An evaluation of tournament angling impacts on a Largemouth Bass population using mark-recapture data

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An evaluation of tournament angling impacts on a Largemouth Bass population using mark-recapture data

by

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Iowa State University

Ames, Iowa

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DEDICATION

This dissertation is dedicated to John-Michael, Mom, Dad and Nick. I could not have accomplished half of what I have in this life without your unwavering support.
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ABSTRACT

Recreational angling for Largemouth Bass (Micropterus salmoides; hereafter referred to as bass) has grown in popularity in recent decades. Bass catch and release angling has become popular, resulting in generally low harvest rates despite high angling effort. Additionally, tournament angling events and anglers have grown exponentially. While many recreational and tournament bass anglers practice catch and release angling with the belief that it is a useful measure for sustaining fish populations, fish subjected to such methods may still be vulnerable to multiple sources of mortality and sub-lethal effects. While many studies have quantified the effects of angling mortality on individual bass, few have been assessed at the population level. Although effort intensive, mark-recapture studies serve as a useful empirical tool to improve assessment and management of sources of mortality in bass populations. Thus, the objectives of this study were 1) determine if angler presence and behavior (fishing depth and movement rate), bass behavioral patterns (movement rate, home range, depth, and size), and environmental conditions affect tournament angler catch rates and bass capture probability at fishing tournaments; 2) estimate daily apparent survival rates of bass to evaluate the duration of delayed tournament mortality and to identify important covariates affecting survival; 3) quantify recreational and tournament angler capture probability and natural, recreational angling, and initial and delayed tournament mortality; and 4) estimate tournament capture probability and survival of two size classes of bass [medium (381-457 mm) and large (>457 mm)] and simulate changes in capture probability and survival to assess potential effects on population size-structure.

To address these objectives, a wide-scale mark-recapture study was employed during a four-year period at Brushy Creek Lake, IA, USA. Bass were captured and tagged both at tournament
events and through electrofishing and recaptures were received through electrofishing and
tournament and recreational angler reporting.

For my first objective, I tracked forty-nine bass implanted with radio telemetry tags
weekly and five tournament anglers at each tournament event during 2018. I then quantified bass
home range, weekly movement rate, depth used, and spatial overlap with anglers, as well as
angler depth use, angler movement rate, and air and water temperature. I then used these
estimates as covariates in a multistate mark-recapture model in program MARK to estimate
capture probability at fishing tournaments. In addition to the mark-recapture model, I also used
the covariates as independent variables to predict bass tournament catch-per-unit-effort (CPUE;
# bass/angler hours) in a multiple regression model. Air temperature and angler overlap were
positively associated with bass capture probability, while bass movement changed across the
sample period and was positively related to tournament CPUE. However, bass size, bass home
range, bass and angler depth use, and angler movement rate were not successful in characterizing
individual variation in capture probability or correlated with tournament CPUE. Tournament
anglers in the study were successful at identifying habitats where bass reside and both bass and
anglers changed patterns as a result of environmental influences. This strong overlap of bass and
tournament anglers creates the potential for population level impacts of tournament angling on
bass populations.

Tournament angling can have significant impacts on bass populations when anglers
successfully target bass; however, assessments of tournament impacts can be difficult, as some
mortality occurs after release from tournaments events. For my second objective, I used a
modified Cormack-Jolly-Seber model in program MARK to evaluate the duration of delayed
tournament mortality and to identify important covariates affecting survival. Multiple monotonic
trends were evaluated to test acute (2, 3, 4, or 7 d) and chronic (15 or 30 d) delayed mortality hypotheses and both environmental and individual covariates were tested to assess additional factors (air and water temperature and bass length, weight, condition, and number of prior tournament captures) influencing delayed tournament mortality. The most supported models revealed a 3-day trend in survival following tournament capture but no support for chronic mortality. Bass tournament mortality ranged from 17% to 33% and increased with increases in water temperature and the number of tournament capture events experienced by an individual bass. Results of the model confirmed the potential for substantial delayed mortality in bass populations and the importance of including delayed mortality when evaluating population-level effects of tournament mortality.

Using estimates from the delayed tournament mortality model, I expanded on my assessment of bass mortality. For my third objective, I used a live-dead multistate mark-recapture model to estimate recreational and tournament angler capture probability. I also evaluated contributions of natural, recreational angling, and initial and delayed tournament mortality to total population level mortality. Average annual tournament angler effort at Brushy Creek was 25.0 hr/ha and resulted in 21% of the bass population captured whereas recreational anglers only captured on average 12% of the bass population. Average total annual mortality was 0.66, with natural mortality representing the largest component (0.57), followed by delayed tournament mortality (0.06), recreational angling mortality (0.03), and initial tournament mortality (0.004). These results showed that tournament angling results in higher mortality than recreational angling but that both angling mortality sources are low compared to natural mortality. Therefore, angling mortality likely has minimal effects on bass abundance.
Although abundance of bass was likely not influenced by tournament mortality, long-term fishing mortality can lead to changes in population size-structure. For my fourth objective, I evaluated differences in tournament capture probability and survival of medium (381 – 457 mm) and large (>457 mm) bass using a multistate mark-recapture model. I then simulated changes in capture and survival rates of each size group to determine the potential for changes in population size-structure. I found that medium bass had higher tournament capture probabilities than large bass and capture probabilities of both size groups increased with air temperature. Medium bass experienced higher survival rates than large bass at tournaments and tournament survival rates of both groups were inversely correlated with water temperature. Simulations indicated increases in tournament capture probability and reductions in survival of large bass resulted in minor reductions in population size-structure whereas changes in tournament capture probability and survival of both size classes had little effect. Thus, reducing the number of large bass weighed in at fishing tournaments may result in only minor increases in bass size-structure.

This holistic assessment of both the capture probability and mortality of a bass populations by recreational and tournament anglers adds to knowledge of population level effects of catch and release angling. Findings from this study reveal that although recreational and tournament anglers can capture large portions of the population (>20%), mortality rates of recreational angling are low compared to natural mortality, resulting in minimal population level effects.
CHAPTER 1. GENERAL INTRODUCTION

Population dynamics of exploited fish populations has been a focus of fisheries management since the early 1940s (Nielsen 1999). Beginning in marine systems, population dynamics became a fundamental part of fisheries science and a useful guide for management decisions. Population assessment techniques quickly spread to inland waters and today incorporate complex understandings of both the natural and human ecosystem (Lorenzen et al. 2016). Effective inland fisheries management now requires information about fishes and their behaviors as well as society that use fishes or benefits from fisheries management (Nielsen 1999). Improvements to this holistic understanding of fisheries are necessary for successful future management.

Micropterus spp., or black bass, are a highly studied genus of freshwater fishes. Due to their recreational fishing popularity, successful management of bass fisheries is critical to meet stakeholder needs. Black bass fishing has consistently risen in popularity since the 1970s as a result of their adaptability and tolerance to a wide range of environmental conditions, making fishing opportunities readily available and highly sought after (Hartley et al. 1995; Blackwell et al. 2007). In 2011, more than 10.6 million participants spent 171 million days fishing for bass, making them the most popular sportfish in North America (US Fish and Wildlife Service 2011). While environmental factors, such as habitat availability and effects of water quality, on bass survival have been well studied, changes in fishing practices of bass anglers have led to a need for a better understanding of effects of fishing on bass populations.

In earlier days of bass fishing (1960s to early 1970s), bass were commonly captured and harvested for consumption (Holbrook 1975). Additionally, harvest regulations throughout the United States were much less stringent than current day regulations, with many systems lacking
bag limits or minimum length limits (Redmond 1986). These angling and management practices paired with increasing angling pressure caused concerns for bass anglers and fishery scientists regarding population level effects of angling, prompting the concept of catch and release angling (Barnhart 1989; Schramm and Gilliland 2015). Catch and release angling for bass has continued to grow in popularity, increasing from 27% in the early 1980s to 68% by 1996 (Quinn 1989, 1996). Today, recreational angling of Largemouth Bass *Micropterus salmoides* (hereafter referred to as bass) is extremely popular and harvest rates have decreased by 50% in North America since the 1990s (Allen et al. 2008) with voluntary release rates approaching 100% in many instances (Henry 2003; Isermann et al. 2013). Thus, while harvest may currently have little effect on populations, the potential for catch and release mortality to affect populations has increased.

In addition to recreational catch and release angling, one of the most rapidly growing segments of black bass fisheries is competitive catch and release fishing events (Schramm et al. 1991). Of an estimated 29,500 competitive fishing events held annually in inland waters in North America, about 78% were directed toward black bass in 1991 (Schramm et al. 1991). More recent studies reported upwards of 40,000 bass tournaments were held in the United States in 2012 (Driscoll et al. 2012). Usually targeting Largemouth Bass, competitive angling events with increased angler participation and multiple tournaments occurring on single systems, makes potential tournament exploitation of bass on lakes extremely high. In the past decade, studies have identified methods to increase survival of tournament captured bass, including improved methods of capture, confinement, and weigh-in procedures (Kwak and Henry 1995; Wilde 1998; Suski et al. 2006). Advances in catch and release angling and tournament angling practices are
believed to maintain quality of bass fisheries and improve future fishing opportunities. Yet, catch and release angling can still result in physiological stressors and potential mortality of bass.

Affinity towards bass fishing both recreationally and in tournament events is especially true in lakes throughout Iowa (Harlan et al. 1987; Mayhew 1987). In 2011, black bass anglers in Iowa comprised 44% of the total anglers in the state, spending 2,440 days targeting bass species in Iowa waters (US Fish and Wildlife Service 2011). Tournament related events in Iowa are also very popular, with some lakes seeing as many as 45 bass tournaments during the open water season every year (Sylvia and Weber in revision). However, bass fishing opportunities in Iowa lakes are inconsistent due to variable population characteristics such as mortality rates (ranging from 10-50%) and catch per unit effort (CPUE). Recently bass tournament anglers as well as the Iowa Department of Natural Resources (DNR) staff have expressed concerns with the quality of bass fisheries (e.g., abundance and size-structure) across the state (Jeff Kopaska, Iowa DNR, personal communication). Even with continued management efforts in the state to improve fisheries, including habitat improvement work, stocking programs, and angling regulations, understanding of underlying population responses of bass to fishing pressure is lacking. Faced with intense fishing pressure, an improved understanding of how to manage bass populations in Iowa and throughout North America is needed.

Effects of fishing on populations are the result of capture probability and fishing mortality. Contributing sources of angling pressure can be high in many bass populations (Isermann et al. 2013), but is generally unknown in most populations. Knowledge of behaviors of bass and anglers that may increase vulnerability of bass to capture, as well as the proportion of bass that are experiencing varying mortality sources is a vital first step in understanding bass population dynamics. Even high mortality rates affecting a small portion of the population can
have negligible influence at the population level (Hayes et al. 1995; Allen et al. 2004), whereas large proportions of a population being vulnerable to capture and combined with associated mortality can cause long-term population effects. Thus, assessing mortality in the framework of capture probability is important when making management decisions.

Bass are vulnerable to multiple mortality sources. While the Iowa DNR has set specific size and harvest limits, harvest mortality can still be significant and additive, increasing mortality rates (Muoneke and Childress 1994; Allen et al. 2008). Harvest of bass is rarely monitored in Iowa lakes, making estimates of fishing mortality difficult to obtain. Even with potentially low harvest of bass in recent years, live-release angling events (i.e., tournaments and recreational angling) can result in “cryptic” mortality and can have substantial effects on bass populations. Immediate mortality from live-release angling can be caused by injury and prolonged confinement in live-wells or other containers (Gingerich et al. 2007; Siepker et al. 2007). Delayed mortality after release can be caused by extended stress, low oxygen conditions, and over handling (Schramm et al. 1987) and result in combined initial and delayed tournament mortality rates up to 77% (Cooke et al. 2002). Thus, combined effects of both harvest and live-release angling may have substantial effects on bass populations.

To fully understand the influence of anthropogenic effects on bass populations, population level analyses are necessary. However, population level studies on bass are uncommon and current results are extremely variable. Reviews of annual exploitation and total mortality estimates over 51 years have varied both temporally (i.e., changing fishing trends) and regionally (Allen et al. 2008). Estimates of catch and release including tournament level mortality have ranged from 18-30% (Allen et al. 2004; Kerns et al. 2016). Such estimates have also primarily been completed in Southern regions of the U.S., including Florida and Texas (e.g.,
Allen et al. 2004; Driscoll et al. 2007; Kerns et al. 2016) where differences in natural mortality rates and genetics (e.g., Florida Largemouth Bass hybridization) compared to Northern regions of the U.S can result in lessened effects of fishing mortality. Additionally, Iowa systems can differ in climate, lake morphology, and fishing pressure, resulting in a continued understanding of what influences bass populations in the Midwest.

Statistical models are useful in estimating dynamic rates of fish populations (Haddon 2010). While effort intensive, mark-recapture studies allow for long-term estimates of capture probability and survival and can be expanded to evaluate state specific effects (see multistate mark-recapture models; Lebreton et al. 1992). Further, mark-recapture techniques allow for the inclusion of both time-varying and individual covariates that can be used to test for specific environmental, fish specific, and angler patterns (White and Burnham 1999). Thus, mark-recapture studies serve as a useful empirical tool to improved assessment of sources of mortality in bass populations.

Quantifying the effects of bass fishing both in terms of probability of capture and mortality is vital to improving our understanding of what drives population changes in bass. Therefore, my objectives were to: 1) evaluate spatial overlap and probability of capture of bass by tournament anglers; 2) quantify delayed tournament mortality; 3) assess the contributions of natural mortality, tournament mortality, harvest mortality, and recreational angling mortality to total population mortality and 4) determine size-dependent population-level effects of tournament mortality. To evaluate these objectives, bass at Brushy Creek Lake were tagged with metal Monel jaw tags at both tournaments and through fishery independent sampling, and recaptured using tournaments, electrofishing, and recreational angler reports during a four-year period. Additionally, 50 bass in Brushy Creek were surgically implanted with radio telemetry
tags and tracked weekly in 2018, as were five tournament anglers at weekly tournament events using handheld GPS units. To address my first objective, I used GIS spatial analyses and a multistate mark-recapture model to determine angler fishing patterns, bass behaviors, and environmental influences on probability of capture at tournaments. Second, I used a Cormack-Jolly-Seber mark-recapture model to identify and quantify patterns (environmental and acute versus chronic effects) of delayed tournament mortality on bass. Third, using estimates from my delayed mortality model, I used a multistate mark-recapture model to determine the recreational and tournament angling capture and mortality rates of bass and compared those to natural mortality in Brushy Creek. Finally, because tournament effects can result in long-term changes in fishery structure, I used a multistate mark-recapture model to assess differences in tournament capture probability and mortality between two size classes of bass (medium: 381-457 mm, and large > 457 mm). I then simulated changes in both mortality and capture probability of the two groups to understand alterations in size-structure as a result of changing fishing practices. My dissertation serves as a holistic assessment of the effects of fishing practices on a bass population in Iowa.

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CHAPTER 2. INFLUENCE OF LARGEMOUTH BASS BEHAVIOR AND ANGLER SPATIAL OVERLAP ON CAPTURE PROBABILITY AT FISHING TOURNAMENTS

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Abstract

Tournament anglers characterize highly specialized abilities in their knowledge of the species they target. While fish-angler behavioral relationships are critical to understand fish catchability, few studies have assessed how bass behavior influences their vulnerability to capture by tournament anglers. Our objectives were to determine if angler presence and behavior (fishing depth and movement rate), Largemouth Bass *Micropterus salmoides* behavioral patterns (movement rate, home range, depth, and size), and environmental conditions affect tournament angler catch rate (CPUE) and bass capture probability at fishing tournaments. Forty-nine bass were tracked weekly using radio telemetry during a four-month period and five tournament anglers were selected at weekly tournament events and tracked using a handheld GPS unit. We quantified bass home range, weekly movement rate, depth used, and spatial overlap with anglers, as well as angler depth use, angler movement rate, and air and water temperature and used these estimates as covariates in a multistate mark-recapture model to estimate capture probability at fishing tournaments. We also used a multiple regression to assess the effects of the above listed covariates on tournament catch-per-unit-effort. Mark-recapture models indicated air temperature
and angler overlap were positively associated with bass capture probability, while bass size, bass home range, movement rate, and depth use were not successful in characterizing individual variation in capture probability. However, bass movement rate showed significant changes across weeks and was highly correlated to tournament CPUE. Our result indicate that bass tournament anglers are successful at identifying habitats where bass reside dependent on environmental influences. Tournament angler’s ability to capture bass creates the potential for population level impacts of tournament angling on bass populations.

**Introduction**

Measurement of the interaction among resource abundance, fishing effort, and catch rate has been coined catchability (Arregúin–Sánchez 1996). Although the traditional concept of catchability assumed fish density was spatially uniform (Baranov 1918; Gulland 1964; Caddy 1979), catchability also depends on the ability of anglers to successfully locate areas where fish are present (Quinn and Deriso 1999; Salthaug and Aanes 2003; Beverton and Holt 2012). Thus, anglers can increase catchability of fish by selectively targeting areas where fish are present. In economically important commercial fisheries, anglers use tactics such as spotters in small planes, sophisticated technology, and intensive effort to locate fish (Pillai et al. 1997; Ruttan and Tyedmers 2007). While technology is also a largely used means of locating fish in recreational fisheries (e.g., global positioning systems (GPS), side scan sonar, depth finders; Leadbitter 2000; Cooke and Cowx 2006), many anglers also rely on their understanding of preferred habitats of the fish they are targeting to increase their chances of capture (Bear and Eden 2011; Beardmore et al. 2013). For example, specialist and tournament anglers focus their efforts on a particular species of fish, compete to catch the largest fish during tournament events, and attempt to replicate behaviors of the fish (location, depth, movement patterns), increasing their overlap with
fish (Loomis and Ditton 1987; Wilde et al. 1998; Bear and Eden 2011), and potentially capturing the target species.

In addition to anglers, fish behavior may also have a large influence on probability of angler capture. Immense effort has been dedicated to understanding fish behavior that is determined by a range of factors, including environmental and individual fish variation. For example, fish movements can vary seasonally, where many species are generally found in shallow water during the spring to spawn, but use deeper water in the summer, fall, and winter to find thermal refuge or feed (Raibley 1997; Sammons et al. 2003; Hanson et al. 2007). Fish movement rates can affect home range size, defined as the area over which an animal regularly travels (Burt 1943; Hayne 1949), that can also vary seasonally in fish, with the largest home ranges observed during summer (Warden and Lorio 1975; Sammons and Maceina 2005) while searching for food due to increased metabolism of fish with increasing temperatures (Brett and Glass 1973; Fraser et al. 1993). Further, fish body size can affect behaviors, as larger fish may travel further in search of food as a result of greater energy demands (McNab 1963; Niimi and Beamish 1974). Finally, distinct sedentary and mobile segments of fish populations have also been identified (Moody 1960; Messing and Wicker 1986) that have different behavioral patterns that may also affect their vulnerability to angling (Alós et al. 2012). Thus, environmental, seasonal, and individual fish variation and its interaction with angler patterns may all play an important role in capture probability. Yet, how individual fish behavior influences their vulnerability to capture by anglers is unknown.

Recently, pairing telemetry data with angler spatial patterns has been identified as a tool to improve our understanding of fish catchability (e.g., Mathias et al. 2014; Weimer et al. 2014). For instance, past assessments of fish movement and behaviors have led to hypotheses that
regions of a system exist where fish are safe from angling due to lack of spatial overlap between fish and anglers (Martin 1958; Cox and Walters 2002). Quantifying fish and angler overlap can allow for a better understanding of areas where fish are more vulnerable to angling. Further, such assessments can identify potential temporal patterns in overlap in an attempt to understand how catchability may change seasonally or in relation to environmental effects. Combined, understanding the intricate relationship between fish, anglers, and the environment may guide fishery management decisions in highly targeted species (e.g., protected areas; Dicenzo et al. 2016; Cooke et al. 2017).

Little information is available regarding the ability of anglers to fish in the same locations as their target species as well as how angler-fish overlap and fish behavior can influence catchability. Even less information is available regarding the fishing behavior of specialist anglers, although such a group may be more likely to find and successfully capture the target species. Tournament anglers are a specialized subset of the population that are highly skilled compared to typical anglers and tournament events continue to gain popularity. For example, one of the most rapidly growing segments of black bass *Micropterus* spp. fisheries is competitive catch and release fishing events (Schramm et al. 1991a). Recent reports estimated upwards of 40,000 bass tournaments were held in the United States in 2012 (Driscoll et al. 2012).

Competitive angling events can involve hundreds of anglers participating in numerous fishing events on a single system annually (Schramm et al. 1991b; Sylvia et al. in progress) that can result in physiological effects (Cooke et al. 2002; Suski et al. 2003) as well as initial and delayed mortality (Schramm et al. 1987; Hartley and Moring 1995; Sylvia and Weber in revision) that may have effects on bass populations (Kerns et al. 2016; Sylvia and Weber in progress). Thus,
understanding the ability of tournament anglers to locate and capture bass, as well as environmental effects and bass behaviors associated with capture, is important.

Our objectives were to quantify spatial overlap of tournament anglers and Largemouth Bass *Micropterus salmoides* (hereafter referred to as bass) and to determine if angler presence, bass behavioral patterns (movement rate, home range, and depth), and environmental conditions affected tournament angler catch rates and probability of individual bass capture at fishing tournaments. We hypothesized that increased angler overlap with bass, as well as increased movement rate and home range of bass, would increase catch rates and probability of capture. We also hypothesized that environmental variables would have little effect on bass capture probability and angler catch rates, as they would be more indicative of bass behavioral changes. Our results are useful in understanding behaviors and patterns of both bass and tournament anglers that can result in increased tournament capture and have the potential to affect bass population dynamics.

**Methods**

**Sampling**

Brushy Creek Lake (hereafter Brushy Creek) is a 279 ha reservoir in Webster County, Iowa, USA. The lake has a mean depth of 8.9 m, a maximum depth of 22.9 m, and is densely covered in both emerged and submerged coarse woody habitat (mean 2.0 SE = 0.004 trees/100 m²). Daytime electrofishing (pulsed DC 300 V and 8 amps) was used to collect bass to be implanted with radio telemetry tags in April 2018. Brushy Creek was divided into four approximately equal quadrants: South, East, West, and North. Approximately 12 bass were collected from each region of the lake during the spring to attain a representation of bass from the entire lake. Fifty-one bass >700 g (<2% tag:body weight; Winter 1996) and ≥381 mm (minimum bass length limit on Brushy Creek) were retained, weighed (g), measured (mm), and
radio tags (Advanced Telemetry Systems (ATS), Isanti, Minnesota; F1835, 14 g in water) were implanted into the intracoelomic cavity using established surgical methods (Adams et al. 2012). Transmitters operated on a frequency of 148.010-151.050 kHz and were programmed to be activated for 897 days with power on for 24 hours per day. Fish were held in a recovery tank with oxygen flow until considered recovered when swimming behavior had returned to normal and returned to initial capture location. Bass implanted with telemetry tags were also tagged on the top left jaw with an individually numbered metal Monel butt end band [selected due to their high retention for black bass; 100% after one year in Smallmouth Bass Micropterus dolomieu (MacCrimmon and Robbins 1979)].

**Tracking**

Tracking began approximately one week following implantation of radio tags and occurred weekly thereafter. Data were censored for the first week of tracking to remove any biased movement or mortality resulting from surgery or relocation of fish. All recorded mortalities occurring during the censored period (n = 2) may have been the result of fish capture and surgery and were removed from analysis. Tracking occurred from boat using a 3 element folding Yagi antennae. Bass were located once gain was at the lowest achievable setting and the fish was considered no more than 2 m away. Bass were tracked every Wednesday during the open water bass tournament season from May 9 to August 15, 2018 to determine location prior to bass tournaments that afternoon. A bass was considered dead if no movement occurred across five consecutive weeks.

**Angler and tournament sampling**

All weekly bass tournaments (occurring every Wednesday from 5:00 pm to dusk) at Brushy Creek were attended and censused (i.e., every tournament captured bass was assessed) from May 9 to August 15, 2018 (n = 15 tournaments; mean anglers per tournament = 28, SE = 1)
and followed a 381 mm (15") minimum length limit and a three bass/angler bag limit. Number of anglers, number of boats, and number of bass weighed-in were recorded for each tournament event. Five tournament anglers were selected at each tournament event and equipped with a Trimble navigation GPS on their boat to record location every 30 seconds throughout the event. Anglers were identified for tracking through contact at boat ramps. Following the fishing event, the GPS’ were returned and movement was uploaded for analysis. Number of anglers, number of boats, and number of bass weighed-in were recorded for each tournament event. Following weigh-in, all bass were placed in an insulated live-well with supplemental oxygen. All fish were weighed (g), measured (mm), searched for telemetry tags, and released at the tournament ramp on the southeastern corner of the lake (same boat ramp was used for all tournaments; Figure 2.1).

Analysis

**Bass depth use, movement, and home ranges**

Bass minimum weekly movement rates (m/week) were calculated by determining the minimum in-water distance (Little et al. 1997) between two consecutive locations divided by the number of weeks between bass locations. To avoid biasing movement rates of tournament captured bass, the distance traveled from the tournament release point to the next recorded location was used to calculate the next consecutive movement rate. Depth at location was determined by overlaying weekly bass locations with a 1 m by 1 m bathymetry contour map of Brushy Creek (Iowa Department of Natural Resources; https://geodata.iowa.gov/; last accessed May 20, 2019) in ArcGIS (ESRI 2011). A global average of bass depth use was used for individuals on dates that bass were not located during tracking. Use of global averages in mark-recapture models allows missing individual covariates to be accounted for without influencing the mean of the observed values (Cooch and White 2001). Although this method can lead to smaller variance estimates due to the small number of missing values, we assumed the influence
would be negligible as only 12% of the total location data were subject to this assumption. Minimum convex polygons (MCP) methods were used to estimate bass home ranges size across the sampling period. Bass locations were plotted in ArcGIS and 90% MCP home ranges, used to remove outliers that may significantly influence home range size (White and Garrot 1990), were estimated using the Home Range Tools for ArcGIS 10 extension (version 2.0.20; Rodgers et al. 2007). Home ranges sizes were only calculated for bass that were located a minimum of five times to adequately estimate home range size, as home range sizes have been found to increase estimation bias with decreasing number of locations (Girard et al. 2002). While the use of a minimum of five locations may influence estimation of home range size, we assumed that such estimates realistically represented relative bass space use trends and their relation to angler capture rates given the sixteen sampling periods. However, interpretation of such home range estimates should be approached with caution (Gautestad and Mysterud 1995). Home range size for one bass could not be estimated due to only three locations and was assigned a global average of home range size in the mark-recapture model. Random effects ANOVA models using the lmer function in program R (RStudio Team 2015), with individual fish as a random effect, and bass TL and time (15 sampling weeks) as fixed effects, were used to evaluate the influence of bass size and differences across time on the movement rate and depth of bass. Post hoc differences were assessed using least squares means. Summary statistics and diagnostic plots in program R assessed assumptions of the models and level of significance was $\alpha \leq 0.05$ for all tests.

**Angler locations**

Maximum boat speed limit on Brushy Creek is 8.0 km/hr and trolling was not an allowed means of fishing during tournament events. Thus, angler movements $> 2.4$ km/hr during the tournament were removed from the analysis, as we assumed movements above such speeds represented moving to a new fishing location and did not represent fishing. Hourly angler
movement rates (m/hr) were calculated by determining the minimum in-water distance between two consecutive locations divided by the number of hours in the tournament. Estimates were averaged across the five sampled anglers for each weekly tournament event. Mean weekly tournament angler depth (m) was calculated by overlaying all tournament angler locations for each individual tournament with a 1 x 1 m bathymetry contour map of Brushy Creek (Iowa Department of Natural Resources; https://geodata.iowa.gov/; last accessed on May 20, 2019) in ArcGIS (ESRI 2011) and extracting depths at each fishing location. We used 95% kernel density estimators to determine weekly tournament angler space use. A rectangle grid was pre-imposed on Brushy Creek using the ArcGIS geostatistical analysis package and an estimate of the angler density probability was obtained for each grid section (Johnston et al. 2001). Bandwidth’s or smoothing parameters are needed for kernel estimators and are used to determine the width of the kernel. A least squares cross validation (LSCV) method was used to select the bandwidth with a minimum score for the error because animal utilization distributions may violate the standard bivariate normal assumption needed for a reference kernel (Seaman and Powell 1996). To visualize monthly angler space use, we repeated the kernel density estimations with all angler locations aggregated across the month for May, June, July, and August. Monthly bass locations were then overlaid on monthly angler space use maps to assess temporal angler-bass overlap.

**Fish-angler overlap estimates and relationships**

Once probability density estimates representing the number of angler locations per every m² were determined for weekly tournament events, we overlaid fish location and calculated the cumulative angler density (Tattersall 2011) within a 10-m radius of each bass location. Total angler density overlap was extrapolated from the five sampled anglers to the total number of anglers fishing during the event by taking the average angler overlap density of individual bass for the five angler locations and then multiplying this value by the total number of anglers during
the event. We chose the 10-m radius by using the estimated hourly movement rate of bass (1.1 m/hr), to account for potential movement between tracking and tournament events. Angler density estimates for each bass at each tournament event was then used in the mark-recapture model as an individual time varying covariate on probability of capture at a tournament. A multiple linear regression using the lm function in program R (RStudio Team 2015) was used to evaluate the relationship and contribution of potential predictors on catch-per-unit-effort (number of bass/number of angler hours fished) of tournament events. Predictors included a continuous variable of mean weekly angler depth use, mean weekly angler movement rate, mean weakly cumulative angler overlap with bass, mean weekly bass movement rate, mean weekly bass depth, and mean air temperature day of tournament. F-test and adjusted R-squared value were reported and used to determine the significance and amount of variance accounted for in the dependent variable by the independent variables in the final main effects model. We chose not to employ independent variable reductions techniques, as the relative effects of each parameter on catch rate were of interest (Harrell 2015). Assumptions of linearity, multivariate normality, and homoscedasticity were assessed by summary statistics and diagnostic plots in program R.

**Multistate mark-recapture model**

We analyzed individual bass encounter histories in program MARK (White and Burnham 1999) using a live capture multistate model for maximum likelihood estimates of survival ($S$), detection probability ($p$), and capture probability (transition of bass from Brushy Creek to the tournament, $Psi$; White et al. 2006). Multistate models are an extension of the Cormack-Jolly-Seber model that use capture-recapture data to understand individual movement of animals among a finite number of states (Lebreton et al. 1992). Assumptions of the model are that every marked animal present in some state immediately following sampling period $i$ have the same probability of detection and every marked animal present in some state immediately following
the sampling period \( i \) has the same probability of surviving until \( i + 1 \) and moving to another state by period \( I + 1 \). Additionally, state at time \( i + 1 \) is dependent only on the state at time \( i \).

Basic notation of the estimation of survival, detection, and transition event follow probabilities associated with each capture occasion conditional on the fish’s first release, where \( S_i^{rs} \) is the probability that fish \( i \) alive in state \( r \) at occasion \( s \), is still alive and in state \( s \) at occasion \( i + 1 \), and \( p_i^{rs} \) is the probability that fish \( i \) alive in state \( s \) at occasion \( i \) is recaptured at time \( i \). For example, a recapture history of three occasions between two states A and B (AAB) would be modelled as

\[
S^{AA}p^A S^{AB} p^B
\]

in the maximum likelihood function.

Bass could reside in one of two states in the multistate model. States were based on location in Brushy Creek (B) using telemetry or capture at a fishing tournament (T; Figure 2.2). Interval duration in the model was alternated between 6.5 days, representing the period between the end of a tournament event to the next telemetry tracking event, and 0.5 days, representing the period between a tracking event and tournament event. Intervals were adjusted in program MARK to calculate daily estimates. Telemetry bass could be observed alive and in Brushy Creek, alive and in a tournament state, unobserved in the lake, or dead in the lake or the tournament state. Transitions could occur from Brushy Creek to a tournament (\( P_{si} B \) to T), from a tournament to Brushy Creek (\( P_{si} T \) to B), or remain in Brushy Creek (\( P_{si} B \) to B). Fish could not stay in a tournament state (i.e., remain in the boat ramp parking lot following the tournament weigh-in); thus, transition probability of individuals from the tournament to Brushy Creek was fixed to one (Figure 2.2). Additionally, detection probabilities in the tournament state were set to one, as all bass captured at a tournament event were examined at weigh-in where tags were not
overlooked. Bass that were released or culled prior to weigh-in were not considered tournament captured bass, as they did not experience the full tournament event. Tournament detection probabilities and transitions into tournaments during events where only lake sampling occurred were set to zero whereas detection probabilities of bass in Brushy Creek during events where only tournaments occurred were also set to zero. Survival rates for bass in tournaments were set to 1 for all tournament events except for July 25, 2018 in which a telemetry bass was observed as an initial tournament mortality. Bass tournament survival was also set to one for all intervals where no tournament event occurred. Tag loss, reporting, and emigration was not relevant in the model, as no bass lost their radio tags during the sampling period, all tournament-captured bass were censused, evaluated for a telemetry tag, and reported, and no bass emigrated from the study area.

Capture histories were created for 49 bass, where an individual received a letter for the state they were observed in during the sampling period and a 0 if it was not observed during the sampling period. Telemetry bass that were known deaths during the study were censored in the model by receiving a -1, thus ignoring all recapture history after the last known capture. Although, censoring known bass mortalities in Brushy Creek within our mark-recapture model has the potential to bias Brushy Creek bass survival estimates high, not removing these bass from the analysis can bias tournament capture probability low. Thus, we chose to accept the potential biases in survival instead of tournament capture probability, as were most interested in factors affecting tournament capture and not survival of bass in Brushy Creek. Time-varying covariates (i.e., covariates that changed on each time interval) were used in the analysis to account for variation in survival rates and detection probability in Brushy Creek and probability of capture at a tournament. Covariates for survival and detection probability included mean daily water
temperature (°C) sampled continuously with temperature loggers (Onset Corporation HOBO Pendant Temperature/Light 64K Data Logger, 15 min sampling intervals) from two locations within the lake at 0 and 4.6 m depth, and mean daily air temperature (°C; attained from NOAA climate data, https://www.ncdc.noaa.gov/cdo-web/, last accessed on May 20, 2019). Mean daily air and water temperature (°C) were also evaluated for tournament capture probability, as were individual covariates for each bass including weekly angler overlap, weekly movement rate, weekly depth use, and home range (Table 2.1, 2.2).

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 detection probability, survival, and capture probability. Models were established in this order to control for the main sources of variation on recapture probability and survival, thus maximizing power to detect patterns in capture probability. Models were first developed to explore variation in bass detection probability as the first step of the hierarchical model selection procedure. We fixed survival and capture probability constant to compare various model combinations and identify the most supported model for explaining variation in detection probability: a model with no variation in detection probability \([p()\)], a linear effect of water temperature \([p(waterT)\]), a quadratic effect of water temperature \([p(waterT + waterT^2)\]), a linear effect of air temperature \([p(airT)\]), and a quadratic effect of air temperature for each group \([p(effort + airT + airT^2)\]; Table 2.3). Next, bass survival in Brushy Creek was assessed after the most supported detection probability model was identified. For bass survival, we considered models with no variation \([S()\]), a linear effect of water temperature \([S(waterT)\]), and a quadratic effect of water temperature \([S(waterT+ waterT^2)\]), as well as a linear \([S(airT)\]) and quadratic effect of air temperature \([S(waterT+ waterT^2)\]; Table 2.4). Once the
best explanatory models for detection probability and survival were determined, we tested variation on capture probabilities for bass at tournaments. First, we considered a model with no variation \( \Psi(.) \), we then tested models of individual effects \( \Psi(\text{waterT}) \), \( \Psi(\text{airT}) \), \( \Psi(\text{depth}) \), \( \Psi(\text{home range}) \), \( \Psi(\text{movement rate}) \), \( \Psi(\text{bass length}) \), \( \Psi(\text{angler movement rate}) \), \( \Psi(\text{angler depth}) \), and combinations of effects (Table 2.5).

**Results**

A total of 51 bass were implanted with telemetry tags. Captured bass averaged 399 mm (SE = 4.5 mm, range was 381 to 534 mm). Two bass died during the censored period and were removed from analysis. Of the remaining 49 bass, seven bass were captured once at bass tournaments (14.3%), but no bass were captured at multiple tournament events (0%). One bass died of initial tournament mortality (2.0%) and nine bass were confirmed dead in Brushy Creek (18.3%). Bass movement rates (m/week) were variable among individuals and weeks. Individual movement rates of fish ranged from 16.1 to 628.9 m/week whereas the global average movement rate was 186.8 m/week (SE = 12.0 m/week) but average weekly movement rates ranged from 80.1 to 305.5 m/week (Table 2.1). Average depth used by bass varied among individuals, ranging from 0.7 m to 4.5 m, with average weekly depth use ranging from 1.9 m to 2.5 m across the 16 weeks (Table 2.1), and a global average depth use of 2.2 m (SE = 0.1 m). Home range was pooled across the study period with an average home range of 9.0 ha (SE = 2.4 ha). Home ranges were also variable among bass, with a minimum of 0.04 ha and a maximum of 76.40 ha. We found no relationship between bass TL and depth \( (F_{1,47} = 1.60, P = 0.21) \) or movement rate \( (F_{1,47} = 0.01, P = 0.92) \). Bass movement rate did vary through time \( (F_{14,672} = 2.45, P < 0.01) \), with significant decreases in movement rates later in the season (June 20, June 27, July 4, July 19, July 25, August 1, August 8, and August 15), compared to the remainder of the dates (Figure
2.3A). In contrast, bass depth use did not change across time ($F_{14,672} = 1.27, P = 0.22$; Figure 2.3B).

Angler movement rates (m/hr) were variable across weeks. Average weekly angler movement rate was 87.6 m/hr (SE = 6.2 m), with a maximum movement rate of 123.4 m/hr on May 9 and a minimum movement rate of 45.0 m/hr on June 6. Average depth used by anglers showed little difference with time, ranging from 2.4 m to 4.3 m with an average depth use of 3.5 m (SE = <0.1 m; Table 2.1). Angler-bass overlap varied temporally and among individual bass (Figure 2.1). All bass experienced intervals with no angler overlap. Average angler overlap across bass and across weeks was 0.0028 angler locations/10 m$^2$ (SE = 0.0002 angler locations/10 m$^2$). The global average for angler overlap was 0.0028 angler locations/10 m$^2$ (SE = 0.0002 angler locations/10 m$^2$; Table 2.1).

Average tournament CPUE was 0.43 bass/angler hour (SE = 0.03 bass/angler hour), with minimum tournament CPUE of 0.28 bass/angler hours on July 25 and maximum tournament CPUE of 0.66 bass/angler hour on May 16 (Figure 2.4A). Bass and angler behaviors were related to tournament CPUE, as the variance explained by the multiple linear regression model was statistically significant ($F_{6,8} = 11.21, P = 0.002$). Five independent variables described 81% of the variance in tournament angler CPUE:

$$
Tournament \ CPUE = 0.118 - 0.06 \ (\text{angler depth}) - 0.0004 \ (\text{angler movement rate}) + 0.070 \ (\text{cumulative angler overlap}) + 0.001 \ (\text{fish movement rate}) + 0.018 \ (\text{fish depth}) + 0.007 \ (\text{air temperature})
$$

However, fish movement rate had the only statistically significant relationship with tournament CPUE ($t = 5.42, P < 0.001$) whereas angler depth ($t = -1.35, P = 0.22$), angler movement rate ($t = -0.85, P = 0.4$), cumulative angler overlap ($t = -1.12, P = 0.28$), and air temperature ($t = -1.68, P = 0.11$) did not.
-0.05, $P = 0.96$), cumulative angler overlap ($t = 0.21, P = 0.84$), fish depth ($t = 0.49, P = 0.64$), and air temperature ($t = 1.04, P = 0.33$) were not related to tournament CPUE.

Of the five models evaluated describing variation in bass detection probability in Brushy Creek, the best-supported model included a quadratic effect of water temperature ($\Delta AIC_c = 0.00, w_i = 0.95$; Table 2.3). Confidence intervals of the beta estimates for all three parameters did not include zero (intercept, waterT, waterT$^2$; Table 2.5). Detection probability was high overall, but highest at lower and higher water temperatures (Figure 2.5). Detection probability estimates ranged from 0.893 (95% CI: 0.827, 0.936) at water temperatures of 23.3 °C to 0.702 (95% CI: 0.627, 0.767) at 18.8 °C. The remainder of the models received little support for explaining variation in detection probability ($\Delta AIC_c \geq 7.70$; Table 2.3).

Of the five models describing bass survival in Brushy Creek, the most supported model was the simplest model where survival was constant ($\Delta AIC_c = 0.00, w_i = 0.34$; Table 2.4). The other four models also received some support for linear and quadratic effects of water and air temperature ($\Delta AIC_c < 2.0$); however, a likelihood ratio test indicated no significant difference between the model with no trend on survival and those that included temperature trends ($\chi^2 = 2.92, P = 0.23$). Bass daily survival in Brushy Creek was estimated at 0.998 (95% CI: 0.996, 0.999) across the 16 weeks. Survival for bass in tournaments were one for all tournament events except for July 25, 2018 in which a telemetry bass was observed as an initial tournament mortality.

Of the models evaluated to describe tournament capture probability, the top model included a linear effect of angler overlap and a linear effect of water temperature ($\Delta AIC_c = 0.00, w_i = 0.24$; Table 2.5). Bass home range ($\Delta AIC_c = 6.64, w_i = 0.01$), movement rate ($\Delta AIC_c = 7.61, w_i = 0.01$), depth use ($\Delta AIC_c = 6.59, w_i = 0.01$), and fish length ($\Delta AIC_c = 6.04, w_i = 0.01$)
showed no influence on tournament capture probability. Angler movement rate ($\Delta AIC_c = 7.00, w_i = 0.01$) and angler depth use ($\Delta AIC_c = 6.85, w_i = 0.01$) were also not influential in describing variability on capture probability, nor did combinations of the models with any of these individual covariates included ($\Delta AIC_c > 2.0$). All three beta estimates (intercept, angler overlap, and airT) in the final capture probability model did not include zero (Table 2.5). Angler overall probability density was positively related to bass tournament capture probability as did increased air temperature, resulting in the highest capture probability of 0.033 (95% CI: 0.009, 0.111) at an air temperature of 27.2 °C and the lowest capture probability of 0.001 (95% CI: 0.001, 0.014) at air temperatures of 17.2 °C (Figure 2.6A and 2.6B). Bass tournament capture probability was highest in late May, early June, and early July and lowest in late June and August (Figure 2.4B).

**Discussion**

Quantifying fine scale patterns of anglers by means of geospatial tracking has been used in commercial and marine fisheries (Hartog 2011; Queiroza 2015). However, assessing angler behaviors in freshwater systems have received less attention (but see Matthias et al. 2014; Weimer et al. 2014). We know of no other studies that have evaluated spatial overlap between bass and tournament anglers that are highly specialized and more successful at capturing fish compared to other angler types (Fisher 1997). Angler overlap with bass was overall high across the summer in Brushy Creek and indicates that tournament anglers are successful at targeting bass. Temporal changes in angler movement patterns likely is reflective of angler’s perceptions of temporal changes in bass habitat in attempts to increase overlap and probability of capture. For example, anglers in May focused fishing effort in shallow, protected reservoir arms, representative of bass spawning habitats (Mesing and Wicker 1986). Alternatively, anglers fished deeper littoral regions of the lake during warmer months when bass generally move to
cooler, deeper waters with increased temperatures (Hubert and Lackey 1980; Sammons et al. 2003; Hanson et al. 2007). However, bass in Brushy Creek did not significantly change depth use over the sampling period and remained in relatively shallow water overall (2.20 m), potentially due to the large amount of available course woody habitat and vegetation. These findings lend support to the concept that anglers change patterns based on environmental conditions in an attempt to match fish’s time-spaces (Bear and Eden 2011), but may represent a potential mismatch in overlap with bass.

Increased fish movement rates, home ranges, and depth use can result in increased encounter rates with fishery gears (Palmer et al. 2011; Parsons et al. 2011). We found no support indicating that bass behaviors affected capture probability in individual fish. However, mean bass movement changed seasonally and was highly correlated to tournament CPUE. Increases in tournament CPUE with increased bass movement rates early in the season may be related to warming water temperatures and spring spawning activity (Breder 1936; Heidinger 1975) when bass exhibit aggressive behaviors (e.g., nest guarding) and may be more vulnerable to angling (Suski et al. 2003; Suski and Philipp 2004). Further, these high movement rates may have increased the probability of tournament anglers occupying the same areas as bass. For example, high movement rates of fish between locations can negate differences in vulnerability of bass, even when some of those locations are not accessible to anglers (Matthias et al. 2014). Alternatively, when movement rates of fish are low, regions of a system can exist where fish are less vulnerable to angling (Cox and Walters 2002). Diminished movement of bass later in the season, potentially due to increases in available habitat (submerged vegetation), may have led to a lower probability of overlap of bass with anglers. Although not quantified in this study, we observed increased aquatic vegetation density later in the season in Brushy Creek, that can result
in decreased movement rates (Ahrenstorff et al. 2009) whereas early in the season, bass use shallow open regions of lakes that are more easily accessed and fished by tournament anglers. Thus, there is likely a connection between fish behavior and angler success at the population level (i.e., tournament angler CPUE), even if not at an individual level (i.e., bass capture probability).

Tournament anglers were highly mobile during tournament events and covered large amounts of the shoreline in an attempt to increase overlap with bass. However, angler movement rates were not correlated with tournament CPUE and did not influence capture probability. Anglers have been found to employ an “optimal foraging strategy” in their fishing (Aswani 1998; Richard et al. 2017), where they must choose to either spend their time in a single area where they believe overlap with bass is high or spend time searching which increases potential chances of overlap with bass. These patterns may change seasonally or in relation to bass behavior. Angler movement did increase with time in our study, potentially indicating difficulty in locating fish. However, we found no benefit of either of these strategies for increasing bass capture rates. These patterns may not be apparent in smaller reservoirs such as Brushy Creek, as anglers can more easily cover large areas of the lake during tournament events while still spending time in single locations, whereas larger reservoirs may see more acute effects of anglers’ decisions to move or stay. For example, anglers in a 870-ha lake were better at locating Bluegills *Lepomis macrochirus* during open water due to the ability to reach more overlapping habitat, as opposed to vertical jigging during ice-up (Weimer et al. 2014).

Angler movement decisions are further influenced by their understanding of the interaction between bass behaviors and environmental variables (Whittaker et al. 2006). Air temperature influenced bass tournament capture probability that may signify changes in bass
behavior. Fishes change behaviors with temperature, such as swimming speed (Watz and Piccolo 2011), foraging patterns (Fraser et al. 1993), and metabolism (Brett and Glass 1973), resulting in the potential for increased vulnerability. Anglers can also change fishing patterns with changing temperatures, including fishing gears and presentation (Lennox et al. 2016). Air temperature may also be correlated with increased tournament angling effort in our model due to increased tournament time (weigh-in occurred at sundown), and angling effort has been positively linked to catch rates (Johnson and Carpenter 1994; Sylvia and Weber in progress).

As hypothesized, our results indicate that bass tournament capture probability is the result of a collection of features. An angler’s knowledge of a system and their target species, the changing behavioral patterns of that species, and the environmental influences that drive such changes are all central in describing catchability of fish through time. The successful alignment of such factors (i.e., anglers successfully locating bass and behavioral and environmental patterns lending themselves to increased vulnerability of bass to fishing) can lead to tournament anglers capturing large portions of the population. As such, it is critical to understand these relationships in the context of fishery management, as systems with high tournament pressure can have the potential to lead to large-scale population level impacts.

**Acknowledgements**

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References


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**Tables**

Table 2.1. Mean, standard error (SE), minimum, and maximum values of Largemouth Bass individual weekly covariates used in multistate models to estimate capture probability ($P_i$) of telemetry tagged fish in Brushy Creek Lake, IA, USA from 9 May 2018 through 15 August 2018.

<table>
<thead>
<tr>
<th>Date</th>
<th>Movement rate (m/week)</th>
<th>Depth use (m)</th>
<th>Angler overlap (anglers locations/10 m$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
</tr>
<tr>
<td>9-May</td>
<td>189.78</td>
<td>47.57</td>
<td>1.20, 1,857.19</td>
</tr>
<tr>
<td>16-May</td>
<td>305.52</td>
<td>90.42</td>
<td>1.41, 3,487.73</td>
</tr>
<tr>
<td>23-May</td>
<td>249.73</td>
<td>53.30</td>
<td>1.50, 1,557.77</td>
</tr>
<tr>
<td>30-May</td>
<td>257.99</td>
<td>64.24</td>
<td>2.84, 2,174.23</td>
</tr>
<tr>
<td>6-Jun</td>
<td>176.47</td>
<td>44.31</td>
<td>1.90, 1,486.20</td>
</tr>
<tr>
<td>13-Jun</td>
<td>214.00</td>
<td>48.77</td>
<td>1.0, 1,486.20</td>
</tr>
<tr>
<td>20-Jun</td>
<td>107.86</td>
<td>21.50</td>
<td>1.0, 617.43</td>
</tr>
<tr>
<td>27-Jun</td>
<td>80.10</td>
<td>18.33</td>
<td>1.30, 617.43</td>
</tr>
<tr>
<td>4-Jul</td>
<td>88.38</td>
<td>17.97</td>
<td>1.30, 617.43</td>
</tr>
<tr>
<td>11-Jul</td>
<td>129.76</td>
<td>36.59</td>
<td>2.13, 1,246.37</td>
</tr>
<tr>
<td>18-Jul</td>
<td>119.22</td>
<td>37.60</td>
<td>1.30, 1,356.89</td>
</tr>
<tr>
<td>25-Jul</td>
<td>108.13</td>
<td>28.88</td>
<td>2.25, 938.62</td>
</tr>
<tr>
<td>1-Aug</td>
<td>130.84</td>
<td>26.51</td>
<td>4.12, 727.46</td>
</tr>
<tr>
<td>8-Aug</td>
<td>128.56</td>
<td>22.52</td>
<td>4.12, 559.70</td>
</tr>
<tr>
<td>15-Aug</td>
<td>135.32</td>
<td>23.06</td>
<td>3.62, 559.70</td>
</tr>
</tbody>
</table>
Table 2.2 Mean values of weekly covariates used in multistate models to estimate angler capture probability ($P_{s_i}$) of telemetry tagged Largemouth Bass in Brushy Creek Lake, IA, USA from 9 May 2018 through 15 August 2018.

<table>
<thead>
<tr>
<th>Date</th>
<th>Water temperature ($^\circ$C)</th>
<th>Air temperature ($^\circ$C)</th>
<th>Angler movement rate (m/hr)</th>
<th>Angler depth use (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9-May</td>
<td>17.22</td>
<td>11.98</td>
<td>3.65</td>
<td>121.19</td>
</tr>
<tr>
<td>16-May</td>
<td>19.44</td>
<td>12.62</td>
<td>3.85</td>
<td>123.40</td>
</tr>
<tr>
<td>23-May</td>
<td>23.89</td>
<td>13.05</td>
<td>3.98</td>
<td>60.66</td>
</tr>
<tr>
<td>30-May</td>
<td>22.22</td>
<td>12.79</td>
<td>3.90</td>
<td>62.43</td>
</tr>
<tr>
<td>6-Jun</td>
<td>25.56</td>
<td>13.09</td>
<td>3.99</td>
<td>45.03</td>
</tr>
<tr>
<td>13-Jun</td>
<td>18.89</td>
<td>15.03</td>
<td>4.58</td>
<td>79.67</td>
</tr>
<tr>
<td>20-Jun</td>
<td>21.11</td>
<td>16.17</td>
<td>4.93</td>
<td>77.11</td>
</tr>
<tr>
<td>27-Jun</td>
<td>22.22</td>
<td>16.80</td>
<td>5.12</td>
<td>93.84</td>
</tr>
<tr>
<td>4-Jul</td>
<td>25.56</td>
<td>17.69</td>
<td>5.39</td>
<td>121.86</td>
</tr>
<tr>
<td>11-Jul</td>
<td>27.22</td>
<td>18.89</td>
<td>5.76</td>
<td>73.35</td>
</tr>
<tr>
<td>18-Jul</td>
<td>23.89</td>
<td>18.57</td>
<td>5.66</td>
<td>85.30</td>
</tr>
<tr>
<td>25-Jul</td>
<td>21.67</td>
<td>19.76</td>
<td>6.02</td>
<td>78.34</td>
</tr>
<tr>
<td>1-Aug</td>
<td>21.11</td>
<td>19.73</td>
<td>6.01</td>
<td>116.28</td>
</tr>
<tr>
<td>8-Aug</td>
<td>22.22</td>
<td>19.33</td>
<td>5.89</td>
<td>87.27</td>
</tr>
<tr>
<td>15-Aug</td>
<td>23.89</td>
<td>20.19</td>
<td>6.15</td>
<td>87.57</td>
</tr>
</tbody>
</table>
Table 2.3 All Cormack-Jolly-Seber multistate models used to estimate transmitter detection probability ($p$) of telemetry tagged Largemouth Bass in Brushy Creek Lake, IA, USA for 31 periods beginning 9 May 2018 through 15 August 2018. Effects evaluated influencing $p$ include linear and quadratic water temperature ($°C$; waterT; waterT$^2$), linear and quadratic air temperature ($°C$; airT, airT$^2$), and a constant rate ($.$). Parameters in the table include $K =$ 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), $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion, and $w_i =$ calculated Akaike weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$ (waterT + waterT$^2$)</td>
<td>743.50</td>
<td>0.00</td>
<td>0.95</td>
<td>5</td>
<td>733.38</td>
</tr>
<tr>
<td>$p$ (airT + airT$^2$)</td>
<td>751.20</td>
<td>7.70</td>
<td>0.02</td>
<td>5</td>
<td>741.08</td>
</tr>
<tr>
<td>$p$ (airT)</td>
<td>751.83</td>
<td>8.33</td>
<td>0.01</td>
<td>4</td>
<td>743.75</td>
</tr>
<tr>
<td>$p$ (.)</td>
<td>752.95</td>
<td>9.45</td>
<td>0.01</td>
<td>3</td>
<td>746.90</td>
</tr>
<tr>
<td>$p$ (waterT + waterT$^2$)</td>
<td>754.97</td>
<td>11.47</td>
<td>0.00</td>
<td>4</td>
<td>746.89</td>
</tr>
</tbody>
</table>
Table 2.4 All Cormack-Jolly-Seber multistate models used to estimate survival (S) of telemetry tagged Largemouth Bass in Brushy Creek, IA, USA for 31 periods beginning 9 May 2018 through 15 August 2018. Effects evaluated influencing \( P_{si} \) include linear and quadratic water temperature (°C; waterT; waterT\(^2\)) and linear and quadratic air temperature (°C; airT, airT\(^2\)). Parameters in the table include \( K \) = 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), \( \text{AIC}_c \) = sample-sized corrected Akaike’s Information Criterion, and \( w_i \) = calculated Akaike weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( w_i )</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>( S \ (.) )</td>
<td>743.50</td>
<td>0.00</td>
<td>0.34</td>
<td>5</td>
<td>733.38</td>
</tr>
<tr>
<td>( S \ (\text{waterT} + \text{waterT}^2) )</td>
<td>744.68</td>
<td>1.19</td>
<td>0.19</td>
<td>7</td>
<td>730.46</td>
</tr>
<tr>
<td>( S \ (\text{waterT}) )</td>
<td>744.83</td>
<td>1.33</td>
<td>0.17</td>
<td>6</td>
<td>732.67</td>
</tr>
<tr>
<td>( S \ (\text{airT} + \text{airT}^2) )</td>
<td>745.06</td>
<td>1.57</td>
<td>0.15</td>
<td>6</td>
<td>732.90</td>
</tr>
<tr>
<td>( S \ (\text{airT}) )</td>
<td>745.10</td>
<td>1.60</td>
<td>0.15</td>
<td>6</td>
<td>732.93</td>
</tr>
</tbody>
</table>
Table 2.5 All Cormack-Jolly-Seber multistate models used to estimate angler capture probability ($\Psi$) of telemetry tagged Largemouth Bass in Brushy Creek Lake, IA, USA for 31 periods beginning 9 May 2018 through 15 August 2018. Effects evaluated influencing $\Psi$ include linear and quadratic air (airT, airT$^2$) and water (waterT, waterT$^2$) temperature (°C), angler overlap, bass home range, bass movement rate, bass depth use, fish length, angler movement rate, and angler depth use. Parameters in the table include K = number of parameters, Deviance = -2 x log-likelihood of the model less -2 x log-likelihood of the saturated models (same number of parameters and degrees of freedom), AIC$_c$ = sample-sized corrected Akaike’s Information Criterion, and $w_i$ = calculated Akaike weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC$_c$</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Psi$ (angler overlap + airT)</td>
<td>737.89</td>
<td>0.00</td>
<td>0.24</td>
<td>7</td>
<td>723.67</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + airT + airT$^2$)</td>
<td>739.80</td>
<td>1.91</td>
<td>0.09</td>
<td>8</td>
<td>723.52</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + airT + angler overlap * airT)</td>
<td>739.87</td>
<td>1.98</td>
<td>0.09</td>
<td>8</td>
<td>723.59</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap)</td>
<td>740.33</td>
<td>2.44</td>
<td>0.07</td>
<td>6</td>
<td>728.16</td>
</tr>
<tr>
<td>$\Psi$ (airT)</td>
<td>740.45</td>
<td>2.55</td>
<td>0.07</td>
<td>6</td>
<td>728.28</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + depth + angler overlap * depth)</td>
<td>740.93</td>
<td>3.04</td>
<td>0.05</td>
<td>8</td>
<td>724.65</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + fish length)</td>
<td>741.01</td>
<td>3.11</td>
<td>0.05</td>
<td>7</td>
<td>726.79</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + home range)</td>
<td>741.18</td>
<td>3.29</td>
<td>0.05</td>
<td>7</td>
<td>726.96</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + depth)</td>
<td>741.44</td>
<td>3.55</td>
<td>0.04</td>
<td>7</td>
<td>727.22</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + angler depth)</td>
<td>741.89</td>
<td>4.00</td>
<td>0.03</td>
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<td>727.67</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + angler movement rate)</td>
<td>741.98</td>
<td>4.08</td>
<td>0.03</td>
<td>7</td>
<td>727.76</td>
</tr>
<tr>
<td>$\Psi$ (airT+airT$^2$)</td>
<td>741.99</td>
<td>4.10</td>
<td>0.03</td>
<td>7</td>
<td>727.77</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + movement rate)</td>
<td>742.30</td>
<td>4.41</td>
<td>0.03</td>
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<td>728.08</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + movement rate + angler overlap * movement rate)</td>
<td>742.76</td>
<td>4.87</td>
<td>0.02</td>
<td>8</td>
<td>726.48</td>
</tr>
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</table>
Table 2.5 Continued

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Psi$ (angler overlap + fish length + angler overlap * fish length)</td>
<td>742.77</td>
<td>4.88</td>
<td>0.02</td>
<td>8</td>
<td>726.49</td>
</tr>
<tr>
<td>$\Psi$ (.)</td>
<td>743.50</td>
<td>5.60</td>
<td>0.01</td>
<td>5</td>
<td>733.38</td>
</tr>
<tr>
<td>$\Psi$ (fish length)</td>
<td>743.93</td>
<td>6.04</td>
<td>0.01</td>
<td>6</td>
<td>731.76</td>
</tr>
<tr>
<td>$\Psi$ (angler overlap + depth + movement rate + home range)</td>
<td>744.18</td>
<td>6.29</td>
<td>0.01</td>
<td>9</td>
<td>725.82</td>
</tr>
<tr>
<td>$\Psi$ (depth)</td>
<td>744.48</td>
<td>6.59</td>
<td>0.01</td>
<td>6</td>
<td>732.31</td>
</tr>
<tr>
<td>$\Psi$ (home range)</td>
<td>744.53</td>
<td>6.64</td>
<td>0.01</td>
<td>6</td>
<td>732.37</td>
</tr>
<tr>
<td>$\Psi$ (angler depth)</td>
<td>744.74</td>
<td>6.85</td>
<td>0.01</td>
<td>6</td>
<td>732.58</td>
</tr>
<tr>
<td>$\Psi$ (angler movement rate)</td>
<td>744.86</td>
<td>6.97</td>
<td>0.01</td>
<td>6</td>
<td>732.70</td>
</tr>
<tr>
<td>$\Psi$ (waterT)</td>
<td>745.19</td>
<td>7.30</td>
<td>0.01</td>
<td>6</td>
<td>733.03</td>
</tr>
<tr>
<td>$\Psi$ (movement rate)</td>
<td>745.50</td>
<td>7.61</td>
<td>0.01</td>
<td>6</td>
<td>733.33</td>
</tr>
<tr>
<td>$\Psi$ (waterT + waterT$^2$)</td>
<td>747.14</td>
<td>9.25</td>
<td>0.00</td>
<td>7</td>
<td>732.92</td>
</tr>
</tbody>
</table>
Table 2.6 Cormack-Jolly-Seber estimates of final model: \([S(.) p (\text{water}T + \text{water}T^2) \Psi_i \text{ (angler overlap + air}T)]\) of telemetry tagged Largemouth Bass in Brushy Creek, IA, USA for 31 periods beginning 9 May 2018 through 15 August 2018. Estimate = beta estimate of parameter. SE = Standard Error of beta estimate. 95 % LCI = 95% lower confidence interval of beta estimate of parameter. 95% UCI = 95% upper confidence interval of beta estimate of parameter. Best model determined by sample-sized corrected Akaike’s Information Criterion (AICc).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate (SE)</th>
<th>95% LCI</th>
<th>95% UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Survival</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>6.229 (0.355)</td>
<td>5.533</td>
<td>6.924</td>
</tr>
<tr>
<td><strong>Detection probability</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>19.742 (5.113)</td>
<td>9.721</td>
<td>29.762</td>
</tr>
<tr>
<td>WaterT</td>
<td>-2.317 (0.639)</td>
<td>-3.569</td>
<td>-1.065</td>
</tr>
<tr>
<td>WaterT(^2)</td>
<td>0.071 (0.020)</td>
<td>0.033</td>
<td>0.109</td>
</tr>
<tr>
<td><strong>Angler capture probability</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-12.915 (4.268)</td>
<td>-21.263</td>
<td>-4.566</td>
</tr>
<tr>
<td>Angler overlap</td>
<td>95.913 (37.450)</td>
<td>22.503</td>
<td>169.323</td>
</tr>
<tr>
<td>AirT</td>
<td>0.347 (0.175)</td>
<td>0.005</td>
<td>0.689</td>
</tr>
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</table>
Figure 2.1 Monthly kernel density estimate maps of angler space-use for May (A), June (B), July (C), and August (D) in Brushy Creek Lake, Iowa. Cooler colors represent low angler density whereas warmer colors represent high angler density. White circles represent locations of 49 telemetry tagged Largemouth Bass for the designated month.
Figure 2.2 Conceptual diagram of multistate model design for estimation of detection, survival and capture probabilities of 49 telemetry tagged Largemouth Bass in Brushy Creek, IA, USA from 9 May 2018 to 15 August 2018. Brushy Creek and Tournament represent states within the model. Arrows represent capture probability ($\psi$) into the tournament states, $p$ represents detection probabilities within states, and $S$ represents survival estimates of each state. $\psi_{B-B} = 1 - \psi_{B-T}$. 
Figure 2.3 Movement rate (A) and depth use (B) changes across time of 49 telemetry tagged Largemouth Bass in Brushy Creek, IA, USA from 9 May 2018 to 15 August 2018. The horizontal lines of the box plot show the median dependent variables response, the box shows the interquartile range, and the whiskers represent the 5th and 95th percentiles. Dots represent data points outside of 5th and 95th percentiles. Lowercase letters denote differences in weekly movement rates.
Figure 2.4 Weekly tournament CPUE (# bass/angler hour ± SE; A) and weekly tournament angler capture probability (B) of 49 telemetry tagged Largemouth Bass in Brushy Creek, IA, USA from 9 May 2018 to 15 August 2018. Solid lines around estimates represent 95% confidence intervals.
Figure 2.5 Estimated detection probability ($p$) of 49 telemetry tagged Largemouth Bass in Brushy Creek, IA, USA in relation to mean daily air temperature from 9 May 2018 to 15 August 2018. Solid lines represent 95% confidence limits.
Figure 2.6 Estimated tournament capture probability ($Psi$) of 49 telemetry tagged Largemouth Bass in Brushy Creek, IA, USA in relation to mean daily air temperature (A) and angler overlap probability density (B), 9 May 2018 to 15 August 2018. Solid lines around estimates represent 95% confidence limits.
CHAPTER 3. USE OF A MARK-RECAPTURE MODEL TO EVALUATE CATCH AND RELEASE DELAYED TOURNAMENT MORTALITY

Modified from a manuscript under review to Fisheries Research

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Iowa State University, Department of Natural Resource Ecology and Management, 339 Science Hall II, Ames, IA 50011, USA

Abstract

Estimating tournament mortality, including both initial and delayed mortality, is necessary to assess potential effects of catch and release tournament fishing events. Traditional studies retaining angler caught fish are useful in understanding total mortality but have associated limitations. As an alternative to traditional tournament mortality studies, we estimated daily apparent survival rates of largemouth bass *Micropterus salmoides* using a modified Cormack-Jolly-Seber model in Program MARK to evaluate the duration of delayed tournament mortality and to identify important covariates affecting survival. Multiple monotonic trends were evaluated to test acute (2, 3, 4, or 7 d) and chronic (15 or 30 d) delayed mortality hypotheses. The most supported models revealed an acute trend in survival following capture but no support for chronic mortality. Largemouth bass survival decreased with increases in water temperature and the number of tournament capture events. Combined, these factors resulted in up to 90% cumulative mortality at temperatures of 18.8°C for individuals captured at five tournament events. Our results confirm the potential for high delayed mortality associated with catch and
release fishing tournaments. Using mark-recapture data to understand tournament fishing mortality can be a valuable tool in managing highly fished systems.

**Introduction**

Competitive tournament angling events are a rapidly growing segment of freshwater and marine fisheries. An estimated 31,000 tournaments were held in inland and marine waters in North America in 1991 (Schramm et al., 1991a). More recent studies reported upwards of 40,000 black bass *Micropterus* spp. tournaments were held just in the southeastern United States in 2012 (Driscoll et al., 2012), whereas a 227% increase in marine tournaments was documented between 1983 and 2003 (Oh et al., 2007). Fishing tournaments are directed at several freshwater and marine species and can involve hundreds to thousands of anglers participating in fishing events lasting just a few hours or up to a year (Schramm et al., 1991b), making the potential for tournament associated mortality considerable. While the overwhelming majority of fishing tournaments today use catch and release as a means to conserve fishery resources and sustain angling quality (Barnhart, 1989; Schramm and Gilliland, 2015), mortality of fishes released following tournaments can be highly variable, dependent on species, study design, and system (Muoneke and Childress, 1994; Killen et al., 2006; James et al., 2007; Cline, et al., 2012; Kerns et al., 2016; Keretz et al., 2018; Sass et al., 2018).

A range of factors can affect fish survival following angling. Gear type (Muoneke and Childress, 1994; Dunmall et al., 2001), hook type and hooking location (Myers and Poarch, 2002; Wilde and Pope, 2008), water depth (St John and Syers, 2005), fish size (Meals and Miranda, 1994; Meka and McCormick, 2005), angling time and level of exhaustion (Dotson, 1982; Suski et al., 2007; Keretz et al., 2018), air exposure (Suski et al., 2007), water temperature (Neal and Lopez-Clayton, 2001; Cooke et al., 2002; Keretz et al., 2018), and angler experience
(Diodati and Richard, 1996; Meka, 2004; Landsman et al., 2011) are all sources of stress that can increase mortality in fish captured and released that vary across water bodies and species (Muoneke and Childress, 1994). Additionally, tournament specific actions including live-well confinement, culling, and weigh-in procedures can result in initial mortality rates up to 50% for black bass and walleye *Sander vitreus* captured during tournaments (Goeman, 1991; Hartley and Moring, 1995; Wilde, 1998). While determining immediate mortality (i.e., mortality occurring before or during weigh-in procedures) of tournament captured fish is relatively simple, catch-and-release tournaments can also result in delayed mortality after fish have been released, which is more difficult to quantify (Cooke et al., 2002). Consequently, considerably less is known about delayed mortality of tournament captured fishes.

Delayed mortality of tournament captured bass was identified and evaluated beginning in the 1980s (Schramm et al., 1987) and continues to be an important topic in current tournament mortality studies (Schramm et al., 2010; Hall et al., 2012; Keretz et al., 2018). Delayed mortality evaluations have focused on black bass due to their popularity among tournament anglers (Wilde, 1998). To measure delayed mortality, traditional post-release mortality studies often use confinement evaluations that involve retaining angler caught and control fish in cages for 12 h – 28 d where surviving fish are counted at the end of the holding period to estimate percent survival, potentially in relation to fish and environmental covariates (e.g., fish size, water temperature and tournament size; Seidensticker, 1975; Bennet et al., 1989; Jackson and Willis, 1991; Steeger et al., 1994; Kwak and Henry, 1995; Weather and Newman, 1997). Delayed mortality rates in bass vary widely but can exceed 50% as a result of cumulative sublethal physiological stressors (Steeger et al., 1994; Weathers and Newman, 1997; Neal and Lopez-Clayton, 2001). While such observational studies have been useful in understanding post-release
mortality of tournament angled fish, they can be difficult to replicate across a broad range of variables (Schramm et al., 1987), are limited in the time and number of tournaments that can be evaluated, number of fish that can be held (Wilde et al., 2003), and can be confounded by mortality due to confinement (Goeman, 1991; Fielder and Johnson, 1994; Edwards et al., 2004; Sass et al., 2018). Additionally, if only conducted on a subset of tournaments, testing for environmental factors associated with delayed mortality can be difficult. Further, confinement delayed mortality evaluations are unable to evaluate the potential for chronic mortality (long term patterns in mortality post release). More recently, assessments of delayed mortality have included telemetry of tournament released fish, assessing survival in natural environments instead of in confinement (Maynard et al., 2013; Taylor et al., 2015; Kerns et al., 2016).

However, much like confinement delayed mortality studies, tagging fish with transmitters may increase stress and mortality and evaluations are limited by the number of individuals that can be tagged and the numbers of tournaments fish are sampled. Thus, these methods may also only include a “snapshot” of a single or few tournaments occurring on the system, limiting inference to the range of environmental conditions fish experience during tournaments, making long-term mortality estimates difficult. Therefore, opportunities exist to improve estimates of tournament mortality and to test for the duration that delayed mortality occurs.

Using mathematical and statistical modelling techniques to understand dynamic rates of fisheries have long been advocated by fisheries professionals (Haddon, 2010). However, the majority of tournament mortality studies still use direct quantification of initial and delayed mortality. Alternatively, the use of mark-recapture methods, such as the Cormack-Jolly-Seber model (Lebreton et al., 1992), would allow for long-term estimates of survival of all individuals captured across multiple tournament events. These models also accept covariates, allowing the
user to tests aspects such as environmental variables, subsequent recapture events, and individual fish characteristics (White and Burnham, 1999). Further, the use of time-varying individual covariates would allow for hypotheses of acute versus chronic mortality to be tested by accounting for days since tournament capture. This improved ability to account for multiple factors affecting survival could provide an increased understanding of tournament associated mortality, but although such methods have been used to evaluate effects of catch and release angling on bass growth and catch rates (Cline et al., 2012; Sass et al., 2018), they have not been applied to these situations.

Herein, we use a mark-recapture dataset from a highly represented tournament species, largemouth bass *Micropterus salmoides* (hereafter referred to as bass), to test for delayed mortality as an alternative to traditional delayed tournament mortality studies. Our objectives were to estimate post-release mortality rates and test for chronic (15 and 30 d) versus acute (2, 3, 4, 7 d) mortality. We also tested a number of covariates (number of tournament captures and fish length, weight, and condition) to test for their potential effects on delayed mortality. Finally, we applied our results to estimate the percent of bass that survive catch-and-release tournaments. We considered multiple competing hypotheses from patterns identified in the literature including acute effects of decreased survival with increasing air and water temperature and increased fish size. We conclude that mark-recapture models serve as useful tools to understand tournament mortality of fish captured in competitive events under a range of conditions in which tournaments occur.
Methods

Sampling

Brushy Creek is a 279 ha reservoir in Webster County, Iowa, USA. The lake has a mean depth of 8.9 m, a maximum depth of 22.9 m, and is densely covered in emergent and submerged coarse woody habitat along the perimeter of the lake. Brushy Creek is used extensively by anglers, hosting over 40 bass tournaments annually (mean 25 tournament angler hours/ha/year from 2015-2017). Electrofishing (pulsed DC 300 V and 8 amps) occurred once monthly on Brushy Creek during the open water season (April - November) for 2015, 2016 and 2017, and from April-June 2018. Electrofishing lasted about five consecutive days each month or until the entire accessible shoreline had been sampled. All bass captured were weighed (g) and measured (mm). Bass ≥381 mm (15” minimum length limit for bass in Iowa, USA) were tagged on the top left jaw with a metal Monel butt end band (selected due to their high retention for black bass; MacCrimmon and Robbins, 1979) for individual bass recognition.

All bass tournaments at Brushy Creek were attended and censused from April 2015 through June 2018 (131 total tournaments). Number of anglers, number of boats, and number of bass weighed-in were recorded for each tournament event. Following weigh-in, all bass were placed in an insulated live-well with supplemental oxygen. All fish were weighed (g), measured (mm), and evaluated for jaw tags; all untagged bass were tagged on the left upper jaw with a metal Monel band and released. Finally, project e-mail and telephone contact information was placed on signs throughout the lake to solicit capture date and bass tag number data from non-tournament anglers.

Model

We analyzed individual bass encounter histories during 2015-2018 in program MARK (White and Burham, 1999) using a Cormack-Jolly-Seber live recapture model (CJS) for
Maximum-likelihood estimates of daily apparent survival ($S$) and detection probability ($p$; Lebreton et al., 1992). Apparent survival represents fish that died and those that left the study area due to permanent emigration; however, emigration of bass from Brushy Creek Lake is minimal and permanent as only two bass during the study period were found to have emigrated over the spillway (<0.001%; A. Sylvia, unpublished data). Further, we assumed temporary emigration (i.e. increased water depth leading to decreased vulnerability of capture during electrofishing) was minimal as bass remained in relatively shallow water (1.88 m; Sylvia et al. in prep) and bass were vulnerable to angling across all depths. Therefore, we refer to apparent survival simply as survival hereafter. Assumptions of the model include that every marked animal in the population has the same probability of recapture and survival, marks are recorded correctly, sampling periods are instantaneous and recaptured fish are released immediately, emigration is permanent, and fish fates are independent of one another (Lebreton et al., 1992).

Although post capture refractory periods for bass may exist for short periods following angling (Cox, 2000; Cline et al., 2012; Sass et al., 2018), bass resume feeding within 16 hours following an angling event (Siepker et al., 2006). Thus, we assumed that all individuals were equally available for recapture by anglers during consecutive sampling events. Basic notation of the estimation of survival and recapture events follow probabilities associated with each capture occasion conditional on the fish’s first release, where $S_{is}$ is the probability that fish $i$ alive at occasion $s$, is still alive at occasion $s + 1$, and $p_{is}$ is the probability that animal $i$ alive at occasion $s$ is captured. For example, a recapture history of five occasions (010110) would be modeled as

$$S_2(1-p_3) S_3 p_4 S_4 p_5 [S_5(1-p_6) + 1 - S_5]$$

in the maximum likelihood function.
Survival for 771 time periods were estimated, representing daily survival rates during the open water season (April-November) from 2015-2018, as well as an ice-up survival rate that began 30 days after the last electrofishing event and ended on the first day of electrofishing the following year. This period consisted of 119 days between 2015-2016, 123 days between 2016-2017, and 134 days between 2017-2018. These intervals were adjusted in Program MARK and calculated a constant daily survival estimate for the entire winter period. Detection probability was estimated for days when electrofishing or tournaments occurred but was set to zero for all remaining days where sampling did not occur. For example, if a tournament occurred on Saturday and Sunday, and no other sampling occurred throughout the week, the detection probabilities were set to zero for Monday - Friday, and the model would estimate detection probability for the tournament events on Saturday and Sunday. Survival rate estimates were not corrected for tag loss rates, as daily tag loss is minimal (0.00065%, A. Sylvia, unpublished data; Arnason and Mills, 1981) and had little effect on survival estimates.

Capture histories were created for 6,770 bass, where an individual received a 1 if it was seen during the sampling period and a 0 if it was not seen during the sampling period. We considered two groups of bass for the model: a reference group consisting of electrofished bass and a treatment group consisting of bass captured during a tournament. To determine short term delayed mortality of tournament-captured bass, electrofishing bass that were subsequently captured at a tournament were censored after capture and moved to the tournament group as a new fish. Additionally, tournament bass successively captured at another tournament were censored and entered into the encounter histories as new tournament fish to account for multiple tournament capture events. Tournament bass that were subsequently captured electrofishing were not censored as tournament to tournament fish were or electrofishing to tournament fish were,
and instead received a 1 in the capture history on the event of electrofishing as a second recapture. This occurred under the assumption, that was later tested and confirmed in the model, that electrofished bass did not experience the same mortality effects as those captured at bass tournaments (i.e., no time spent in a live well, going through weigh-in procedures, or angling stress) and that electrofishing does not affect bass survival (Dolan and Miranda, 2002). Capture histories of bass included individual covariates of number tournament captures, length-at-capture (mm), weight-at-capture (mm), and relative weight-at-capture ($W_r$, Neumann et al., 2012; Table 3.1). Time-varying covariates, covariates that changed on each time interval, were also used in the analysis, including mean daily air temperature (°C), mean daily water temperature (°C) sampled continuously with temperature loggers (Onset Corporation HOBO Pendant Temperature/Light 64K Data Logger, 15 min sampling intervals) from two locations within the lake at 0 and 4.6 m depth, and daily effort for electrofishing (seconds) and tournaments (hours). Time varying individual covariates included a monotonic trend from time since capture, where covariates were coded as 0 until the first day of capture (Holt et al., 2009). Once captured at a tournament, bass received individual covariates counting down from the number of days of hypothesized acute or chronic delayed mortality, followed by zeros for the remaining days. We chose six time periods, representative of common time periods tested in the literature (Seidensticker, 1975; Bennet et al., 1989; Jackson and Willis, 1991; Steeger et al., 1994; Kwak and Henry, 1995; Weather and Newman, 1997) of delayed mortality to test for acute versus chronic mortality, where survival followed a monotonic trend for 2, 3, 4, 7, 15, and 30 days. For example, a bass captured during the third sampling event had a 30-day covariate of

0 0 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1 0 0...

whereas that same individual had a 3 day covariate of
Alternatively, bass captured only via electrofishing received 0 for all days of their delayed mortality covariate models, as they never experienced a tournament. The 4-, 3-, and 2-day periods were tested as they are commonly used in traditional confinement delayed mortality studies (e.g., Wilde et al., 1998; Graeb et al., 2005) whereas the 30-, 14-, and 7-day periods were chosen to test longer term, potentially chronic, effects of delayed tournament mortality.

Using hierarchical model-selection procedures based on Akaike’s Information Criterion corrected for small sample size (AICc), where lower AICc values and higher Akaike weights represent the most parsimonious model (Akaike, 1973), we characterized variation in recapture probability, acute survival effects, and survival due to additional covariates. For all models, we assumed that the most parsimonious model was one in which the ΔAICc was two or greater, indicating substantial evidence of model fit (Anderson and Burnham, 2004). If the ΔAICc was less than two for multiple models, we chose the top model for simplicity; however, evidence ratios were evaluated for model pairs with the top model to further assess supporting models (Anderson and Burnham, 2004). Models were first developed for explaining variation in bass recapture probability as the first step of the hierarchical model selection procedure, followed by survival. Models were established in this order to control for the main sources of variation on recapture probability, thus maximizing power to detect patterns in survival. First, we fixed survival to group effects (tournament bass and electrofishing bass) to compare various model combinations and identify the most supported model for explaining variation in detection probability: a group effect (largemouth bass captured by electrofishing coded as group one in the model and largemouth bass captured by tournament angling coded as group zero in the model) \[ p(g) \], a linear effect of effort for each group \[ p(g + \text{effort}) \] and water temperature for each
Once the best explanatory model for recapture probability was determined, we compared model combinations that included time varying individual covariates describing the acute effect of time since tournament capture on survival estimates. We included the six hypothesized linear trends of tournament capture effects between 2 and 30 d on bass survival as explained above. A group effect (electrofishing versus tournament captured bass) was maintained in each of the models to serve as a surrogate for differences between tournament and electrofishing bass, but later removed when additional covariates were added to the models that instead directly quantified differences in conditions experiences between these two groups (i.e., survival trends and number of tournament captures). Survival trends of 30 d \([S (g+ 30 \text{ day trend}) p (\text{best})]\), 14 d \([S (g+15 \text{ day trend}) p (\text{best})]\), 7 d \([S (g+7 \text{ day trend}) p (\text{best})]\), 4 d \([S (g+4 \text{ day trend}) p (\text{best})]\), 3 d \([S (g+3 \text{ day trend}) p (\text{best})]\), and 2 d \([S (g+2 \text{ day trend}) p (\text{best})]\) were chosen.

After the best survival time-trend model was determined, we tested additional linear individual and time-dependent covariates that were hypothesized to potentially affect survival of fish, including mean water temperature \([S (\text{best + water T}) p (\text{best})]\), mean air temperature \([S (\text{best + air T}) p (\text{best})]\), bass length-at-capture \([S (\text{best + initial length}) p (\text{best})]\), bass weight-at-capture \([S (\text{best + initial weight}) p (\text{best})]\), bass relative weight-at-capture \([S (\text{best + } W_i) p (\text{best})]\), and number of tournaments an individual bass was captured at \([S (\text{best + # tournaments}) p (\text{best})]\)]. Additive combinations of the covariates were also tested. Once the best covariate model
structure for survival was identified, the surrogate group effect (electrofishing and tournament captured bass) was removed to determine if the covariates adequately described differences between the tournament and electrofishing bass. We concluded that the additional covariates adequately described the group differences if the top model no longer included the group effect and carried majority of the support according to AICc weights.

**Cumulative mortality estimates**

Using estimates from the most parsimonious model, cumulative survival of bass captured at multiple tournament events was calculated by multiplying survival estimates of fish captured at one tournament for day of capture, one day since capture, and two days since capture to determine total survival of the first tournament event. This process was then repeated for survival estimates of fish captured at second, third, fourth, and fifth tournament events. The 3-day mortality calculations for each event were then multiplied by each prior tournament until the fifth event was reached. Cumulative mortality estimates were completed four times to estimate cumulative survival for the 20th, 40th, 60th and 80th percentiles of water temperature observed during the Brushy Creek tournament season during 2015-2018.

**Application of survival rates to a theoretical tournament event**

Finally, we evaluated the fate of 100 theoretical bass captured at a tournament, where number of tournament captures was related to the number of times bass were brought into tournaments at Brushy Creek from 2015-2017. We chose four events to evaluate water temperatures representing the 20th, 40th, 60th, and 80th percentiles of average tournament water temperature during the Brushy Creek Lake tournament season. We then applied the estimated daily survival rates for day of capture to the initial 100 fish. Using the most supported time since capture trend model, survival rates for the remainder of hypothesized days were applied to the number of surviving bass at the end of each time period. For example, if 90 fish survived day of
capture, the survival rate for one day since capture would then be applied to the remaining 90 bass.

**Results**

A total of 3,423 bass >381 were captured at 131 bass tournaments and an additional 2,168 bass were captured during 129 hours of electrofishing between 2015 and 2018 (Table 3.1). Of the recaptures, 1,196 were captured at tournaments and 745 were captured during electrofishing, with 1,388 (71.2%) bass captured once, 419 (21.5%) bass captured twice, 107 (5.5%) bass captured three times, 26 (1.3%) bass captured four times, eight (0.4%) bass captured five times, and two (< 0.1%) bass captured six times either from a tournament or electrofishing. After classifying bass into an electrofishing or tournament group, 2,168 were characterized as electrofishing bass, of which 306 were censored in the model and subsequently reclassified as a tournament bass after subsequent tournament captures. An additional 4,602 fish were characterized as tournament captured bass, of which 873 were censored in the model and re-characterized as a new tournament bass after subsequent tournament captures.

Of the nine models evaluated to describe variation in detection probability, the most supported model included linear water temperature and sampling effort, a two-way interaction between sampling effort and water temperature, and a three-way interaction between bass group, effort, and water temperature (\(\Delta AIC_c = 0.0\), \(W_i = 1.0\); Table 3.3). Detection probability beta estimates of the final model resulted in 95% confidence intervals for five of the six parameters not including zero (Table 3.4). Detection probability was higher for tournament captured bass than electrofishing bass and increased with water temperature and sampling effort. Detection probabilities ranged from 0.006 during an electrofishing event consisting of 1.7 hours of effort at 6.9 °C (Figure 3.1A) to 0.044 for a tournament event with a combined angler effort of 731 hours at 18.7 °C (Figure 3.1B).
All of the trend models describing acute effects on survival of tournament captured bass performed better than a model with no trend ($\Delta AIC_c > 7$, $W_i=0.0$; Table 3.5). Monotonic trends were best described by a 3 d pattern ($\Delta AIC_c=0.0$, $W_i=0.20$). However, 2 d and 4 d trends were also highly supported in the candidate model list ($\Delta AIC_c=0.10$, $W_i=0.20$), whereas the 7 d and 30 d trends also received some support ($0<\Delta AIC_c<2$). Evidence ratios of zero indicated that 2 d and 4 d trends were equally as likely as the 3 d trend, whereas the 3 d trend was twice as likely as the 7 d and 30 d trends. The beta estimate of the 3 d trend in the final model did not include zero (Table 3.5) and the slope indicated an increase in survival in relation to time since capture. At average water temperature (15.5 °C), survival of bass was lowest on day of capture (0.85, 95% CI: 0.77, 0.91) and increased one (0.95, 95% CI: 0.93, 0.97) and two (0.99, 95% CI: 0.98, 0.99) days since capture. Tournament bass survival three days since capture returned to average daily survival of all uncaptured bass (0.99, 95% CI: 0.99, 0.99; Figure 3.2).

Additional covariates describing survival in the final step of the hierarchical model resulted in 15 candidate models (Table 3.6). The top model did not include the group effect between tournament and electrofishing bass, indicating that the addition of covariates successfully described differences between these groups ($W_i=0.44$). Survival in the top model was best described by the 3 d trend, water temperature, and number of tournaments. All three of the covariate beta parameters did not include zero in the 95% confidence intervals (Table 3.4).

Bass survival decreased as water temperatures increased (Figure 3.3A). Water temperature during tournaments ranged from 3.8 to 23.3 °C, with majority of tournaments occurring during warmer temperatures in June, July, and August. Water temperature had the greatest influence on bass survival on day of capture ranging from 0.9569 (95% CI: 0.9138, 0.9788) at 3.8 °C to 0.6938 (95% CI: 0.5762, 0.8002) at 23.3°C, a 28% decrease in survival. One
day since capture, survival of bass ranged from 0.9874 (95% CI: 0.9774, 0.9929) to 0.8888 (95% CI: 0.8488, 0.89235) between 3.8 and 23.3 °C, a 10% decrease in daily survival. Two days since capture, survival ranged from 0.9964 (95% CI: 0.9942, 0.9977) at 3.8 °C to 0.9657 (95% CI: 0.9572, 0.9742) at 23.3 °C, a 3% decrease in survival. Three days since capture, survival ranged from 0.9990 (95% CI: 0.9985, 0.9993) at 3.8°C and 0.9900 (95% CI: 0.9877, 0.9924) at 23.3 °C, <1% decrease in survival.

Survival of bass decreased with each capture event and was closely associated with days since capture (Figure 3.3B). Bass were captured in tournaments up to five times in the three and a half years sampled, with 82% of bass captured once, 15% of bass captured twice, 2% of bass captured three times, 0.09% of bass captured four times, and 0.01% of bass captured five times. Day of capture showed the largest change in survival across number of tournament captures, where survival on average decreased 11% from 0.8390 (95% CI: 0.7748, 0.9121) for fish captured at one tournament to 0.7500 (95% CI: 0.4861, 0.6430) for fish captured at five tournaments. One day since capture, survival for fish captured at one tournament was 0.9484 (95% CI: 0.9264, 0.9641), whereas fish captured at five tournaments was 0.9135 (95% CI: 0.8494, 0.9521). Average survival trends for two days since capture were similar, with a change in survival from 0.9848 (95% CI: 0.9822, 0.9870) for bass captured at one tournament to 0.9739 (95% CI: 0.9524, 0.9854) for bass captured at five tournaments, a difference of 1%. Finally, on three days since capture, survival of bass captured once had an estimated survival rate of 0.9956 (95% CI: 0.9952, 0.9960) while those captured at five tournaments had a survival rate of 0.9924 (95% CI: 0.9914, 0.9934), a difference of <1%.

Cumulative bass survival decreased with increasing tournament capture events and decreased with increasing water temperatures (Figure 3.4). Water temperature the day of a
tournament was 12.4 °C for the 20th percentile, 15.7 °C for the 40th percentile, 17.6 °C for the 60th percentile, and 18.8 °C for the 80th percentile. Survival estimates of two tournament capture events were 0.6751, 0.5697, 0.5021 and 0.4560 for 12.4 °C, 15.7 °C, 17.5 °C, and 18.8 °C, respectively. Differences increased across water temperature for three (0.5319, 0.4056, 0.3317, 0.2846) and four tournament captures (0.4056, 0.2760, 0.2075, 0.1671). Finally, bass captured five times had cumulative survival rates ranging from 0.2980 at 12.4 °C to 0.0917 at 18.8 °C indicating that few bass survived being captured at five tournaments.

**Application of survival rates to a theoretical tournament event**

Application of survival rates to four tournament scenarios showed the number of surviving tournament bass decreased with consecutive days since capture (Figure 3.6). The number of surviving bass decreased on the day of capture (day 0) from 100 to 87, 83, 78 and 76 bass for the 20th, 40th, 60th, and 80th water temperature percentiles. Across the range of water temperatures, number of bass decreased by an average of 6.61% (SE = 0.53) between day of capture and one day since capture, 1.81% (SE = 0.46) between one day and two days since capture, and 0.65% (SE = 0.18) between two days and three plus days since capture. Overall, of the theoretical initial 100 tournament captured bass, 83% would survive the 3 d delayed mortality period at 12.4 °C, 75% would survive at 15.7 °C, 71% would survive at 17.6 °C, and only 67% bass would survive at 18.8 °C.

**Discussion**

Delayed mortality of tournament captured bass may be a result of an inability to recover from physiological stress (Gustaveson et al., 1991; White et al., 2008). Additionally, relocation and accumulation of bass at tournament release sites may result in increased competition for food, inability to find appropriate habitat, and increased predation (Stang et al., 1996; Gilliland,
We found that bass delayed mortality was an acute effect, occurring between two and four days post tournament. Prior studies of black bass typically retained fish between one and three days post tournament (Bennet et al., 1989; Jackson and Willis, 1991; Steeger et al., 1994; Kwak and Henry, 1995), with mortality past four days reported as negligible (Weathers and Newman, 1997; Neal and Lopez-Calyton, 2001; Keretz et al., 2018). However, variability in the duration of delayed mortality across studies is large. For example, bass were found to be fully recovered from physiological disturbances after 24 hours in a Utah reservoir (Gustaveson et al., 1991), whereas others have found support for delayed mortality up to six days in Florida and Georgia (Plumb et al., 1975; Schramm et al., 1987). We identified similar support for two, three, and four day delayed mortality, as well as some support for a seven day delayed mortality. In contrast, we found less evidence in our models of 15 and 30 day mortality, suggesting chronic tournament mortality is unlikely. Although we chose three day trends to model our results, duration of delayed mortality is likely specific to individual fish, depending upon a suite of individual-level factors occurring during the angling process (e.g., angler gear type, hooking injuries, livewell duration, etc; Dunmall et al., 2001; Wilde and Pope, 2008; Keretz et al., 2018). Although there have been a few observations of delayed mortality lasting past one week (Archer and Loycano, 1975; Gravel and Cooke, 2008), this may be a result of differences in tournament bass handling practices among studies and challenges in confining bass for extended periods.

Our most supported models also included water temperature, but not air temperature, as an important explanatory covariate of tournament mortality. While air temperature has been suggested to potentially affect survival of tournament angled fish due to the increases in stress response of fish exposed to air (Suski et al., 2004), direct relationships of air temperature and survival have been tested but rarely found (Schramm et al., 1985; Schramm et al., 1987; Edwards
et al., 2004). Prior studies have found variable trends in the effects of water temperature on tournament mortality (Wilde, 1998), where correlation coefficients of water temperature and initial and delayed mortality varied from 0.71 (Watson and Johnson, 1997) to 0.01 (Steeger et al., 1994). Marked declines in bass survival rates were observed at water temperatures exceeding 17.6 °C (Seidensticker, 1975; Bennett et al., 1989), explaining up to 30% of variability in mortality at some tournaments (Wilde, 1998). This trend has also been observed in other species, including smallmouth bass *Micropterus dolomieu* (Welborn and Barkley, 1974), walleye (Goeman, 1991; Fielder and Johnson, 1994), and sauger *Sander canadensis* (Boland, 1990; Hoffman et al., 1996). Increases above ambient temperature in live-wells (Keretz et al, 2018) during weigh-ins and at release sites lead to increased physiological stress and mortality (Cooke and Suski, 2005). We observed that the largest effect of water temperature occurred on day of capture that included mortality as a result of capture and weigh-in procedures whereas water temperature had less of an effect days following release.

Initial and delayed tournament mortality rates of bass in Brushy Creek ranged from 17% at 12.4 °C to 33% at 18.8°C. Similar tournament mortality of black bass at higher temperatures was observed in two Florida lakes where mortality was 33% after four days (Schramm et al., 1985). Tournament mortality ranging from 14-32% has also been observed in other Southern states including Texas, Mississippi, Georgia, and Alabama, USA (May, 1973; Welborn and Barkley, 1974; Plumb, 1975; Seidensticker, 1975; Schramm et al., 1987). Conversely, our tournament mortality estimates were higher than similar total mortality studies in higher latitudes conducted at the same temperatures, including Maine, USA (5.2%; Hartley and Moring, 1995), Connecticut, USA (3.2%; Edwards et al., 2004), Minnesota, USA (4.5%; Kwak and Henry, 1995), South Dakota, USA (4.9%; Jackson and Willis, 1991), and Idaho, USA (10.5%; Bennet et
al., 1989). The difference between our findings and other bass mortality rates at northern latitude could be a result of our ability to incorporate data from a wide range of conditions and tournaments over more than 130 tournaments across three years.

Although rarely considered, we found the effect of multiple tournament captures to be an important determinant of bass survival. Within the three years we evaluated, bass were captured up to five times at tournaments, a rate that has been observed in other bass populations (Sass et al., 2018). However, while studies with similar bass tournament recapture rates have indicated little evidence of catch and release mortality, increased recaptures of bass in our study lead to a daily mortality rate of nearly 20% on day of capture at warmer water temperatures. Additionally, cumulative mortality of bass captured multiple times at tournaments was substantially higher, approaching 90% after five capture events during at tournaments where water temperatures surpassed 20 °C. Similarly, cumulative catch-and-release mortality of marine fishes can approach 100% for fish with high capture probabilities (Bartholomew and Bohnsak, 2005). Thus, high cumulative mortality after multiple tournament recaptures likely explains the low proportion of bass captured at tournaments multiple times, as survival of those individuals is lower than individuals that have only been captured at a single tournament. Methods to quantify cumulative mortality after multiple captures is especially important in species that are long-lived and experience intense fishing pressure, resulting in the potential for multiple captures throughout their lifetime (Musick, 1999). When multiple captures do occur, reduced survival rates of these potentially “trap-happy” individuals may be further explained by selective forces of recreational angling on largemouth bass populations (see Philip et al., 2009).

Tournament mortality (Meals and Miranda, 1994; Meka and McCormick, 2005) can be size-specific, but the influence of bass length, weight, and condition on delayed mortality were
not supported in our models. Considerable variation in responses to angling among regions, regulations, and populations is common (Cooke and Suski, 2005). For example, larger bass (>457 mm) experienced significantly more mortality than bass between 304 and 355 mm in Mississippi, USA (Meals and Miranda, 1994) whereas correlations between mean weight of captured fish of initial and delayed mortality were not found to be significant in Florida, USA lakes (Schramm et al., 1987). Tournaments held at Brushy Creek required bass retained in tournaments to be >381 mm, with a majority of the bass captured at tournaments <457 mm (~82%) and in good condition (mean Wt each year >100). Thus, although maximum TL of bass in tournaments was 658 mm, the small number of large bass in our study and high condition factor of most individuals encountered may account for the lack of support for size-related mortality.

Our theoretical tournament results reflected the survival rates and trends in temperature observed in our model. Tournaments held when water temperatures were cooler showed a loss of up to 13% of bass on day of capture and only an additional 4% in the days post release. This supports findings of minimal delayed mortality at lower temperatures (Kwak and Henry, 1995; Edwards et al., 2004; Keretz et al., 2018). However, tournaments occurring at higher water temperatures (>15.7 °C) showed increased rates of mortality, resulting in a loss of up 25% of bass on day of capture and increasing to 33% of bass three days post capture. Even with improved ability to decrease physiological stress of tournament angled bass in recent decades, our results indicate that mortality can still be high, especially in systems that experience multiple tournament events throughout the season. Although the number of bass experiencing multiple tournament captures was not large in our hypothetical scenario, the likelihood of multiple
tournament captures may increase as tournament pressure increases, further decreasing the number of surviving tournament bass.

While delayed tournament mortality in Brushy Creek was markedly high when compared to other studies in similar regions and is often negatively perceived, catch and release angling mortality may also provide some benefits. Recent work has shown that regulations enacted to increase bass abundance (e.g., length-limits, bag limits and seasonal closures) rely on the assumption that anglers will harvest fish. High voluntary release rates of bass (near 100%, Henry, 2003) paired with increased regulations have the potential to result in negative effects on population growth and size-structure (see Hansen et al., 2015; Miranda et al., 2017). Thus, some low level of catch and release mortality may be beneficial in releasing bass from density dependent growth, increasing population size-structure.

A vital component of understanding the total mortality of fish captured during competitive catch-and-release events is the ability to accurately estimate delayed mortality. Our use of mark-recapture data further highlights the usefulness of such assessments in sportfish populations (see Cline et al., 2012, Kerns et al., 2016; Sass et al., 2018; Shaw et al., 2019). This study improves upon previous study designs and can be completed across multiple tournament events and extended periods of time, improving findings of traditional mortality studies. Further, the use of this mark-recapture method removes the arbitrary choice of holding time and allows for multiple hypotheses to be tested regarding factors related to delayed mortality. While our study evaluated only tournament mortality, this model could be extended to assess recreational catch-and-release angling (e.g., Muoneke and Childress, 1994), marine bycatch (e.g., Davis, 2002), and tagging mortality of released fish (e.g., Brattey and Cadigan, 2004) across various
water bodies. Assessing post-release mortality is a challenging task; pursuing objective and repeatable methods are fundamental to its continued understanding.

**Acknowledgements**

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**References**


Table 3.1 Mean, standard error (SE), and range of individual covariates used in Cormack-Jolly-Seber models to estimate apparent survival ($S$) of jaw tagged largemouth bass in Brushy Creek, IA, USA for 771 periods April 2015 through June 2018. Tournament captures = number of time a bass was captured at a tournament. Length-at-capture = length of fish (mm) at time of capture. Weight-at-capture = weight of fish (g) at time of capture. $W_r$-at-capture = relative weight at time of capture.

<table>
<thead>
<tr>
<th></th>
<th>2015</th>
<th></th>
<th></th>
<th>2016</th>
<th></th>
<th></th>
<th>2017</th>
<th></th>
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<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
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<td>SE</td>
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<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
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<td>Tournament captures</td>
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<td>0.84</td>
<td>0.02</td>
<td>0, 5</td>
<td>0.89</td>
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<td>0, 5</td>
<td>0.44</td>
<td>0.03</td>
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<td>Length-at-capture</td>
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<td>381, 658</td>
<td>425.87</td>
<td>0.76</td>
<td>381, 553</td>
<td>428.06</td>
<td>0.82</td>
<td>380, 561</td>
<td>424.32</td>
<td>2.23</td>
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<td>8.37</td>
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<td>1258.66</td>
<td>8.15</td>
<td>461, 2813</td>
<td>1227.5</td>
<td>8.53</td>
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<td>1202.67</td>
<td>23.99</td>
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<td>0.22</td>
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<td>0.23</td>
<td>60, 137</td>
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Table 3.2 Tagged and recaptured largemouth bass with electrofishing and tournaments by year at Brushy Creek, IA. Data in table represents modified data including censored and re-entered tournament and electrofishing bass used in Cormack-Jolly-Seber mark-recapture models.

<table>
<thead>
<tr>
<th>Capture method</th>
<th>Year</th>
<th>Number tagged</th>
<th>2015</th>
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<th>2017</th>
<th>2018</th>
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</thead>
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<td>503</td>
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<td>2</td>
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<td></td>
<td>2016</td>
<td>1,423</td>
<td>-</td>
<td>112</td>
<td>253</td>
<td>23</td>
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<tr>
<td></td>
<td>2017</td>
<td>1,621</td>
<td>-</td>
<td>-</td>
<td>498</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>109</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5</td>
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<td>325</td>
<td>615</td>
<td>786</td>
<td>59</td>
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<td>7</td>
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<tr>
<td></td>
<td>2016</td>
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<td>-</td>
<td>96</td>
<td>50</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>603</td>
<td>-</td>
<td>-</td>
<td>65</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>313</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>2,168</td>
<td>154</td>
<td>185</td>
<td>129</td>
<td>81</td>
</tr>
<tr>
<td>Total bass</td>
<td></td>
<td>6,770</td>
<td>479</td>
<td>800</td>
<td>915</td>
<td>140</td>
</tr>
</tbody>
</table>
Table 3.3 Cormack-Jolly-Seber models used to estimate detection probability ($p$) of jaw tagged largemouth bass in Brushy Creek, IA, USA for 771 periods beginning 13 April 2015- June 2018. Effects evaluated influencing $p$ include electrofishing or tournament captured bass ($g$), water temperature (Water T), and electrofishing sampling effort and tournament fishing effort (effort). $K =$ number of parameters. Deviance = -2 x log-likelihood of the model less -2 x log-likelihood of the saturated models (same number of parameters and degrees of freedom). $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$ (g + water T + effort + water T x effort + g x water T x effort)</td>
<td>106,583.18</td>
<td>0.00</td>
<td>1.0</td>
<td>8</td>
<td>98,180.32</td>
</tr>
<tr>
<td>$p$ (g + effort)</td>
<td>106,692.20</td>
<td>109.02</td>
<td>0.0</td>
<td>5</td>
<td>98,295.35</td>
</tr>
<tr>
<td>$p$ (g + water T$^2$ + effort)</td>
<td>106,693.47</td>
<td>110.29</td>
<td>0.0</td>
<td>6</td>
<td>98,294.63</td>
</tr>
<tr>
<td>$p$ (g + water T + water T$^2$ + effort)</td>
<td>106,693.56</td>
<td>110.38</td>
<td>0.0</td>
<td>7</td>
<td>98,292.71</td>
</tr>
<tr>
<td>$p$ (g + water T + effort + water T x effort)</td>
<td>106,695.35</td>
<td>112.17</td>
<td>0.0</td>
<td>7</td>
<td>98,294.49</td>
</tr>
<tr>
<td>$p$ (g + water T + water T$^2$)</td>
<td>106,697.18</td>
<td>114.00</td>
<td>0.0</td>
<td>6</td>
<td>98,298.33</td>
</tr>
<tr>
<td>$p$ (g)</td>
<td>106,700.86</td>
<td>117.68</td>
<td>0.0</td>
<td>4</td>
<td>98,306.01</td>
</tr>
<tr>
<td>$p$ (g + water T)</td>
<td>106,702.30</td>
<td>119.12</td>
<td>0.0</td>
<td>5</td>
<td>98,305.45</td>
</tr>
<tr>
<td>$p$ (.)</td>
<td>106,706.03</td>
<td>122.85</td>
<td>0.0</td>
<td>3</td>
<td>98,313.20</td>
</tr>
</tbody>
</table>
Table 3.4 Cormack-Jolly-Seber estimates of most supported model: \[ S (3 \text{ day trend} + \text{water T} + \# \text{tournaments}) \] \[ p (g + \text{water T} + \text{effort} + \text{water T} \times \text{effort} + g \times \text{water T} \times \text{effort}) \] of jaw tagged largemouth bass in Brushy Creek, IA, USA for 771 periods from April 2015 through June 2018. Estimate = Beta estimate of parameter. SE = Standard error of beta estimate. 95% LCI = 95% lower confidence interval of beta estimate of parameter. 95% UCI = 95% upper confidence interval of beta estimate of parameter. Best model determined by sample-sized corrected Akaike’s Information Criterion (AIC_c).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>95% LCI</th>
<th>95% UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Survival (S)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>7.32629</td>
<td>0.267452</td>
<td>6.802080</td>
<td>7.850491</td>
</tr>
<tr>
<td>3 day trend</td>
<td>-1.26042</td>
<td>0.093797</td>
<td>-1.444257</td>
<td>-1.076574</td>
</tr>
<tr>
<td>Water T</td>
<td>-0.11704</td>
<td>0.016207</td>
<td>-0.148804</td>
<td>-0.085272</td>
</tr>
<tr>
<td># tournaments</td>
<td>-0.13843</td>
<td>0.047710</td>
<td>-0.231942</td>
<td>-0.044919</td>
</tr>
<tr>
<td><strong>Detection probability (p)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-4.85657</td>
<td>0.146773</td>
<td>-5.144246</td>
<td>-4.568895</td>
</tr>
<tr>
<td>Group</td>
<td>-0.31937</td>
<td>0.096928</td>
<td>-0.509352</td>
<td>-0.129392</td>
</tr>
<tr>
<td>Effort</td>
<td>0.00001</td>
<td>0.000045</td>
<td>-0.000076</td>
<td>0.000099</td>
</tr>
<tr>
<td>Water T</td>
<td>0.01440</td>
<td>0.007843</td>
<td>-0.000974</td>
<td>0.029770</td>
</tr>
<tr>
<td>Effort x water T</td>
<td>0.00011</td>
<td>0.000011</td>
<td>0.000089</td>
<td>0.000131</td>
</tr>
<tr>
<td>g x effort x water T</td>
<td>-0.00011</td>
<td>0.000010</td>
<td>-0.000128</td>
<td>0.000088</td>
</tr>
</tbody>
</table>
Table 3.5 Cormack-Jolly-Seber models used to estimate apparent survival ($S$) of jaw tagged largemouth bass in Brushy Creek, IA, USA for 771 periods beginning April 2015 through June 2018. Effects evaluated influencing $S$ include 2, 3, 4, 7, 15, and 30 day trends in survival post tournament capture. $K =$ number of parameters. Deviance = $-2 \times \text{log-likelihood of the model}$ less $-2 \times \text{log-likelihood of the saturated models (same number of parameters and degrees of freedom)}$. $b =$ beta parameter estimate for tournament mortality effects of a specific duration. 95% CI = 95% confidence interval for beta parameter estimate for tournament mortality effects of a specific duration. $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion.

<table>
<thead>
<tr>
<th>Model</th>
<th>b</th>
<th>95% CI</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>S (3 day trend)</td>
<td>-1.256</td>
<td>[-1.444, -1.077]</td>
<td>106,575.30</td>
<td>0.00</td>
<td>0.20</td>
<td>9</td>
<td>106,557.28</td>
</tr>
<tr>
<td>S (2 day trend)</td>
<td>-2.107</td>
<td>[-2.473, -1.740]</td>
<td>106,575.35</td>
<td>0.10</td>
<td>0.20</td>
<td>9</td>
<td>106,557.33</td>
</tr>
<tr>
<td>S (4 day trend)</td>
<td>-0.980</td>
<td>[-1.169, -0.792]</td>
<td>106,575.42</td>
<td>0.10</td>
<td>0.20</td>
<td>9</td>
<td>106,557.40</td>
</tr>
<tr>
<td>S (7 day trend)</td>
<td>-0.497</td>
<td>[-0.609, -0.384]</td>
<td>106,576.14</td>
<td>0.80</td>
<td>0.10</td>
<td>9</td>
<td>106,558.12</td>
</tr>
<tr>
<td>S (30 day trend)</td>
<td>-0.064</td>
<td>[-0.089, -0.039]</td>
<td>106,576.20</td>
<td>0.90</td>
<td>0.10</td>
<td>9</td>
<td>106,558.18</td>
</tr>
<tr>
<td>S (15 day trend)</td>
<td>-0.176</td>
<td>[-0.232, -0.121]</td>
<td>106,577.31</td>
<td>2.00</td>
<td>0.10</td>
<td>9</td>
<td>106,559.29</td>
</tr>
<tr>
<td>S (g)</td>
<td>-</td>
<td>-</td>
<td>106,583.18</td>
<td>7.90</td>
<td>0.00</td>
<td>8</td>
<td>98,180.32</td>
</tr>
</tbody>
</table>
Table 3.6 Cormack-Jolly-Seber models used to estimate apparent survival ($S$) of jaw tagged largemouth bass in Brushy Creek, IA, USA for 771 periods beginning 13 April, 2015 - 1 June 2018. Effects evaluated influencing $S$ include a three day monotonic trends in survival post tournament capture (3 day trend), electrofishing or tournament bass ($g$), mean daily water temperature (water $T$), number of tournament captures (# tournaments), mean daily air temperature (air $T$), $W_r$-at-capture ($W_r$), weight-at-capture (initial weight), and length-at-capture (initial length). $K$ = 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). $b =$ beta parameter estimate for tournament mortality effects of a specific duration. 95% CI = 95% confidence interval for beta parameter estimate for tournament mortality effects of a specific duration. $AIC_c =$ sample-sized corrected Akaike’s Information Criterion.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$ (3 day trend + water $T$ + # tournaments)</td>
<td>106,513.81</td>
<td>0.00</td>
<td>0.44</td>
<td>10</td>
<td>106,493.79</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + water $T$ + # tournaments)</td>
<td>106,515.76</td>
<td>1.95</td>
<td>0.16</td>
<td>11</td>
<td>106,493.73</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + $W_r$ + water $T$ + # tournaments)</td>
<td>106,516.08</td>
<td>2.27</td>
<td>0.14</td>
<td>12</td>
<td>106,492.04</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + $W_r$ + air $T$ + water $T$ + # tournaments)</td>
<td>106,516.33</td>
<td>2.52</td>
<td>0.12</td>
<td>13</td>
<td>106,490.28</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + air $T$ + water $T$ + # tournaments)</td>
<td>106,516.88</td>
<td>3.07</td>
<td>0.09</td>
<td>12</td>
<td>106,492.84</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + $W_r$ + air $T$)</td>
<td>106,518.51</td>
<td>4.70</td>
<td>0.04</td>
<td>12</td>
<td>106,494.47</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + $W_r$ + air $T$)</td>
<td>106,541.02</td>
<td>27.21</td>
<td>0.00</td>
<td>11</td>
<td>106,518.98</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + initial weight + air $T$)</td>
<td>106,541.32</td>
<td>27.51</td>
<td>0.00</td>
<td>11</td>
<td>106,519.28</td>
</tr>
<tr>
<td>$S$ ($g$ + 3 day trend + initial length + air $T$)</td>
<td>106,542.12</td>
<td>28.31</td>
<td>0.00</td>
<td>11</td>
<td>106,520.08</td>
</tr>
</tbody>
</table>
Table 3.6 Continued

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S(g + 3$ day trend + # tournaments)</td>
<td>106,570.54</td>
<td>56.73</td>
<td>0.00</td>
<td>10</td>
<td>106,550.51</td>
</tr>
<tr>
<td>$S(g + 3$ day trend)</td>
<td>106,575.30</td>
<td>61.49</td>
<td>0.00</td>
<td>9</td>
<td>106,557.28</td>
</tr>
<tr>
<td>$S(g + 3$ day trend + $W_r$)</td>
<td>106,575.36</td>
<td>61.55</td>
<td>0.00</td>
<td>10</td>
<td>106,555.33</td>
</tr>
<tr>
<td>$S(g + 3$ day trend + initial weight)</td>
<td>106,575.64</td>
<td>61.83</td>
<td>0.00</td>
<td>10</td>
<td>106,555.61</td>
</tr>
<tr>
<td>$S(g + 3$ day trend + initial length)</td>
<td>106,576.52</td>
<td>62.71</td>
<td>0.00</td>
<td>10</td>
<td>106,556.49</td>
</tr>
<tr>
<td>$S(g)$</td>
<td>106,583.18</td>
<td>69.37</td>
<td>0.00</td>
<td>8</td>
<td>106,567.16</td>
</tr>
</tbody>
</table>
Figures

Figure 3.1 Detection probability of jaw tagged largemouth bass captured by electrofishing (a; coded as group one in final MARK model) and largemouth bass captured by tournament angling (b; coded as group zero in the final MARK model) across effort in hours at 12.4 °C (solid line), 15.7 °C (dotted line), 17.6 °C (dashed line), and 18.8 °C (dashed and dotted line) for 771 time periods from April 2015 to June 2018 in Brushy Creek, IA, USA. Water temperatures represent the 20th, 40th, 60th and 80th percentiles of water temperatures across the tournament season.
Figure 3.2 Apparent survival rate of jaw tagged largemouth bass in Brushy Creek IA, USA, on day of capture (day zero), one day since capture, two days since capture, and three + days since capture at a mean water temperature during tournaments of 15.5°C with 95% confidence bands (shaded area).
Figure 3.3 Apparent survival of jaw tagged largemouth bass in Brushy Creek, IA, USA, three plus days since capture (solid line), two days since capture (dotted line), one day since capture (dashed line), and day of capture (dashed and dotted line) in relation to water temperature (°C).
Figure 3.4 Apparent survival of jaw tagged largemouth bass in Brushy Creek, IA, USA, three plus days since capture (solid line), two days since capture (dotted line), one day since capture (dashed line), and day of capture (dashed and dotted line) in relation to number of tournament captures (bottom).
Figure 3.5 Cumulative apparent survival from April 2015 to June 2018 of jaw tagged largemouth bass in Brushy Creek, IA, USA, captured on one, two, three, four, and five tournaments at 12.4 °C (solid line), 15.7 °C (dotted line), 17.6 °C (dashed line), and 18.8 °C (dashed and dotted line). Water temperatures represent the 20th, 40th, 60th and 80th percentiles of water temperatures across the tournament season.
Figure 3.6 Number of surviving largemouth bass in Brushy Creek, IA, USA on day of capture (represented by zero), one day since capture, two days since capture, and three plus days since capture for a at 12.4 °C (solid line), 15.7 °C (dotted line), 17.6 °C (dashed line), and 18.8 °C (dashed and dotted line). Assuming a theoretical tournament with 100 original captured bass at the 20th, 40th, 60th and 80th percentiles of water temperatures across the tournament season.
CHAPTER 4. TOURNAMENT AND RECREATIONAL ANGLERS HAVE LITTLE EFFECT ON A LARGEMOUTH BASS POPULATION COMPARED TO NATURAL MORTALITY

Modified from a manuscript to be submitted to Ecological Applications

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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 successful identification and focus of management. We conducted monthly electrofishing, solicited recreational angler tag returns, and censused Largemouth Bass *Micropterus salmoides* tournaments at Brushy Creek, IA, USA from April 2015 to June 2018. We then used a live-dead multistate mark-recapture model to evaluate the effects of air temperature, water temperature, tournament bass per angler, and tournament initial mortality on electrofishing and recreational and tournament angler capture probability and natural, recreational angling, and initial and delayed tournament mortality. A total of 3,893 bass were captured at 142 bass tournaments while 1,250 bass were captured during 139 hours of electrofishing. Increased air temperatures resulted in increased capture probability for recreational anglers whereas increased water temperature and tournament catch-per-unit effort
resulted in increased tournament capture probability. Air temperature followed a quadratic trend for recreational and tournament captured bass survival, and tournament bass survival decreased with increased number of bass per angler and initial tournament mortality. Bass survival in Brushy Creek showed a quadratic relationship with water temperature. Average total annual mortality was 0.66, with natural mortality representing the largest component (0.57), followed by delayed tournament mortality (0.06), recreational angling mortality (0.03), and finally initial tournament mortality (0.004). Our results reveal that both recreational and tournament angling mortality are low compared to natural mortality. Therefore, cumulative angling mortality likely has minimal population level effects on bass populations.

**Introduction**

Determining fish mortality rates and sources are essential to understanding population level changes but can often be difficult to assess (Quinn and Deriso 1999). Total mortality is a combination of fishing mortality and natural mortality (Beverton and Holt 2012). While fishing mortality has traditionally been considered the removal of fish from a population through direct harvest, increases in anglers choosing to release fish (e.g., due to ethical considerations, social trends, etc.) has led to the expansion of fishing mortality to include mortality associated with catch and release angling (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005). Catch and release angling has grown immensely in both marine and freshwater systems (Schroeder and Love 2002; Cooke and Suski 2005; Brownscombe et al. 2017) and is used to increase recreational angling opportunities, support sustainable fisheries, and protect vulnerable fishes (Barnhart and Roelofs 1977; Policansky 2002; Arlinghaus et al. 2007). Although many anglers and fishery managers believe that catch and release mortality represents only a small component of total mortality, catch and release mortality at the population level is highly
variable (0-50%) but is difficult to evaluate (Cooke and Schramm 2007; Taylor et al. 2015; Kerns 2016). Consequently, catch and release mortality is typically assessed on the individual level (e.g., Cooke et al. 2002; Cooke et al. 2003; Ferter et al. 2017) but population level effects of catch and release mortality has received substantially less attention.

Largemouth Bass (*Micropterus salmoides*; hereafter referred to as bass) represent an example of shifts in angler behaviors and motivations. Historically, overharvest of bass was common (Holbrook 1975; Redmond 1986; Long et al. 2015). More recently, voluntary 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 bass populations (0.42, Gardner Lake, Connecticut; Edwards et al. 2004; 0.58 Luchetti Reservoir, Puerto Rico; Waters et al. 2005). Even when anglers release bass alive, they can still experience mortality because of hooking wounds (Cooke et al. 2003), exhaustion during capture (Schreer et al. 2001), air exposure (Gingerich et al. 2007), warm temperatures (Suski et al. 2003), and handling stress (Williamson et al. 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).

Bass fishing tournament represent a common example of catch and release angling mortality. Bass tournament angling events have grown exponentially in number in recent decades (Driscoll et al. 2014; Bernthal et al. 2015; Long et al. 2015), potentially leading to considerably more fish being captured and subjected to tournament stressors, resulting in higher catch and release mortality than bass captured through recreational angling. While similarities exist between factors affecting mortality of competitive and recreationally captured bass (e.g., increased air and water temperature; Cooke et al. 2003a; Cooke et al. 2004), additional stressors
imposed on bass during tournament events, including live-well and weigh-in bag confinement and increased air exposure during weigh-ins (Kwak et al. 1995; Weathers and Newman 1997), may further increase bass mortality.

Bass mortality at an individual tournament can be as high as 61% (Wilde 1998; Neal and Lopez-Clayton 2001; Gravel and Cooke 2008) and is comprised of both initial and delayed mortality. Initial mortality, accounting for 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 bass prior to weigh-in can result in disqualification from a tournament. In contrast, delayed mortality occurring post-release is cryptic and is difficult to assess (Schramm et al. 1987; Sylvia and Weber in revision). While relationships between initial and delayed tournament mortality exist (i.e., increased initial mortality can be related to increased delayed mortality; Wilde 1998), there can be high variability associated with extent of delayed mortality as a result of environmental and tournament conditions (e.g., water temperature, prior tournament capture, bass density in live-well; Schramm et al. 1987; Kwak and Henry 1995; Sylvia and Weber in revision). However, delayed mortality may be high and account 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 not been assessed.

Bass fishing mortality can arise from multiple sources. When sources of fishing mortality are additive, populations with high angler harvest or catch and release angling and tournament mortality may lead to higher total mortality of bass populations (Allen et al. 1998). Alternatively,
tournament mortality may have negligible population-level effects when natural mortality rates are high (Driscoll et al. 2007), offsetting tournament mortality effects. Thus, understanding the 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 bass capture and mortality probabilities of tournament and recreational anglers and assess their effect on a population compared to natural mortality. A multistate, live-dead, mark-recapture approach was used to estimate distinct sources of natural mortality compared to fishing mortality, that included both initial and delayed tournament mortality as well as recreational angling mortality. We also tested multiple covariates on bass survival and capture probability, including mean water and air temperature, angling effort, average tournament bag/angler, and initial tournament mortality. Finally, we estimated abundance of bass in the lake and applied our model estimates to determine relative mortality rates of each source. Our results provide new insights into potential population-level effects of tournament and recreational anglers on bass.

Methods

Sampling

Brushy Creek Lake (hereafter Brushy Creek) is a 279 ha reservoir in Webster County, Iowa, USA. The lake has a mean depth of 8.9 m, a maximum depth of 22.9 m, and is densely covered in both emerged and submerged coarse woody habitat along the perimeter of the lake. Brushy Creek is used extensively by anglers, hosting more than 40 bass tournaments annually between April and October (mean = 32.3; SE = 18.0 tournament angler hours/ha/year from 2015-2017). Electrofishing (pulsed DC 300 V and 8 amps) occurred once monthly on Brushy Creek during the open water season (April - November) for 2015, 2016, and 2017 and from April-June
2018. Electrofishing lasted approximately three to five consecutive days each month until the entire accessible shoreline had been sampled. Electrofishing effort averaged 242 minutes (SE = 26 minutes SE) per month. All Largemouth Bass (hereafter referred to as bass) captured were weighed (g) and measured (mm). Bass \( \geq 381 \text{ mm (15”)} \) 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).

All bass tournaments at Brushy Creek 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 of 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”) minimum length limit and a three fish/angler bag limit. Number of anglers, number of boats, and number of bass weighed-in were recorded for each tournament event. Following weigh-in, all bass were placed in an insulated live-well with lake water and supplemental oxygen. All bass were weighed (g), measured (mm), and evaluated for jaw tags: all untagged bass were tagged on the left upper jaw with a metal Monel band and released. Finally, project e-mail and telephone contact information was placed on signs throughout the lake and capture date and bass tag number, harvest, length, and weight were reported by non-tournament anglers. To estimate reporting rates, ~10% of bass in Brushy Creek were tagged with reward tags ($99) during each tagging event while the remainder of bass received non-reward tags.

**Model**

Individual bass encounter histories were analyzed during 2015-2018 in program MARK (White and Burham 1999) using a multistate, live-dead encounter model for maximum-
likelihood estimates of survival ($S$; hereafter referred to as survival), recapture probability (representing electrofishing capture; $p$), transition probabilities (representing recreational and tournament angler capture probabilities; $P_{si}$), and dead recovery rate ($r$; Lebreton et al. 1992; Figure 4.1). 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). Assumptions of the model include that every marked animal present in some state immediately following sampling period $i$ have the same probability of recapture and every marked animal present in some state immediately following the sampling period $i$ has 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, the reporting rates of dead animals depend only on the state of the animal in the immediately preceding live-recapture.

Survival in Brushy Creek represents fish that died and those that left the study area due to permanent emigration; however, emigration of bass from Brushy Creek is minimal, as only two bass during the study period were found to have emigrated over the spillway (<0.001%; A. Sylvia, unpublished data). Further, we assumed temporary emigration (i.e. increased water depth leading to decreased vulnerability of capture during electrofishing) was minimal as bass remained in relatively shallow water (1.88 m; Sylvia et al. in prep) and bass were vulnerable to angling across all depths. Although post capture refectory periods for bass may exist for short periods following angling (Cox, 2000; Cline et al., 2012; Sass et al., 2018), bass resume feeding within 16 hours following an angling event (Siepker et al. 2006). 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).

Survival was estimated for 378 days during the open water seasons. Only days with a tournament or electrofishing or a weekend were included as dates across the three years, where intervals between events were adjusted in program MARK. 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. This period consisted of 150 days between November 8, 2015 and April 3, 2016, 148 days between November 13, 2016 and April 7, 2017, and 165 days between November 4, 2017 and April 15, 2018. These intervals were adjusted in program MARK and calculated a single daily survival estimate that was constant across the entire winter period. Tag loss can result in negative bias in survival, capture probability and recapture probability estimates (Nichols and Hines 1993; Pine et al. 2012); as such, survival rate estimates were corrected for tag loss by including an additional state in the final model that applied a constant daily tag loss rate of 0.0000065 that was estimated using secondary marks on tagged bass (Pine et al. 2012). This state thereby removed that portion of fish from the population and adjusted estimates of survival, recapture, and transition probability for tag loss (Figure 4.1).

Fish could reside in one of four states in the multistate model (Figure 4.1). The four states were the electrofishing sample in Brushy Creek (B), recreational angling (R), fishing tournaments (T), and a delayed mortality state post tournament capture (D). Tagged and recaptured bass could be observed alive or dead in the Brushy Creek, alive or dead and in a tournament state, or alive or harvested in the recreational angling state. Transitions could occur from Brushy Creek to a tournament state \((\Psi)\) B to T, from Brushy Creek to a recreational
angling state ($P_{si} B$ to $R$), from a tournament state back to Brushy Creek ($P_{si} T$ to $B$), from a recreational angling state back to Brushy Creek ($P_{si} R$ to $B$), from a tournament state to a delayed mortality state ($T$ to $D$), or remain in Brushy Creek ($P_{si} B$ to $B$; Figure 4.1). Bass could not stay in a tournament or recreational angling state, move between tournament and recreational angling states without first returning to Brushy Creek, move out of the delayed mortality state, or move from recreational angling to the delayed mortality state; thus, transition probability between these states were fixed to zero (Figure 4.1). Recapture probabilities ($p$) were fixed to one for the tournament state, as all 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. Additional constants in the model included reporting rate and dead recovery rates ($\lambda$) of fish captured through recreational angling. We calculated a reporting rate of 0.32 across years using the formula:

$$\lambda = \frac{R_s N_r}{R_r N_s}$$

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 were necessary to achieve 100% reporting (Nichols et a. 1991; Pollock et al. 2001; Meyer et al. 2012). We used the same reporting rate for both live release and harvested bass, as adjustments for biases in reporting rates are needed as a result of the decision to remove the tag from a fish (Myer et al. 2012) or when all tags were removed regardless of harvest or capture (Smith et al. 2000), both of which were not required in this study.
Transition probabilities from the tournament to delayed mortality were fixed using daily estimates from a prior analysis assessing delayed mortality post tournament capture (Sylvia and Weber in revision). 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 in revision) to increase the accuracy of our population model. Estimates of delayed mortality from one, two, and three days post release were multiplied together to obtain a cumulative delayed mortality estimate. Delayed mortality was evaluated using a Cormack-Jolly-Seber mark-recapture model of jaw-tagged Brushy Creek bass, where estimates across the time period varied with the most supported covariates of the model including a three-day delayed mortality trend and mean water temperature. Additional details of the delayed mortality model can be found in Sylvia and Weber (in revision).

Capture histories were created for 5,143 bass ≥ 381 mm (Table 4.1), where an individual bass received a letter representing the state they were captured in during the sampling period in a live column (i.e., B, R, T; Figure 4.1) 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. 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 mean daily water temperature (°C) sampled continuously with temperature loggers (Onset Corporation HOBO Pendant Temperature/Light 64K Data Logger, 15 min sampling intervals) 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/angler calculated by dividing the
total number of captured 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 4.2).

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 bass recapture probability in Brushy Creek, transition (or capture) probability, and finally 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 bass recapture probability in Brushy Creek as the first step of the hierarchical model selection procedure. First, we fixed survival and transition probability to state effects (Brushy Creek, tournament, recreational angling, delayed mortality) to compare various model combinations and identify the most supported model for explaining variation in recapture probability. We tested a model with no variation in recapture probability \([p(.)]\), a linear effect of electrofishing effort \([p\ (\text{effort})]\) and water temperature \([p\ (\text{water T})]\), a quadratic effect of water temperature \([p\ (\text{water T} + \text{water T}^2)]\), and a linear effect of effort and a quadratic effect of temperature for each group \([p\ (\text{effort} + \text{water T} + \text{water T}^2)]\). Similar combinations of models for air temperature \([p\ (\text{effort} + \text{air T} + \text{air T}^2)]\) were also tested (Table 4.3).

Using the best explanatory model for recapture probability in Brushy Creek, we tested variation on angler capture probabilities for bass within Brushy Creek to recreational angling and tournament states. First, we tested a model assuming capture probabilities were the same \([\Psi i (B-T = B-R)]\) and different \([\Psi i (B-T \neq B-R)]\) for bass from Brushy Creek to both the recreational angling and tournament states. Once the best state capture probability was determined, we tested
linear and quadratic effects of water temperature and air temperature \(\Psi (\text{state} + \text{water } T)\), \(\Psi (\text{state} + \text{water } T + \text{water } T^2)\), \(\Psi (\text{state} + \text{air } T)\), and \(\Psi (\text{state} + \text{air } T + \text{air } T^2)\), a linear effect of tournament effort for the tournament states \(\Psi (\text{B-T} + \text{effort})\), and a linear effect of effort and a quadratic effect of temperature for Brushy Creek to the tournament state \(\Psi (\text{B-T} + \text{effort} + \text{water } T + \text{water } T^2)\), \(\Psi (\text{B-T} + \text{effort} + \text{air } T + \text{air } T^2)\). We also tested combinations of models that used tournament CPUE for tournament angling capture probabilities (\(\Psi (\text{state} + \text{CPUE})\); Table 4.4).

Bass survival in each state was assessed after both recapture and capture probability models were determined. For bass survival, first we tested models estimating survival in Brushy Creek, recreational angler, and tournament states separately \(S(\text{state})\), models where survival in the tournament state was equal to the recreational angler state \(S(\text{Brushy Creek, Tournament=Recreational angler})\), models where survival in all states were equal \(S(.)\), and models where either tournament \(S(\text{Brushy Creek = Tournament, Recreational angler})\) or recreational angler \(S(\text{Brushy Creek, Recreational angler, Tournament})\) survival was equal to survival in Brushy Creek. We then tested a linear effect of water temperature on the best combination of survival by states \(S(\text{state} + \text{water } T)\), and a quadratic effect of water temperature \(S(\text{state} + \text{water } T + \text{water } T^2)\) as well as a linear \(S(\text{state} + \text{air } T)\) and quadratic effect of air temperature \(S(\text{state} + \text{water } T + \text{water } T^2)\). For bass survival in the tournament state, we also included a linear effect of average bag/angler \(S(\text{state} + \text{bag/angler})\) as well as the number of initial mortalities occurring at each tournament event \(S(\text{state} + \text{initial mortality})\). Additive combinations of the covariates were also tested (Table 4.5).

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. Original maximum likelihood parameter estimates from
the top model were used as starting values, and the simulation ran 4,000 tuning iterations, 1,000
burn-in iterations, followed by 10,000 iterations used in the final estimates. Parameters and their
standard errors were estimated by the mean and standard deviations from the MCMC iterations.
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 bass ≥381 mm in Brushy
Creek were estimated for a 2015, 2016, and 2017 using Schnabel models calculated by

\[
\hat{N} = \frac{\sum_{i=1}^{t} n_i M_i}{\sum_{i=1}^{t} m_i + 1}
\]

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

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

(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 and lasting three 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
recreational angling effort and the period was short enough that tag loss did not influence estimates.

Once population size was determined, we first applied the daily capture probability to determine the number of bass that were captured at individual tournament events for each year. We then applied the initial survival rate to the number of bass captured at tournaments to estimate initial mortality. Of the remaining surviving tournament bass, we applied the transition probability from the tournament to the delayed mortality state to determine the number of bass lost to delayed tournament mortality. We summed the total number of 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 bass captured and lost to cumulative tournament mortality. We repeated the steps for recreational 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 bass captured through recreational angling and mortality due to recreational angling. Finally, we applied extrapolated daily survival estimates to the bass population in Brushy Creek to determine population level natural mortality.

Results

A total of 3,893 bass ≥381 mm was captured at 142 bass tournaments and an additional 1,250 bass were captured during 139 hours of electrofishing at Brushy Creek from April 2015-June 2018. A total of 1,955 bass were recaptured during the sampling period, with 1,412 (29.8%) recaptured once, 330 (7.0%) recaptured twice, 140 (3.0%) recaptured three times, and 73 (1.5%) recaptured four times. Of the total recaptures, 742 (38.0%) were recaptured by electrofishing, 848 (43.4%) were recaptured by tournament anglers, and 365 (18.7%) were recaptured and
reported by recreational anglers (Table 4.1). Forty-four (12.0%) of the total bass recaptured by recreational 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 31.98%, with 3.9% of the released non-reward tags reported by recreational anglers, while 12.2% of released reward tags were reported by recreational anglers.

Of the ten models evaluated to describe variation in bass recapture probability in Brushy Creek, the most supported model included a linear effect of sampling effort and a quadratic effect of water temperature ($\Delta AIC_c = 0.00, w_i = 0.63$; Table 4.3). There was some support for models that included a linear effect of water temperature ($\Delta AIC_c = 1.41, w_i = 0.33$); 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 bass in Brushy Creek (Table 4.3). Recapture probability beta estimates of the final model resulted in 95% confidence intervals not including zero for all three of the estimated parameters (intercept, waterT, waterT$^2$, electrofishing effort; Table 4.6). Recapture probability decreased with increased water temperatures (Figure 4.2A) and increased with electrofishing effort (Figure 4.2B). Recapture probabilities of bass within Brushy Creek ranged from 0.00144 (95% CI: 0.00119, 0.00170) during an electrofishing event lasting 1,833 seconds and at an air temperature of 16.17 °C to 0.01690 (95% CI: 0.01250, 0.02179) during an electrofishing event lasting 18,354 seconds at 19.7 °C.

Of the models describing capture probability to the tournament and recreational angling states, those that estimated capture probabilities from Brushy Creek to tournament and Brushy to recreational angling states separately ($\Delta AIC_c = 0.00, w_i = 1.0$) outperformed models that set capture probabilities equal to each other ($\Delta AIC_c = 1,396.93, w_i > 0.001$) prior to inclusion of
additional covariates, suggesting rates of capture from Brushy Creek to tournament and recreational angling states are different. The most supported model included a quadratic effect of air temperature on both tournament and recreational angling capture probabilities as well as tournament catch-per-unit effort on the tournament state (\(\Delta AIC_c = 0.00, w_i = 1.0\); Table 4.4). All five beta estimates describing capture probability included zero in the final model (Table 4.6). Capture probabilities into tournaments ranged from 0.00245 (95% CI: 0.00183, 0.00282) to 0.01132 (95% CI: 0.00922, 0.01345) and was eleven fold higher than recreational angling state capture probability [0.00024 (95% CI: 0.00009, 0.00039) to 0.00099 (95% CI: 0.00081, 0.00120)].

Capture probabilities of both tournament and recreational angling increased with increasing air temperatures whereas tournament capture probability also increased with increasing tournament CPUE (Figure 4.3). The additional transition of tournament to delayed mortality (Sylvia and Weber in revision) was positively related to water temperature and number of prior tournament captures. 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 indicated the strongest support for survival estimated separately for each state (\(\Delta AIC_c = 0.00, w_i = 0.96\)), followed by models that set tournaments and recreational angling equal (\(\Delta AIC_c = 6.51, w_i = 0.03\)), models that set Brushy and recreational angling states equal (\(\Delta AIC_c = 107.18, w_i < 0.001\)), models that set Brushy and tournament states equal (\(\Delta AIC_c = 130.25, w_i < 0.001\)), and finally models that set all state survivals equal (\(\Delta AIC_c = 141.36, w_i < 0.001\)). Setting all state survivals separate, the top model included a quadratic effect of air temperature on recreational
and tournament states, a quadratic effect of water temperature on the Brushy Creek state, and an
effect of average bag/angler and initial mortality on the tournament survival estimates ($\Delta AIC_c = 0.00, w_i = 0.98$; Table 4.5). The most supported model included separate intercepts; thus, state
effects and covariates were estimated individually. Mean daily survival probability of bass was
highest in Brushy Creek, followed by tournament captured bass and finally recreationally angled
bass. Average percent differences in survival of bass in Brushy Creek was 1.6% higher than that
of tournament captured bass and 14% higher than recreationally captured bass whereas average
tournament bass survival was 12.5% higher than that of recreationally angled bass.

Eight of the eleven beta estimates on survival in the final model did not include zero
(Brushy Creek water$T^2$, Tournament intercept, Tournament air$T$, Tournament bag/angler,
Tournament initial mort, Recreational intercept, Recreational air$T$, Recreational air$T^2$; Table
4.6). Survival of bass in Brushy Creek showed a quadratic pattern with temperature, resulting in
highest survival [0.99787 (95% CI: 0.99721, 0.99847)] at 10.4 °C and lowest survival [0.99573
(95% CI: 0.99340, 0.99802] at water temperatures of 22.9 °C (Figure 4.4). Similar relationships
between air temperature and survival of recreationally angled bass were observed, with rates
ranging from 0.98107 (95% CI: 0.95808, 0.99706) at -3.89 °C to 0.67003, (95% CI: 0.49611,
0.83670) at 29.0 °C (Figure 4.6A). For tournament bass, survival followed a quadratic pattern
with water temperature (Figure 4.5A) and was also inversely related to bag/angler and initial
mortality (Figure 4.6B; Figure 4.6C). Survival was lowest on days with increased air
temperature, increased initial mortality, and increased bag/angler. Survival rates of tournament
bass were highest [0.98792 (95% CI: 0.98053, 0.99461)] when air temperature was 14.4 °C,
bag/angler was 3.0, and initial mortality was zero whereas lowest survival rates [0.77914 (95%
CI: 69423, 0.88542) occurred with air temperatures of 22.2 °C, a bag/angler of 1.9, and 27 initial mortalities.

The annual population estimate of bass ≥381 mm in Brushy Creek during 2015 was 6,122 (95% CI: 5,578, 6,436; mean = 22 bass/ha, 95% CI: 20-23), the 2016 population estimate was 6,183 (95% CI: 5,536, 6,830; mean = 22 bass/ha, 95% CI: 20-25), and the 2017 estimate was 6,236 (95% CI: 5,468, 7,003; mean = 22 bass/ha, 95% CI: 20-25). Tournament anglers captured four times as many bass throughout the year than recreational anglers. On average, 1,274 bass (SE = 66 bass) were captured at tournament across the three sample years (20.6%), whereas only 752 bass (SE = 50 bass) were estimated as captured by recreational anglers (12%; Figure 4.7). Tournament mortality was also greater than that of recreational angling mortality. An average of 23 (SE = 1 bass; 0.4%) bass were lost to initial tournament mortality annually whereas 353 (SE = 39 bass) were estimated to be lost to delayed tournament mortality (5.5%; Figure 4.8). Cumulatively, an average of 378 bass (SE = 38 bass) were lost to tournament mortality, representing 5.8% of the population. Alternatively, 153 bass (SE = 17 bass) were harvested or experienced delayed recreational angling mortality, representing only 2.8% of the total bass population. Conversely, natural mortality accounted for greatest loss of bass, with an average of 57% of the bass population annually (Figure 4.8).

**Discussion**

Understanding the scale and influence of harvest and catch and release angler practices are important to population management in Largemouth Bass. Recreational and tournaments angler capture probabilities were high, with anglers capturing a combined 33% of the population annually. Average annual tournament angler effort at Brushy Creek was 32.3 hr/ha across the tournament season. While tournament pressure is variable across systems (0.2 hr/ha, 0.1 ha/hr in
North central Florida, Schramm et al. 1987; 3.3 in Texas, Driscoll et al. 2007; 27.8 hr/ha in Connecticut, Edwards et al. 2004; and 59.5 hrs/ha 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 recreational (2.8%) and initial tournament mortality (0.4%). While delayed tournament mortality made up the largest proportion of fishing mortality (5.5%), it was still ten times less than that of natural mortality (57%). Thus, cumulative angling mortality likely has little effect on bass in Brushy Creek and many other bass populations.

Understanding capture rates are important when evaluating fisheries, as relatively small proportions of the total population captured annually, even paired with high mortality rates, can result in trivial population level effects (Chapman and Fish 1985; Schramm et al. 1987; Edwards et al. 2004). Daily capture rates of recreationally angled bass were relatively low, but varied within and among years as a result of environmental effects that may have affected bass feeding habits and behavior. Increasing air temperature was an important factor resulting in increases in recreational 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 bass metabolism and foraging (Fry 1971; Brett and Glass 1973); however, water temperature can remain relatively buffered to large 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 bass (Stoner 2004) that may have had more of an effect on bass activity levels and feeding rates, and hence, angler capture probabilities (Johnson et al. 1960; Coutant 1975; Sylvia and Weber in progress).
Low daily recreational capture rates corresponded to a relatively low proportion of the total population (10.6-13.0%) captured by recreational 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 bass (Philipp et al. 2009; Sylvia et al. in prep), or influences of tournament angling (Hackney and Linkous 1978). For example, recreational anglers using smaller lure sizes may have selected for and captured smaller bass (<381 mm) that were not included in this assessment. Bass can also experience multiple capture events by recreational anglers (Myers 2008; Brownscombe et al. 2017), resulting in a small, highly vulnerable segment of the population comprising a large portion of recreational angling events (Colgan 1986; Philipp et al. 2009). Recreational anglers throughout the study captured approximately 10% of bass multiple times, indicating that while a small proportion of the bass in Brushy Creek lake are captured multiple times, many of the fish have never been captured by tournament anglers previously, or are newly recruited to the fishery. Finally, increased angling pressure can lead to decreases in catch rates because of bass recovery time between captures (Mankin et al. 1984; Burkett et al. 1986), as well as learned behaviors of bass including lure avoidance (Clark 1983) and loss of naivety (Hessenauer et al. 2016). High tournament activity on Brushy Creek may have resulted in less success by recreational anglers, whereas angler skill (Beardmore et al. 2011; Sylvia et al. in prep) may play an important role in increased capture rates at tournament angling events.

While high overall, 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 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, bass tournament capture probabilities also increased with air temperatures. The effect of air temperature on 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.

Combined, recreational harvest and catch and release mortality accounted for only 2.8% of total annual mortality. Harvest was approximately 10% of the total reported recreational angler recaptures, indicating high rates of voluntary catch and release practiced by anglers in Brushy Creek, similar to other systems (Henry 2003; Isermann et al. 2013). Catch and release mortality of recreationally angled bass is generally low (5-10%; Muoneke and Childress 1994; Hayes et al. 1995). Numerous factors are known to increase mortality of recreationally captured bass (e.g., hooking injury, increased fight time and air exposure, depressurization; Cooke et al. 2003; Suski et al. 2004; Siepker et al. 2007). We found that increases in air temperature led to decreases in survival of released bass, 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 recreational mortality was low, air temperature is important in describing variation in mortality of bass through time.

In contrast to recreational angling capture, the high proportion of the bass population (upwards of 22%) captured at tournament events during any given year increased the number of
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 that delayed mortality had a larger effect than initial mortality. Daily initial mortality estimates were <1% in Brushy Creek 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 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 Newmann 1997) can all contribute to increased initial tournament mortality. However, lower bass bag limits in Iowa (three bass/angler), as opposed to five bass/angler regulations in many other states (American Bass 2001; Mississippi Wildlife, Fisheries and Parks 2018) may account for the lower number of fish dying before or during the weigh-in process. Instead, combined stressors throughout the tournament capture, restraining, weigh-in, and release process may have led to increased delayed mortality in bass.

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 bass size (Sylvia and Weber in revision). Water temperature may explain up to 30% of the 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 recreational angling recapture, only 11% of 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. Although tournament mortality can be size-specific (Meals and Miranda 1994), the effects of bass length, weight, and condition were not supported. While larger 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 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 was within the range of other estimates populations, but were higher on average. This is unusual for a high latitude system, as natural mortality in bass is negatively correlated with latitude and positively correlated with mean air temperature (Beamesderfer and North 1995). However, similar independent estimates of bass natural mortality have been reported near this latitude (Pitlo and Bonneau 1992, Sylvia et al. in progress), indicating that natural mortality of 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). However, daily natural mortality rates were 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 recreational fishing mortality combined and likely has the most influential effect
on the population. High natural mortality rates have the potential to offset high fishing pressure,
as the population likely grows and dies quickly. Population abundance across the study period
remained constant, indicating potentially high recruitment into the ≥ 381 mm bass population,
and offsetting the effects of natural mortality, resulting in little population level impacts of
fishing mortality (Churchill et al. 1995; Driscoll et al. 2007). Further assessment to understand
the relationship between recruitment, population growth and the high natural mortality rate in
this population may be useful in understanding of the impacts of angling mortality on other 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, 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 bass (Hysmith et al. 2014). However,
even with three and a half years of tournament census data and fishery independent sampling,
multistate models require large amounts of data and 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. Further, 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 recreational capture probability. Supplemental creel data would have been useful in our estimation of recreational angling capture probability, but would have required substantial additional sampling effort. While we are confident that we met the assumptions associated with multistate mark-recapture models, there is potential for bias. Segments of fish populations may exhibit higher or lower likelihood of capture through angling events (Colgan 1986; Philipp et al. 2009), leading to bass having unequal detection and probability of transition. If this is occurring in Brushy Creek, our estimates of population level capture probability and mortality may be over or under estimated. Inclusion of monthly fishery independent sampling is useful in preventing assumption violations; however, future work should consider potential differences in bass vulnerability to angling.

With release rates approaching 100% in some systems (Henry 2003), understanding additional sources of mortality, including that from catch and release and tournaments, is imperative. Our results indicate that while initial and delayed tournament mortality can be substantially higher compared to recreational catch and release angling and harvest mortality, both sources of fishing mortality are low compared to natural mortality, potentially providing some protection from long-term population level effects. With high natural mortality in systems, additional regulations implemented to reduce fishing pressure are likely unnecessary. Increased management of bass paired with high catch and release rates has resulted in negative effects on growth and size-structure of bass in some populations (see Hansen et al. 2015 and Miranda et al. 2017). Thus, some level of mortality due to recreational and tournament angling may actually be
beneficial in releasing bass from density dependent growth response and potentially increasing size-structure in bass populations.

Acknowledgements

We thank the technicians and Brushy Creek recreational and tournament anglers that assisted with data collection. Funding for this project was provided by an Iowa State University Presidential Wildlife grant, the Department of Natural Resource Ecology and Management, and the Iowa Department of Natural Resources contract number 18CRDFBGSCHO-0004.

References


Coutant, C. C. 1975. Responses of bass to natural and artificial temperature regimes (No. CONF-750205-1). Oak Ridge National Lab., Tennessee, USA.


Table 4.1 Number of Largemouth Bass tagged and recaptured by electrofishing and tournaments at Brushy Creek, IA, USA from 2015-2018.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number tagged</th>
<th>Tournament</th>
<th>Electrofishing</th>
<th>Total bass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2015</td>
<td>2016</td>
<td>2017</td>
<td>2018</td>
</tr>
<tr>
<td>Tournament</td>
<td>1,183</td>
<td>260</td>
<td>138</td>
<td>42</td>
</tr>
<tr>
<td>2015</td>
<td>1,250</td>
<td>-</td>
<td>128</td>
<td>86</td>
</tr>
<tr>
<td>2016</td>
<td>1,460</td>
<td>-</td>
<td>-</td>
<td>243</td>
</tr>
<tr>
<td>2017</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td>2018</td>
<td>3,893</td>
<td>260</td>
<td>266</td>
<td>371</td>
</tr>
<tr>
<td>Electrofishing</td>
<td>353</td>
<td>123</td>
<td>91</td>
<td>18</td>
</tr>
<tr>
<td>2015</td>
<td>364</td>
<td>-</td>
<td>84</td>
<td>44</td>
</tr>
<tr>
<td>2016</td>
<td>269</td>
<td>-</td>
<td>-</td>
<td>55</td>
</tr>
<tr>
<td>2017</td>
<td>264</td>
<td>-</td>
<td>-</td>
<td>31</td>
</tr>
<tr>
<td>2018</td>
<td>1,250</td>
<td>123</td>
<td>175</td>
<td>117</td>
</tr>
<tr>
<td>Total bass</td>
<td>5,143</td>
<td>383</td>
<td>441</td>
<td>488</td>
</tr>
</tbody>
</table>
Table 4.2 Mean, standard error (SE), and range of covariates used in multistate models to estimate survival ($S$), capture probability ($Psi$), and recapture probability ($p$) of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018.

<table>
<thead>
<tr>
<th></th>
<th>2015</th>
<th>2016</th>
<th>2017</th>
<th>2018</th>
<th>Min, Max</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Mean daily water temperature ($°C$)</td>
<td>16.1</td>
<td>0.3</td>
<td>6.3, 21.3</td>
<td>17.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Mean daily air temperature ($°C$)</td>
<td>17.7</td>
<td>0.5</td>
<td>4.0, 28.0</td>
<td>17.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Tournament angling effort (h)</td>
<td>223.3</td>
<td>4.1</td>
<td>20.0, 738.0</td>
<td>168.8</td>
<td>2.3</td>
</tr>
<tr>
<td>Tournament CPUE</td>
<td>0.2</td>
<td>0.0</td>
<td>0.1, 0.5</td>
<td>0.2</td>
<td>0.0</td>
</tr>
<tr>
<td>Electrofishing effort (s)</td>
<td>5,271.8</td>
<td>93.1</td>
<td>1,305.0, 11,527.0</td>
<td>6,318.7</td>
<td>150.2</td>
</tr>
<tr>
<td>Average tournament bass/angler</td>
<td>1.4</td>
<td>0.0</td>
<td>0.4, 3.0</td>
<td>1.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Initial tournament mortality</td>
<td>1.1</td>
<td>0.4</td>
<td>0.0, 27.0</td>
<td>0.1</td>
<td>0.1</td>
</tr>
</tbody>
</table>
Table 4.3 Live-dead multistate models used to estimate recapture probability ($p$) of jaw tagged Largemouth Bass in Brushy Creek, IA, USA for 377 periods beginning 13 April, 2015 through 1 June 2018. Effects evaluated influencing $p$ include a constant model (.), electrofishing sampling effort ($s$), linear and quadratic water temperature ($°C$; $\text{waterT}$; $\text{waterT}^2$), and linear and quadratic air temperature ($°C$; $\text{airT}$, $\text{airT}^2$). Parameters in the table include $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion, $\Delta \text{AIC}_c =$ 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).

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta \text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$ (waterT + waterT$^2$ + effort)</td>
<td>192,871.91</td>
<td>0.00</td>
<td>0.67</td>
<td>9</td>
<td>192,853.88</td>
</tr>
<tr>
<td>$p$ (waterT + effort)</td>
<td>192,873.32</td>
<td>1.41</td>
<td>0.33</td>
<td>8</td>
<td>192,857.30</td>
</tr>
<tr>
<td>$p$ (airT + effort)</td>
<td>192,896.98</td>
<td>25.07</td>
<td>0.00</td>
<td>8</td>
<td>192,880.96</td>
</tr>
<tr>
<td>$p$ (airT + airT$^2$ + effort)</td>
<td>192,898.05</td>
<td>26.14</td>
<td>0.00</td>
<td>9</td>
<td>192,880.02</td>
</tr>
<tr>
<td>$p$ (effort)</td>
<td>192,958.04</td>
<td>86.13</td>
<td>0.00</td>
<td>7</td>
<td>192,944.02</td>
</tr>
<tr>
<td>$p$ (waterT)</td>
<td>193,087.05</td>
<td>215.14</td>
<td>0.00</td>
<td>7</td>
<td>193,073.03</td>
</tr>
<tr>
<td>$p$ (waterT + waterT$^2$)</td>
<td>193,088.60</td>
<td>216.69</td>
<td>0.00</td>
<td>8</td>
<td>193,072.58</td>
</tr>
<tr>
<td>$p$ (airT)</td>
<td>193,110.48</td>
<td>238.57</td>
<td>0.00</td>
<td>7</td>
<td>193,096.46</td>
</tr>
<tr>
<td>$p$ (airT + airT$^2$)</td>
<td>193,110.56</td>
<td>238.65</td>
<td>0.00</td>
<td>8</td>
<td>193,094.54</td>
</tr>
<tr>
<td>$p$ (.)</td>
<td>193,191.21</td>
<td>319.30</td>
<td>0.00</td>
<td>7</td>
<td>193,177.19</td>
</tr>
</tbody>
</table>
Table 4.4 Live-dead multistate models used to estimate capture probability ($Psi$) from recreational angling and tournament angling (state) of jaw tagged Largemouth Bass Brushy Creek, IA, USA for 377 periods beginning 13 April, 2015 through 1 June 2018. Effects evaluated influencing $Psi$ include tournament angler effort (h), tournament catch-per-unit-effort (#/h; CPUE), linear and quadratic water temperature ($^\circ$C; waterT; waterT$^2$), and linear and quadratic air temperature ($^\circ$C; airT, airT$^2$). Parameters in the table include

$AIC_c =$ sample-sized corrected Akaike’s Information Criterion, $\Delta AIC_c =$ relative difference between the particular model and the best model, $w_i =$ Akaike weight, $K =$ number of parameters, Deviance = -2 x log-likelihood of the model less -2 x log-likelihood of the saturated models (same number of parameters and degrees of freedom).

<table>
<thead>
<tr>
<th>Model</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Psi$ (state + airT + airT$^2$ + Tournament CPUE)</td>
<td>192,669.66</td>
<td>0.00</td>
<td>1.00</td>
<td>11</td>
<td>192,647.62</td>
</tr>
<tr>
<td>$Psi$ (state + airT + Tournament CPUE)</td>
<td>192,779.70</td>
<td>110.04</td>
<td>0.00</td>
<td>11</td>
<td>192,755.65</td>
</tr>
<tr>
<td>$Psi$ (state + waterT + waterT$^2$ + Tournament CPUE + Tournament effort)</td>
<td>192,784.36</td>
<td>114.70</td>
<td>0.00</td>
<td>12</td>
<td>192,760.31</td>
</tr>
<tr>
<td>$Psi$ (state + waterT + Tournament CPUE)</td>
<td>192,812.30</td>
<td>119.94</td>
<td>0.00</td>
<td>11</td>
<td>192,767.56</td>
</tr>
<tr>
<td>$Psi$ (state + Tournament CPUE)</td>
<td>192,832.28</td>
<td>142.64</td>
<td>0.00</td>
<td>10</td>
<td>192,792.27</td>
</tr>
<tr>
<td>$Psi$ (state + airT)</td>
<td>192,832.28</td>
<td>162.62</td>
<td>0.00</td>
<td>10</td>
<td>192,812.25</td>
</tr>
<tr>
<td>$Psi$ (state + waterT + Tournament CPUE)</td>
<td>192,845.72</td>
<td>176.06</td>
<td>0.00</td>
<td>12</td>
<td>192,821.67</td>
</tr>
<tr>
<td>$Psi$ (state + waterT$^2$ + Tournament CPUE)</td>
<td>192,840.29</td>
<td>190.63</td>
<td>0.00</td>
<td>10</td>
<td>192,840.26</td>
</tr>
<tr>
<td>$Psi$ (state + waterT)</td>
<td>192,875.33</td>
<td>205.67</td>
<td>0.00</td>
<td>9</td>
<td>192,857.30</td>
</tr>
<tr>
<td>$Psi$ (state)</td>
<td>194,067.92</td>
<td>1,398.26</td>
<td>0.00</td>
<td>8</td>
<td>194,051.90</td>
</tr>
</tbody>
</table>
Table 4.5 Live-dead multistate models used to estimate survival ($S$) of jaw tagged Largemouth Bass in Brushy Creek, IA, USA for 377 periods beginning 13 April, 2015 through 1 June 2018. Survival was evaluated in Brushy Creek (B), tournament angler (T), and recreational angler (R) 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 $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion, $\Delta \text{AIC}_c =$ relative difference between the particular model and the best model, $w_i =$ Akaike weight, $K =$ number of parameters, Deviance = -2 x log-likelihood of the model less -2 x log-likelihood of the saturated models (same number of parameters and degrees of freedom).

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta \text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$ (state + airT + airT$^2$ (R,T) + bag/angler (T) + initial mortality (T) + waterT + waterT$^2$ (B), different intercepts)</td>
<td>192,639.23</td>
<td>0.00</td>
<td>0.98</td>
<td>21</td>
<td>192,597.09</td>
</tr>
<tr>
<td>$S$ (state + airT + airT$^2$ (R,T) + bag/angler (T) + initial mortality (T) + waterT + waterT$^2$ (B), same intercept)</td>
<td>192,647.20</td>
<td>7.96</td>
<td>0.02</td>
<td>19</td>
<td>192,609.08</td>
</tr>
<tr>
<td>$S$ (state + airT + airT$^2$ (R,T) + bag/angler (T) + initial mortality (T) + waterT (B))</td>
<td>192,668.33</td>
<td>29.09</td>
<td>0.00</td>
<td>18</td>
<td>192,632.22</td>
</tr>
<tr>
<td>$S$ (state + waterT + bag/angler (T) + initial mortality (T))</td>
<td>192,677.99</td>
<td>38.75</td>
<td>0.00</td>
<td>17</td>
<td>192,643.89</td>
</tr>
<tr>
<td>$S$ (state + waterT + waterT$^2$ + initial mortality (T))</td>
<td>192,682.91</td>
<td>43.67</td>
<td>0.00</td>
<td>16</td>
<td>192,650.82</td>
</tr>
<tr>
<td>$S$ (state + waterT + initial mortality (T))</td>
<td>192,692.25</td>
<td>53.01</td>
<td>0.00</td>
<td>16</td>
<td>192,660.16</td>
</tr>
<tr>
<td>$S$ (state + airT (R,T) + bag/angler (T) + initial mortality (T))</td>
<td>192,695.91</td>
<td>56.67</td>
<td>0.00</td>
<td>15</td>
<td>192,665.83</td>
</tr>
<tr>
<td>$S$ (state + airT (R,T) + initial mortality (T))</td>
<td>192,702.07</td>
<td>62.83</td>
<td>0.00</td>
<td>16</td>
<td>192,669.98</td>
</tr>
<tr>
<td>$S$ (state + airT + airT$^2$ (R,T) + bag/angler (T))</td>
<td>192,702.72</td>
<td>63.49</td>
<td>0.00</td>
<td>15</td>
<td>192,672.65</td>
</tr>
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</table>
Table 4.5 Continued

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>S (state + initial mortality (T))</td>
<td>192,722.50</td>
<td>83.26</td>
<td>0.00</td>
<td>16</td>
<td>192,690.41</td>
</tr>
<tr>
<td>S (state + waterT)</td>
<td>192,732.59</td>
<td>93.35</td>
<td>0.00</td>
<td>14</td>
<td>192,704.52</td>
</tr>
<tr>
<td>S (state + waterT + bag/angler (T))</td>
<td>192,744.91</td>
<td>105.67</td>
<td>0.00</td>
<td>14</td>
<td>192,716.84</td>
</tr>
<tr>
<td>S (state + airT (T,R))</td>
<td>192,746.39</td>
<td>107.15</td>
<td>0.00</td>
<td>15</td>
<td>192,716.31</td>
</tr>
<tr>
<td>S (state + airT (T,R) + bag/angler (T))</td>
<td>192,748.36</td>
<td>109.12</td>
<td>0.00</td>
<td>14</td>
<td>192,720.29</td>
</tr>
<tr>
<td>S (state)</td>
<td>192,749.16</td>
<td>109.93</td>
<td>0.00</td>
<td>15</td>
<td>192,719.09</td>
</tr>
<tr>
<td>S (state + bag/angler (T))</td>
<td>192,780.58</td>
<td>141.34</td>
<td>0.00</td>
<td>13</td>
<td>192,754.52</td>
</tr>
<tr>
<td>S (R = T, B)</td>
<td>192,782.44</td>
<td>143.20</td>
<td>0.00</td>
<td>14</td>
<td>192,754.37</td>
</tr>
<tr>
<td>S (B = R, T)</td>
<td>192,790.18</td>
<td>150.94</td>
<td>0.00</td>
<td>13</td>
<td>192,764.12</td>
</tr>
<tr>
<td>S (B = T, R)</td>
<td>192,890.57</td>
<td>251.33</td>
<td>0.00</td>
<td>13</td>
<td>192,864.51</td>
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<tr>
<td>S (.)</td>
<td>192,999.95</td>
<td>360.71</td>
<td>0.00</td>
<td>13</td>
<td>192,973.89</td>
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Table 4.6 Final live-dead multistate model parameter estimates: $[S (Brushy\ Creek + waterT + waterT^2,\ Tournament + airT + airT^2 + bag/angler + initial\ mortality,\ Recreational + airT + airT^2)\ Psi\ Brushy\ (Intercept + B\ to\ T + airT + airT^2 + tournament\ CPUE),\ p (Intercept + waterT + waterT^2 + electrofishing\ effort)]$ of jaw tagged Largemouth Bass in Brushy Creek, IA, USA for 378 periods beginning 13 April, 2015 through 1 June 2018. Estimate = Mean Beta estimate of parameter from MCMC iterations. SE = Standard error of beta estimate from MCMC iterations. 95% LCI = 95% lower credible interval of beta estimate of parameter from MCMC iterations. 95% UCI = 95% upper credible interval of beta estimate of parameter from MCMC iterations. Best model determined by sample-sized corrected Akaike’s Information Criterion ($\text{AIC}_c$).

<table>
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<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>95% LCI</th>
<th>95% UCI</th>
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<td>Survival</td>
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Figure 4.1 Conceptual diagram of multistate model design that includes Brushy Creek, tournament and recreational angling, delayed mortality, and tag loss of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018. Arrows represent transition probabilities ($\Psi$) 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. $\Psi_{B-B} = 1 - (\Psi_{B-T} + \Psi_{B-R})$. 
Figure 4.2 Estimated recapture probability of jaw tagged Largemouth Bass in Brushy Creek, IA, 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.
Figure 4.3 Estimated tournament (dashed line) and recreationally (dotted line) angled capture probabilities of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C; B) and tournament CPUE (B). Solid lines around estimates represent the 95% credible intervals of the Markov Chain Monte Carlo estimates.
Figure 4.4 Estimated survival rates of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily water temperature (°C). Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 4.5 Estimated survival rates of jaw tagged tournament captured Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C; A), average bag/angler (B), and number of initial tournament mortalities (C). Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 4.6 Estimated survival rates of jaw tagged, recreationally captured Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature (°C). Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 4.7 Cumulative percentage of Largemouth Bass population captured at tournaments (dashed line) and by recreational angling (dotted line) during 2015 (A), 2016 (B), and 2017 (C) in Brushy Creek, IA, USA. Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 4.8 Cumulative percentage of Largemouth Bass population mortality in Brushy Creek, IA, USA from natural mortality (dashed line), delayed tournament mortality (dashed and dotted line), initial tournament mortality (solid line), and recreational angling (dotted line) during 2015 (A), 2016 (B), and 2017 (C).
CHAPTER 5. ASSESSING SIZE-DEPENDENT POPULATION-LEVEL EFFECTS OF LARGEMOUTH BASS TOURNAMENT MORTALITY

Modified from a manuscript to be submitted to Fisheries Management and Ecology

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Abstract

As black bass tournaments continue to grow in popularity, so too must evaluations on the population-level effects of live-release angling events. However, while factors influencing tournament mortality are well studied, assessments at the population-level are lacking. We evaluated differences in tournament capture probability and survival of two size classes of Largemouth Bass [Micropterus salmoides; medium (381-457 mm) and large (>457 mm)] using a multistate mark-recapture model. Changes in estimated capture and survival rates of medium and large bass were then simulated to assess potential effects on population size-structure. Medium bass had higher tournament capture probabilities than large bass and tournament capture probabilities of both size classes increased with air temperature. Medium tournament bass also experienced higher survival rates than large tournament bass and survival rates of both groups were inversely correlated with water temperature. Our simulations indicated that increases in tournament capture probability and reductions in survival of large bass resulted in minor reductions in population size-structure whereas changes in tournament capture probability and survival of medium or medium and large bass had little effect. Our results are important to
understanding potential disproportional differences in capture and survival of tournament bass and are useful to managing fishery effects of tournament angling.

**Introduction**

One of the most popular segments of black bass (*Micropterus* sp.) fisheries is competitive catch and release fishing events (Schramm et al. 1991). Of an estimated 29,500 competitive fishing events held annually in inland waters in North America, about 78% were directed toward black bass in 1991 (Schramm et al. 1991). More recent studies reported upwards of 40,000 bass tournaments were held in the United States from 2009 to 2011 and membership of Bass Angler Sportsman Society (B.A.S.S.) grew to more than 500,000 members in 2013 (Bassmaster 2013; Driscoll et al. 2013). Competitive angling events can involve hundreds of anglers participating in multiple fishing events on a single system per open water season, making potential tournament associated mortality of bass high, even with live release regulations in place. Consequently, a long-term focus has been to identify factors affecting survival of tournament-captured bass (e.g., Kwak and Henry 1995; Wilde 1998; Suski et al. 2006).

Black bass tournament mortality studies usually involve assessing initial and delayed mortality rates. Numerous studies have shown that factors such as increased water temperature, air temperature and exposure, inexperienced anglers (Cooke et al. 2003a, 2003b; Cooke et al. 2004), increased livewell confinement and density, and relaxed tournament regulations (Weathers and Newman 1997) can be related to tournament mortality rates of individuals. However, an understanding of how tournament mortality can ultimately affect bass populations remains elusive, as mortality rates have almost exclusively been estimated on the individual-level (but see Driscoll et al. 2007; Kerns et al. 2016; Sylvia et al in prep). Yet, tournaments to affect bass populations, they need to capture a large portion of the population and have an
adverse effect on survival rate of captured fish. Due to a relatively small proportion of the total population captured annually at tournaments, tournament mortality may not affect bass populations, even when tournament mortality is high (Chapman and Fish 1985; Schramm et al. 1987; Lee et al. 1993; Edwards et al. 2004; Sylvia et al. in prep). However, even if only a small portion of the population is captured, certain segments of the population may be captured at higher rates that could still result in population-level effects (Hayes et al. 1995; Allen et al. 2004). For example, larger bass (> 457 mm), those approaching memorable size (Gabelhouse 1984), make up less of the population and consequently, may be captured less frequently. Conversely, a common goal of tournament angling events is to capture the largest fish in the population (Wilde et al. 1998) that are typically only present in populations at low abundance compared to smaller individuals (Gabelhouse 1984). Thus, tournament practices targeting large bass may alter the size-structure of the fishery (Meals and Miranda 1994), even if only a small portion of the total population is captured. However, little information is available regarding tournament capture probability and survival rates of different sizes of bass (Schramm et al. 1985; Meals and Miranda 1994; Burleson et al. 2001).

Statistical models are useful tools for understanding and explaining fish population dynamics (Haddon 2010). For example, methods such as multistate mark-recapture models are effective in answering such questions due to the ability to test for differences in tournament capture probability and survival rates of different size bass at tournament events (Lebreton et al. 2009). Such studies can account for temporal changes in survival and capture rates and allow for the inclusion of covariates, such as environmental variables and tournament angler patterns (White and Burnham 1999). Therefore, empirical mark-recapture analyses could be useful in
understanding changes in population structure in response to tournament fishing but have rarely been used to address these important questions.

Our objectives were to estimate tournament capture probability and survival of medium (381-457 mm) and large (>457 mm) Largemouth Bass (*Micropterus salmoides*; hereafter referred to as bass) at fishing tournaments at Brushy Creek Lake, Iowa, USA. We also tested a number of covariates (mean water temperature, mean air temperature, average number of bass/angler, initial tournament mortality, and angler effort) to evaluate potential effects on tournament capture probability and survival. Next, we estimated abundance of medium and large bass in the lake and applied our model results to assess population level mortality for each size class. Finally, we simulated changes in survival and tournament capture probabilities of each size to understand changes in abundance of each size group and size-structure changes within the system. We conclude that the use of mark-recapture methods to understand potential non-proportional differences in survival and capture of tournament bass is useful to better understand and manage fishery effects of tournament angling.

**Methods**

**Sampling**

Brushy Creek Lake (hereafter Brushy Creek) is a 279 ha reservoir in Webster County, Iowa, USA. The lake has a mean depth of 8.9 m, a maximum depth of 22.9 m, and is densely covered in both emerged and submerged coarse woody habitat throughout the lake. Brushy Creek is used extensively by anglers, hosting more than 40 bass tournaments annually (mean 32.3, SE = 18.0 tournament angler hours/ha/year from 2015-2017). Electrofishing (pulsed DC 300 V and 8 amps) occurred once monthly on Brushy Creek during the open water season (April - November) during 2015, 2016, and 2017 and from April-June 2018. Electrofishing lasted
approximately five consecutive d each month or until the entire accessible shoreline had been sampled. All Largemouth Bass captured were weighed (g) and measured (mm). Bass ≥381 mm (15” minimum length limit at Brushy Creek) were tagged on the top left jaw with a metal Monel butt end band that have high retention on black bass (0% loss after one year in Smallmouth Bass *Micropterus dolomieui*; MacCrimmon and Robbins 1979).

All bass tournaments at Brushy Creek were attended and censused from April 2015 through June 2018 (n = 142 tournaments; mean anglers per tournament = 25.7, SE = 1.8, mean 25 tournament angler hours/ha/year). Number of anglers, number of boats, number of bass weighed-in, and number of initial mortalities were recorded for each tournament event. Following weigh-in, all bass were placed in an insulated live-well with supplemental oxygen. All fish were weighed (g), measured (mm), and evaluated for jaw tags: all untagged bass were tagged on the left upper jaw with a metal Monel band and released. Finally, project e-mail and telephone contact information was placed on signs throughout the lake and capture date and bass tag number, length, and weight were reported by non-tournament anglers.

**Model**

We analyzed individual encounter histories during 2015-2018 in program MARK (White and Burnham 1999) using a live capture multistate model for maximum likelihood estimates of daily survival (\(S\)), detection probability (\(p\)), and tournament capture probability (\(Psi\), White et al. 2006). Multistate models are an extension of the Cormack-Jolly-Seber model that use capture-recapture data to understand individual movement of animals among a finite number of states (Lebreton et al. 1992). Assumptions of the model include that every marked animal present in some state immediately following sampling period \(i\) have the same probability of detection and every marked animal present in some state immediately following the sampling period \(i\) has the same probability of surviving until \(i + 1\) and moving to another state by period \(i + 1\).
Additionally, state at time $i + 1$ is dependent only on the state at time $i$. Survival in Brushy Creek represents fish that died and those that left the study area due to permanent emigration; however, emigration of bass from Brushy Creek is minimal and permanent as only two bass during the study period were found to have emigrated over the spillway (<0.001%; A. Sylvia, unpublished data). Further, we assumed temporary emigration (i.e., bass using increased water depth leading to decreased vulnerability of capture during electrofishing) was minimal as bass remained in relatively shallow water (1.88 m; Sylvia et al. *in prep*) and bass were vulnerable to angling across all depths. Although post-capture refrectory periods for bass may exist for short periods following angling (Cox, 2000; Cline et al., 2012; Sass et al., 2018), bass resume feeding within 16 hours following an angling event (Siepker et al., 2006). Thus, we assumed that all individuals were equally available for recapture by anglers during consecutive sampling events. Basic notation of the estimation of survival, detection, and transition event follow probabilities associated with each capture occasion conditional on the fish’s first release, where $S_{i|rs}$ is the probability that fish $i$ alive in state $r$ at occasion $s$, is still alive and in state $s$ at occasion $i + 1$, and $p_{i|j}$ is the probability that fish $i$ alive in state $s$ at occasion $i$ is recaptured at time $i$. For example, a recapture history of three occasions between two states A and B (AAB) would be modelled as 

$$S^{AA}p^{A}S^{AB}p^{B}$$

in the maximum likelihood function.

Survival for 256 time periods were estimated representing daily survival estimates during the open water seasons from 13 April 2015 through 01 June 2018. Only days when either a tournament or electrofishing occurred were included as periods across the three years and interval duration between events was adjusted in program MARK. A daily ice-up survival rate
that began after the last electrofishing event and ended on the first day of electrofishing the following year were also included in the model. This period consisted of 150 days between 2015-2016, 148 days between 2016-2017, and 153 days between 2017-2018. These intervals were adjusted in program MARK and calculated a constant daily survival estimate for the entire winter period, when tournaments did not occur. Survival rate estimates were not corrected for tag loss rates, as daily tag loss is minimal and had little effect on survival estimates (0.00065%, A. Sylvia, unpublished data; Arnason and Mills 1981).

Bass could reside in one of four states in the multistate model. States were based on fish size (medium: 381-457 mm or large: >457 mm; where larger bass represented those approaching memorable size (Gabelhouse 1984), and represented a lower proportion of the tournament captured bass ~ 18%) and capture in Brushy Creek or at a fishing tournament, and delayed tournament mortality (Figure 5.1). Thus, a Brushy Creek state for all fish (B), a tournament state for medium fish (MT), a tournament state for large fish (LT), and a tournament delayed mortality state (D) were used (Figure 5.1). Tagged and recaptured bass could be observed alive and in Brushy Creek, alive and in a tournament, unobserved in the lake, dead in the lake or the tournament, or dead due to delayed tournament mortality. Transitions could occur from Brushy Creek to a tournament ($\Psi B$ to MT and $\Psi B$ to LT), from a tournament to Brushy Creek ($\Psi MT$ to B or $\Psi LT$ to B), from a tournament to delayed mortality ($\Psi MT$ to D or $\Psi LT$ to D), or remain in Brushy Creek ($\Psi B$ to B). Fish could not stay in a tournament state, move from a tournament to another tournament without first returning to Brushy Creek, or leave the delayed mortality state; thus, transition probability of individuals between these states were fixed to zero, and survival in the delayed mortality state was also set to zero (Horton et al. 2011; Figure 5.1). Additionally, detection probabilities were set to one for both tournament states, as all bass
captured at a tournament event were censused. We set transition probabilities from the
tournaments to the delayed mortality state as constants using daily estimates from a prior
analysis assessing delayed mortality post tournament capture (Sylvia and Weber in revision).
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, we chose to use robust estimates of a
3-day delayed mortality rate model (Sylvia and Weber in review) to increase the accuracy of our
population model. Estimates of delayed mortality from one, two, and three days post release
were multiplied together to obtain a cumulative delayed mortality estimate. Transition rates to
the delayed mortality state were set equal for both medium and large bass, as we found no size-
specific differences in delayed mortality rates. Details of the models can be found in Sylvia and
Weber (in review).

Capture histories were created for 5,962 bass (Table 5.1), where an individual received a
letter for the state they were observed in during the sampling period and a 0 if it was not
observed during the sampling period. Time-varying covariates (i.e., covariates that changed on
each time interval) were used in the analysis to potentially account for variation in survival,
detection probability, and tournament capture probability. Covariates for bass in Brushy Creek
included mean daily water temperature (°C) sampled continuously with temperature loggers
(Onset Corporation HOBO Pendant Temperature/Light 64K Data Logger, 15 min sampling
intervals) from three locations within the lake at 0 and 4.6 m depth and daily electrofishing effort
(seconds). Tournament state time-varying covariates included mean daily air temperature (°C),
mean daily water temperature (°C), daily effort for tournaments (hours), and mean number of
bass/angler calculated by dividing the total number of captured bass by the total number of
anglers for each tournament event (Table 5.2).
Using hierarchical model-selection procedures based on Akaike’s Information Criterion (AIC) corrected for small sample size, where lower $AIC_c$ values and higher Akaike weights represent the most parsimonious model (Akaike 1973), we characterized variation in detection probability, tournament capture probability, and survival. 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 first developed to explore variation in bass detection probability as the first step of the hierarchical model selection procedure. We fixed survival and tournament capture probability to state effects (Brushy Creek, tournament medium, tournament large) to compare various model combinations and identify the most supported model for explaining variation in detection probability: a model with no variation in detection probability $p(.)$, a linear effect of electrofishing effort $p(\text{effort})$ and water temperature $p(\text{water T})$, a quadratic effect of water temperature $p(\text{waterT + water T}^2)$, a linear effect of effort and a quadratic effect of temperature for each group $p(\text{effort + water T + water T}^2)$, and a similar combination of models for air temperature $p(\text{effort + air T + air T}^2)$ (Table 5.3).

Once the best explanatory model for detection probability was determined, we tested variation on tournament capture probabilities for bass at medium and large tournament states. First, we tested a model without the size effect to determine if tournament capture probability differed between medium and large fish captured at tournaments $[\Psi_i(\cdot)\text{ and } [\Psi_i(\text{state})]$. Once the best state tournament capture probability was determined, we tested linear and quadratic effects of water temperature and air temperature $[\Psi_i(\text{state + water T}), [\Psi_i(\text{state + water T + waterT}^2)], [\Psi_i(\text{state + air T})], \text{ and } [\Psi_i(\text{state + air T + air T}^2)]$, a linear effect of tournament effort for the tournament states $[\Psi_i(\text{state + effort})]$, and a linear effect of effort and a quadratic
effect of temperature for each group \( \Psi_1 (\text{state + effort + water } T + \text{water } T^2) \), and \( \Psi_2 (\text{state + effort + air } T + \text{air } T^2) \) (Table 5.4).

Next, survival was assessed after the most supported detection and tournament capture probability models were identified. For bass survival, we first tested models estimating survival in Brushy Creek, medium tournament, and large tournament states separately \( S (\text{state}) \), models where survival in tournament states was equal \( S (\text{Brushy, Tournament}) \), models where survival in all states were equal \( S (.) \), and models where survival in either medium \( S (\text{Brushy, Medium}) \) \( S (\text{Large}) \) or large \( S (\text{Brushy, Large}) S (\text{Medium}) \) tournament states were similar to survival in Brushy Creek. We then tested a linear effect of water temperature on the best combination of survival by states \( S (\text{state + water } T) \), and a quadratic effect of water temperature \( S (\text{state + water } T + \text{water } T^2) \), as well as a linear \( S (\text{state + air } T) \) and quadratic effect of air temperature \( S (\text{state + water } T + \text{water } T^2) \). For survival of medium and large tournament bass, we also included a linear effect of average number of bass/angler \( S (\text{state + bass/angler}) \), as well as the number of initial mortalities occurring at each tournament event \( S (\text{state + initial mortality}) \). Additive combinations of the covariates were also tested (Table 5.5).

Markov Chain Monte Carlo (MCMC) simulations were used in the final most supported model to obtain estimates of standard error for model parameters in program MARK. Original MLE parameter estimates from the top model were used as starting values, and the simulation ran 4,000 tuning iterations, 1,000 burn-in iterations followed by 10,000 iterations used in the final estimates. Parameters and their standard error were estimated by the mean and standard deviations from the MCMC iterations. All results are reported as mean parameter values, their standard deviations, and 95% credibility intervals from the simulations.
**Population estimation**

Yearly population estimates and 95% confidence intervals of medium and large bass were calculated separately using Schnabel models estimated by

\[ \hat{N} = \frac{\sum_{i=4}^{t} n_i M_i}{\sum_{i=4}^{t} m_i + 1} \]

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

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

(Hayes et al. 2007). Four weeks in May of 2015, 2016, and 2017 were used as sampling periods in the model, as these times represent time periods when the most sampling effort occurred within a closed period throughout the year that resulted in more accurate population estimates.

Once population size was determined for each of the two size classes, we applied the daily capture probability and total tournament survival rates (initial and delayed) of each tournament event from the most supported multistate model to the abundance of medium and large size bass separately. Total number of tournament mortalities across all tournaments for each year were then subtracted from the total yearly population estimate.

**Simulations**

Simulations were conducted on the 2016 data for both tournament survival rates and tournament capture rates of medium and large tournament bass. Survival and transition probabilities were increased in 10% increments to 90% and similarly reduced. Proportion of the population captured and proportion of population lost to tournament mortality was evaluated by
applying true and simulated tournament survival and capture probabilities to the population estimated for an example year (2016). Proportion of fish 381-457 mm and >457 mm were modelled to evaluate the effects of changes in size-structure of the population as a result of fishing tournaments by applying the proportion at size captured by electrofishing to the estimated population size and then removing the total number of fish lost by true tournament estimates or adjusted tournament estimates for each size class. Proportions were then summarized by the equations

\[ Proportion \ of \ medium \ bass = \frac{Number \ of \ fish \ \leq \ 457 \ mm}{Number \ of \ fish \ \geq \ 381 \ mm} \]

and

\[ Proportion \ of \ large \ bass = \frac{Number \ of \ fish \ > \ 457 \ mm}{Number \ of \ fish \ \geq \ 381 \ mm} \]

Results

A total of 4,712 bass ≥381 mm were captured at 144 bass tournaments and an additional 1,250 bass were captured during 139 hours of electrofishing from 2015 to 2018. Of the tournament captured bass, 3,888 (82.5%) were between 381 and 457 mm and 824 (17.5%) were >457 mm. Of the electrofishing bass, 1,012 (81.0%) were between 381 and 457 mm and 238 (19.0%) were >457 mm (Figure 5.2). A total of 1,454 bass were recaptured with 1,148 (78.5%) recaptured once, 250 (17.1%) recaptured twice, 47 (3.2%) recaptured three times, five (0.3%) recaptured four times, and four (0.3%) recaptured five times. Of the recaptured fish, 946 (65.1%) were recaptured at fishing tournaments, while 508 (34.9%) were recaptured electrofishing (Table 5.1).
Of the ten models evaluated describing variation in bass detection probability in Brushy Creek, the most supported model included a linear effect of sampling effort and air temperature (ΔAIC_c = 0.00, w_i = 0.45; Table 5.3). Confidence intervals of the beta estimates for both parameters did not include zero (sampling effort and air temperature; Table 5.6): detection probability decreased with increasing air temperature and increased with increasing electrofishing effort (Figure 5.3). Detection probabilities of an individual bass in Brushy Creek ranged from 0.0014 (95% CI: 0.0010, 0.0018) during an electrofishing event lasting 4,000 seconds and at air temperatures of 27.2 °C to 0.0200 (95% CI: 0.0140, 0.0260) during an electrofishing event lasting 4,627 seconds at -2.2 °C.

Of the eleven models describing tournament capture probability, the most supported model included separate estimates for bass in Brushy Creek into medium and large tournament states and a linear effect of air temperature (ΔAIC_c = 0.00, W_i = 0.38; Table 5.4). The second (ΔAIC_c = 0.15, W_i = 0.35) most supported model also included tournament angler effort as a covariate on tournament capture probability (ΔAIC_c < 2.00, W_i > 0.14). However, a likelihood ratio test indicated no significant difference between the models with the inclusion of angler effort (χ^2 = 1.85, p = 0.17). In contrast, models with similar tournament capture probability for medium and large tournament bass had no support (ΔAIC_c = 279.18, W_i = 0.00), indicating different capture probabilities for medium and large tournament bass at fishing tournaments. Confidence intervals for one of the three beta estimates describing tournament capture probability did not include zero (Intercept; Table 5.6). Tournament capture probability was higher for medium bass, ranging from 0.0030 (95% CI: 0.0022, 0.0038) when air temperature was 4.4 °C to 0.0082 (95% CI: 0.0070, 0.0093) when air temperature was 28.3 °C. Tournament capture probability of large bass was generally three times lower than that of medium bass across
air temperatures (Figure 5.4). Tournament capture probability of large bass ranged from 0.0007 (95% CI: 0.0005, 0.0010) at an air temperature of 4.4 °C to 0.0021 (95% CI: 0.0017, 0.0025) at 28.3 °C. For both medium and large bass, tournament capture probability increased with increasing air temperatures on average by 4% with each additional degree rise in temperature (Figure 5.4).

Models estimating survival of bass in Brushy Creek and in the medium and large tournament states separately were more supported over models where survival was similar between tournament states (ΔAICₖ = 33.39, \( W_i = 0.00 \)), models where survival in all states was equal (ΔAICₖ = 36.94, \( W_i = 0.00 \)), and where survival of either medium (ΔAICₖ = 33.58, \( W_i = 0.00 \)) or large (ΔAICₖ = 36.62, \( W_i = 0.00 \)) bass was equal to bass in Brushy Creek (Table 5.5). The top model also identified a quadratic effect of water temperature on survival in all states and a linear effect of average number of bass/angler on the tournament states (ΔAICₖ = 0.00, \( W_i = 1.00 \); Table 5.5). No other models received support (ΔAICₖ > 21.00, \( W_i = 0.00 \)).

Four of the six beta estimates (Brushy Creek bass, medium tournament bass, water Temperature\(^2\) and number of bass/angler) in the final survival model did not include zero (Table 5.6). Bass survival and temperature exhibited a quadratic trend, resulting in highest survival at water temperatures around 13.0 °C for bass in Brushy Creek (mean = 0.9960; 95% CI: 0.9953, 0.9967), as well as medium (mean = 0.9929; 95% CI: 0.9790, 0.9999) and large (mean = 0.9914; 95% CI: 0.9709, 0.9999) tournament bass. Survival rates among the three states decreased by 0.3% between Brushy Creek and medium tournament bass, and by 0.5% between Brushy Creek and large tournament bass. Differences in survival were magnified among groups at both cooler and warmer water temperatures (Figure 5.5). At low water temperatures (4.2 °C), survival of Brushy Creek bass was 0.9958 (95% CI: 0.9938, 0.9982), 0.9926 (95% CI: 0.9798, 0.9999) for
medium tournament bass (a 0.3% reduction), and 0.9608 (95% CI: 0.9080, 0.9893) for large tournament bass (a 3.5% reduction). The largest differences in survival among states were observed at the warmest temperatures (23.0 °C), where survival for Brushy Creek bass was 0.9926 (95% CI: 0.9892, 0.9956), survival decreased to 0.9870 (95% CI: 0.9657, 0.9999), for medium tournament bass (a 0.6% decrease), and 0.9294 (95% CI: 0.8435, 0.9925) for large tournament bass (a 6.3% decrease; Figure 5.5).

Number of bass/angler was also a supported covariate describing fish survival rates; however, the effect was less important than that of water temperature, based on the beta estimate. With water temperatures held constant, bass survival was variable in relation to number of bass/angler. At one bass/angler, survival for medium tournament bass was 0.9830 (95% CI: 0.9695, 0.996) which increased to 0.9885 (95% CI: 0.9565, 0.9999) for three bass/angler, a 0.6% increase in survival rate. Similar trends were seen with large tournament bass, where survival at one bass/angler was 0.9492 (95% CI: 0.8792, 0.9921) which increased to 0.9688 (95% CI: 0.9223, 0.9946) at a three bass/angler, a 2.0% increase in survival. Differences between survival rates of medium and large tournament bass as a function of the number of bass/angler were also minimal and likely more influenced by water temperatures.

Annual population estimates of medium and large bass within Brushy Creek were similar among years. Estimates of medium bass ranged from 5,136 fish in 2017 to 5,046 fish in 2015 (Table 5.7). Alternatively, abundance of large bass each year ranged from 1,013 in 2015 to 1,137 in 2017, ranging from 77% to 80% less than that of the population of medium bass (Table 5.7). Capture rates and mortality of medium and large bass due to tournament angling events differed among years and bass size group. The percent of the population captured at tournaments ranged from 27.1-29.8% for medium bass (Figure 5.6A) and 27.5-37.1% for large bass (Figure 5.6B),
resulting in 7.0-7.6% of the medium Largemouth Bass population (Figure 5.6C) and 7.3-9.8% of the large bass population (Figure 5.6D) lost to total tournament mortality.

Increases in tournament capture probabilities altered the proportions of the population captured through tournament angling for each size class. For medium bass, 90% increases in tournament capture probabilities increased the proportion of the population captured to 54.7%, whereas decreases of 90% resulted in only 2.9% of the population captured (Figure 5.7A). Changes in tournament capture probability for large bass increased to 63.3% of the population captured with 90% increases and was reduced to 3.3% with 90% decreases in tournament capture probability (Figure 5.7A). Changes in survival rates showed similar trends between medium and large bass, representing at most 13.7% population level mortality for large bass and 11.7% population level mortality for medium bass when survival rates were decreased by 90%. Ninety percent decreases in survival resulted in population level mortality of <1.0% for both medium and large bass (Figure 5.7B).

Changes in tournament capture probability and survival rates resulted in relatively small changes to proportions of medium and large bass (Figure 5.8A-E). Proportions were 0.818 medium bass and 0.182 large bass in 2016. Changes in tournament capture probabilities resulted in larger effects on changes in population proportions than did changes in survival. Greater influences in population proportions were observed when changes in tournament capture probabilities and survival were applied to only one size group, particularly, large bass. Proportion of large bass increased to 0.193 with a 90% increase in large bass tournament capture probability (Figure 5.8B) or a 90% decrease in large bass tournament survival (Figure 5.8D). Simulations of changes in both tournament capture probability and survival of tournament bass showed the largest effects on changes in proportions of medium and large bass within Brushy
Creek (Figure 5.8E, 5.8F). When tournament capture probability was increased by 90%, and survival was decreased by 90% for medium bass only, large bass proportions increased to 0.212. Alternatively, when such changes were applied to only the large bass population, large bass proportions dropped to 0.151 (Figure 5.8F).

**Discussion**

Successful understanding of population-level changes as a result of tournament fishing mortality requires two primary pieces of information: 1) proportion of the population captured by tournament anglers and 2) tournament mortality. We found strong support for differences between medium and large bass tournament capture probabilities. Tournament capture probability of medium bass was on average three times that of large bass. However, tournament anglers captured a larger proportion of the large bass population (27-37%) compared to medium bass (27-30%), suggesting tournament anglers are efficient at capturing the largest bass in the population. With intraspecific differences in vulnerability to angling a possible result of lure recognition and avoidance (Hackney and Linkous 1978; Clark 1983), loss of naivety of individuals (Burkett et al. 1968; Anderson and Heman 1969; Farabee 1970; Hessenauer et al. 2016), behavioral changes post-capture (O’Hara 1986), and selection for or against vulnerability to angling (Philipp et al. 2009), we hypothesized that the largest, and likely oldest and most experienced bass in population would have lower capture probability as a result of previous selective angling mortality and learned behaviors. The higher percentage of the large bass captured at tournaments is indicative of tournament goals and angler motivations that focus on capturing the largest fish in the population (Fisher 1997). Practices such as angler gear selectivity (Gabelhouse and Willis 1986), culling of small fish with larger ones (Staggs 2005), and
environmental variables may result in differences between medium and large bass tournament capture probabilities.

Air temperature described tournament capture probability of both medium and large bass, indicating weather plays an important role in vulnerability of bass to angling. Capture probability of bass at tournaments consistently increased with air temperatures, although water temperature was less effective at describe capture rates. Water temperature has been linked to fishes physiological processes including foraging patterns (Fraser et al. 1993) and metabolism (Brett 1964; Fry 1971; Brett and Glass 1973), leading to potential increases in vulnerability to angling. While air temperature and water temperature are correlated, the importance of air temperature likely indicates that primary mechanisms of bass vulnerability are not limited to metabolism alone. Instead, they likely include sensory limitations related to light and turbidity, as well as additional variables associated with fish activity and feeding capability, including wind and barometric pressure (Stoner 2004).

Although large bass had lower tournament capture probabilities than medium bass, large bass exhibited higher initial mortality rates. Survival of tournament captured bass can decrease with fish size (Weathers and Newman 1997; Meals and Miranda 2004). Though prior estimates of delayed mortality used in this analysis showed no size-specific differences (Sylvia and Weber in review), it is reasonable that differences would be more apparent in initial survival, as larger fish experience higher stressors during the tournament event. Increased mortality of larger individuals is attributed to an inverse relationship between aerobic metabolism and body size, higher oxygen demands, longer landing times, longer air exposure at weigh-ins, and higher live-well densities (Schmidt-Nielsen 1984; Kieffer et al. 1996; Ostrand et al. 1999; Burleson et al. 2001; Cooke et al. 2002). The effects of angling on bass survival may also be mediated by
temperature. Temporal trends across the fishing season were evident in both medium and large bass and were described by quadratic patterns in water temperature. Larger bass were more affected by warmer water temperatures than medium bass, and warmer temperatures resulted in significantly larger affects than did cooler temperatures. Higher water temperatures can lead to disproportionately greater negative effects on larger bodied fish (Schmidt-Nielsen 1984) as a result of increased metabolic activity compounded by low oxygen conditions in live-wells and plastic bags during weigh-in procedures (Meals and Miranda 1994; Weathers and Newman 1997).

Our estimates of population-level mortality were lower than prior size based mortality estimates (9% for medium tournament bass and 29% for large bass, Meals and Miranda 1994; 30.8%, Weathers and Newman 1997), but approached estimates from studies conducted in Northern latitudes where total mortality regardless of fish size was 5.2% in Maine (Hartley and Moring 1995), 3.2% in Connecticut (Edwards et al. 2004), 4.5% in Minnesota (Kwak and Henry 1995), 4.9% in South Dakota (4.9%; Jackson and Willis 1991), and 10.5% in Idaho (Bennet et al. 1989). Bass captured during tournaments at Brushy Creek experienced little initial mortality (~1% annually; Sylvia and Weber in review) and models that include initial mortalities as covariates on survival rates were not supported, suggesting delayed mortality accounts for the majority of the total tournament mortality. Inclusion of estimates of delayed mortality accounted for 6.00% of the total 6.05% population level tournament mortality for medium bass, and 6.8% of the 7.3% population level tournament mortality for large bass, whereas initial mortality only accounted for 0.1% and 0.5% of the total population mortality for medium and large bass. The large influence of delayed tournament mortality on total tournament mortality estimates
demonstrates the importance of assessing both sources when evaluating the effects of
tournaments on population dynamics.

Despite a high proportion of the bass population being captured annually at tournaments,
we found little support for potential effects on population size-structure. Simulations have
suggested that tournament mortality has the potential to be an additive source of mortality and
reduce the number of large bass when it exceeds harvest mortality (Hayes et al. 1995; Allen et al.
2004). For instance, a simulated 50% decrease in tournament fishing pressure resulted in a
proportionally greater increase in abundance of fish >457 mm than fish >356 mm (Hysmith et al.
2014). Conversely, our simulations indicated that even a 90% decreases in tournament fishing
pressure resulted in negligible changes in population size-structure. Differential tournament
effects on population size-structure may be compounded if size-specific tournament mortality
occurs (Meals and Miranda 1994; Weathers and Newman 1997). It is worth noting that
adjustments in only tournament capture probability and survival rates of large fish resulted in
greater population size-structure changes than did changes in tournament survival rates and
capture probabilities of medium fish, or both. Thus, for systems with higher tournament pressure,
methods that decrease the capture or increase survival of larger bass at tournaments (e.g., paper
tournaments, limits on number of bass exceeding certain sizes; Willis and Hartmann 1986;
Ostrand et al. 1999) may be more successful at mitigating tournament effects on bass
populations. While many national tournament angling associations (e.g., Major League Fishing,
B.A.S.S., Fishing League Worldwide) were traditionally hesitant to implement additional
regulations, catch-weigh-immediate release events and slot limits tournaments (i.e., one fish
above the slot limit) are beginning to be implemented at a national level (Bassmaster 2019;
B.A.S.S. 2019, Major League Fishing 2018) and may be a tool to reduce potential population-levels effects of tournament mortality.

Meeting fisheries goals can be challenging when attitudes, motivations, and characteristics of anglers vary, even when targeting the same species (Wilde et al. 1998). Goals of fishing tournaments are to capture the biggest fish within populations. However, this practice may result in fewer large fish may become available over time. Assessing differences in capture and survival rates of various size classes of fish can serve useful in understanding potential size-structure changes within the populations. Our results indicate that significant differences exist between tournament capture probability and survival of medium and large bass and should be assessed when evaluating fishery effects and making management decisions. However, even when a substantially large proportion of the population is captured at tournaments, low initial mortality rates appear to result in limited population level effects.

**Acknowledgements**

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**References**


Table 5.1 Number of Largemouth Bass tagged and recaptured by electrofishing and by tournaments at Brushy Creek, IA from 2015-2018.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number Tagged</th>
<th>2015</th>
<th>2016</th>
<th>2017</th>
<th>2018</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tournament</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>1,183</td>
<td>260</td>
<td>138</td>
<td>42</td>
<td>4</td>
</tr>
<tr>
<td>2016</td>
<td>1,250</td>
<td>-</td>
<td>128</td>
<td>86</td>
<td>12</td>
</tr>
<tr>
<td>2017</td>
<td>1,460</td>
<td>-</td>
<td>-</td>
<td>243</td>
<td>28</td>
</tr>
<tr>
<td>2018</td>
<td>819</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td><strong>Tournament total</strong></td>
<td>4,712</td>
<td>260</td>
<td>266</td>
<td>371</td>
<td>49</td>
</tr>
<tr>
<td><strong>Electrofishing</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>353</td>
<td>123</td>
<td>91</td>
<td>18</td>
<td>24</td>
</tr>
<tr>
<td>2016</td>
<td>364</td>
<td>-</td>
<td>84</td>
<td>44</td>
<td>4</td>
</tr>
<tr>
<td>2017</td>
<td>269</td>
<td>-</td>
<td>-</td>
<td>55</td>
<td>34</td>
</tr>
<tr>
<td>2018</td>
<td>264</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>31</td>
</tr>
<tr>
<td><strong>Electrofishing total</strong></td>
<td>1,250</td>
<td>123</td>
<td>175</td>
<td>117</td>
<td>93</td>
</tr>
<tr>
<td><strong>Total bass</strong></td>
<td>5,962</td>
<td>383</td>
<td>441</td>
<td>488</td>
<td>142</td>
</tr>
</tbody>
</table>
Table 5.2 Mean, standard error (SE), and range of environmental covariates used in multistate models to assess variation in Largemouth Bass survival ($S$), capture probability ($P_s$), and detection probability ($p$) in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018.

<table>
<thead>
<tr>
<th></th>
<th>2015</th>
<th></th>
<th>2016</th>
<th></th>
<th>2017</th>
<th></th>
<th>2018</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
<td>Mean</td>
<td>SE</td>
<td>Min, Max</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Mean daily water temperature (°C)</td>
<td>16.46</td>
<td>0.04</td>
<td>6.31, 21.32</td>
<td>17.21</td>
<td>0.06</td>
<td>7.14, 22.91</td>
<td>16.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Mean daily air temperature (°C)</td>
<td>18.63</td>
<td>0.02</td>
<td>5.56, 27.22</td>
<td>17.75</td>
<td>0.09</td>
<td>1.11, 28.33</td>
<td>17.80</td>
<td>0.10</td>
</tr>
<tr>
<td>Tournament angling effort (h)</td>
<td>223.33</td>
<td>4.06</td>
<td>20.00, 738.00</td>
<td>168.81</td>
<td>2.34</td>
<td>84.00, 512.00</td>
<td>158.19</td>
<td>1.83</td>
</tr>
<tr>
<td>Electrofishing effort (s)</td>
<td>5,271.75</td>
<td>93.11</td>
<td>1,305.00, 11,527.00</td>
<td>6,318.73</td>
<td>150.20</td>
<td>1,374.00, 18,354</td>
<td>5,652.00</td>
<td>128.72</td>
</tr>
<tr>
<td>Average tournament bass/angler</td>
<td>1.38</td>
<td>0.02</td>
<td>0.40, 3.00</td>
<td>1.33</td>
<td>0.02</td>
<td>0.30, 3.00</td>
<td>1.52</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 5.3 All Cormack-Jolly-Seber multistate models used to estimate Largemouth Bass recapture probability ($p$) in Brushy Creek, IA, USA during 256 periods from 13 April, 2015 through 1 June 2018. Effects evaluated influencing $p$ include a constant model (.), sampling effort (s), linear and quadratic water temperature ($^\circ$C; waterT; waterT$^2$), and linear and quadratic air temperature ($^\circ$C; airT, airT$^2$). Parameters in the table include $K =$ 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), $\text{AIC}_c =$ sample-sized corrected Akaike’s Information Criterion, and $w_i =$ Akaike weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p$ (airT + effort)</td>
<td>954,223.80</td>
<td>0.00</td>
<td>0.45</td>
<td>5</td>
<td>9,43074.22</td>
</tr>
<tr>
<td>$p$ (airT + airT$^2$)</td>
<td>954,223.88</td>
<td>0.08</td>
<td>0.43</td>
<td>6</td>
<td>9,43072.30</td>
</tr>
<tr>
<td>$p$ (airT)</td>
<td>954,227.95</td>
<td>4.14</td>
<td>0.06</td>
<td>4</td>
<td>9,43080.36</td>
</tr>
<tr>
<td>$p$ (airT + airT$^2$)</td>
<td>954,228.09</td>
<td>4.29</td>
<td>0.05</td>
<td>5</td>
<td>9,43078.50</td>
</tr>
<tr>
<td>$p$ (waterT + effort)</td>
<td>954,257.67</td>
<td>33.87</td>
<td>0.00</td>
<td>6</td>
<td>9,43106.09</td>
</tr>
<tr>
<td>$p$ (waterT + waterT$^2$ + effort)</td>
<td>954,259.42</td>
<td>35.63</td>
<td>0.00</td>
<td>7</td>
<td>9,43105.84</td>
</tr>
<tr>
<td>$p$ (waterT)</td>
<td>954,262.41</td>
<td>38.61</td>
<td>0.00</td>
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<td>9,43114.82</td>
</tr>
<tr>
<td>$p$ (waterT + waterT$^2$)</td>
<td>954,263.93</td>
<td>40.13</td>
<td>0.00</td>
<td>5</td>
<td>9,43114.34</td>
</tr>
<tr>
<td>$p$ (.)</td>
<td>954,319.21</td>
<td>95.42</td>
<td>0.00</td>
<td>3</td>
<td>9,43173.64</td>
</tr>
<tr>
<td>$p$ (effort)</td>
<td>954,319.32</td>
<td>95.52</td>
<td>0.00</td>
<td>4</td>
<td>9,43171.73</td>
</tr>
</tbody>
</table>
Table 5.4 All Cormack-Jolly-Seber multistate models used to estimate Largemouth Bass tournament capture probability ($\Psi$) in Brushy Creek, IA, USA during 256 periods from 13 April, 2015 through 1 June, 2018. Effects evaluated influencing $\Psi$ include a constant model (.), tournament effort (h), linear and quadratic water temperature (°C; waterT; waterT$^2$), and linear and quadratic air temperature (°C; airT, airT$^2$). Parameters in the table include K = number of parameters, Deviance = -2 x log-likelihood of the model less -2 x log-likelihood of the saturated models (same number of parameters and degrees of freedom), AICc = sample-sized corrected Akaike’s Information Criterion, $w_i$ = Akaike weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Psi$ (state + airT)</td>
<td>953,944.61</td>
<td>0.00</td>
<td>0.38</td>
<td>7</td>
<td>942,791.03</td>
</tr>
<tr>
<td>$\Psi$ (state + effort + airT)</td>
<td>953,944.77</td>
<td>0.15</td>
<td>0.35</td>
<td>8</td>
<td>942,789.18</td>
</tr>
<tr>
<td>$\Psi$ (state + airT + airT$^2$)</td>
<td>953,946.59</td>
<td>1.97</td>
<td>0.14</td>
<td>8</td>
<td>942,790.99</td>
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<tr>
<td>$\Psi$ (state + effort + airT + airT$^2$)</td>
<td>953,946.70</td>
<td>2.09</td>
<td>0.13</td>
<td>9</td>
<td>942,789.11</td>
</tr>
<tr>
<td>$\Psi$ (state + effort)</td>
<td>953,966.50</td>
<td>21.89</td>
<td>0.00</td>
<td>7</td>
<td>942,812.91</td>
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<tr>
<td>$\Psi$ (state)</td>
<td>953,967.05</td>
<td>22.44</td>
<td>0.00</td>
<td>6</td>
<td>942,815.47</td>
</tr>
<tr>
<td>$\Psi$ (state + effort + waterT)</td>
<td>953,967.46</td>
<td>22.84</td>
<td>0.00</td>
<td>8</td>
<td>942,811.87</td>
</tr>
<tr>
<td>$\Psi$ (state + waterT)</td>
<td>953,968.10</td>
<td>23.49</td>
<td>0.00</td>
<td>7</td>
<td>942,814.52</td>
</tr>
<tr>
<td>$\Psi$ (state + effort + waterT + waterT$^2$)</td>
<td>953,968.62</td>
<td>24.01</td>
<td>0.00</td>
<td>9</td>
<td>942,811.02</td>
</tr>
<tr>
<td>$\Psi$ (state + waterT + waterT$^2$)</td>
<td>953,969.42</td>
<td>24.80</td>
<td>0.00</td>
<td>8</td>
<td>942,813.83</td>
</tr>
<tr>
<td>$\Psi$ (.)</td>
<td>954,223.80</td>
<td>279.18</td>
<td>0.00</td>
<td>5</td>
<td>943,074.22</td>
</tr>
</tbody>
</table>
Table 5.5 All Cormack-Jolly-Seber multistate models used to estimate Largemouth Bass survival ($S$) in Brushy Creek, IA, USA during 256 periods from 13 April, 2015 through 1 June 2018. Effects evaluated influencing $S$ include a constant model (.), linear and quadratic air ($\text{airT}$, $\text{airT}^2$) and water ($\text{waterT}$, $\text{waterT}^2$) temperature ($^\circ$C), average number of bass per angler (bag/angler), and initial tournament mortalities. Parameters in the table include $K$ = 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), $\text{AIC}_c = \text{sample-sized corrected Akaike’s Information Criterion}$, $w_i = \text{Akaike weight}$.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
<th>$K$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$ (state + waterT + waterT$^2$ + bass/angler)</td>
<td>953,911.22</td>
<td>0.00</td>
<td>1.00</td>
<td>11</td>
<td>942,749.62</td>
</tr>
<tr>
<td>$S$ (state + airT + airT$^2$ + bass/angler)</td>
<td>953,932.88</td>
<td>21.66</td>
<td>0.00</td>
<td>9</td>
<td>942,775.28</td>
</tr>
<tr>
<td>$S$ (state + waterT + waterT$^2$ + bass/angler + initial mortality)</td>
<td>953,933.20</td>
<td>21.98</td>
<td>0.00</td>
<td>12</td>
<td>942,769.58</td>
</tr>
<tr>
<td>$S$ (state + waterT + initial mortality)</td>
<td>953,935.07</td>
<td>23.84</td>
<td>0.00</td>
<td>10</td>
<td>942,775.46</td>
</tr>
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<td>$S$ (state + waterT + waterT$^2$)</td>
<td>953,935.08</td>
<td>23.86</td>
<td>0.00</td>
<td>9</td>
<td>942,777.49</td>
</tr>
<tr>
<td>$S$ (state + waterT + bass/angler)</td>
<td>953,936.00</td>
<td>24.77</td>
<td>0.00</td>
<td>10</td>
<td>942,776.39</td>
</tr>
<tr>
<td>$S$ (state + waterT + waterT$^2$ + initial mortality)</td>
<td>953,937.90</td>
<td>26.68</td>
<td>0.00</td>
<td>11</td>
<td>942,776.29</td>
</tr>
<tr>
<td>$S$ (state)</td>
<td>953,943.69</td>
<td>32.46</td>
<td>0.00</td>
<td>8</td>
<td>942,788.10</td>
</tr>
<tr>
<td>$S$ (state + initial mortality)</td>
<td>953,943.69</td>
<td>32.46</td>
<td>0.00</td>
<td>8</td>
<td>942,788.10</td>
</tr>
<tr>
<td>$S$ (state + bass/angler)</td>
<td>953,944.57</td>
<td>33.35</td>
<td>0.00</td>
<td>9</td>
<td>942,786.98</td>
</tr>
<tr>
<td>$S$ (Brushy, tournament)</td>
<td>953,944.61</td>
<td>33.39</td>
<td>0.00</td>
<td>7</td>
<td>942,791.03</td>
</tr>
<tr>
<td>$S$ (Brushy, medium tournament) $S$ (large tournament)</td>
<td>953,944.80</td>
<td>33.58</td>
<td>0.00</td>
<td>7</td>
<td>942,791.22</td>
</tr>
<tr>
<td>$S$ (state + airT + bass/angler)</td>
<td>953,946.35</td>
<td>35.12</td>
<td>0.00</td>
<td>10</td>
<td>942,786.74</td>
</tr>
<tr>
<td>$S$ (state + airT + airT$^2$)</td>
<td>953,946.79</td>
<td>35.56</td>
<td>0.00</td>
<td>10</td>
<td>942,787.18</td>
</tr>
<tr>
<td>$S$ (state + bass/angler + initial mortality)</td>
<td>953,947.37</td>
<td>36.14</td>
<td>0.00</td>
<td>10</td>
<td>942,787.76</td>
</tr>
<tr>
<td>$S$ (Brushy, large tournament) $S$ (medium tournament)</td>
<td>953,947.84</td>
<td>36.62</td>
<td>0.00</td>
<td>7</td>
<td>942,794.26</td>
</tr>
<tr>
<td>$S$ (.)</td>
<td>953,948.16</td>
<td>36.94</td>
<td>0.00</td>
<td>6</td>
<td>942,796.58</td>
</tr>
</tbody>
</table>
Table 5.6 Cormack-Jolly-Seber estimates the most supported model \[ S (\text{state} + \text{waterT} + \text{waterT}^2 + \text{bass/angler}) \psi (\text{state} + \text{airT}) p (\text{airT} + \text{effort}) \] explaining Largemouth Bass survival, tournament capture and detection probability in Brushy Creek, IA, USA during 256 periods from 13 April, 2015 through 1 June 2018. Estimate = Beta estimate of parameter. SE = Standard error of beta estimate. 95% LCI = 95% lower confidence interval of beta estimate of parameter. 95% UCI = 95% upper confidence interval of beta estimate of parameter.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>95% LCI</th>
<th>95% UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Survival</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.19656</td>
<td>1.15505</td>
<td>-2.11358</td>
<td>2.40168</td>
</tr>
<tr>
<td>Brushy Creek</td>
<td>2.41992</td>
<td>1.05293</td>
<td>0.50147</td>
<td>4.57203</td>
</tr>
<tr>
<td>Medium bass</td>
<td>-2.88786</td>
<td>0.73443</td>
<td>-4.33655</td>
<td>-1.51302</td>
</tr>
<tr>
<td>WaterT</td>
<td>0.00887</td>
<td>0.06810</td>
<td>-0.11498</td>
<td>0.14572</td>
</tr>
<tr>
<td>WaterT^2</td>
<td>-0.00844</td>
<td>0.00031</td>
<td>-0.00900</td>
<td>-0.00781</td>
</tr>
<tr>
<td>Bass/angler</td>
<td>-0.36026</td>
<td>0.03497</td>
<td>-0.42613</td>
<td>-0.29089</td>
</tr>
<tr>
<td><strong>Tournament capture probability</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.15212</td>
<td>0.23027</td>
<td>0.69623</td>
<td>1.58889</td>
</tr>
<tr>
<td>Medium bass</td>
<td>0.00546</td>
<td>1.75927</td>
<td>-3.42467</td>
<td>3.65256</td>
</tr>
<tr>
<td>AirT</td>
<td>-0.00052</td>
<td>0.06172</td>
<td>-0.12148</td>
<td>0.11817</td>
</tr>
<tr>
<td><strong>Detection probability</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.91269</td>
<td>0.37145</td>
<td>0.18312</td>
<td>1.62589</td>
</tr>
<tr>
<td>AirT</td>
<td>0.06670</td>
<td>0.03841</td>
<td>0.00239</td>
<td>0.14259</td>
</tr>
<tr>
<td>Effort</td>
<td>0.00007</td>
<td>0.00001</td>
<td>0.00006</td>
<td>0.00008</td>
</tr>
</tbody>
</table>
Table 5.7 Schnabel model estimates for medium (381-457 mm) and large (>457 mm) bass in Brushy Creek by from 2015-2017. $\hat{N}$ represents the estimated number of bass, $SD(\hat{N})$ is the estimated standard deviation, and 95% LCI and UCI are the upper and lower confidence intervals calculated from the estimator and variance estimator.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\hat{N}$</th>
<th>SD($\hat{N}$)</th>
<th>95% LCI</th>
<th>95% UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Medium bass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>5,109</td>
<td>120</td>
<td>4,879</td>
<td>5,109</td>
</tr>
<tr>
<td>2016</td>
<td>5,046</td>
<td>150</td>
<td>4,751</td>
<td>5,340</td>
</tr>
<tr>
<td>2017</td>
<td>5,136</td>
<td>217</td>
<td>4,709</td>
<td>5,562</td>
</tr>
<tr>
<td><strong>Large bass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>1,013</td>
<td>160</td>
<td>699</td>
<td>1,327</td>
</tr>
<tr>
<td>2016</td>
<td>1,137</td>
<td>179</td>
<td>785</td>
<td>1,490</td>
</tr>
<tr>
<td>2017</td>
<td>1,100</td>
<td>173</td>
<td>759</td>
<td>1,441</td>
</tr>
</tbody>
</table>
Figure 5.1 Conceptual diagram of multistate model design used to estimate Brushy Creek, tournament medium, tournament large, and delayed tournament mortality of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018. Arrows represent capture probabilities ($\Psi$) in the tournament states, $p$ represents detection probabilities within states, and $S$ represents survival estimates of each state. $\Psi^{B-B} = 1 - (\Psi^{B-TM} + \Psi^{B-TL})$. 
Figure 5.2 Largemouth Bass length-frequency histograms for individuals captured with electrofishing and tournament angling in Brushy Creek Lake, IA, USA from 13 April 2015 to 11 November 2017. Vertical line at 457 mm represents the separation of medium (left) and large (right) bass designations within model.
Figure 5.3 Estimated detection probability of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to electrofishing effort (A) and mean daily air temperature (B). Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 5.4 Estimated medium (dashed line) and large (dotted line) tournament capture probabilities of jaw tagged Largemouth Bass in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily air temperature. Solid lines around estimates represent the 95% credibility intervals of the Markov Chain Monte Carlo estimates.
Figure 5.5 Estimated survival rates of jaw tagged Largemouth Bass in Brushy Creek (dashed and dotted line), in medium (dashed line), and in large (dotted line) tournaments in Brushy Creek, IA, USA from 13 April 2015 through 1 June 2018 in relation to mean daily water temperature.
Figure 5.6 Cumulative percentage of the Brushy Creek Lake, IA, USA Largemouth Bass population captured at tournaments during 2015 (solid line), 2016 (dotted line), and 2017 (dashed line) for medium (A) and large (B) bass, and cumulative percentage of Largemouth Bass population mortality from tournaments during 2015 (solid line), 2016 (dotted line), and 2017 (dashed line) for medium (C) and large (D) size groups.
Figure 5.7 Percent of medium (solid line) and large (dotted line) Largemouth Bass population in Brushy Creek Lake, IA, USA captured at tournaments with simulated decreases (-10% to -90%) and increases (10% to 90%) in tournament capture probabilities (A) and percent of medium (solid line) and large (dotted line) Largemouth Bass population mortality at tournaments with simulated decreases (-10% to -90%) and increases (10% to 90%) in tournament survival probabilities (B).
Figure 5.8. Proportion of medium and large Largemouth Bass population in Brushy Creek Lake, IA, USA with simulated decreases (-10% to -90%) and increases (10% to 90%) in tournament capture probabilities (A, B), in tournament survival probabilities (C, D), and tournament capture and survival probabilities (E, F) of both medium and large bass (solid line), only medium bass (dotted line) and only large bass (dashed line).
CHAPTER 6. GENERAL CONCLUSION

Population dynamics of fishes continues to be a growing field and represents some of our best attempts at guiding fisheries management decisions and improving fisheries (Nielsen 1999; Lorenzen et al. 2016). While much attention has been focused on bass management, many studies have lacked a comprehensive understanding of factors potentially influencing populations that have largely transformed from harvest to catch and release fisheries. For example, studies at the individual level (Cooke et al. 2002; Cooke et al. 2003), while useful for suggesting strategies to improve fishing practices (Siepker et al. 2007), lack the ability to quantify such effects into translatable fisheries management decisions. Of the population level studies that have been conducted on Largemouth Bass (Allen et al. 2004; Driscoll et al. 2007; Kerns et al. 2016), focus has largely been on Southern U.S. systems (e.g., Arkansas, Florida, Texas). However, Largemouth Bass fishing is popular across the world, including Iowa reservoirs (U.S. Fish and Wildlife Service 2011), with a large portion of that effort consisting of tournament events. However, despite the popularity of bass recreational fisheries, little was known regarding the effects of catch and release angling in populations. Through our use mark-recapture methods, we have quantified population-level influences of angling on an Iowa bass population in Brushy Creek Lake (hereafter Brushy Creek), furthering our knowledge on an extremely popular and important species to the recreational angling community.

While mortality can be a primary driver in fish population changes, understanding vulnerability of fish to mortality sources is an important first step in assessing population-level impacts. If bass have low capture probability, initial and delayed catch and release mortality rates have little influence on populations (Hayes et al. 1995; Allen et al. 2004). However, bass tournament anglers are highly skilled at capturing the fish they target (Fisher 1997) and
subsequently may capture large portions of populations and inflict high mortality rates on captured individuals (Wilde 1998). However, no studies have assessed the spatial relationships between bass and tournament anglers. Results presented in my dissertation show that bass tournament anglers use their understanding of bass behavior to increase overlap with bass during angling events (Chapter 2). This intricate balance between angler knowledge, bass behavior, and environmental patterns can lead to intervals during the spring when bass are especially vulnerable to capture (e.g., times when bass movement is high and anglers can use sight fishing; Chapter 2). These periods of strong overlap between bass and tournament anglers can lead to potential impacts of tournament angling on bass populations.

After gaining an understanding of the potential for capture of bass at tournaments, I then evaluated what this meant in terms of mortality in Brushy Creek. In what is likely one of the more difficult assessments of mortality sources, delayed mortality is either ignored or has traditionally been done with some associated limitations (Schramm et al. 1987; Wilde et al. 2003; Edwards et al. 2004; Chapter 3). Through using a mark-recapture framework, we were not only able to quantify delayed tournament mortality, but determine both the length of its effects and additional factors that influenced it. Delayed tournament mortality in Brushy Creek was acute, lasting on average three days. Further, delayed mortality increased with water temperature and with number of prior tournament captures. Effect of prior capture has been considered in marine systems (Bartholomew and Bohnsak 2005), but has received little attention in freshwater systems. However, it was extremely important in describing variability in survival of tournament captured bass in Brushy Creek. Bass cumulative mortality approached 90% after five tournament captures with water temperature above 20 °C. Although not assessed, the effect of prior capture history on survival may explain why so few bass were captured multiple times across the study.
period (Chapter 3). Surprisingly, fish size did not influence delayed tournament mortality. Additional factors not related to size of bass likely drives post release survival, including ability to find food, appropriate habitat, and avoid predation (Stang et al. 1996; Gilliland 1999). Overall, I estimated delayed tournament mortality in Brushy Creek to vary from 17 to 33% for individuals and demonstrated the importance of incorporating such estimates when conducting comprehensive assessments of bass population dynamics.

Using our estimated of delayed mortality, we were able to assess tournament mortality in relation to total mortality at the population level. Understanding additional sources of mortality acting on bass populations including natural mortality, harvest, mortality, and recreational catch-and-release mortality, are necessary to understand the relative effects of individual sources (Kerns et al. 2012). My results indicated that more than 20% of the legal-sized Largemouth Bass population is captured at fishing tournaments during any given year, compared to only 12% of the bass population captured through recreation angling (Chapter 4). These capture rates translated to low (2.8%; Chapter 4) harvest and catch-and-release angling mortality in Brushy Creek, as harvest is minimal and catch-and-release mortality may be as low as 5-10% for captured individuals (Muoneke and Childress 1994; Hayes et al. 1995). However, harvest and catch and release mortality were greater than initial tournament mortality, which did not surpass one percent of the population (0.4%). Delayed tournament mortality resulted in the highest angler induced mortality (5.5%); however, the combined influences of each source still only constituted (13%) of total mortality. On average, natural mortality was 57%, which is surprisingly high compared to other Northern latitude systems (e.g., 35% in Michigan, Cooper and Latta 1962; 19-29% in Minnesota, Kwak and Henry 1995; 30% Connecticut, Edwards et al. 2004). Thus, although a substantial percent of the bass population in Brushy Creek is captured
and may experience some type of angling induced mortality, natural mortality likely provides a buffer to such effects. As such, angling mortality likely has little effect on bass abundance.

Although our assessment of total mortality showed that tournaments contribute marginally to total mortality and abundance is likely unaltered in bass populations, other population level effects, such as reductions in size-structure, may result if capture and mortality rates if tournament bass are skewed towards large bodied individuals targeted by tournament anglers (Hayes et al. 1995; Allen et al. 2004; Hysmith et al. 2014). Although medium bass (≥ 381 mm) were captured more frequently than large bass (>457 mm), a larger portion of the large bass population was captured at tournaments and large bass had higher mortality rates (Chapter 5). Thus, in addition to bass anglers successfully capturing bass for fishing tournaments (Chapter 2), they successfully capture larger bass within the population (Gabelhouse and Willis 1986; Fisher 1997; Staggs 2005). While we hypothesized that these unequal capture and mortality rates may result in long-term size-structure effects, changes in mortality and capture probability of bass in each size groups only showed marginal differences in population size-structure (Chapter 5).

While each assessment in this study added to our understanding of bass population dynamics, some common themes were apparent. The importance of environmental influence in both capture probability and mortality was a reoccurring pattern. Air temperature was commonly positively related to increased capture probability (Chapters 2, 3, 4, 5), indicating that weather patterns play a large role in recreational and tournament anglers ability to capture bass. Increased temperature is a known driver in fish metabolism (Fry 1971; Brett and Glass 1973), likely leading to increased vulnerability of bass to angling through increased foraging rates. Further, air temperature is related to large-scale weather patterns that may result in changes of light levels,
water clarity, turbidity, and pressure. These changes may alter both the feeding activity and sensory abilities of fishes (Stoner 2004; Coutant 1975), further driving bass capture probability. These findings are important especially in Northern latitude systems where seasonality is more apparent and changes in weather patterns may result in dramatic shifts in fish behaviors (Niimi and Beamish 1974). Seasonal and environmental influences were also important in describing bass mortality rates (Chapters 2, 3, 4, 5). Increases in air temperature led to decreases in survival of bass captured by recreational and tournament anglers (Chapter 4). Temperature can influence survival of bass due to warmer water in live-wells and bags during weigh-in procedures with angling mortality disproportionately affecting larger bodied bass (Chapter 5). Water temperature described both bass natural and delayed tournament mortality (Chapters 2, 4). While water temperature can influence feeding and growth of bass (Beamesderfer and North 1995), increased water temperatures can also lead to decreased recovery of bass after release and increase delayed tournament mortality (Cooke and Suski 2005).

Several questions remain concerning potential effects of tournament angling on bass populations in Iowa. First, is Brushy Creek representative of other Largemouth Bass populations in Iowa? While we know of other Iowa lakes that experience high levels of tournament fishing pressure (Twelve Mile and Three Mile lakes, Union County, IA), these systems do not approach the number of tournaments experienced on Brushy Creek each year. Further, Brushy Creek is a relatively new system (impounded in 1998), resulting in large amounts of course woody habitat and vegetation and is relatively deep for an Iowa reservoir (22.9 m maximum depth). As a younger reservoir, with reasonable water quality and notable habitat availability, Brushy Creek may have high bass recruitment, leading to increased ability to replace fish lost to mortality sources (Ahrenstorff et al. 2011; Sass et al. 2012). However, other Iowa systems are older and
more degraded in water quality and habitat, leading to the potential for less resilient bass populations. Future assessments should evaluate the interactions of lake ageing and environmental influences with angler mortality on bass populations in Iowa.

Secondly, how variable are natural mortality rates of other bass populations, what factors are driving variation in natural mortality, and what is the interplay between angler and natural mortality rates? Traditionally, natural mortality rates in Largemouth Bass increase with latitude, mean air temperature, and degree-days exceeding 10 °C (Beamesderfer and North 1995). Thus, high bass natural mortality in Brushy Creek was unexpected, it was higher than many systems in Southern regions and lower than many Northern systems (Beamesderfer and North 1995). However, other Iowa systems exhibited similar rates (0.40 to 0.50, Pitlo and Bonneau 1992; 0.65 in Smallmouth Bass, Jansen et al. 2008), giving some support for this pattern. Additionally, many Northern latitude bass populations are considered slow growing. The statewide average length of bass at age four in Iowa is 343 mm and 381 mm at age five (Hayes et al. 2016), whereas age four bass in Brushy Creek were on average 395 mm, and age five bass were 414 mm (Sylvia et al. in prep), indicating growth of bass in Brushy Creek lake is higher than other bass populations in the state. Higher than average growth rates in bass populations may result in higher natural mortality rates (Stroud 1948; Pauly 1980; Moreau 1987). Thus, opportunities exist to expand our understanding of how growth rates and natural mortality rates interact with angling mortality to affect bass populations.

Third, to what degree are long term learned and evolutionary behaviors acting on bass capture probability at Brushy Creek? Although Brushy Creek is considered a young lake, high fishing pressure can lead to long-term changes in capture probability and survival of fish. Both learned behaviors (lure avoidance, Hackney and Linkous 1978; Clark 1983; loss of naivety,
Burkett et al. 1968; Anderson and Heman 1969; Farabee 1970; Hessenauer et al. 2016), behavioral changes post capture (O’Hara 1986), and selective forces (Philipp et al. 2009) paired with fishing mortality can drive changes across populations. If high angling pressure resulted in faster growing, capture prone segments of the population, estimates of capture probabilities may not be representative of the entire population. Evaluating fishery-induced changes in Brushy Creek may also help to understand potential future changes in the population. For example, selection against high vulnerably lines of bass can lead to decreases in reproductive fitness, aggressiveness and metabolic rates (Philipp et al. 2009; Sutter et al. 2012; Hessenauer et al. 2015). Assessing the degree, if any, to which this highly angled bass population is influenced by angling induced evolution will allow for preemptive management against such forces.

Finally, with the high levels of release rates of bass (Henry 2003; Isermann et al. 2013), is management of bass populations needed? High natural mortality rates of bass in Brushy Creek paired with low angler induced mortality lead us to reasonably conclude that recreational angling of bass in Iowa likely have little effect on the survival and structure of populations. These findings are growing across bass studies (Hansen et al. 2015; Miranda et al. 2017) and recent work has suggested that catch and release fishing mortality can help release bass from density dependent growth and increase size-structure in populations (Hansen et al. 2015; Miranda et al. 2017). Thus, catch and release mortality that releases bass from density-dependent growth may be one reason why Brushy Creek is considered the best bass fishery in the state of Iowa and one to the top 25 best bass fishing lakes in the central U.S. (Bassmaster 2016). Future management of bass populations in Iowa should begin with assessments of natural mortality to determine if some protection against angling induced mortality exists. If there is concern for population level impacts, assessment of relative influences of mortality sources on populations would be valuable.
in guiding management decisions (i.e. seasonal fishing closures; reduction in number of
tournament events; catch-weigh-immediate release events and slot limits tournaments). Further
in-depth evaluations of other Iowa lakes will continue to add to our current knowledge. Although
several questions are still unanswered, this study has set a strong foundation for future
assessments of bass population dynamics in Iowa and will be useful in continued efforts to
understand and manage tournament angling on Largemouth Bass populations.

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