) recaptured four times. Of the total recaptures, 742 (38.0%) were recaptured by electrofishing, 843 (43.2%) were recaptured by tournament anglers, and 365 (18.7%) were recaptured and reported by non-tournament anglers (Table 1). Forty-four (12.0%) of the total largemouth bass recaptured by non-tournament anglers were reported harvested, 0.6% of the total number of tags in the population. Reporting based on return rates of reward versus non-reward tags was estimated at 32%, where 3.9% of all released non-reward tags were reported by non-tournament anglers, and 12.2% of all released reward tags were reported by non-tournament anglers.

Of the ten models evaluated to describe variation in largemouth bass recapture probability in Brushy Creek Lake, the most supported model included a linear effect of sampling effort and a quadratic effect of water temperature (ΔAIC_c = 0.00, w_i = 0.63; Table 3). There was some support for models that included a linear effect of water temperature (ΔAIC_c = 1.41, w_i = 0.33); however, the quadratic trend of water temperature garnered more support than that of the linear effect and was used in further analyses. The remainder of the models had little to no support in describing variation in recapture probability of largemouth bass in Brushy Creek Lake (Table 3). Recapture probability beta estimates of the final model resulted in 95% credibility intervals not including zero for all three of the estimated parameters (intercept, waterT, $waterT^2$, electrofishing effort). Recapture probability increased with increased water temperatures (Fig. 2A) and electrofishing effort (Fig. 2B). Recapture probabilities of largemouth bass within Brushy Creek Lake ranged from 0.00081 (95% CI: 0.00063, 0.00102) during an electrofishing event lasting 1833 seconds and at an air temperature of 16.17 °C to 0.014159 (95% CI: 0.01090, 0.01796) during an electrofishing event lasting 18 354 seconds at 19.7 °C.

Of the models describing capture probability to the tournament and non-tournament angling states, those that estimated capture probabilities from Brushy Creek Lake to the tournament and Brushy to non-tournament angling states separately (ΔAIC_c = 0.00, w_i = 1.0) outperformed models that set capture probabilities equal to each other (ΔAIC_c = 1396.93, w_i < 0.001) prior to inclusion of additional covariates, suggesting rates of capture from Brushy Creek Lake to tournament and non-tournament angling states are different. The most supported model for capture probability also included a quadratic effect of air temperature on both tournament and non-tournament angling capture probabilities as well as tournament catch-per-unit effort on the tournament state (largemouth bass·h^{-1}; ΔAIC_c = 0.00, w_i = 1.0; Table 4). All five beta estimates describing capture probability included zero in the final model. Capture probabilities into tournaments ranged from 0.00210 (95% CI: 0.00127, 0.00256) to 0.01526 (95% CI: 0.01212, 0.01854) and were twelve fold higher than non-tournament angling state capture probability [0.00031 (95% CI: 0.00015, 0.00052) to 0.00126 (95% CI: 0.00104, 0.00149)].

Capture probabilities of both tournament and non-tournament angling increased with increasing air temperatures, whereas tournament capture probability also increased with increasing tournament CPUE (Fig. 3). The additional transition of tournament to delayed mortality was positively related to water temperature and number of prior tournament captures (Sylvia and Weber 2019). Cumulative three-day delayed mortality ranged from 0.09 to 0.43, with an average rate of 0.27 (SE = 0.08).

Evaluation of survival models, prior to inclusion of additional covariates, with all states set equal, all states set separate, and combinations of states equal to and separate from each other

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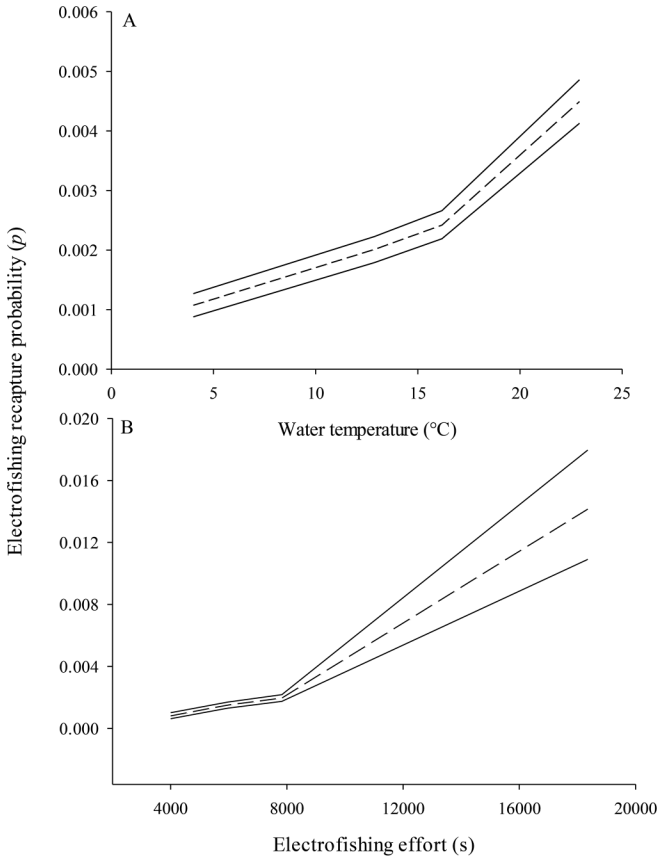
Table 5. Live–dead multistate models used to estimate survival (*S*) of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, for 377 periods beginning 13 April 2015 through 1 June 2018.

Model	AIC_c	ΔAIC_c	w_i	*K*	Deviance
S (state + airT + airT^2 (NT,T) + bag/angler (T) + initial mortality (T) + waterT + waterT^2 (B), different intercepts)	192 639.23	0.00	0.98	21.00	192 597.09
S (state + airT + airT^2 (NT,T) + bag/angler (T) + initial mortality (T) + waterT + waterT^2 (B), same intercept)	192 647.20	7.96	0.02	19.00	192 609.08
S (state + airT + airT^2 (NT,T) + bag/angler (T) + initial mortality (T) + waterI (B))	192 668.33	29.09	0.00	18.00	192 632.22
S (state + waterT + bag/angler (T) + initial mortality (T))	192 682.91	43.67	0.00	16.00	192 650.82
S (state + waterT + waterT^2 + initial mortality (T))	192 692.25	53.01	0.00	16.00	192 660.16
S (state + waterI + initial mortality (T))	192 695.91	56.67	0.00	15.00	192 665.83
S (state + airT (NT,T) + bag/angler (T) + initial mortality (T))	192 702.07	62.83	0.00	16.00	192 669.98
S (state + airT (NT,T) + initial mortality (T))	192 702.72	63.49	0.00	15.00	192 672.65
S (state + airT + airT^2 (NT,T) + bag/angler (T))	192 722.50	83.26	0.00	16.00	192 690.41
S (state + initial mortality (T))	192 732.59	93.35	0.00	14.00	192 704.52
S (state + waterT)	192 744.91	105.67	0.00	14.00	192 716.84
S (state + waterT + bag/angler (T))	192 746.39	107.15	0.00	15.00	192 716.31
S (state + airT (NT,T))	192 748.36	109.12	0.00	14.00	192 720.29
S (state + airT (NT,T) + bag/angler (T))	192 749.16	109.93	0.00	15.00	192 719.09
S (state)	192 780.58	141.34	0.00	13.00	192 754.52
S (state + bag/angler (T))	192 782.44	143.20	0.00	14.00	192 754.37
S (NT = T, B)	192 790.18	150.94	0.00	13.00	192 764.12
S (B = NT, T)	192 890.57	251.33	0.00	13.00	192 864.51
S (B = T, NT)	192 999.95	360.71	0.00	13.00	192 973.89
S (.)	193 132.00	492.76	0.00	12.00	193 107.95

Note: Survival was evaluated in Brushy Creek Lake (B), tournament angler (T), and non-tournament angler (NT) states. Effects evaluated influencing *S* include a constant model (.), linear and quadratic air (airT, airT^2) and water (waterT, waterT^2) temperature (°C), average number of bass per angler (bag/angler), and initial tournament mortalities. Parameters in the table include AIC_c = sample-sized corrected Akaike's information criterion, ΔAIC_c = relative difference between the particular model and the best model, w_i = Akaike weight, *K* = number of parameters, Deviance = $-2 \times$ log-likelihood of the model less $-2 \times$ log-likelihood of the saturated models (same number of parameters and degrees of freedom).

Fig. 2. Estimated recapture probability of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018 in relation to mean daily water temperature (A) and electrofishing effort (B). Solid lines around estimates represent the 95% credible intervals of the Markov chain Monte Carlo estimates.



indicated the strongest support for survival estimated separately for each state (ΔAIC_c = 0.00, w_i = 0.96) followed by models that set tournaments and non-tournament angling equal (ΔAIC_c = 6.51, w_i = 0.03), models that set Brushy and non-tournament angling states equal (ΔAIC_c = 107.18, $w_i < 0.001$), models that set Brushy and tournament states equal (ΔAIC_c = 130.25, $w_i < 0.001$), and finally models that set all state survivals equal (ΔAIC_c = 141.36, $w_i < 0.001$). Setting all state survivals separate, the top model included a quadratic effect of air temperature on non-tournament and tournament states, a quadratic effect of water temperature on the Brushy Creek Lake state, and an effect of average bag per angler and initial mortality on the tournament survival estimates (ΔAIC_c = 0.00, w_i = 0.98; Table 5). The most supported model included separate intercepts; thus, state effects and covariates were estimated individually. Mean daily survival probability of largemouth bass was highest in Brushy Creek Lake, followed by tournament captured largemouth bass and finally non-tournament angled largemouth bass. Average percent differences in survival of largemouth bass in Brushy Creek Lake was 2.9% higher than that of tournament captured largemouth bass and 23% higher than non-tournament captured largemouth bass, whereas average tournament largemouth bass survival was 20% higher than that of non-tournament angled largemouth bass.

Eight of the eleven beta estimates on survival in the final model did not include zero (Brushy Creek Lake waterT^2, Tournament intercept, Tournament airT, Tournament bag per angler, Tournament initial mort, Non-tournament intercept, Non-tournament airT, Non-tournament airT^2). Survival of largemouth bass in Brushy

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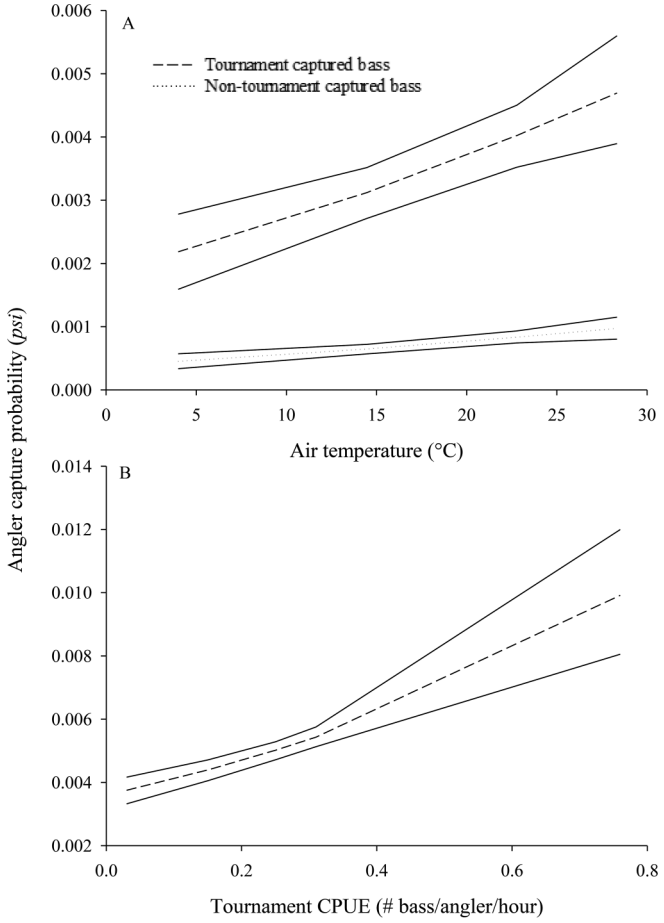
Fig. 3. Estimated tournament (dashed line) and non-tournament (dotted line) angled capture probabilities of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C; A) and tournament CPUE (B). Solid lines around estimates represent the 95% credible intervals of the Markov chain Monte Carlo estimates.



Creek Lake showed a quadratic pattern with temperature, resulting in highest survival [0.998094 (95% CI: 0.99759, 0.99876)] at 10.4 °C and lowest survival [0.99252 (95% CI: 0.98981, 0.99514] at water temperatures of 22.9 °C (Fig. 4). Similar relationships between air temperature and survival of non-tournament angled largemouth bass were observed, with rates ranging from 0.82025 (95% CI: 0.73228, 0.74962) at −3.89 °C to 0.71535, (95% CI: 0.52989, 0.84601) at 29.0 °C (Fig. 5). For tournament largemouth bass, survival followed a quadratic pattern with water temperature (Fig. 6A) and was also inversely related to bag per angler and initial mortality (Figs. 6B, 6C). Survival was lowest on days with increased air temperature, increased initial mortality, and increased bag per angler. Survival rates of tournament largemouth bass were highest [0.97274 (95% CI: 0.96325, 0.99363)] when air temperature was 14.4 °C, bag per angler was 3.0, and initial mortality was zero, whereas lowest survival rates [0.75190 (95% CI: 64844, 0.85969)] occurred with air temperatures of 22.2 °C, a bag per angler of 1.9, and 27 initial mortalities.

The annual population estimate of largemouth bass ≥381 mm in Brushy Creek Lake during 2015 was 6122 (95% CI: 5578, 6436; mean = 22 bass·ha^{-1}, 95% CI: 20–23), the 2016 population estimate was 6183 (95% CI: 5536, 6830; mean = 22 bass·ha^{-1}, 95% CI: 20–25), and the 2017 estimate was 6236 (95% CI: 5468, 7003; mean = 22 bass·ha^{-1}, 95% CI: 20–25). Tournament anglers captured three times as many

Fig. 4. Estimated survival rates of jaw tagged largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018 in relation to mean daily water temperature (°C). Dashed lines around estimates represent the 95% credibility intervals of the Markov chain Monte Carlo estimates.

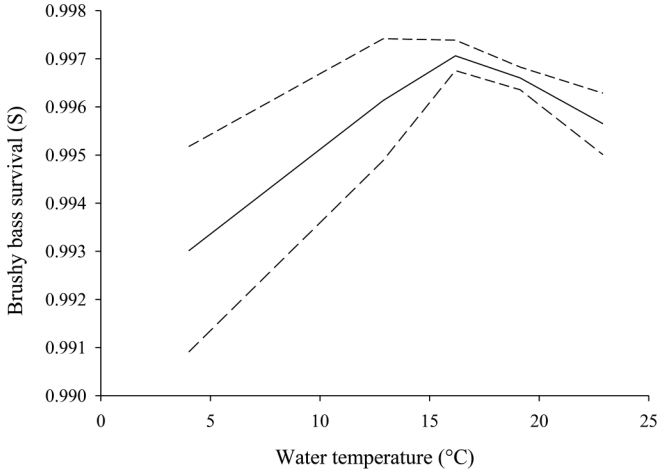
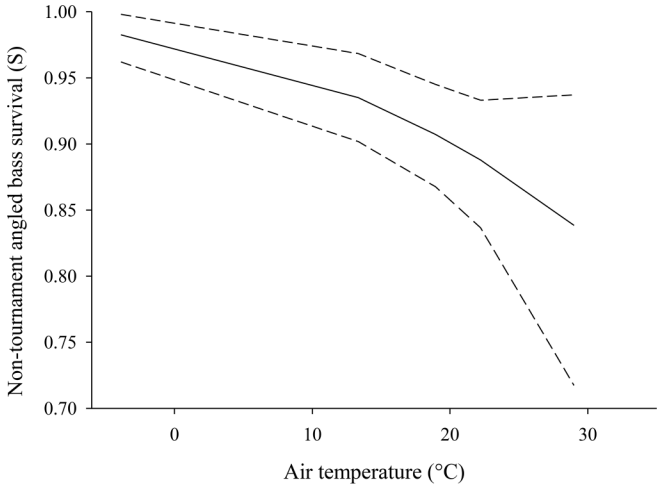


Fig. 5. Estimated survival rates of jaw tagged, non-tournament captured largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C). Dashed lines around estimates represent the 95% credibility intervals of the Markov chain Monte Carlo estimates.



largemouth bass throughout the year than non-tournament anglers. On average, 1215 bass (SE = 62 bass) were captured at tournaments across the three sample years (20.0%), whereas only 590 largemouth bass (SE = 32 bass) were estimated as captured by non-tournament anglers (9.8%; Fig. 7). Tournament mortality was also greater than that of non-tournament angling mortality. An average of 37 (SE = 2 bass; 0.6%) largemouth bass were lost to initial tournament mortality annually, whereas 277 (SE = 49 bass) were estimated to be lost to delayed tournament mortality (4.5%; Fig. 8). Cumulatively, an average of 314 largemouth bass (SE = 47 bass) were lost to tournament mortality (25.8%), representing 5.1% of the population. Alternatively, 125 largemouth bass (SE = 7 bass) were harvested or experienced delayed non-tournament angling mortality, representing only 2.0% of the total largemouth bass population. Natural mortality accounted for the greatest loss of largemouth bass, with an average of 57% of the largemouth bass population annually (Fig. 8).

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Fig. 6. Estimated survival rates of jaw tagged tournament captured largemouth bass in Brushy Creek Lake, Iowa, USA, from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C; A), average bag per angler (B), and number of initial tournament mortalities (C). Dashed lines around estimates represent the 95% credibility intervals of the Markov chain Monte Carlo estimates.

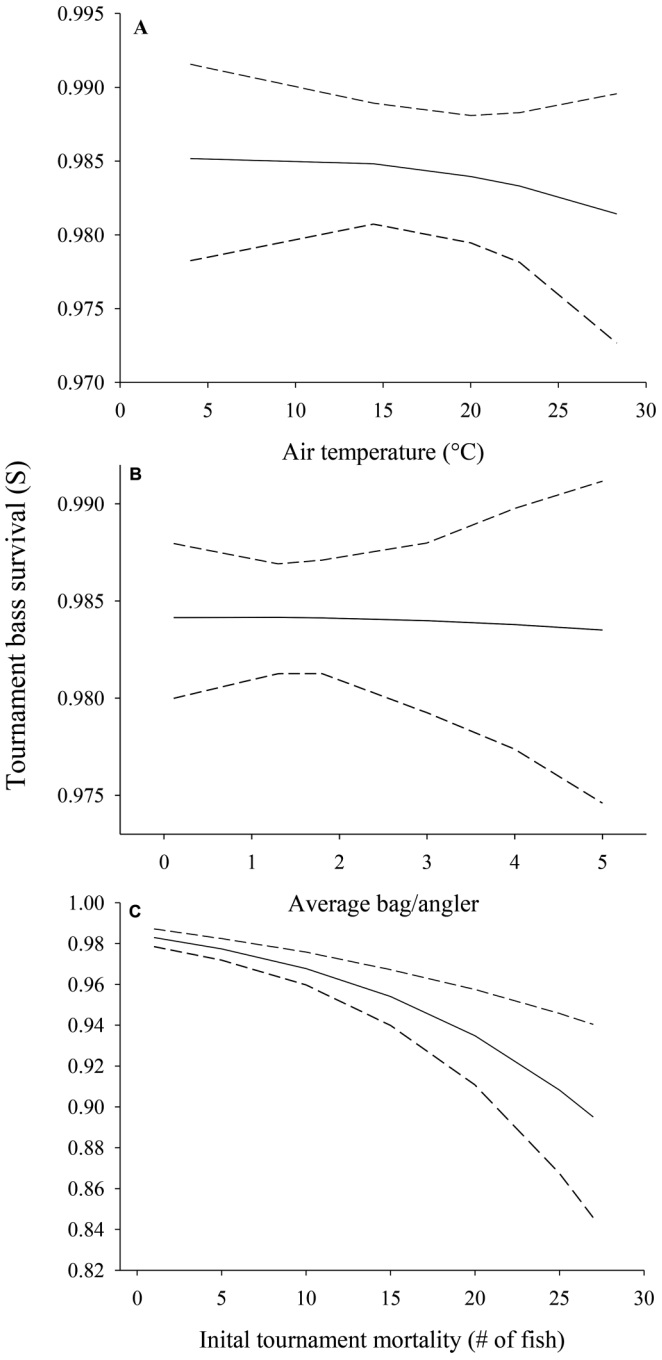
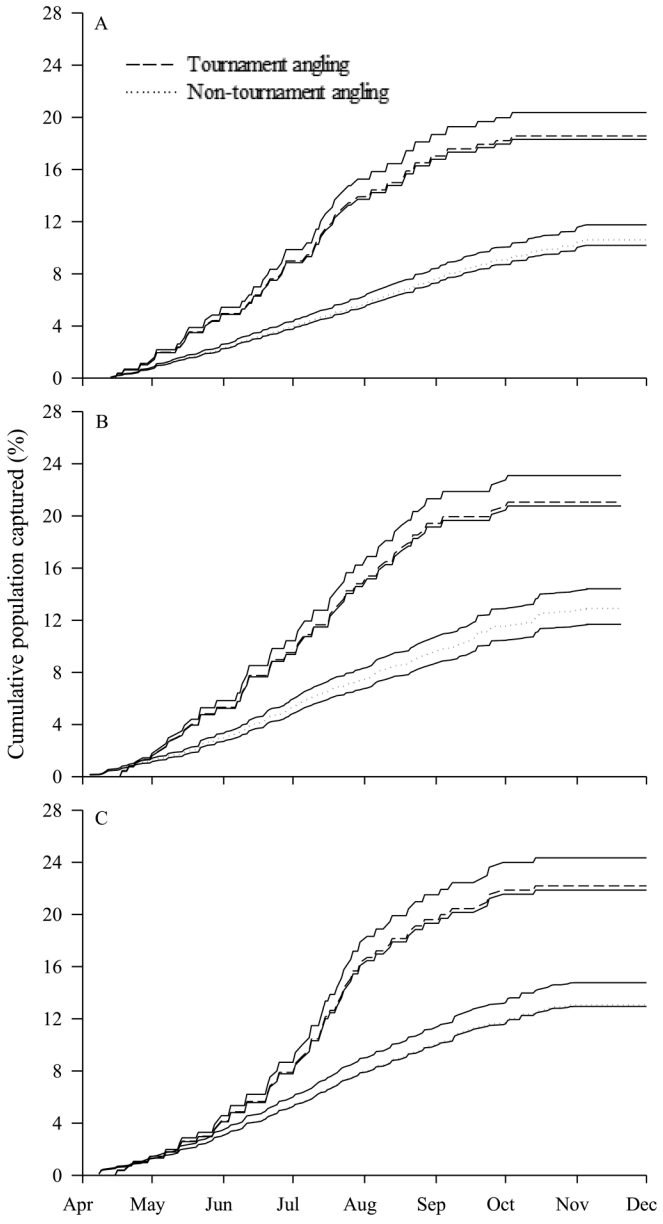


Fig. 7. Cumulative percentage of largemouth bass population captured at tournaments (dashed line) and by non-tournament angling (dotted line) during 2015 (A), 2016 (B), and 2017 (C) in Brushy Creek Lake, Iowa, USA. Solid lines around estimates represent the 95% credibility intervals of the Markov chain Monte Carlo estimates.



Discussion

Understanding the scale and influence of harvest and catch and release angler practices are important to population management in largemouth bass. Non-tournament and tournament angler capture probabilities were high, with anglers capturing a combined 29% of the population annually. Average annual tournament angler effort at Brushy Creek Lake was 32.3 h·ha^{-1} across the tournament season. While tournament pressure is variable across systems (0.2 h·ha^{-1}, 0.1 ha·h^{-1} in north central Florida, Schramm et al. 1987; 3.3 in Texas, Driscoll et al. 2007; 27.8 h·ha^{-1} in Connecticut, Edwards et al. 2004; and 59.5 h·ha^{-1} in Puerto Rico, Neal and Lopez-Clayton 2001), Brushy Creek Lake is above the average for tournament angling effort. However, corresponding angling mortality was relatively low, especially for non-tournament (2.0%) and initial tournament mortality (0.6%). While delayed tournament mortality made up the largest proportion of fishing mortality (4.5%), it was still more than ten times less than that of natural mortality (57%). Thus, cumulative angling mortality likely has little effect on largemouth bass in Brushy Creek Lake and these patterns may also occur in other black bass populations similar to this one.

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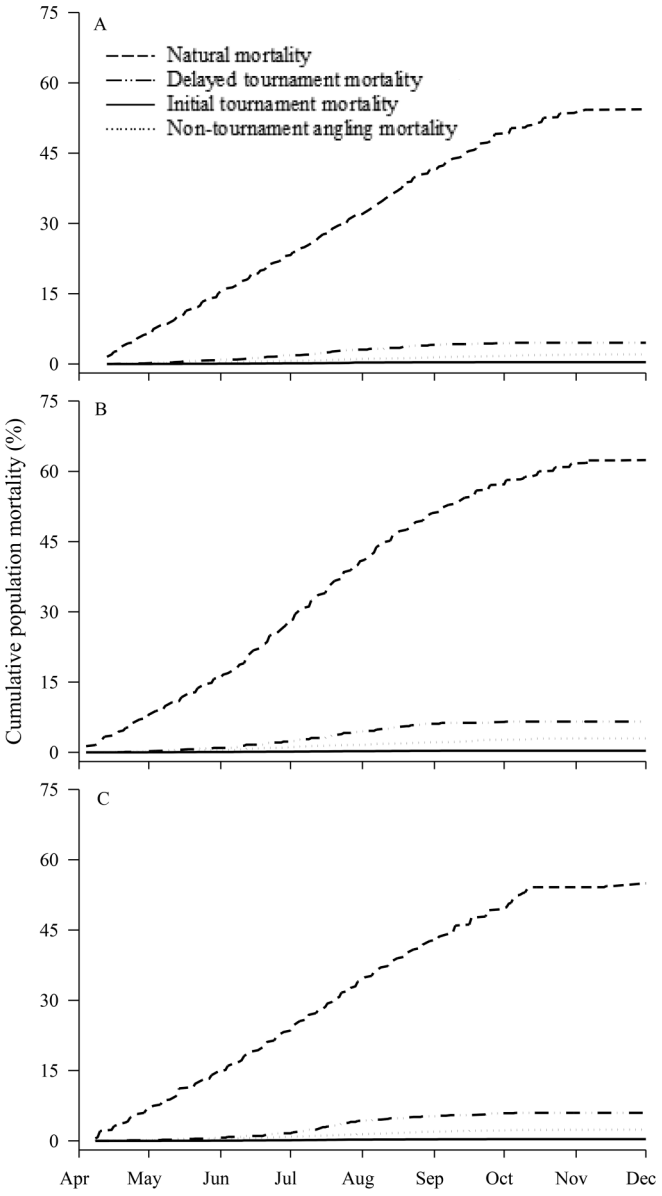
Fig. 8. Cumulative percentage of largemouth bass population mortality in Brushy Creek Lake, Iowa, USA, from natural mortality (dashed line), delayed tournament mortality (dashed and dotted line), initial tournament mortality (solid line), and non-tournament angling (dotted line) during 2015 (A), 2016 (B), and 2017 (C).



Daily capture rates of non-tournament angled largemouth bass were relatively low but varied within and among years because of environmental effects that may have affected largemouth bass feeding habits and behavior (Sylvia et al. 2020). Increasing air temperature was an important factor resulting in higher non-tournament angling capture rates, whereas water temperature was less important in describing variability in capture rates. Water temperature and air temperature can be highly correlated in structuring black bass metabolism and foraging (Fry 1971); however, water temperature can remain relatively buffered to short-term fluctuations in air temperature and weather patterns. Weather events, such as storms and fronts leading to changes in wind, barometric pressure, light and turbidity levels, can influence feeding and sensory capability of black bass (Stoner 2004) that may have had more of an effect on largemouth bass activity levels and feeding rates, and hence, angler capture probabilities (Johnson and Charlton 1960; Coutant 1975).

Low daily non-tournament capture rates (0.00031–0.00126) corresponded to a relatively low yearly proportion of the total population (8.5%–11.0%) captured by non-tournament anglers. Low capture rates, despite high angling effort in systems, may occur for many reasons, including angler practices (Wilde et al. 2003), behavioral patterns of black bass (Philipp et al. 2009; Sylvia et al. 2020), or influences of tournament angling (Hackney and Linkous 1978). For example, non-tournament anglers using smaller lure sizes may have selected for and captured smaller largemouth bass (<381 mm) that were not included in this assessment. Largemouth bass can also experience multiple capture events by tournament and non-tournament anglers (Burkett et al. 1986; Myers 2008; Sylvia and Weber 2019), resulting in a small, highly vulnerable segment of the population comprising a large portion of angling events (Colgan 1986; Philipp et al. 2009). Increased angling pressure can lead to decreases in catch rates because of recovery time between captures (Mankin et al. 1984; Burkett et al. 1986), as well as learned behaviors including lure avoidance (Clark 1983) and loss of naivety (Hessenauer et al. 2016). High tournament activity on Brushy Creek Lake may have resulted in less success by non-tournament anglers, whereas angler skill (Beardmore et al. 2011) may play an important role in increased capture rates at tournament angling events. Non-tournament anglers throughout the study captured approximately 10% of largemouth bass multiple times, indicating that while a small proportion of the largemouth bass in Brushy Creek Lake are captured multiple times, many of the fish have never been captured previously or are newly recruited to the fishery.

Largemouth bass tournament capture probabilities varied depending on tournament angler catch per unit effort, where higher tournament angler catch rates resulted in a higher probability of a largemouth bass coming into a tournament. Tournament catch per unit effort varied with time, where tournaments held in June and July tended to have higher catches per angler per hour (0.26, 0.28, respectively) compared to other months (mean = 0.19). In addition to tournament angler catch rates, largemouth bass tournament capture probabilities also increased with air temperatures. The effect of air temperature on largemouth bass capture probability is likely reflective of increased bass metabolism, foraging rates, and sensory abilities (Coutant 1975). Large deviations in air temperatures can lead to changes in the feeding habits of fishes (Niimi and Beamish 1974), as well as environmental factors in systems such as turbidity and light levels, affecting the ability of fish to see prey. Thus, evaluation of combined effects of angler effort and environmental influences are useful in further understanding capture success at fishing tournaments. Non-tournament harvest and catch and release mortality accounted for only 2.0% of total annual mortality. Harvest was approximately 10% of the total reported non-tournament angler recaptures, indicating high rates of catch and release practiced by anglers in Brushy Creek Lake, similar to other systems (Henry 2003; Isermann et al. 2013). Catch and release mortality of non-tournament angled black bass is generally low (5%–10%; Muoneke and Childress 1994; Hayes et al. 1995). Numerous factors are known to increase mortality of non-tournament captured black bass (e.g., hooking injury, increased fight time and air exposure, depressurization; Cooke et al. 2003; Suski et al. 2003; Siepker et al. 2007). Given data limitations, we were unable to include an additional state of delayed non-tournament angling mortality in our model. While prior work has indicated much of delayed mortality is the results of long-term stressors and containment (Steeger et al. 1994; Weathers and Newman 1997; Neal and Lopez-Clayton 2001), which does not occur with non-tournament angling, there is the potential for mortality occurring past one day for these fish. It would be useful to examine the impacts of delay non-tournament angling mortality in future assessments.

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Moreover, we found increases in air temperature led to decreases in survival of released largemouth bass (see Table 2) whereas water temperature was less supported in our models. Air temperature has been empirically linked to recovery time after capture (Suski et al. 2007) and handling mortality (Gingerich et al. 2007), all leading to increased stress in fish. Thus, although non-tournament mortality was low, air temperature is important in describing variation in mortality of largemouth bass through time.

In contrast to non-tournament angling capture, the high proportion of the largemouth bass population (upwards of 22%) captured at tournament events during any given year increased the number of largemouth bass exposed to tournament stressors and potential initial and delayed tournament mortality. Tournament mortality is well-studied (Schramm et al. 1987; Edwards et al. 2004; Moon et al. 2017) and initial and delayed tournament mortality is highly variable spatially and temporally (Schramm et al. 1987; Hartley and Moring 1995; Schramm and Gilliland 2015). Our results indicate delayed mortality had a larger effect than initial mortality. Daily initial mortality estimates were <1% in Brushy Creek Lake and accounted for only 0.4% of population level mortality. Tournament mortality was positively associated with air temperature, number of initial tournament mortalities, and number of largemouth bass per angler. Increased air and water temperatures (Chapman and Fish 1985; Schramm et al. 1987; Wilde 1998), increased handling times (Hartley and Moring 1995), increased number of fish per angler (Wilde et al. 2002), and high live-well densities (Weathers and Newman 1997) can all contribute to increased initial tournament mortality. Lower largemouth bass bag limits in Iowa (three fish per angler), as opposed to five fish per angler regulations in many other states (Mississippi Wildlife, Fisheries and Parks 2018) may account for the lower number of fish dying before or during the weigh-in process, although recent evidence suggests this may not be the case (Maahs 2020).

Average delayed tournament mortality was seven times greater than initial mortality (17%–33%) and was previously related to water temperature and prior tournament captures but was not related to largemouth bass size (Sylvia and Weber 2019). Water temperature may explain up to 30% of variability in mortality across tournaments (Wilde 1998) and can influence delayed mortality because of increased temperatures in live-wells, during weigh-ins, and at release sites leading to increased physiological stress and decreased recovery post-tournament (Cooke and Suski 2005). We found that prior tournament capture can also increase cumulative stressors at each tournament event. Similar to non-tournament angling recapture, only 11% of largemouth bass were captured at multiple tournament events, suggesting high propensity for increased delayed tournament mortality. Size differences in delayed mortality were not evident in our prior analysis (Sylvia and Weber 2019). Although tournament mortality can be size-specific (Meals and Miranda 1994), the effects of largemouth bass length, weight, and condition were not supported. While larger black bass can experience more stressors during a tournament (higher oxygen demands, longer landing times, longer air exposure at weigh-ins, and higher live-well densities; Burleson et al. 2001; Cooke et al. 2002), after release, additional influences such as relocation, accumulation of largemouth bass at tournament release sites, inability to find appropriate habitat, and increased predation during recovery (Stang et al. 1996; Gilliland 1999) are likely more critical to post-tournament survival.

Largemouth bass natural mortality was high (57%: 95% CI: 45%, 72%) across years. When compared to mortality across other largemouth bass populations (mean: 37%, 95% CI: 2%–71%; Beamesderfer and North 1995), largemouth bass natural mortality in Brushy Creek Lake was within the range of other estimates populations but was higher on average. This is unusual for a high latitude system, as natural mortality in largemouth bass is generally negatively correlated with latitude and positively correlated with mean air temperature (Beamesderfer and North 1995). However, similar independent estimates of largemouth bass natural mortality have been reported in this region (Pitlo and Bonneau 1992), indicating that natural mortality of largemouth bass can be high even at northern latitudes. We did observe increased natural mortality at both high and low water temperatures, likely due to physiological effects on growth, feeding outside of optimum temperatures, and environmental productivity (Beamesderfer and North 1995). Daily natural mortality rates were still highly variable, especially at lower than average water temperatures, likely due to little recapture data occurring during the winter periods of our model. Even with high variability, natural mortality was approximately seven times greater than tournament and non-tournament fishing mortality combined and likely has the most influential effect on the population. High natural mortality rates have the potential to minimize adverse effect of high fishing pressure, as the population likely grows and dies quickly. Population estimates across the study period remained constant, suggesting potentially high recruitment into the ≥381 mm largemouth bass population, offsetting the effects of natural mortality, and resulting in little population level impacts of fishing mortality (Churchill et al. 1995; Driscoll et al. 2007). Further assessments to understand relationships among recruitment, population growth, and natural mortality rates may be useful in understanding of the impacts of angling mortality on largemouth bass populations.

Prior population level mortality models have evaluated total mortality multiple ways, including simulations (Allen et al. 2004), combined tag-telemetry models (Kerns et al. 2016), Leslie matrix models (Hayes et al. 1995), and tagging studies (Hysmith et al. 2014). We know of no previous study that has used live–dead multistate mark–recapture models and censused tournament data to quantify population level mortality of largemouth bass. While mark–recapture studies can be effort intensive (more than 140 tournaments attended and nearly 100 hours electrofishing in this study), they serve great value in understanding capture probability, mortality rates, and variables associated with designated model states (Lebreton et al. 1992). Multiple issues encountered in prior methodologies have been avoided with such techniques including transmitter failure of telemetry tags (Kerns et al. 2016), unaccounted tag loss, and unknown capture probabilities of tournament black bass (Hysmith et al. 2014). However, even with three and a half years of tournament census data and fishery independent sampling, multistate models can fail to estimate specific states, especially if recapture probabilities are low or unknown (Kendall 2004). For example, a lack of data during the winter season likely led to a less precise estimation of natural mortality during those periods. Lacking appropriate descriptive covariates within the model can also influence model estimates. Catch and effort information influenced capture probability in tournament events, but we were unable to include a similar covariate on non-tournament capture probability. Supplemental creel data would have been useful in our estimation of non-tournament angling capture probability but would have required substantial additional sampling effort. While we are confident we met the assumptions associated with multistate mark–recapture models, there is potential for bias in our estimation of the largemouth bass populations size. The Schnabel model estimated a single population estimate at the beginning of each year, not accounting for recruitment offsetting mortality in the model. However, assessment of the relative numbers of largemouth bass lost to each mortality type across the year is still useful as all comparisons were made based on the same assumptions. Segments of fish populations may also exhibit higher or lower likelihood of capture through angling events (Colgan 1986; Philipp et al. 2009), leading to largemouth bass having unequal detection and probability of transition. If this is occurring in Brushy Creek Lake, our estimates of population level capture probability and mortality may be over or underestimated. Inclusion of monthly fishery independent sampling is useful in preventing assumption

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violations; however, future work should consider potential differences in largemouth bass vulnerability to angling.

With release rates approaching 100% in some systems (Henry 2003), understanding additional sources of mortality, including from catch and release and tournaments, is imperative. Our results indicate in Brushy Creek Lake, initial and delayed tournament mortality can be substantially higher compared to non-tournament catch and release angling and harvest mortality, but both sources of fishing mortality are low compared to natural mortality, potentially providing some protection from long-term population level effects. This is not to say that instances do not exist in which increases in capture probability (e.g., bed fishing; Suski and Philipp 2004; Philipp et al. 2009) and survival rates (angler experience; Sylvia 2019; Siepker et al. 2007) have the potential to negatively influence black bass populations through other mechanisms. For example, largemouth bass in Brushy Creek Lake preside in the lower end of black bass thermal ranges and likely experienced lower air and water temperatures compared to black bass populations in other regions of the country where high air and water temperatures may have more impact on angling mortality. However, additional analyses conducted on this data set where large simulated increases (10%–100%) in capture probabilities and decreases (10%–100%) in survival probabilities resulted in relatively minor population level impacts on the largemouth bass abundance and size structure (Sylvia 2019). Consequentially, when largemouth bass natural mortality is high, additional regulations implemented to reduce fishing pressure are likely to be unnecessary or provide intended benefits (Sylvia 2019; Maahs 2020). Increased management of black bass paired with high catch and release rates has resulted in negative effects on growth and size structure in some populations (see Hansen et al. 2015; Miranda et al. 2017). Thus, some level of mortality due to non-tournament and tournament angling may be beneficial in releasing bass from density dependent growth response and potentially increasing size structure in largemouth bass populations.

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