INFLUENCES OF CATCH-AND-RELEASE ANGLING ON FISH AVOIDANCE
BEHAVIOR

by

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Newly opened recreational fisheries provide the opportunity to explore direct social impacts on controlled (i.e., managed), naïve (i.e., previously unexploited by anglers) population of fish. Herein, we examine the direct influence of angling on wild fish populations, and aim to identify the behavioral outcomes in fish resulting from angling through laboratory experiments. Using two naïve fish populations from newly opened reservoirs in Nebraska, we assessed the short-term (30 d) response of fish populations to recreational angling. At one reservoir, we noted declining catch rates in catch-and-release regulated fish but not in harvested-regulated fish. We hypothesized that caught-and-released fish were given the opportunity to alter behavior, whereas harvested fish were presumably removed from the waterbody after capture with no opportunity to alter behavior. In addition, we evaluated behavioral types (i.e., bold and shy) in fish and whether they affect ability to learn to avoid subsequent recapture in the laboratory. Ration level and gear type, which consisted of a straightened hook with a worm (no hooking potential), a hook with a worm, and a lure with a worm, were varied across treatments to assess the role of hunger and visual cues on a fish's propensity to be caught. We observed that both shy and bold individuals had a decreased probability of capture over the seven-day experiment. Bolder individuals exhibited a greater probability of capture across gear types compared to shyer individuals. Ration level appeared to have little influence on the

probability of capture. Fish exposed to the control gear showed little change in the probability of capture. Fish exposed to lures exhibited lower probability of capture than the hook and control gears across behavioral types. The learned avoidance of capture has strong implications for fishing-induced evolution, efficacy of management regulations and satisfaction of anglers.

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TABLE OF CONTENTS

List of Tables

List of Figures

Appendix figures

Glossary

Behavioral syndrome – correlated behaviors that are repeated across contexts at a

population or species level

Behavioral type – an individual's unique "personality", or repeatable behavioral

characteristics (e.g., how active, and explorative an individual is)

Boldness – an individual's propensity to be active, explorative and aggressive

Catchability coefficient (q) – the proportion of the fish population that an angler can

expect to catch with one unit of effort

Learning – behavioral change resulting from the introduction of negative stimuli

Naïve – previously unexposed to recreational angling

Vulnerability – an individual's susceptibility to being caught by anglers

CHAPTER 1. INTRODUCTION

Understanding the complex influences that humans exert on ecological systems is essential in a rapidly changing world. The web of interactions and feedbacks between the social system (humans and the social dynamics that regulate them) and the ecological system (abiotic and biotic factors of ecosystems) make up social-ecological systems (Folke 2006). It is important to recognize that social systems exert powerful, direct pressures on ecological systems, but it is also important to explore the unintentional or indirect effects that occur in the interaction between social and ecological systems (Liu 2007). For example, unintended behavioral change in species can occur from social-ecological interactions (Díaz Pauli and Sih 2017; Arlinghaus et al. 2017). The resulting behavioral changes may lead to "landscapes of fear," where prey populations alter their foraging or movement behavior because of perceived predation risk (Laundré et al. 2001). Humans impose landscapes of fear through their interactions with wild populations (Frid and Dill 2002; Ciuti et al. 2015a, 2015b), but it can be difficult to accurately isolate behavioral outcomes resulting from human influence due to the complexity of ecological systems.

Systems that are naïve (i.e., where some, or all, of the organisms in the system have no previous interactions with human influences) offer the chance to observe organisms in the absence of human interaction. However, systems unaffected by humans are rare (Parmesan and Yohe 2003). Recreational fisheries are one of the few opportunities to explore social impacts on naïve (i.e., previously unexploited by anglers) populations of fish (Hessenauer et al. 2015; Hessenauer et al. 2016). Herein, we examine the direct influence of angling on wild fish populations, and aim to identify the

behavioral outcomes in fish resulting from angling through both field observation and laboratory experiments.

Population-level effects in an ecosystem may have the power to influence the overall resiliency of the ecosystem, or how much disturbance the system can endure before it is driven into an alternative stable state [Holling 1973]). Humans put significant pressure on ecological systems (Steffen et al. 2004; Folke et al. 2004), which can drive regime shifts where an ecosystem switches from one stable state to another stable state (whether desirable or undesirable) (Scheffer et al. 2001, Scheffer and Carpenter 2003). Normal predator-prey interactions incorporate both mortality and perceived predation risk that results in prey behavioral change (Lima 1998), and the interactions between humans and wildlife have similar outcomes. Thus, the mechanisms that drive a human-induced regime shift between states may be indirectly initiated through behavioral changes resulting from encounters with humans and perceived predation risk, in addition to directly initiated through mortality or removal of a species (Sih et al. 2011). However, humans also can exploit wild populations (e.g., species extinctions, commercial fisheries collapse) and induce evolution by consistently selecting for certain desirable individuals from the population (Palumbi 2001; Allendorf and Hard 2009; Sullivan et al. 2017), thereby decreasing resiliency in populations and increasing the rate of potential regime shifts (Folke et al. 2004).

Naïve study systems can help isolate the outcomes of social influences on ecological components of a system by ensuring that the populations in question have not been previously influenced by humans and thus observed behavioral changes will likely be a result of the human influence. Recreational fisheries management often creates naïve

systems each time a reservoir is opened or restored. Stocked fish populations in newly opened reservoirs allow for observation of how a previously inexperienced population of fish responds to human influence in the form of recreational angling. A response can be tracked using relative population catchability and angler catch rates.

Recreational fisheries populations often display reduced catchability over time (Post et al. 2002; van Poorten and Post 2005; Díaz Pauli and Sih 2017). Commonly, reductions or variations in catchability are attributed to seasonal and yearly affects (i.e., fish spawning, temperature shifts, food availability), unrelated to angler effort (Lux and Smith 1960; van Poorten and Post 2005; Guy and Willis 1991). However, there are many instances where variation in catchability is unclear and may be driven by anglers (Cox and Walters 2002; Heermann et al. 2013; Askey et al. 2006). Particularly in catch-and-release-regulated fisheries (i.e., where fish species are regulated through restrictive length limits or managed as no-take), fish respond to the threat of angling by altering behavior to avoid hooks (e.g., Van Poorten and Post 2005; Askey et al. 2006; Alós et al. 2015; Arlinghaus et al. 2017). The concept of behavioral change resulting from catch-and-release fishing was described as "angling-induced timidity syndrome" where fish are driven to be less catchable by the experience of capture (Arlinghaus et al. 2017).

The role of individual fish may be integral to understanding population-level change in response to social pressures. Many fish species display a boldness continuum where individuals fall along a spectrum from aggressive and active (bold) to timid and inactive (shy) (Wilson et al. 1994; Coleman and Wilson 1998; Sneddon 2003). Bold individuals are typically less risk averse, display more aggressive and active behaviors, and tend to distribute themselves in open water more often than shy individuals (Wilson

and McLaughlin 2007). In contrast, shy individuals are more risk averse, display less aggressive behaviors and tend to stay close to shelter in the littoral zone (Wilson and McLaughlin 2007). The boldness continuum is known as a behavioral syndrome, in which populations are constrained in their potential responses to stimuli by certain tendencies in their behavior (Sih et al. 2004). The behaviors by which an individual is constrained has been described as personality or behavioral type (Sih et al. 2004). Individual behavioral types are thought to be linked to underlying genetic dispositions (Dingemanse et al. 2002; Ariyomo et al. 2013; Dochtermann et al., 2015). Several studies have demonstrated that fish display varying levels of vulnerability to angling based on their relative boldness (Fernö 1983; Härkönen et al. 2014; Philipp et al. 2009; Biro and Post 2008; Wilson and Godin 2009). If fish respond to the threat of capture by learning to avoid hooks, then an individual's behavioral type my play a critical role in their ability respond effectively. Currently, no studies explore the potential influence behavioral type plays on an individual's ability to learn to avoid capture, which directly influences its vulnerability to angling over time.

Fisheries are traditionally managed under the assumption that all fish of catchable sizes are vulnerable to be caught and that catchability can only be affected through increasing population abundances or more efficient gear. However, the traditional view ignores the nonlinear relationship of catch rates with effort and the possible behavioral changes that may occur because of multiple captures of individuals (Cox and Walters 2002; Askey et al. 2006). It is theorized that there are four states that a fish can exist in at any one time: 1) available and reactive to anglers (i.e., vulnerable), 2) fish harvested by anglers, 3) fish unavailable and unreactive to anglers (i.e., invulnerable), 4) fish in a

refractory state (i.e., temporarily invulnerable) after being released by anglers (Cox and Walters 2002). Fish are available to anglers based on size (i.e., gear limitations [Wilde et al. 2003]), physiological state, and location within a waterbody, and fish are reactive or unreactive to anglers based on the behavior of the fish (Cox and Walters 2002).

There is a lack of research conducted on the factors influencing the movement between vulnerable and invulnerable states, but it is likely that behavioral types may play a significant role. Behavioral type likely influences how a fish perceives and responds to risk (Wolf et al. 2008; Dingemanse and Wolf 2010; Klefoth et al. 2012), and resource availability (i.e., prey abundance) (Biro and Stamps 2008). For example, risk allocation theory predicts that frequent periods of high risk in conjunction with resource limitation will force individuals to forage under the threat of predation to acquire the nutrients necessary to subsist (Lima 1998; Lima and Bednekoff 1999). Individuals that are more aggressive may be less likely to alter their behavior in response to risk (Huntingford and Adams 2005), and therefore may consume more but be at higher risk for predation (Biro and Stamps 2008). Furthermore, differences in space use between behavioral types (e.g., occupying the littoral or limnetic zones) (Wilson and Mclaughlin 2007) can also influence risk assessment (Stankowich and Blumstein 2005) by altering when and how an individual reacts to a predator. Given the adaptive variation among behavioral types, behavioral type may play a key role in vulnerability to angling and the ability to learn after being caught and released. Within the concept of learning, individuals can be described as informed or naïve based on whether they have knowledge of an experience (e.g., previous hooking experience). Here, we define learning as a behavioral change in response to negative stimuli (Dill 1983; Warburton 2003).

Few studies have attempted to explore the interplay between behavioral types and learning (Sneddon 2003), and those that have produced contradictory results (Nomakuchi et al. 2009; Kurvers et al. 2010a). However, studies indicate that bold individuals are more likely to be leaders, and shy individuals are more capable of utilizing social information (Harcourt et al. 2009; Kurvers et al. 2010). If bold and shy individuals learn at different rates, the rate at which individuals move between vulnerable and invulnerable pools in recreational fisheries may depend on behavioral type, making one type consistently more, or less, vulnerable to angling than the other. If there is individual variance in learning capability, then it is likely that a continuum of vulnerability will exist. For example, a fish that is caught several times may move into increasingly less vulnerable states with each successive capture. As fish experience hooking and survive, they may advance into a more knowledgeable, and less vulnerable state (i.e., become less catchable). However, advancement may depend on an individual's ability to learn, such that a less perceptive individual may remain in the same vulnerable state even after subsequent captures.

If unique behavioral types learn and exist in different vulnerability states, then angling should impose different selective pressures on different behavioral types and their underlying genetic components. Several studies have aimed to identify the selective pressures recreational angling places on populations (e.g., Biro and Post 2008; Philipps et al. 2009; Saura et al. 2010; Hessenauer et al. 2017). Bold, rapidly growing fish were shown to be selectively harvested over shy individuals in a simulation of a commercial gillnet fishery (Biro and Post 2008). Additionally, vulnerability to angling in largemouth bass was identified as a heritable trait and demonstrated, through controlled angling

experiments, that vulnerability increased over successive generations (Philipp et al. 2009). Selection on a behavioral type may lead to less vulnerable and less diverse fish populations over time, which may have severe consequences for the resiliency of the population and the fishery (Conrad et al. 2011).

Using two naïve populations in newly opened reservoirs in Nebraska, we assessed the short-term (30 d) response of fish populations to recreational angling. Additionally, we performed laboratory experiments on rock bass *Ambloplites rupestris* to evaluate individual behavioral types and their effect on angling vulnerability and ability to alter behavior after capture. We included level of satiation, lure type, and behavioral type as important variables in vulnerability to fishing pressure. Though individual variance will always be present, identifying a driving factor of vulnerability will help to determine when and why individuals fluctuate between vulnerable and invulnerable states, and the role learning and behavioral type plays in dictating movement between vulnerability states. Identifying the most influential factors in determining fish vulnerability and behavioral change will allow managers to make informed decisions regarding regulations, and will lead to more sustainable fisheries.

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CHAPTER 2. INTRODUCTION OF ANGLING TO NAÏVE FISHERIES

INTRODUCTION

From city dwellers traversing crowded streets to farmers interacting with livestock, humans are immersed in social-ecological systems at a multitude of geographic and temporal scales (Birge et al. 2016). Social-ecological systems are defined by the interactions and feedbacks between humans and the abiotic and biotic factors of the environment, and are difficult to study because of the complexity of the interactions (Arlinghaus et al. 2017). Additionally, each component in the social-ecological system is inherently dynamic, further complicating attempts to tease out interactions, feedbacks, and outcomes (Folke et al. 2004; Post 2013). Understanding the outcomes that result from human impact on wild populations is necessary for both conservation and management of wild species.

An ecosystem's resilience, or how much disturbance a system can endure before it is driven into an alternative stable state (Holling 1973), is an important topic as humans continue to put pressure on ecological systems (Steffen et al. 2007). Often, humans can drive regime shifts (i.e., where an ecosystem is forced to transition from one stable state to another because of human-induced disturbance [Folke et al. 2004]). Naïve study systems (i.e., no previous interactions with humans) can help isolate the social influences on ecological components of the system by ensuring that the population has not been previously influenced by humans. Naïve systems are rare and may be difficult to identify, but recreational fisheries management often create naïve systems each time a reservoir is opened or restored. These new recreational fisheries offer the opportunity to study social-ecological interactions because newly built or stocked reservoirs allow for the

observation of how a previously unexploited population of fish responds to human influence.

Angler catch rates are often used as measures of success in recreational fisheries but are also a useful tool to assess the condition of a fishery (Hilborn and Walters 2013). Studies of dynamic catch rates in recreational angling have historically focused on biotic rather than social variables (Hunt et al. 2013). Seasonal changes such as food availability, habitat conditions, temperature, and predator abundance influence catch rates (Lux and Smith 1960; Cox and Walters 2002; van Poorten and Post 2005), but these factors do not account for all the variation observed in catch rates (van Poorten and Post 2005). Recent studies have sought to identify social-ecological interactions to account for variation in catch rates (Cox and Walters 2002; Post et al. 2002; van Poorten and Post 2005). Human social variables are inexplicitly tied to the dynamics of fished populations and aquatic ecosystems (Post 2013). Angling can have physiological and life history effects on fish populations, including angling-induced evolution (i.e., selection in the form of removal through harvest) (Biro and Post 2008; Heino et al. 2015). In harvest-regulated (i.e., species managed to be harvested by anglers) fish populations, it is common for angling practices to truncate size and age ranges and decrease biomass in exploited populations (Goedde and Coble 1981; Paukert and Willis 2001). Alternatively, catch-and-release-regulated (i.e., species managed with restricted or no harvest regulations) populations avoid direct mortality from human interaction, but can still experience physiological stress, behavioral changes, and sub-lethal effects that can alter recreational fisheries (Klefoth et al. 2008; Cox and Walters 2002). For example, many studies of recreational fisheries demonstrate that populations display reduced catchability over time (e.g., Van

Poorten and Post 2005; Philipp et al. 2009) and in catch-and-release regulated fisheries, fish may respond to the threat of angling by learning to avoid hooks (e.g., Askey et al. 2006; Alós et al. 2015).

Understanding how fish behave post-release is fundamental to assessing the influences of catch-and-release angling. The potential exists for caught-and-released fish to subsist in 'refractory' states after experiencing the negative stimuli (e.g., hooking, being taken out of the water, and handled) associated with a catch-and-release event, during which time fish may be invulnerable to angling due to the stress of the experience (Cox and Walters 2002). Gaining a better understanding of the vulnerable and invulnerable sub-populations of fish, and whether angler effort shifts fish between vulnerable states is a critical component to successfully managing a productive recreational fishery (Cox and Walters 2002). If enough angling effort is exerted on a system, much of the fish population may experience capture-related stress and subsequently become invulnerable to angling for an undetermined amount of time (Cox and Walters 2002), resulting in a regime shift to an exploited system. Additionally, behavioral shifts in fish resulting from the stress of capture may cause behavioral cascades (i.e., behavioral changes affecting interactions with other trophic levels such as prey), leading to a destabilization of the community and disrupting fish recruitment (Post 2013; Romare and Hansson 2003). Low-quality fisheries not only lead to a decrease in satisfaction among anglers, but also result in management expenditures to improve angling and waterbody condition (e.g., supplemental stocking, prey stocking, and fish renovations) (Cox and Walters 2002).

In assessing recreational fisheries, angler efficiency is generally determined by the catchability coefficient, or the efficiency of the gear used by the fisherman (i.e., rod and reel). Using information collected from angler surveys on catch and effort, and based on the assumption that the stocking information describes the relative abundance of the populations available to be caught, we can calculate a numerical representation of the catchability of the population at the onset of angling and at the completion of the 30-days, providing another tool to assess the potential outcomes of social-ecological interactions on the fish population.

A better understanding of the impact of the social component on the ecological component is crucial in successfully managing social-ecological systems like recreational fisheries (Hunt et al. 2013; Pope et al. 2014). Through identification of these critical interactions, we can promote sustainable systems by altering our own behavior in the social sphere to achieve desired outcomes from the ecological sphere. The objectives of the study were to assess two naïve systems during the first 30-days post introduction of angling to determine: (1) if we can identify a decline in catch rate and catchability over the 30-day period, and (2) whether catch rate differed among harvest-regulated and catch-and-release-regulated species. The short 30-day time scale does not afford the opportunity to observe the long-term structural and physiological outcomes of exploitation on harvested-regulated and catch-and-release populations, but it should provide enough time to observe short-term behavioral changes in the populations.

METHODS

Study area

Lake Wanahoo. -- Lake Wanahoo (Fig. 2-1A) is a 258-ha reservoir located in the Sand

Creek Watershed in Saunders County, Nebraska that is managed by the Nebraska Game

and Parks Commission (NGPC). The reservoir provides flood protection, environmental

restoration, and recreational opportunities. Construction of the dam and lake

enhancements was completed in 2009 and the reservoir was filled by late 2010. Stocked

fish were given a minimum of 11 months (354 days) and a maximum of 29 months (898

days) development time prior to the onset of angling (Table 2-1). Wanahoo was stocked

with largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*, black

crappie *Pomoxis nigromaculatus,* northern pike *Esox lucius*, walleye *Sander vitreus,* and

channel catfish *Ictalurus punctatus.* The reservoir was opened to recreational angling on

April 28, 2012 at sunrise (0800). During the study period, there was a 533-mm length

limit on largemouth bass, no harvest on northern pike, a bag limit of 15 for panfish (e.g.,

crappie and bluegill), and a no wake regulation throughout the lake. The study was

concluded on May 29, 2012.

Prairie Queen Lake. -- Prairie Queen Lake (Fig. 2-1B) is a 53-ha reservoir located in

Sarpy County, Nebraska that is managed by NGPC. The reservoir provides flood control

and recreational use. Construction on the reservoir and lake enhancements was completed

in the summer of 2014 and the reservoir was filled by late 2014. Stocked fish were left to

develop for a minimum of 6 months (187 days) and a maximum of 23 months (706 days)

prior to the introduction of angling. Prairie Queen Lake was stocked with largemouth

bass, bluegill, black crappie, redear Sunfish *Lepomis microlophus* and channel catfish. It was opened to recreational angling on Tuesday, March 31, 2015. At the time, there was a 381-mm length limit on largemouth bass, a bag limit of 15 panfish, and a no wake regulation throughout the lake. The study was concluded on April 30, 2015.

Angler surveys

To assess catch per unit effort (CPUE), we surveyed anglers during the first 30-days following the opening of the reservoir. The in-person survey was approved by the University of Nebraska – Lincoln Institutional Review Board (IRB # 27616). We used a stratified multi-stage probability-sampling regime (Malvestuto 1996) to determine days of interviews. Each interview day was further stratified into a morning (sunrise to 1330) and evening (1330 to sunset) period. A survey period consisted of instantaneous counts from several vantage points to assess angling effort and roving in-person interviews to assess catch. Instantaneous counts were conducted at randomized times within the survey period and were performed by circling the lake and counting active anglers. Survey technicians gathered information from anglers about trip length (duration of angling for that day), species sought, access method (boat or bank) and species caught-and-harvested, and caught-and-released. To explore catch rate differences between harvest-regulated and catch-and-release regulated species, we were specifically interested in the CPUE relative to largemouth bass (essentially catch-and-release-regulated given no harvest at Wanahoo and extremely low harvest at Prairie Queen) and northern pike (a catch-and-release-regulated species) and bluegill and crappie (harvest-regulated species).

Lake Wanahoo. -- During opening weekend (Saturday, April 28, 2012 – Monday, April 30, 2012), Lake Wanahoo was surveyed from 0630 to 2030, with instantaneous counts taken every hour. Following opening weekend, eight weekday afternoons, seven weekday mornings, two weekend afternoons, and three weekend mornings were randomly selected from the next 29 days. The greatest length between survey days was three days. During these sampling times, two instantaneous counts were conducted during each survey period. Lake Wanahoo's opening was considered a hard opening because it was scheduled on a weekend (Saturday).

Prairie Queen. -- During Prairie Queen's opening (Tuesday, March 31, 2015 – Wednesday, April 1, 2015) and the first weekend following opening (Saturday, April 4, 2015 – Sunday, April 5, 2015), surveys were conducted from 0700 to 2100, with instantaneous counts taken twice during each period (for a daily total of four). Following opening, six weekday afternoons, five weekday mornings, two weekend afternoons, and three weekend mornings were randomly selected from the next 29 days. The greatest length between survey days was two days. During these sampling times, two instantaneous counts were conducted during each survey period. Prairie Queen's opening was considered a soft opening because it was scheduled on a weekday (Tuesday).

Temperature information. -- Temperature data were collected from the historical weather information portion of Weather Underground's website (Weather Underground INC, 2016). Air temperatures were collected from the nearest airport to Lake Wanahoo

(Wahoo Municipal Airport) and Prairie Queen Lake (Milliard Municipal Airport) during

the study periods. Temperatures were transformed from Fahrenheit to Celsius.

Analysis

Angler effort. -- We calculated daily angling effort ($E_{angling}$) per hectare from the

instantaneous counts following Malvestuto et al. (1978). Effort was calculated by:

$$E_{angling} = \frac{\overline{C}_{period} * L_{period} * \frac{1}{P_{period}}}{hectare}$$

where $\overline{C}_{period}$ is the mean number of anglers counted during the instantaneous counts,

L_{period} is the period length (7 hrs), and P_{period} is the probability of selecting the period

(0.5 for both waterbodies). During the opening weekend of Wanahoo, both periods were

surveyed each day, therefore P_{period} was unnecessary and daily effort was calculated as:

$$E_{angling} = \sum \overline{C}_{period} * L_{period}$$

Catch per unit effort. -- Catch-per-unit-effort (R) was calculated using the mean of ratios

estimator, with all trips less than 30 minutes disregarded following Hoenig et al. (1997).

$$R = \frac{1}{N} \sum_{j=1}^{N} \frac{C_j}{L_j * n_j}$$

where C_j was the catch of angler party j up to the time of interview, L_j be the length of the

trip (hours) to the time of interview, n_j is the number of anglers in the party, and N is the

total number of parties interviewed during that survey period. During the opening

weekend of Wanahoo, CPUE was calculated separately for each period. A separate

CPUE was calculated separately for each of the species of interest. In addition, harvest

rates were calculated similarly except rather than the number of fish caught by the party

(C_j) the number of fish harvested H_j was used.

Extrapolated effort. -- The total angling effort and number of fish harvested for the 30-d

study period was calculated using the strata-estimator approach described in Rasmussen

et al. (1998). Briefly, effort and harvest estimates and associated variances within a

stratum (i.e., weekday and weekend) were estimated by multiplying the mean effort and

mean harvest rates and then multiplying by the number of days during that month in the

strata. The strata harvest estimates and associated variances were then summed to get a

total harvest estimate.

Catchability coefficient. -- The catchability coefficient represents the relationship

between the catch per effort (CPUE) exhibited by the fishery and the number of fish

available to be caught, and can be thought of as the proportion of fish in a population that

an angler can catch with one unit of effort (Arreguín-Sánchez 1996). We can estimate the

catchability coefficient of a fish population using the following equation:

$$q = \frac{C}{E*N},$$

where q is the catchability coefficient, C is the catch, E is effort and N is the assumed

number of fish in the population. The q variable provides a simple way to assess the

relationship between discard mortality (a potential source of mortality for catch-and-

release-oriented species in the study lakes given the lack of harvesting) and the effects of

human-induced behavior change. Because q is determined by both the catch per effort of

anglers and the number of fish in the population, it allows us to model assumptions about the population dynamics of fish sought by anglers. Herein, we assume that the stocked densities prior to opening the reservoir represent N_0 or the initial assumed number of fish in the population. N_{t+1} is then calculated as,

$$N_{t+1} = C_t * D_i ,$$

where D_i is a deterministic percent of fish that die post capture (Di=30%, 10%, and 0%). In this case, we will only estimate each q_i based on the catch and effort values for largemouth bass at Lake Wanahoo and Prairie Queen Lake. Using the stocking information to estimate our N and assuming no recruitment or natural mortality, we can demonstrate the tradeoffs between mortality (i.e., harvest or discard) and human-induced behavior change within the population of largemouth bass at Lake Wanahoo and Prairie Queen Lake.

Statistical analysis. -- We were interested in how angler catch rates varied during the 30-d study at each reservoir. We assessed the relationship between angler catch rates and time (days) at each reservoir using linear regression with date since reservoir opening as the dependent variable and angler catch rates as the independent variable. The significance of each relationship was assessed using a simple analysis of variance test (ANOVA). For each test, we provide the associated p-value for the ANOVA. In addition, we provide the coefficients for all the linear regression models including F statistic, residual degrees of freedom, and variance explained (i.e., R^2).

A simple t-test was conducted to assess whether there was a statistical difference between the mean temperatures observed throughout the study period at Lake Wanahoo and Prairie Queen Lake.

RESULTS

Lake Wanahoo. -- A total of 825 interviews were conducted at Wanahoo during the first 30 days. The total effort on opening day was 11.1 hours per hectare. The catch for opening day included 7945 ± 1359 (SE) largemouth bass, 503 ± 106 northern pike, 15 ± 10 bluegill, and 382 ± 125 crappie. Over opening weekend, mean catch rates for largemouth bass fell consistently from 2.77 ± 0.47 (opening day Saturday) to 2.49 ± 0.37 (Sunday) and 2.04 ± 0.38 (Monday) fish per angler hour, and then spiked to 6.47 ± 4.18 on the Tuesday following opening weekend (Fig. 2-8).

Largemouth bass catch rates ranged from 0.28 ± 0.46 (SE) to 6.47 ± 0.46 fish per angler hour on weekdays and from 0.07 ± 0.37 to 2.77 ± 0.37 fish per angler hour on weekends. Northern pike catch rates ranged from 0.0 ± 0.02 to 0.26 ± 0.02 on weekdays and from 0.00 ± 0.03 to 0.18 ± 0.03 fish per angler hour on weekends. Bluegill catch rates ranged from 0.02 ± 0.11 to 1.39 ± 0.11 fish per angler hour on weekdays, and from 0.01 ± 0.07 to 0.49 ± 0.07 fish per angler hour on weekends. Crappie catch rates ranged from 0.04 ± 0.40 to 6.25 ± 0.40 fish per angler hour on weekdays, and from 0.00 ± 0.10 to 0.88 ± 0.10 fish per angler hour on weekends.

Daily angling effort per hectare ranged from 1.2 ± 0.6 to 9.2 ± 0.6 hours during weekdays and from 2.9 ± 1.1 to 13.9 ± 1.1 hours on weekends (Fig. 2-2). Total angling effort for bank anglers during the study was 15,938.73 ± 1,160.70 hours and total angling

effort for boat anglers during the study was 14,175.00 ± 1,178.11. Totals of 58,043 ± 5,016 largemouth bass, 3,435 ± 369 northern pike, 26,284± 3,627 crappie, and 35,529 ± 2,291 bluegill were reported caught during the study period. Of those, zero largemouth bass, zero northern pike, 15,335 ± 2,469 crappie, and 7,633 ±1,087 bluegill were harvested.

Prairie Queen Lake. -- A total of 391 interviews were conducted at Prairie Queen during the first 30 days. The total effort on opening day was 4.6 hours per hectare. The total catch for opening day was 380 ± 105 largemouth bass (CPUE 1.6 ± 0.4). No other species of fish were reported caught during opening day.

Largemouth bass catch rates ranged from 0.00 ± 0.40 to 5.07 ± 0.40 fish per angler hour on weekdays, and 0.00 ± 0.30 to 2.75 ± 0.30 fish per angler hour on weekends. Bluegill catch rates ranged from 0.00 ± 0.00 to 0.04 ± 0.00 fish per angler hour on weekdays, and 0 bluegill were caught on weekends.

Daily angling effort ranged from 0.1 ± 0.4 to 6.7 ± 0.4 hours per hectare during weekdays and 0.7 ± 0.9 to 11.8 ± 0.9 hours per hectare on weekends (Fig. 2-3). Total angling effort for bank anglers during the study was 3,616 ± 564 hours and total angling effort for boat anglers during the study was 2,144 ± 297 hours. Largemouth bass and bluegill were the only species indicated caught in the angler survey. The total catch estimates were 10, 833 ± 1882 largemouth bass and 574 ± 533 bluegill. The only fish reported harvested during the survey were two largemouth bass (both 381-mm), which predicted a harvest estimate of 20 ± 15 largemouth bass.

Catchability. -- The catchability model for Lake Wanahoo (Fig. 2-4) demonstrates what the population catchability of largemouth bass (based on stocking density and no natural recruitment or natural mortality) would be assuming discard mortality rates of 30% (red), 10% (green), and 0% (gold). Models used observed data of Lake Wanahoo largemouth bass catch rates to predict catchability under the varying discard mortality rates. Discard mortality rates of 30% and higher resulted in a negative population number of largemouth bass given the observed catch rates at Lake Wanahoo. Catchability estimates ranged from 0.0002061 ± 0.00007 (95% CI) to 0.0002505 ± 0.0002189 on opening day (April 28, 2012) for all discard mortalities (Table A-1). Assuming a discard mortality of 10% provided the greatest catchability coefficient (0.0006480 ± 0.00061), but it resulted in a drastic population decrease from 13,452 to 1,425 largemouth bass over the study period (Fig. 2-5). Using a 0% discard mortality did not allow for any population change, but resulted in a maximum catchability coefficient of 0.000322 ± 0.00027.

The catchability model for Prairie Queen Lake (Fig. 2-6) demonstrates what the population catchability (based on stocking density and no natural recruitment) would be assuming a discard mortality of 30% (red), 10% (green), and 0% (gold). Catchability estimates ranged from 0.0000845 ± 0.00004 to 0.0000850 ± 0.00005 on opening day (March 31, 2015) for all discard mortalities (Table A-2). Assuming a discard mortality of 30% provided the greatest catchability coefficient (0.0004100 ± 0.00032), but it resulted in a population decrease from 11,400 to 7,762 largemouth bass over the study period (Fig. 2-7).

Catch rates over time. -- We assessed the relationship between angler catch rates and time (days) at each reservoir using linear regression with date since reservoir opening as the dependent variable and angler catch rates as the independent variable. Angler catch rates at Lake Wanahoo for catch-and-release-regulated largemouth bass declined over the study period ($F_{1,21} = 15.50$, p-value < 0.001, $R^2 = 0.43$ [Fig. 2-8]), as did the catch rates for catch-and-release-regulated northern pike ($F_{1,21} = 26.17$, p-value < 0.001, $R^2 = 0.55$). Angler catch rates for harvest-regulated bluegill ($F_{1,21} = 1.33$, p-value $= 0.26$, $R^2 = 0.06$) and crappie ($F_{1,21} = 1.87$, p-value $= 0.19$, $R^2 = 0.08$) did not change over the study period. We did not see a significant change over the study period for any of the species caught at Prairie Queen, whether they were catch-and-released-regulated or harvest-regulated (Largemouth bass: $F_{1,23} = 0.26$, p-value $= 0.61$, $R^2 = 0.01$. Bluegill: $F_{1,23} = 1.909$, p-value $= 0.18$, $R^2 = 0.08$ [Fig. 2-9]).

Temperature. -- Lake Wanahoo had a mean $\pm$ SE temperature of 19.34 ± 0.84 °C that was significantly different (T statistic $= -6.73$, degrees of freedom $= 56.13$, P < 0.001) from Prairie Queen Lake's mean temperature of 12.22 ± 0.64 °C (Fig. 2-11).

DISCUSSION

The introduction of angling at Lake Wanahoo resulted in a decline in catch rates similar to other studies that investigated declining catch rates (e.g., Van Poorten and Post 2005) and behavioral change in fished populations (Askey et al. 2006; Alós et al. 2015). We observed decreases in angler catch rates for largemouth bass and northern pike (both catch-and-release-regulated species) over the first 30-days, but we did not observe

changes in angler catch rates for bluegill and crappie (both harvest-regulated species). However, we did not observe a similar relationship in Prairie Queen Lake with largemouth bass and could not assess a relationship with bluegill or crappie given so few caught during the study period. The varying results between reservoirs exemplify the complexity inherent to social-ecological systems and the difficulty in studying human-induced disturbance. Given the results of the study, there are many mechanisms that influence the social-ecological relationship between anglers and fished populations.

The declining catch rates among catch-and-release-regulated species at Lake Wanahoo could indicate an exploitation-driven regime shift in behavioral states (Fig. 2-10). However, the lack of relationship observed at Prairie Queen Lake provides an opportunity for careful consideration of the mechanistic differences between the two waterbodies and associated fisheries. The trend observed at Lake Wanahoo for both largemouth bass and northern pike suggests that both populations may have been partially driven into refractory or invulnerable states from catch-and-release angling after the opening of the reservoir (Cox and Walters 2002). Harvested fish have no ability to alter behavior due to mortality, however caught-and-released fish are returned to the waterbody and if they survive the effects of being caught-and-released, can potentially alter their behavior to avoid further capture. Thus, under catch-and-release practices we would expect to see a decline in catchability and little to no decline in harvested fish (unless total abundance was rapidly decreased).

The lack of a significant change in catch rate in the Prairie Queen largemouth bass population suggest that other factors may have also influenced the decline at Lake Wanahoo. Some of the contributing social factors may be varying levels of angler skill

(within a waterbody and during the 30 days) and different opening day management strategies of the reservoirs (i.e., hard [Wanahoo] versus soft [Prairie Queen] opening). Biologically, stocking densities, stocking timing, seasonality, fish life history and behavioral changes are all possible contributing factors.

Angler skill. -- It is difficult to assess skill among anglers, and furthermore, to estimate variation in skill over time. It is common that fisheries are skewed in favor of a small number of anglers catching a disproportionate number of fish (Baccante 1995; Seekell et al. 2011), suggesting some anglers are more adapt at catching and harvesting fish. However, in fisheries with high catch rates (e.g., > 1 fish per angler per hour), the distribution of catch among anglers may be more evenly distributed (Baccante 1995; van Poorten and Post 2005). During high use, variation in angler skill may have the potential to indirectly affect the effort at a water body. For example, at Wanahoo, highly skilled anglers may have avoided situations of overcrowding, which may have caused them to refrain from angling early in the study period (Hunt et al. 2007). After the initial period of high pressure, unskilled anglers may have stopped participating because of declining catch rates, and skilled anglers may have begun participating and continued to drive down catch rates (Post 2013). At Prairie Queen Lake, we may have observed the opposite effect; instead of skilled anglers replacing a portion of unskilled anglers and continuing to drive down catch rates, skilled anglers may have stepped in and masked the decline in catch rates by maintaining the same catch rates as the unskilled anglers despite an overall decrease in catchability of the fish population (Post 2013). An important consideration when assessing effort at a waterbody is the total effort may be consistent across a period

(i.e., Prairie Queen), but the skill (and effectiveness of anglers at catching fish) may not be consistent (Pope et al. 2017).

Hard versus soft opening. -- Lake Wanahoo's opening day fell on a Saturday (hard opening), whereas Prairie Queen Lake's opening day was on a Tuesday (soft opening). Lake Wanahoo experienced more effort opening day than Prairie Queen (11.11 hours per hectare versus 4.62 hours per hectare respectively), and more fish were caught (7,945 ± 1,359 largemouth bass versus 380 ± 105 largemouth bass, respectively). If we compare the number of largemouth bass caught on opening day compared to the total number of largemouth bass over the 30-day period at each reservoir (60,707 at Lake Wanahoo and 10,833 at Prairie Queen), we see that a greater proportion of the largemouth bass population was caught at Wanahoo (0.13) on opening day than at Prairie Queen on opening day (0.04). Therefore, a larger proportion of catch-and-release-regulated individuals at Wanahoo likely experienced the negative stimuli associated with catch-and-release than those at Prairie Queen. A smaller proportion of individuals caught may be an explanation for the lack of declining catch rates at Prairie Queen. If we take catchability into account, the largemouth bass stocked at Lake Wanahoo were larger than the individuals stocked at Prairie Queen (Table 2-1), which may have made individuals at Lake Wanahoo more catchable, or available to anglers, than the individuals stocked at Prairie Queen Lake.

Seasonality. -- Prairie Queen opened in late March, whereas Wanahoo opened late April, which may have also influenced catch rates (McMichael and Kaya 1991). Lake Wanahoo

was significantly warmer than Prairie Queen during first 30 days (Fig. 2-11) after

opening, which may have influenced fish behavior. Additionally, largemouth bass often

spawn when water temperatures are within an appropriate range (typically around 18 -

30°C) (Heidinger 2000), and nest defense is a common practice among males of the

species, which may make them more vulnerable to angling (Suski and Philipp 2004).

Therefore, aggression associated with male nest defense may have played a role in the

increased catch rates observed at Lake Wanahoo. The survey period at Prairie Queen

likely fell prior to intense spawning, which suggest fish may not have been in an

aggressive, territorial state. Furthermore, fisheries are complex systems with many

interactions. There is the potential for many other unforeseeable, biotic or abiotic

seasonal interactions that may account for the discrepancies between catch rates at Prairie

Queen and Wanahoo.

Catchability. -- Fish at Prairie Queen were stocked at smaller size distributions than those

at Wanahoo (Table 2-1), and therefore may have been inherently less catchable than the

populations at Wanahoo. Reduced catchability, in addition to seasonality, may help

explain the lack of an obvious response to angling effort among the largemouth bass

population. Furthermore, it may explain the lack of any significant capture of bluegill and

crappie at Prairie Queen. Modeling the catchability coefficients assuming varying levels

of discard mortality at Prairie Queen (Fig. 2-6) demonstrated a tradeoff between human-

induced behavior change and discard mortality. A discard mortality (30%) was equally

likely to result in the catch rates observed at Prairie Queen as a low discard mortality rate

in conjunction with rapidly decreasing catchability due to behavior change (10%).

Alternatively, even a low discard mortality rate (10%) resulted in an extremely low population (821 largemouth bass) at Lake Wanahoo given the observed catch rates (Fig. 2-4). The instability of the population in the model suggests that it is unlikely discard mortality alone would have resulted in the catch rate decline observed at Lake Wanahoo without irreparably altering the population structure and leading to collapse (Fig. 2-5) (which was not observed).

The results of the catchability coefficient model support the effects of seasonality as an important factor influencing catch rates. The increase in catch rates present at Prairie Queen in the middle of the month (Fig. 2-9) were likely a result of a slight increase in temperature in and around April 13, 2012 (Fig. 2-11) which increased fish's foraging activity and propensity to bite. At all discard mortality levels tested (30%, 10%, 0%), an increase in estimated catchability was described which coincided with the increase in temperature around April 13, 2012.

A caveat to the assumptions used in the catchability model is that no natural recruitment or mortality was included in the estimation of population abundance. In Prairie Queen Lake, the stocking schedule did not likely allow for the recruitment of new individuals to the population (Table 2-1). Lake Wanahoo was an exception, as 10-inch largemouth bass were stocked 898 days prior to reservoir opening. Stocking 898 days in advance would allow for at least one recruitment class to reach catchable sizes. Estimating the average number of recruits from a cohort is difficult without estimating a stock recruit curve, and those data were not available.

Angling-induced behavioral change. -- Anglers primarily practiced catch-and-release of largemouth bass at both reservoirs (no reported harvest of largemouth bass at Lake Wanahoo and 20 harvested at Prairie Queen Lake). In addition, there was little evidence of discard mortality on the shores of the lakes observed during roving creel surveys (Chizinski personal communication). Though discard mortality is always a factor in catch-and-release, it is difficult to accurately quantify and varies between both species and individual fish (Muoneke and Childress 1994, Wilde and Pope 2008). In catch-and-release angling, the opportunity exists for individual fish that are caught and thrown back to alter behavior in the future to avoid subsequent recapture (Askey et al. 2006, Alós et al. 2015).

Fish, in addition to many other species, display predictable, repeatable behaviors in various situations, termed behavioral syndromes (Sih et al. 2004). Within a behavioral syndrome, individuals have a behavioral type that represents the individual's unique expression of the behaviors that exist in the syndrome (e.g., aggression level) (Sih et al. 2004). There is evidence for an underlying genetic component to behavioral types (Dingemanse et al. 2002; Ariyomo et al. 2013; Dochtermann et al., 2015). In fish, behavioral types are often described within the context of a boldness syndrome, where some fish are more active, aggressive, exploratory and bold, whereas others are more docile, inactive, neophobic, and shy. Studies suggest that these individual behavioral types may play a role in a fish's vulnerability to angling, with bold fish being more likely to be caught by anglers (Biro and Post 2008; Härkönen et al. 2014; Alós et al. 2015). If angling selects for bold individuals, then in harvested species we may be removing the bold, aggressive individuals from the population (Biro and Post 2008; Philipp et al.

2009), which could have a drastic effect on the population as it becomes composed of dominantly shy individuals (Sutter et al. 2012). In catch-and-release-regulated species, behavioral changes may cause bold and shy individuals to behave more shyly (Arlinghaus et al. 2017), depending on the inherent plasticity of behavioral types, leading to a homogenization of behavior like what we would see if harvest is removing bold individuals.

CONCLUSION

Social-ecological systems are inherently complex, and our understanding of the dynamics of social-ecological systems is crucial in successful management of wild populations. A disconnect between the studies of the social and biological components of a system is common, and exists in past recreational fisheries research (Arlinghaus et al. 2007; Hunt et al. 2013). In the study, we attempted to identify a direct outcome of social impact on a naïve system in two newly-opened reservoirs where the fish populations were naïve to angling.

The inherent complexity of social-ecological systems makes it impossible to identify and account for all the potential interactions. We noted a change in catch rates for catch-and-release-regulated populations at Lake Wanahoo that was not present in a catch-and-release regulated population at Prairie Queen, and though we conjectured about the potential causes for the discrepancy, further research in similar systems is necessary to help isolate other factors that may have contributed to the variation in our results. Further field and laboratory research that can account for the behavioral aspects

of the social and biological components of natural systems will likely shed light on some of the more nuanced and convoluted interactions that exists.

The ability of animals to alter their behavior in response to human activity will only become more pressing with human population increase and the continued strain on resources and ecosystems. Studies of whether unique behavioral types differ in their response to social inputs will likely have far reaching consequences for human-induced evolution and genetic diversity in wild and managed populations.

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Table 2-1

Stocking records for Lake Wanahoo and Prairie Queen Lake. Stocking information is

broken down per reservoir and in order of earliest stocking event to latest stocking event

prior to opening at each reservoir.

Waterbody	Date	Species	Size (mm)	Number	Development days
Lake Wanahoo	11/12/09	Largemouth Bass	254.0	500	898
	4/22/10	Largemouth Bass	88.9	5507	737
	7/15/10	Largemouth Bass	76.2	5398	653
	8/18/10	Largemouth Bass	71.12	2047	619
	5/3/10	Northern Pike	38.1	26650	726
	5/10/11	Northern Pike	33.02	64900	354
	4/22/10	Bluegill	20.32	101622	737
	4/27/10	Bluegill	33.02	21147	732
	4/27/10	Bluegill	20.32	27481	732
	8/18/10	Bluegill	20.32	60060	619
	8/18/10	Bluegill	38.1	26272	619
	9/22/10	Bluegill	33.02	113130	584
	9/22/10	Bluegill	30.48	178700	584
	9/29/10	Bluegill	25.4	82860	577
	10/22/10	Bluegill	76.2	30000	554
	9/28/10	Black Crappie	71.1	39890	578
Prairie Queen Lake	4/24/13	Largemouth Bass	198.1	480	706
	6/26/13	Largemouth Bass	38.1	10961	643
	7/18/14	Largemouth Bass	406.4	104	256
	10/3/13	Bluegill	35.6	36047	544
	10/3/13	Bluegill	76.2	5772	544
	9/25/14	Black Crappie	76.2	47979	187
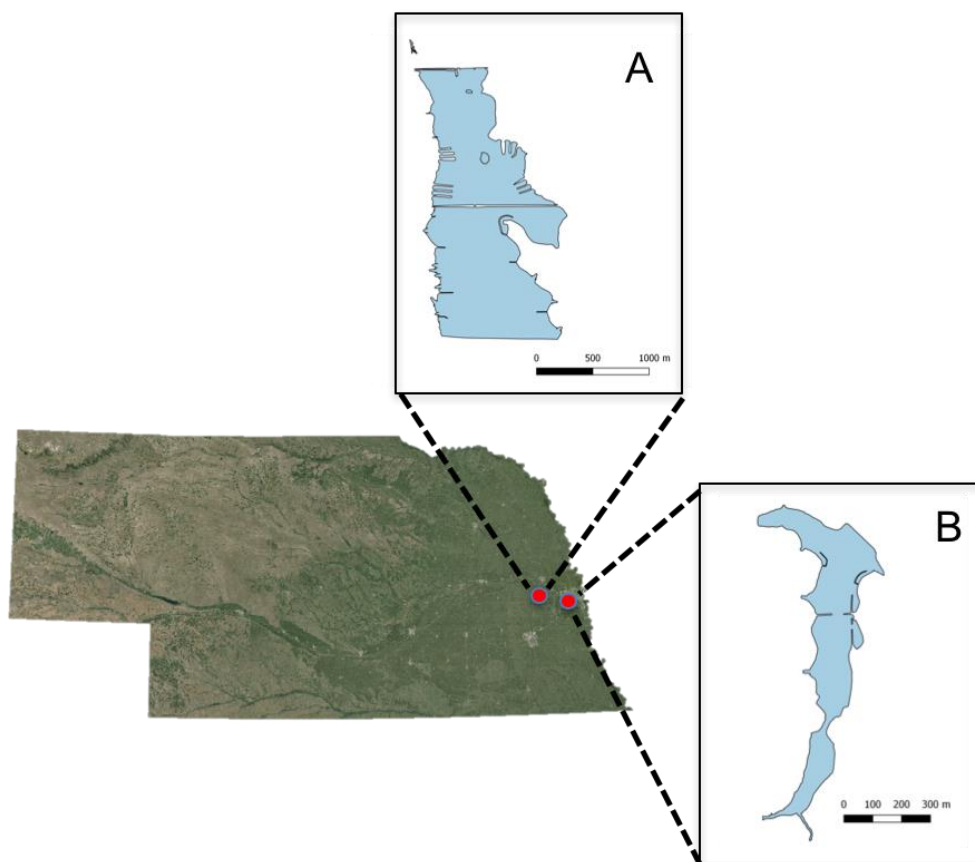
Figure 2-1

Lake Wanahoo(A) and Prairie Queen Lake (B) in Eastern Nebraska. Lake Wanahoo

(258-ha) is located in Saunders County, and Prairie Queen Lake (53-ha) is located in

Sarpy County.
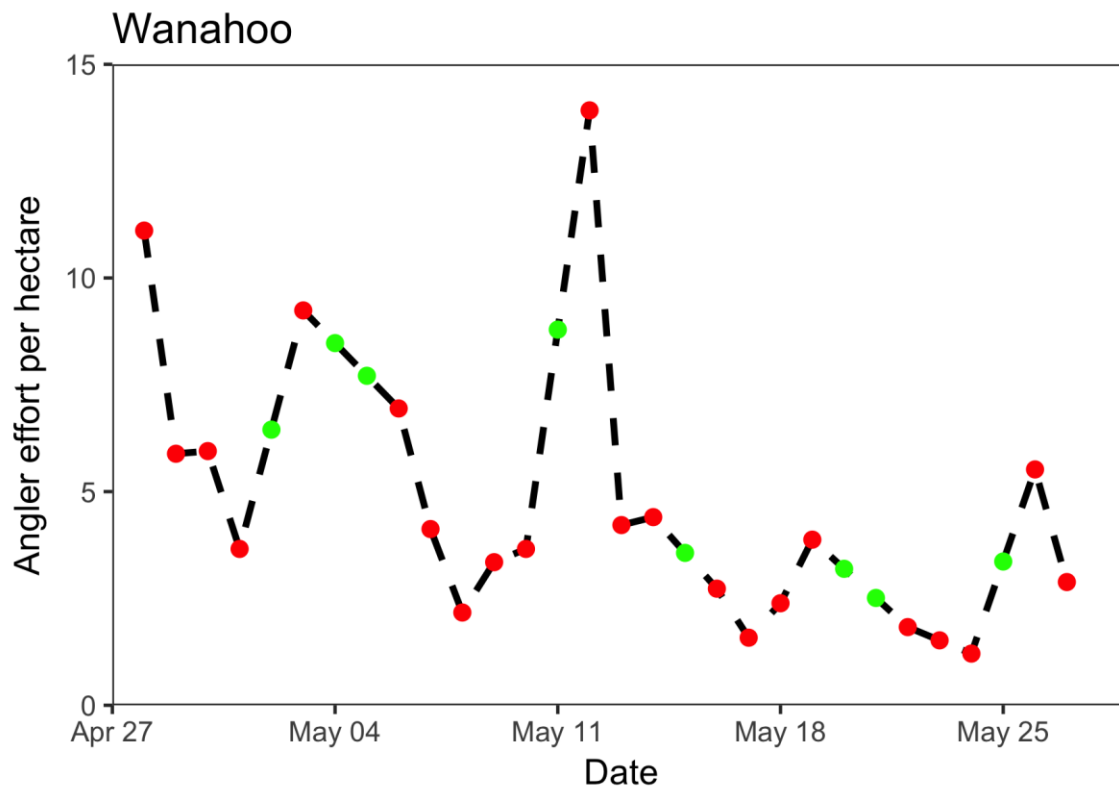
Figure 2-2

Daily angler effort (hour per hectare) from opening day on April 28, 2012 to the end of

the study period on May 29, 2012 at Lake Wanahoo. Red dots represent observed effort

values, and green dots represent interpolated effort values.
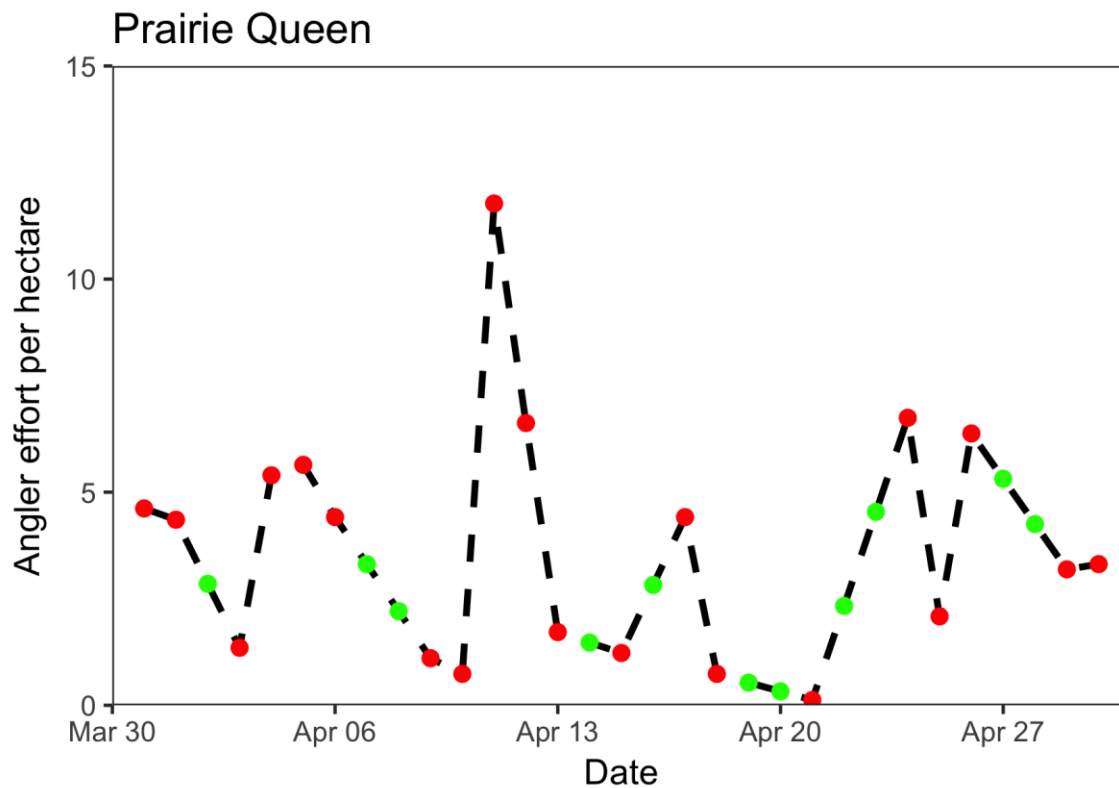
Figure 2-3

Daily angling effort (hour per hectare) from opening day on March 31, 2015 to the end of

the study period on April 30, 2015 at Prairie Queen Lake. Red dots represent observed

effort values, while green dots represent interpolated effort values.
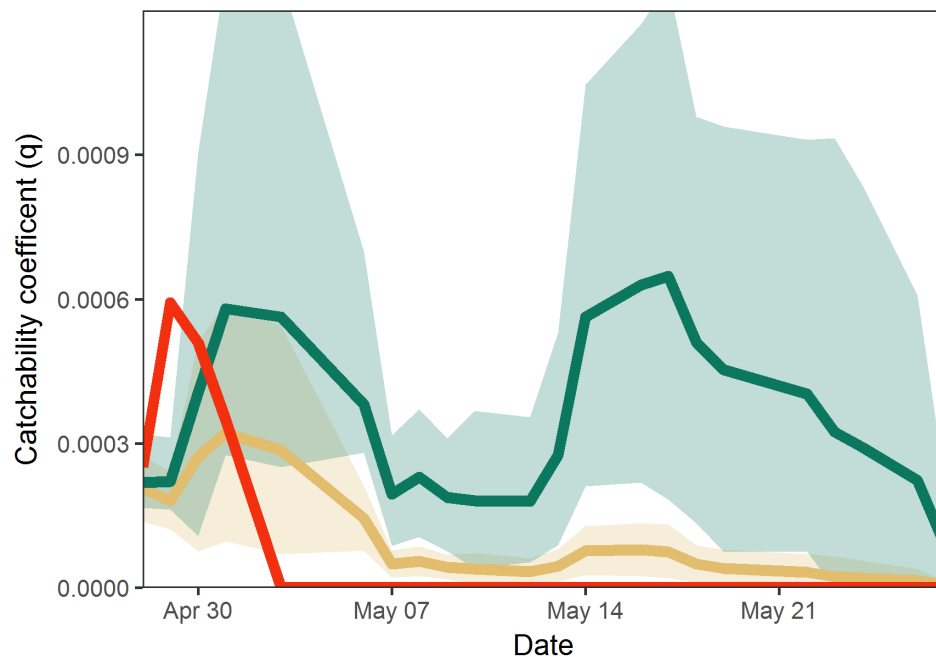
Figure 2-4

Catchability model for Wanahoo largemouth bass population for the study period (April 28, 2012 – May 29, 2012) assuming a 30% discard mortality (red line), a 10% discard mortality (green line), and a 0% discard mortality (gold line). The green and gold ribbons represent a 95% confidence interval.
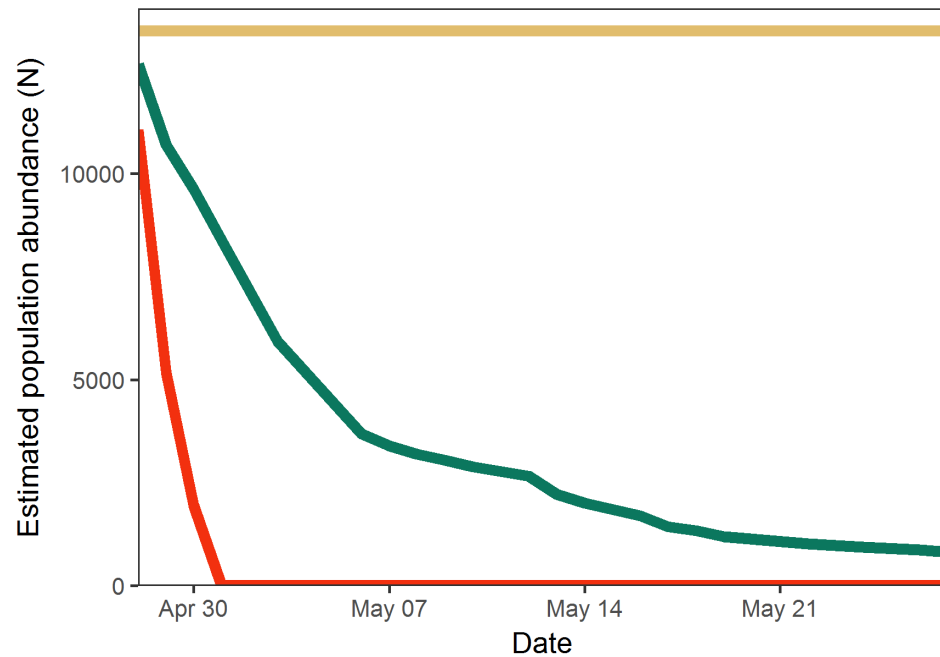
Figure 2-5

Estimated population abundance given different discard mortality rates for the Lake

Wanahoo largemouth bass population for the study period (April 28, 2012 – May 29,

2012). The red line represents a 30% discard mortality. The green line represents a 10%

discard. The gold line represents a 0% discard mortality.
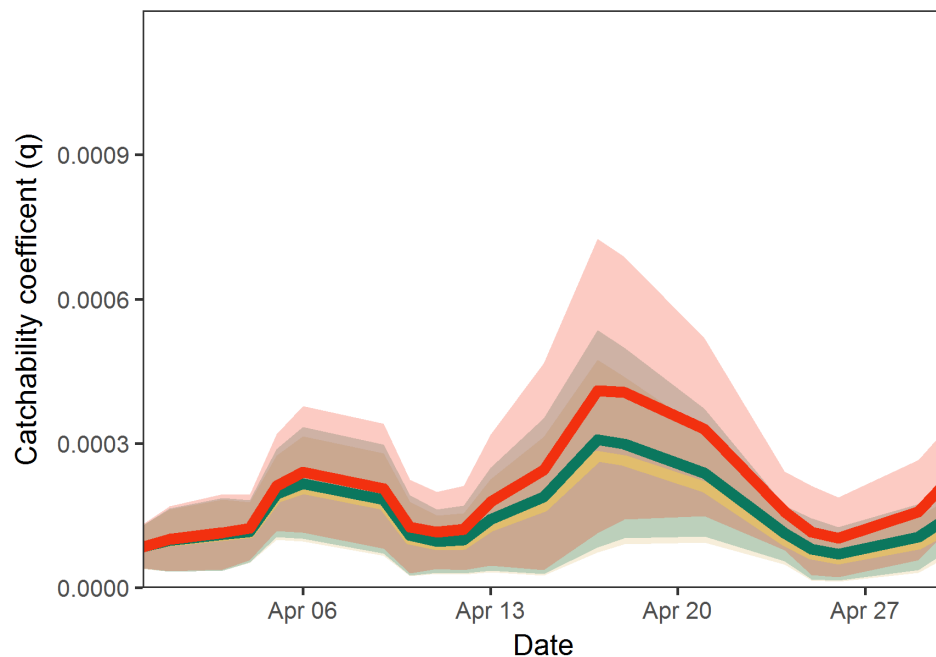
Figure 2-6

Catchability model for Prairie Queen largemouth bass population for the study period
(March 31, 2015 – April 30th, 2015) assuming a 30% discard mortality (red line), a 10%
discard mortality (green line), and a 0% discard mortality (gold line). The red, green, and
gold ribbons represent a 95% confidence interval.
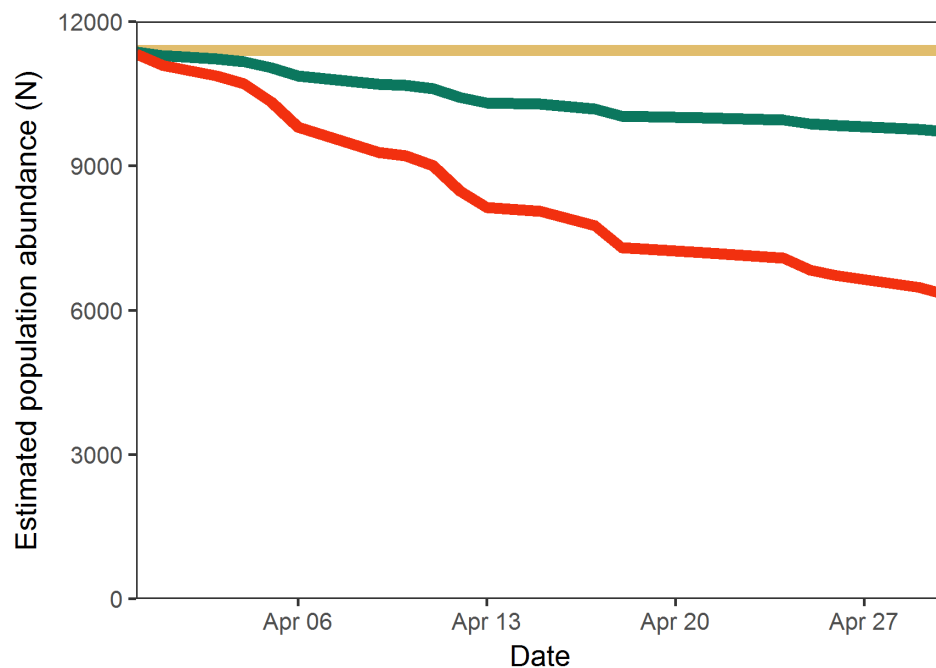
Figure 2-7

Estimated population abundance given different discard mortality rates for the Prairie Queen Lake largemouth bass population for the study period (March 31, 2015 – April 30th, 2015). The red line represents a 30% discard mortality. The green line represents a 10% discard. The gold line represents a 0% discard mortality.
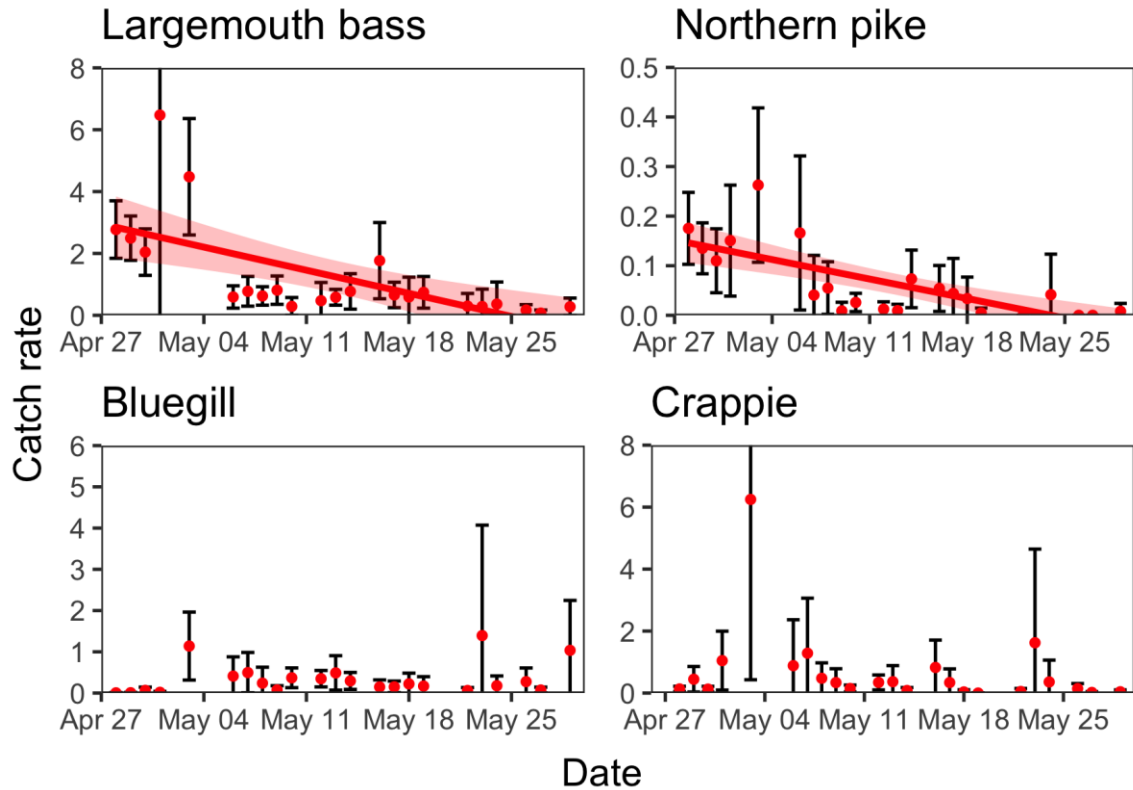
Figure 2-8

Daily angler catch rates (fish per angler hour) for largemouth bass, northern pike, bluegill and crappie at Lake Wanahoo from April 28, 2012 to May 29, 2012. The red dots represent the mean daily catch rate and the error bars represent a 95% confidence interval. The grey lines with grey ribbon represent the significant regression of catch rates as a function of time. Bluegill and crappie did not have significant relationships between catch rate and time.
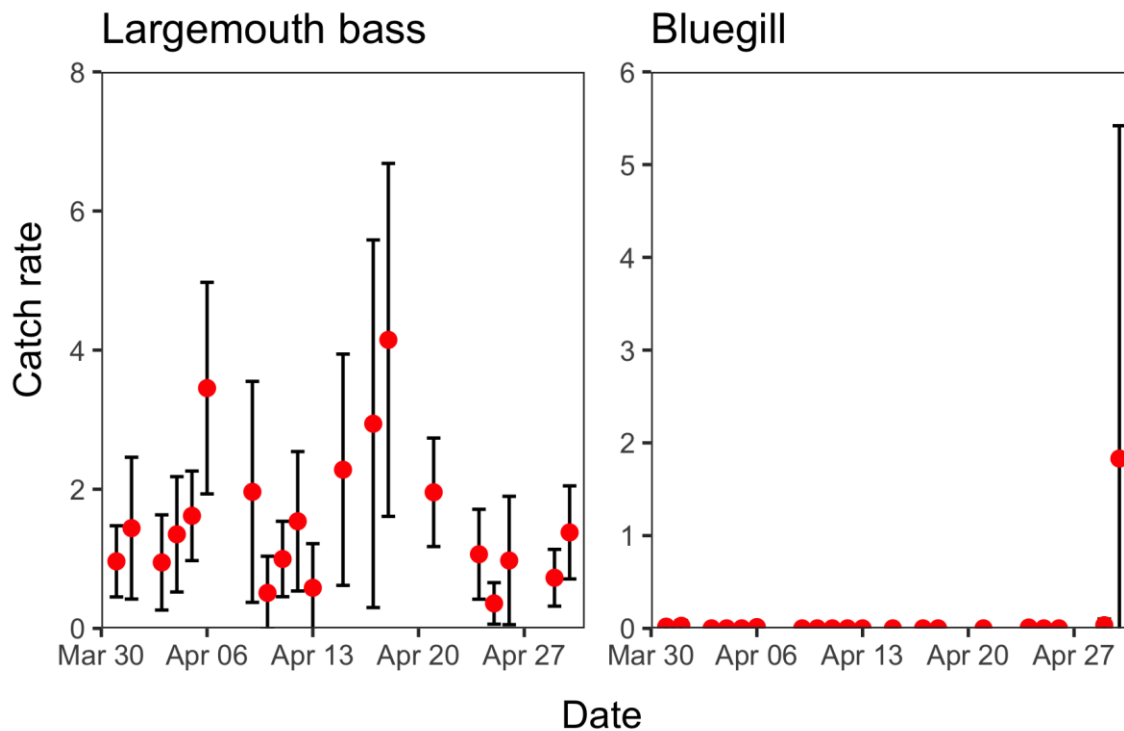
Figure 2-9

Angler catch rates (number of fish per angler hour) for largemouth bass and bluegill at Prairie Queen during the survey period, March 31, 2015 to April 30, 2015. The red dots represent the mean daily catch rate and the error bars represent a 95% confidence interval.
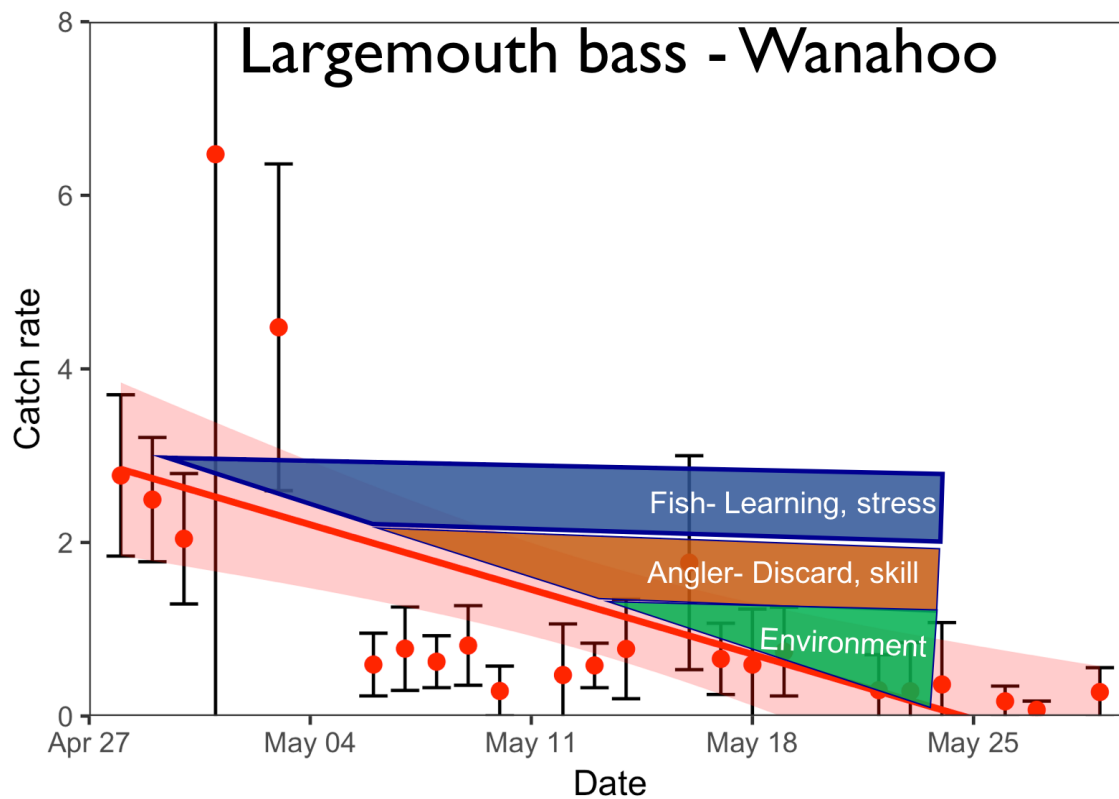
Figure 2-10

Diagram of potential causes of reduced catch rates in the Lake Wanahoo largemouth bass population. Potential contributing factors may include fish learning, fish stress, discard mortality, varying angler skill, and seasonality and environmental factors.
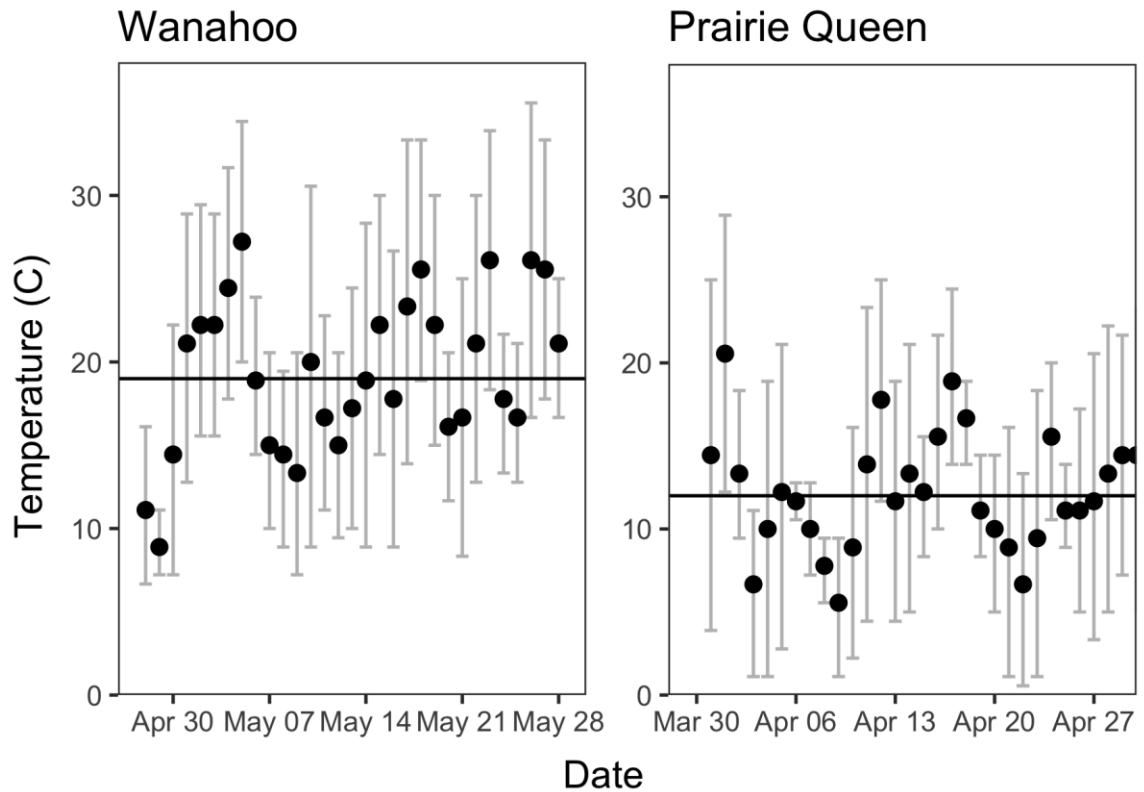
Figure 2-11

Daily air temperatures at Wanahoo (left) and Prairie Queen (right) during the study periods. The points represent mean air temperature for each day and the error bars represent maximum and minimum air temperatures for each day. The mean temperatures (black horizontal lines) were different ($p < 0.05$) between Lake Wanahoo and Prairie Queen Lake.

CHAPTER 3. BEHAVIORAL SYNDROMES AND LEARNING

INTRODUCTION

The predation risk allocation hypothesis assumes that individuals alter their foraging and vigilance behavior in response to predation risk (Lima and Bednekoff 1999). However, it is not always easy for prey to anticipate predator presence, and therefore prey-perceived predation risk can also lead to alterations in foraging and vigilance patterns (Brown 1999). These behavioral shifts in response to perceived predation risk (i.e., fear of predator encounter) are termed "landscapes of fear," and are often generated due to the natural foraging dynamics of predator and prey populations (Brown 1999; Laundré et al. 2001; Laundré et al. 2010). A classic, though highly contested, observation of a landscape of fear occurred in Yellowstone National Park, where an absence of wolves *Canis lupus* led to populations of elk *Cervus elaphus* that were released from the fear that had normally been imposed on them, resulting in increasing home ranges and an over-consumption of vegetation in the park (Laundré et al. 2001). Humans have influenced the spatial layout of wild prey populations directly through predation, and indirectly through fear, for thousands of years (Sullivan et al. 2017). Whether intentionally through hunting (Bonnot et al. 2012; Ciuti et al. 2012a) and fishing (Pauly 1995; Philipp et al. 2009; Sutter et al. 2012) or unintentionally through traffic disturbance, construction, and habitat degradation (Ciuti et al. 2012b; Bonnot et al. 2012), humans may generate landscapes of fear in target populations.

Human exploitation of wild populations is often directed toward certain desirable physical traits or characteristics of individuals, such as size (Allendorf and Hard 2009; Heino et al. 2015). For example, in trophy hunting and fishing (e.g., intent to harvest a

deer with the largest antlers, or the largest fish), the strongest, largest, or most impressive individuals are sought. Some individuals are directly removed through harvest, while non-target individuals are influenced through experiencing fear associated with the activities, often resulting in a behavioral change among affected individuals (Ciuti et al. 2012b; Alós et al. 2015; Arlinghaus et al. 2017; Messinger 2015). Recreational exploitative activities create direct selective pressure through harvest and indirect selective pressure through fear on individuals.

How an individual experiences fear may depend on its behavioral type (also referred to as animal personality). There are five proposed categories for animal personality traits: (1) shyness–boldness, (2) exploration–avoidance, (3) activity, (4) aggressiveness, and (5) sociability (Réale et al. 2007). Animal behavioral syndromes (Sih et al. 2004) are considered repeatable behaviors that are often correlated (i.e., bold individuals also tend to be aggressive [Huntingford 1976], exploratory, and active [Wilson and Godin 2009]), and expressed by organisms across contexts at the population or species level (Sih et al. 2004). Boldness is the most common behavioral trait studied in fish (reviewed by Conrad et al. 2011). The individual expression of boldness within a population exists along a continuum, for example some individuals express consistently bold and aggressive behaviors, though others systematically respond with shy, timid behaviors (Sneddon 2003, Conrad et al. 2011). These behavioral types can occupy different niches within their environment, often maintaining unique foraging strategies, space use, and life-history strategies (McLaughlin et al. 1992), which also show some consistency in laboratory settings (Wilson and McLaughlin 2007). Behavioral types also tend to use information differently, with bold individuals often acting in leadership roles

(Beauchamp 2000, Kurvers et al. 2010a) and shy individuals using social information more efficiently (van Oers et al. 2005; Harcourt et al. 2009; Kurvers et al. 2010b). Further, the subtle distinctions between individuals may influence population dynamics including differences in dispersal, with bold individuals being more likely to disperse (Fraser et al. 2001; Dingemanse et al. 2003; Cote et al., 2010), and differences in sociality, with shy individuals more likely to form social connections (Harcourt et al. 2009; Pike et al. 2008; Croft et al. 2009).

When human exploitation selects for segments of a population with a specific trait (e.g., size, physical trait, aggression), the selected individuals likely share similar behavioral types that contribute to their desirable traits (i.e., bold and aggressive individuals may have better foraging success and therefore grow to be large). Behavioral types are thought to have an underlying genetic component, and therefore would also be affected by the selective removal of sought-after traits (Dingemanse et al. 2002; Philipp et al. 2009; Dochtermann et al. 2015). By selectively targeting one behavioral type from a population, the behavioral traits those individuals contributed to the population are disproportionately removed. Selective removal could have negative influences at a population level, limiting the population's reproductive capabilities (e.g., by removing large reproductive individuals), decreasing body size (e.g., by trophy hunting and selecting for the biggest individuals), limiting dispersal (e.g., by removing bold behavioral types who are more likely to disperse) and a whole suite of effects that have not been considered yet. Additionally, dominance of one behavioral type in a population could result in imbalances at the trophic level (e.g., relaxation of predation on a specific prey species because of variance in foraging strategy between behavioral types), which

could cascade to affect other trophic levels in the ecosystem (Romare and Hansson 2003; Ioannou and Krause 2008; Conrad et al. 2011; Díaz Pauli and Sih 2017).

Behavioral tendencies in a population can shift as result of indirect selective pressures as well as direct. Though behavioral types are defined as an individual's repeatable expression of behaviors in a given behavioral syndrome (Sih et al. 2004), there is still a certain amount of individual plasticity (i.e., the ability to alter behavior) present (Frost et al. 2007; Réale et al. 2010). For example, individuals may shift their behaviors or uncouple certain correlated behaviors throughout early growth and development (Bell and Stamps 2004). Thus, individuals may alter their behavior within the bounds of their behavioral type to diminish their likelihood of mortality.

Recreational fisheries provide an opportunity to view behavioral change resulting from the practice of catch-and-release fishing (i.e., where fish are hooked and then returned to the water alive) and the potential landscape of fear that results. Typical predators shape landscapes of fear through the threat of predation (Brown 1999; Laundré et al. 2001; Laundré et al. 2010), and anglers subject fish to catch-and-release practices. Fish experience a stressful stimulus that can lead to mortality (and does, in harvested individuals), but instead many are frequently returned to the waterbody, simulating a failed predatory event. Caught-and-released fish must contend with the possibility of discard mortality from physical harm, or cognitive and physiological stress post-release (Cooke et al. 2002; Arlinghaus et al. 2007; Arlinghaus et al. 2009). Bold fish are often more likely to be caught by passive angling gear (Biro and Post 2008; Härkönen et al. 2014; Alós et al. 2015). Therefore, by repeatedly catching and releasing individuals, anglers may be driving populations to behave more shyly through fishes' behavioral

change in response to the experience and continued threat of catch-and-release
(Arlinghaus et al. 2017).

The extent of behavioral plasticity that an individual possesses is still unknown.
The concept of behavioral syndromes assumes a limited amount of plasticity, as
behaviors are often shown to be repeatable across contexts, even when they may be
maladapted in certain contexts (Sih et al. 2004). For example, an individual that benefits
from being aggressive through better foraging success, may be at higher risk of predation
under predator-dense conditions because of its associated boldness (Sih et al. 2004; Bell
and Stamps 2004). However, individuals do adapt behavior in response to the risk of
predation (e.g., landscapes of fear), thus individuals have the capability to assess the
dangers in its environment and respond appropriately if possible (e.g., if body condition
and reproductive strategy allow) (Lima and Dill 1990; Frost et al. 2007; Ferrari et al.
2009).

Assessing a situation and altering behavior in response to an assessment may be
considered a form of learning (Dill 1983). Various types of learning in fish have been
demonstrated (reviewed by Kieffer and Colgan 1992). However, it has yet to be fully
understood whether behavioral types learn at different rates, or differ in the degree of
behavioral plasticity, in the face of negative stimuli. Furthering our knowledge of the
differences between behavioral types in their responses to negative stimuli and human-
induced pressure will contribute to our ability to better manage and preserve the
behavioral diversity among populations. Herein, we explore the response of fish to
negative stimuli in a laboratory across a continuum of behavioral types. Our objective is
to quantify how different behavioral types respond to the negative stimuli associated with

catch-and-release angling, and whether we can assess a difference between learning

capabilities among behavioral types.

METHODS

Fish. -- Juvenile (less than 1-year old) rock bass (*Ambloplites rupestris*) were acquired

from the Nebraska Fish Hatchery in Valentine, Nebraska on October 15, 2015. Fish were

transported (transit time approx. 5 hours) with aeration to the laboratory at the University

of Nebraska in Lincoln, Nebraska. Fish were randomly placed among two, 1892-L

fiberglass tanks and allowed to acclimate to the laboratory for 6 weeks. Temperature was

maintained at $20°C \pm 1°C$. Full spectrum lights were set at a 12-hour light:12-hour dark

cycle. Fish were fed and tanks cleaned daily.

Experimental set-up and fish holding conditions. -- Behavioral tests were conducted in

twelve, 132-L tanks with a constant flow of water (Fig 3.1, Fig A.1). Dividers were used

to create a refuge of approximately 44 L. The divider had a 10-cm x 10-cm door that

could be raised to allow the fish to move into the larger arena. Burlap drapes covered the

tanks to minimize disturbance to the fish in the experimental tank and to minimize

exposure to the researcher.

Behavioral trials. -- Behavioral methodology was adapted from Wilson and Godin

(2009). Fish were netted from an 1892-L holding tank at random, mass recorded (g), and

then placed into the refuge side of a testing tank. Each fish was allowed a 24-hour

acclimation period in their refuge. Fish were not fed during the acclimation period. After

the acclimation period, each fish began behavioral testing. The three tests were an exit

test, a model predator test (largemouth bass *Micropterus salmoides*), and a novel object

test (salad shrimp) (Fig. 3-2), aimed at assessing exploration, boldness and activity of

individual fish.

The order that the tests were administered was randomly assigned, and each fish

was given a two-hour rest period between trials. A GoPro HERO4 Silver™ (1080p, 12

megapixels, wide-angle lens) camera was placed above each tank prior to the initiation of

the test to record video. For day two of behavioral testing, the order of the three

behavioral tests were randomized again and run for a second day following the above

protocol. Fish were not fed during the behavioral trials. However, they were given the

opportunity to consume the salad shrimp if they chose to do so.

Exit test. -- During the exit test, the fish was presented with an empty arena. A researcher

would manually lift the door and the fish was given 60 minutes to exit the refuge and

explore the arena. Video was recorded for the full 60 minutes, regardless of whether the

fish exited the refuge during that time. At the completion of 60 minutes, the door was

manually closed and recording was stopped. If a fish was still located in the arena

segment of the tank, it would be netted and placed back into the refuge. The fish was then

given a 2-hour break until the next test.

Model predator test. -- For the model predator test, the same procedure was followed as

presented above, except a model largemouth bass (Fig. 3-3) was suspended in the arena

prior to opening the door. The fish was then given 60-minutes to exit the refuge and

explore the arena and the bass. Video was recorded for the full 60-min, regardless of whether the fish exited the refuge during that time. The fish was then given another 2-hour break until the next test.

Novel object test. -- For the novel object test, the same procedure was followed as presented in the exit test, but in addition, salad shrimp (novel object) was suspended below a yellow and orange bobber attached to a fishing line with a weight on the bottom (Fig. 3-4). The novel object was positioned at the back third of the tank, in the center. The fish was then given 60 minutes to exit the refuge and explore the arena, novel object, and apparatus. Video was recorded for the full 60 minutes, regardless of whether the fish exited the refuge during that time. The fish was then given a 2-hour break until the next test.

Fishing trials. -- At the completion of behavioral trials, the refuge divider was removed from the tank, and fish were given a 10-cm x 10-cm PVC collar as a refuge. We used a full factorial design for gear and ration treatments. Each fish was randomly assigned one of two ration treatments (maintenance and satiation). Fish assigned a maintenance ration were fed 0.5% of their body weight each day over the 7-day fishing trials. Fish assigned a satiation ration were fed 2% of their body weight each day over the 7-day fishing trials. In addition, fish were randomly assigned one of three gear treatments. Gear treatments included a control treatment group that consisted of a straightened hook with the barb pinched, which allowed the fish to remove the worm without the possibility of being hooked (i.e., no negative stimulus). The second gear treatment was a simple fish hook

with the barb pinched. The third treatment was a red Road Runner™ jig head with a blade (Fig. 3-5). All gear treatments were baited with a wax worm (family Pyralidae).

Each fishing trial was recorded using a GoPro HERO4 Silver™ camera mounted directly over the tank. An ice fishing rod (3.5' rod with 6 lbs. test monofilament line, drag maintained at 50%) with the baited treatment gear was introduced to the tank for 15 minutes, or until the fish was hooked. Lines were periodically jigged by the researcher. If hooking occurred, the researcher attempted to engage the fish for ten seconds, remove it from the water, remove the hook, and then return the fish to the water (a goal of ~ 10 s out of the water). Fish were then recorded for an additional ten minutes to observe post-hooking event behavior. When fishing trials were completed, fish were fed per their randomly assigned ration type. Food was removed from the tanks using nets approximately 5 hours after feeding and a wet weight was recorded. Fish were then left alone until the next day's fishing trials. The process was repeated for 7 days. Tanks were flushed daily (i.e., ball valve was opened to clear debris in drain [Fig. A-1]) and vacuumed at the end of the fourth day of fishing trials.

Behavioral analysis

All videos were analyzed using Behavioral Observation Research Interactive Software (BORIS) (Friard and Gamba 2016). Individual behavior codes were generated and assigned to each behavior of interest (Table 3-1). Spatial location and behavior were continuously recorded as time (seconds) spent in a location or performing a behavior. Behavior was not recorded when fish were in the refuge, during which time the only measurement was spatial location (simply recorded as in refuge). In addition to

continuous or "state" events, several singular or "point" behavioral events occurred at a specific time (i.e., a fish stole a worm or swallowed a gear treatment [i.e., gut hooked]). Latency object and latency refuge were also recorded as the initial time the fish approached the given object, and the initial time the fish emerged from the refuge. Each behavior was broken down by test and day (e.g., Bass_proximal, Bass2_proximal, Exit_Activeswim, Exit2_Activeswim). BORIS outputs all behaviors as cumulative time (in seconds) spent enacting each behavior or in each spatial location.

Fishing analysis:

Fishing videos were analyzed in BORIS (Friard and Gamba 2016). Individual behavior codes were generated and assigned to each behavior of interest (Table 3-2) Spatial location and behavior were constantly recorded, except when a fish was in the refuge (during which time the fish was recorded as in refuge) or when an individual was hooked (during which time the fish was recorded as hooked).

Statistical analysis

Behavioral PCA. -- A Principal Component Analysis (PCA) was performed in R (R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.) to determine the proportion of variation explained by the recorded behaviors. Only behaviors thought to be most relevant to an individual's behavioral type were included in the PCA. Many behaviors were highly correlated (Fig. A-2), so we kept only the behaviors that we believed were the most representative of the boldness continuum. The selected behaviors

were: time spent in the arena, time spent in the refuge, and latency to exit the refuge. The behavioral score for each fish was its location on the first principal component in the PCA.

Fishing behavioral model. -- A logistic mixed-model was used to predict capture over each trial using the package *lme4* (Bates et al. 2014). The dependent unique individual fish ID (*Fish_ID*) was a random effect. The first dimensions from the PCA (*Dim.1*) was included as fixed effect variables to represent the shy-bold continuum observed from the behavior trials. Interactions were assumed between the trial day (*Day*) and the gear type (*Control, Hook, Lure*), and the individual mass of the fish in the trial (*Weight*) and the ration treatment (*Ration*).

$$P(capture) = Caught \sim Day * Gear + Dim.1 + Weight * Ration$$

We report the coefficient estimate, standard error, t statistic (i.e., coefficient estimate divided by the standard error) and associated p value for each of our fixed effects and interaction terms. We log transformed *Weight* to minimize the spread in the weight data (i.e., majority of fish were < 50 g but some fish were > 100 g [Fig A.3]). Given the relatively normal distribution of our data along Dimension 1 of the PCA (Fig. 3-8), we determined bold individuals would be represented by the 25th quantile of the Dimension 1 and shy individuals would be represented by the 75th quantile for illustrative purposes.

RESULTS

Behavioral tests performed on the first and second day indicated a range from weak (minimum of 0.3) to moderate (maximum of 0.5) correlation between days depending on the behavior assessed (Table 3-3). We selected only the first day for

inclusion in the behavioral PCA. Moderate to strong negative correlations existed between bold and shy behaviors (ranging from -0.5 to -0.9), and moderate correlation existed among shy behaviors (ranging from 0.6 to 0.7) (Fig. 3-6). The mean proportion of time spent in the arena was greatest for the exit trial (0.376), and least for the bass and novel trials (0.226) (Table 3-4). The mean latency to emerge (represented by the proportion of time at which the event occurred) from the refuge was quickest for the bass trial (0.188) and slowest for the novel object trial (0.253). The mean time spent in the refuge was greatest for the novel trial (0.691) and least for the exit trial (0.614).

The behavioral PCA results demonstrated that the behaviors we determined to be associated with the boldness continuum fell primarily along the first principal component axis, which accounted for 52.2% of the variation (Fig. 3-7). Negative values of Dimension 1 encompassed bold behaviors (time spent in the arena), while positive values of Dimension 1 encompassed shy behaviors (time spent in the refuge and latency to exit the refuge). The relative boldness of the individual fish, represented by their associated value in the first principal component, fell in a distribution that was close to normal, with a slight skew toward more bold individuals (Fig. 3-8). The second principal component accounted for 16.1% of the variation in addition to the variation accounted for by the first component.

Our model indicated a significant interaction between day and both the lure and hook treatment (Table 3-5), which suggests that the longer fish are exposed to a gear type, the less likely they are to be caught by it. Fish are therefore continuing to evaluate the risk involved with the hook or lure treatment and becoming less likely to be caught over time in response to their assessment. The first dimension of the PCA had a

significant effect on probability of capture, which suggests that behavioral types do have different vulnerabilities to angling because a fish's associated value on the first dimension affects that fish's probability of capture. Finally, increasing weight had a significant negative effect on probability of capture.

Our model predicted outcomes based on values of the 25th and 75th quantile of Dimension 1 (-0.286 and 0.264 respectively). We selected the 25th and 75th quantile because they were representative of most individuals from both the bold and shy groups. Bold individuals (defined by those that fell within the 25th quantile in the model) had a higher probability of capture across treatment (Fig. 3-9) than shy individuals, (defined by those that fell within the 75th quantile in the model) (Fig. 3-9). For both bold and shy individuals, the model predicts a consistent probability of capture for control treatments. Hook and lure gears interacting with day of trial result in a significant decline in probability of capture across the seven-day trial period. Lures started out at the lowest probability of capture for both bold and shy individuals.

We were also interested in predicting probability of capture across the continuum of fish involved in experimental trials. To explore this, we looked at probability of capture across all the values of Dimension 1, broken down by day and gear treatment type (Fig. 3-10).

DISCUSSION

Our results indicated that shy and bold individuals altered their behavior over the 7-d trial period, resulting in a decreased probability of capture independent of behavioral type. The observed behavioral alteration was in direct response to the gear treatment,

indicating that we may have induced a fear response among experimental fish similar to what could be expected in a landscape of fear (Laundré et al. 2001). Fish may be forgoing the opportunity to continue to consume high-quality forage (e.g., wax worms) because of the negative stimuli associated with the worms, thus altering their foraging strategy in response to a perceived risk. Bold and shy individuals assessed risk differently, prior to any experience with angling. Shy individuals were less likely to be caught by all three gear types at the initiation, and throughout the length of the trial, than bold individuals (Fig. 3-9, Fig. 3-10).

Probability of capture represents vulnerability to angling, and our results parallel past research that states bold individuals are more vulnerable to capture than shy (Biro and Post 2008, Härkönen et al. 2014). However, vulnerability traditionally assesses a fish's likelihood to encounter angling gear, based on the characteristics that make it more apt to do so (e.g., bold, aggressive, active, exploratory). In our study, fish are presented with angling gear within a defined space, and therefore their vulnerability is not dependent on their activity or exploration. Given that detection and encounter probabilities should be equal between behavioral types in the defined space, our results support correlation between exploration and aggression in fish. In addition to being more likely to encounter angling gear, bold fish are also more likely to attack angling gear given an encounter.

To determine behavioral type, we measured eleven different behaviors for each behavioral test (Table 3-1), but chose the factors that we considered to be most relevant to our examination of boldness (including assessments of exploration and activity), and those that explained the most variation in the first dimension of our behavioral PCA. We

chose to include only the first day of behavioral trials in the PCA to attempt to capture

behavioral reactions under circumstances where the tests were most novel (i.e., on day

two, fish had prior experience with the tests). Several of our measured behaviors were

highly correlated (e.g., active swimming and time spent in the arena, and latency object

and latency refuge [Fig. A-2]) allowing us to select one for representation in the PCA.

Latency to exit the refuge has high relevance to the field in terms of predicting dispersal

distance in killifish (Fraser et al. 2001), which is also often associated with bold

individuals (Fraser et al. 2001, Dingemanse et al. 2003, Cote et al., 2010).

The behavioral PCA indicated that factors associated with boldness (e.g., time

spent in the arena) fall in the negative values of Dimension 1, while factors associated

with shyness (e.g., time spent in the refuge) fall in the positive values of Dimension 1,

thus we can assume Dimension 1 to be a description of a boldness continuum. Dimension

1 explains 52.2% of the variation, and Dimension 2 accounts for an additional 16.1% of

the variation, which is unrelated to the variation explained in Dimension 1. Therefore

Dimension 2 may be describing variation accounted for by other components of a

behavioral type such as sociality (Réale et al. 2007), which we will not attempt to

describe given our focus on factors pertaining to, and associated with, boldness.

Therefore, we chose not to include Dimension 2 in our model assessing probability of

capture over time.

The lure gear indicated a lower initial probability of capture for both behavioral

types, suggesting that fish were influenced by the additional visual cues provided by the

color and silver blade attachment (Fig. 3-5). The control treatment exhibited a slight

increase over the seven days, reflecting the positive feedback of the worm without the

added negative stimulus associated with the other two treatments. Our results indicate that shy individuals assessed the cues from the fishing treatments differently than bold individuals, as each treatment started out at a lower probability of capture. Thus, shy individuals perceived each treatment as inherently riskier compared to bold individuals' perceived risk.

The continuum of behavior types (Fig. 3-10) demonstrates the decline in probability of capture over the 7-day trial period, independent of behavioral type. It also represents bold individuals starting out at a higher probability of capture (left side of the figure in each panel) than shy individuals. More variation is observed in the intermediate ranges of Dimension 1 than at the extremes, suggesting that intermediate behavioral types may have more flexibility in behavioral response than those at the extreme ends of the continuum.

The interaction between weight and probability of capture was significant, which parallels previous studies that assessed an increase in length and weight with decreasing boldness (Brown and Braithwaite 2004; Brown et al. 2005). The relationship between length and weight has implications for trophy fisheries that aim to increase catch rates of large individuals. Sought after size groups may be inherently less likely to get caught due to a potential inverse relationship between size and boldness.

There was no influence of ration type on probability of capture of bold or shy individuals. We hypothesized that we would observe an increased probability of capture for individuals that were fed a maintenance ration based on the concept that hungry individuals would be more likely to take risks (Stephens and Krebs 1986; Damsgard and Dill 1998). Perhaps if there was more of a disparity between the ration types, or if there

was an extended period at which the rations were maintained, we may have observed an influence from ration type on probability of capture.

An assumption of our experiment is that the tests we chose to perform can distinguish bold individuals from shy. While measurements such as latency to exit a refuge and latency to approach a novel object are accepted tests within behavioral literature (especially regarding fish behavioral analysis [reviewed by Conrad et al. 2011]), they may not be an accurate representation of boldness and rather simply an outcome of assessments that we presume to measure boldness (Toms et al. 2010; Conrad et al. 2011). However, we noted a difference in behavioral types between individuals in our study and therefore the tests identified unique behavioral responses among individuals. Additionally, our results were focused on individual response of one species to behavioral tests and negative stimuli. It is important to consider that behavioral syndromes may not be consistent across species or even between populations (Bell and Stamps 2004). Moreover, individual responses in behavior may be subject to social interactions as well. Several studies note that behavior of individuals may be influenced by the behavior of neighboring conspecifics (Stöwe and Kotrschal 2007; Harcourt et al. 2009), which may have implications for how schooling fish, and other social animals, alter behavior in response to fear.

CONCLUSION

Fish in our study demonstrated an ability to alter behavior to avoid capture, independent of behavioral type, reinforcing the concept that humans impose landscapes of fear through their interactions with wildlife. Our results indicated that bold individuals

had a greater probability of capture across treatment types compared to shy individuals. Thus, our study supports the idea that angling may be driving populations to be shyer through harvest (higher probability of removal of bold individuals [Biro and Post 2008; Härkönen et al. 2014]). Catch-and-release appears to drive both bold and shy fish to alter their behavior to avoid capture (Arlinghaus et al. 2017; Díaz Pauli and Sih 2017]).

More research is needed to determine if the plasticity of behavioral types shifts across contexts (e.g., in their interaction with other prey and conspecifics), or simply in response to anglers. Research that pursues the ramifications of population-level shifts in behavior across trophic levels may provide critical information for maintaining the resiliency of ecosystems in the face of societal pressure. Observing whether bold and shy behavioral types have different effects on other trophic levels following behavioral alteration would also provide a unique insight into community dynamics. Additionally, future studies should assess the length of time that individuals maintain their aversion to angling (i.e., the length of the refractory period). Length of memory retention of negative stimuli could be crucial to assessing possible rebound periods for exploited systems and species. In fisheries, the length of a typical refractory period may also help managers adapt management techniques, such as assessing an appropriate period for temporary closures that allow fish to recover from capture and return to a vulnerable state. The pursuit of maintaining genetic diversity is well accepted and understood, but perhaps behavioral diversity should be thought of in the same vein and with the same importance. Both are linked, and ultimately connected to a population's ability to react and adapt to environmental change. Challenges in maintaining both genetic and behavioral diversity

will only continue to increase with pressures from a rising global population and the effects of climate change.

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Table 3-1

Measured behaviors, behavioral codes in BORIS, and their associated descriptions. Event

type is listed as either "state" meaning continuous, or "point" meaning at a specific time

within the trial.

Behavior	Description	BORIS Code	Event type
Proximal	Proximal to a test object (e.g. bass or novel object)	0	state
Active swim	Time spent actively swimming	1	state
Refuge	Time spent in refuge	2	state
Arena	Time spent in arena	3	state
Hover	Time spent hovering	4	state
Peek	Peeking out of refuge, but not fully emerging	5	state
Interacting	Interacting (i.e. biting or contacting) with test object	7	state
Surface	Time spent at the water's surface	9	state
Consume novel	Consume novel object (shirmp)	@	point
Latency to exit refuge	First instance of exiting refuge	-	-
Latencty to approach object	First instance of approaching object	-	-

Table 3-2

Measured behaviors, behavioral codes in BORIS, and their associated descriptions. Event

type is listed as either "state" meaning continuous, or "point" meaning at a specific time

within the trial.

Behavior	Description	BORIS code	Event type
Proximal	Proximal to a fishing treatment	0	state
Active swim	Time spent actively swimming	1	state
Refuge	Time spent in refuge	2	state
Arena	Time spent in arena	3	state
Hover	Time spent hovering	4	state
Interacting	Interacting (i.e. biting or contacting) fishing treatment	7	state
Surface	Time spent at the water's surface	9	state
Hooked	Time spent fully hooked (i.e. controlled by researcher)	6	state
Out of water	Time spent removed from the water	/	state
Stationary	Time spent stationary (i.e. resting on floor of tank) post-hooking event	*	state
Steal worm	When an individual stole a worm without getting hooked	&	point
Gut hooked	When an individual swallowed the treatement and the line needed to be cut	%	point
Latencty to approach object	First instance of approaching object	-	-

Table 3-3

Correlation factor between first and second day trials of selected behavioral factors,

broken down by trial type and behavior.

Behavior	Correlation factor
Exit	
Time spent in arena	0.380
Latency to emerge from refuge	0.451
Time spent in refuge	0.408
Bass	
Time spent in arena	0.308
Latency to emerge from refuge	0.434
Time spent in refuge	0.416
Novel	
Time spent in arena	0.389
Latency to emerge from refuge	0.516
Time spent in refuge	0.493

Table 3-4

Spread, mean and standard error of selected behavioral factors for each of the three

behavioral tests used to determine fish individual behavioral type. Units are proportion of

the total time (s) for the given trial. (n = 79)

Behavior	Minimum	Mean	SE	Maximum
Exit				
Time spent in arena	0.051	0.376	0.025	0.850
Latency to emerge from refuge	0.013	0.214	0.016	0.780
Time spent in refuge	0.148	0.614	0.016	0.948
Bass				
Time spent in arena	0.009	0.226	0.016	0.569
Latency to emerge from refuge	0.018	0.188	0.020	0.789
Time spent in refuge	0.119	0.625	0.025	0.972
Novel				
Time spent in arena	0.004	0.226	0.016	0.692
Latency to emerge from refuge	0.019	0.253	0.022	0.826
Time spent in refuge	0.291	0.691	0.021	0.990

Table 3-5

Model summary of the mixed effects logistic predicting the probability of being caught over seven consecutive days. Each coefficient in the model is represented with its associated estimate, standard error, z value and level of significance. Significant effects are highlighted in bold.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.377	1.332	3.285	**0.001**
Day	-0.056	0.119	-0.474	0.635
Gear: Hook	0.555	0.847	0.655	0.513
Gear: Lure	-2.636	0.925	-2.850	**0.004**
Behavioral type: Dim.1	-2.234	0.717	-3.114	**0.002**
Weight	-0.838	0.361	-2.321	**0.020**
Ration	-0.147	0.499	-0.295	0.768
Day * Gear: Worm	-0.449	0.157	-2.853	**0.004**
Day * Gear: Lure	-0.340	0.174	-1.952	0.051
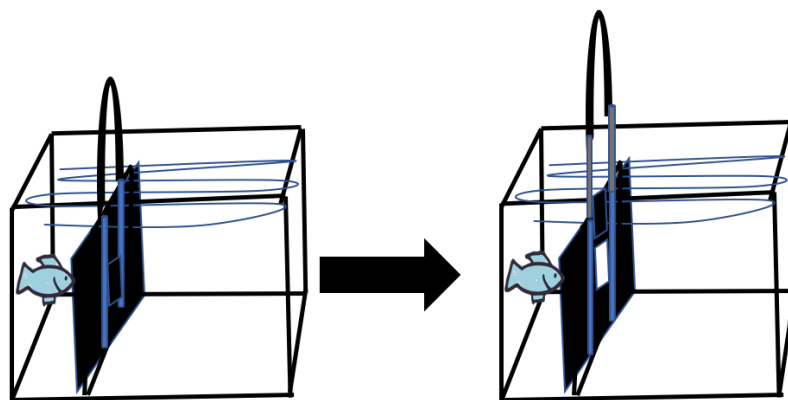
Figure 3-1

Refuge and door setup in experimental tanks. The refuge is located on the left of the

divider in each image, and the arena is located to the right of the divider.
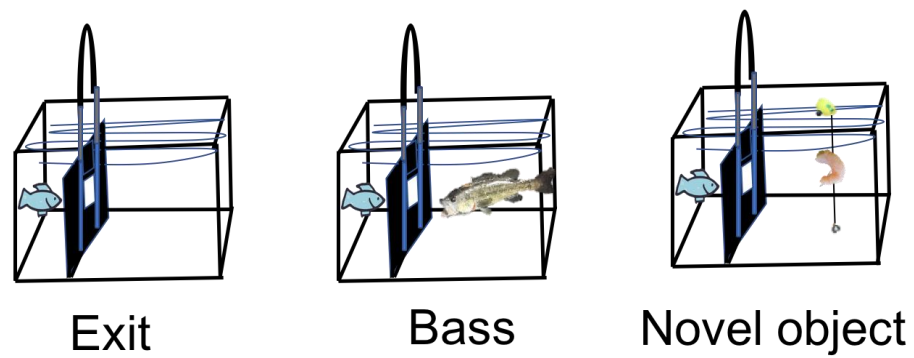
Figure 3-2

Tests for behavioral type assessment. Exit tests featured an open arena, model predator

(bass) tests featured a suspended model of a largemouth bass in the arena, and novel

object tests featured a suspended salad shrimp in the arena.

Figure 3-3

Model largemouth bass used in predator exposure test. The bass was suspended by

fishing line attached to a medal rod that rested across the top of the experimental tanks.

Figure 3-4

Novel object apparatus. The salad shrimp was attached to fishing line by threading it
through small wire. The line was weighted down with a lead weight and suspended
using a yellow and orange bobber.
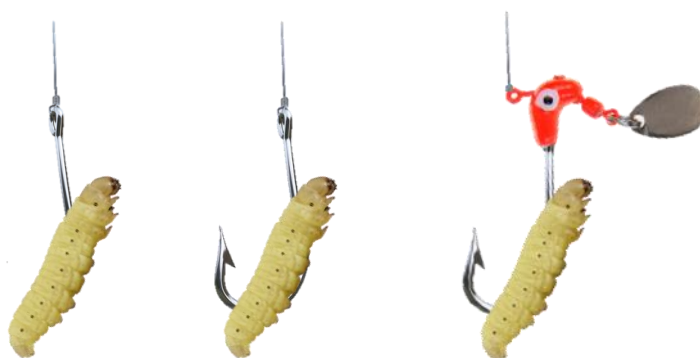
Figure 3-5

Gear treatments. Each fish was randomly assigned either a control treatment with a straightened hook (left), a regular hook (center), or a lure (right).

Figure 3-6

Correlation coefficients between selected behaviors. The circles indicate correlations that are greater than or equal to 0.5 in magnitude, with pink circles indicating negative correlations and blue circles indicating positive correlations.
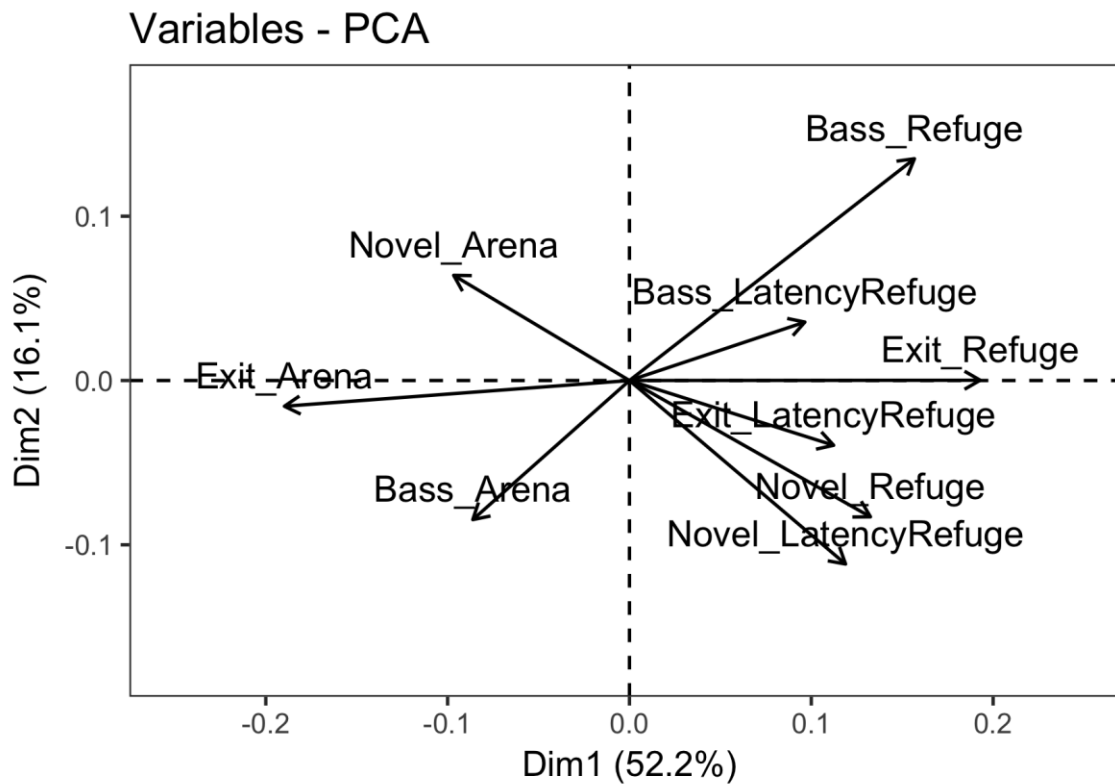
Figure 3-7

Behavioral PCA: spread of assessed behavioral factors. Dim1 describes 52.2% of the

variation in our behavioral data. Dim2 describes an additional 16.1% of the variation in

the data. Factors we associate with being bold fall among the negative values of Dim1,

and factors we associate with being shy fall among the positive values of Dim1.
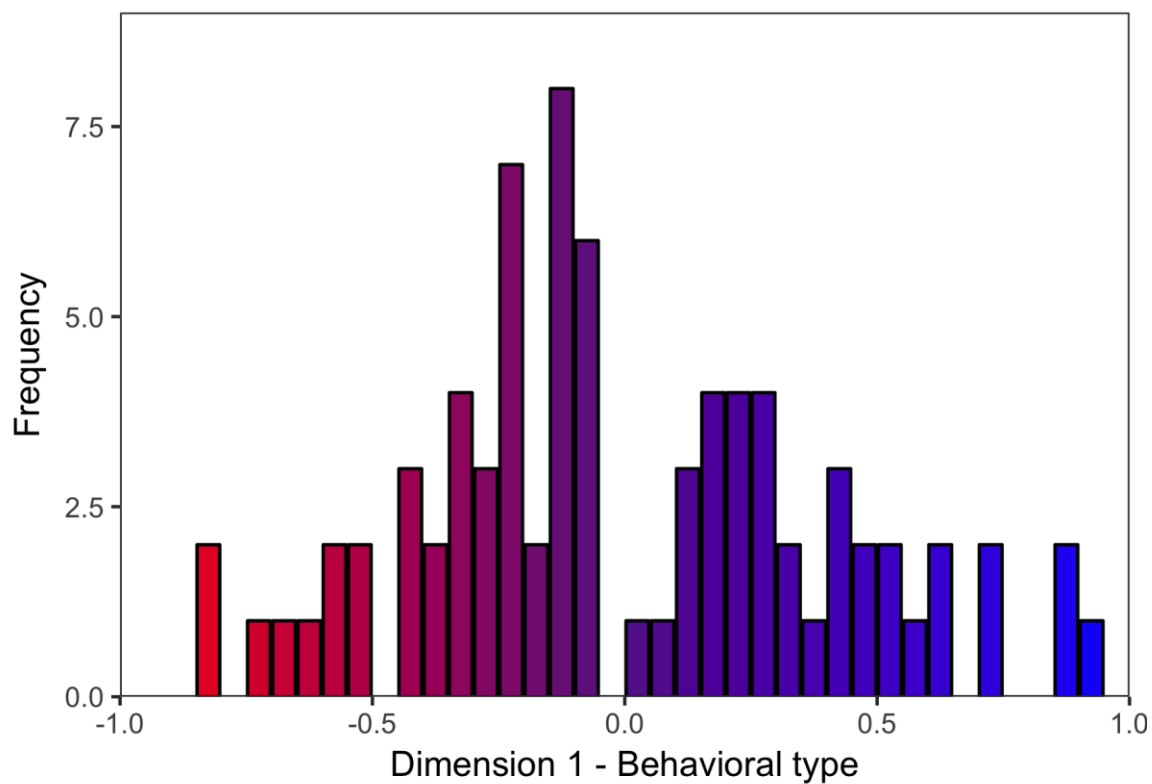
Figure 3-8

Spread and frequency of individual fish along Dimension 1 of PCA. Individuals that fall

to the left of zero are those we consider to be bolder individuals (red), and those that fall

to the right of zero are those we considered to be shyer (blue). Total sample size was 79

fish.
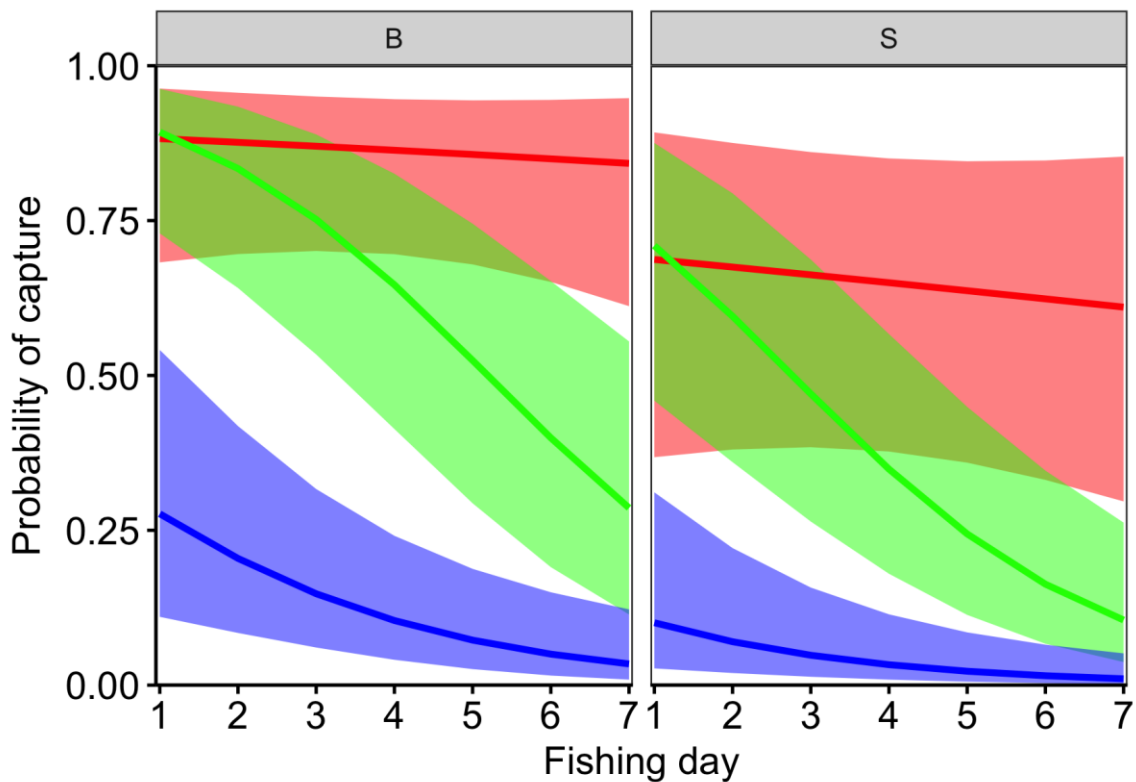
Figure 3-9

Predicted probability of capture for bold (left panel, 25th quantile) and shy rock bass (right panel, 75th quantile) across the 7-day trial period. The red line represents the control and the corresponding red ribbon represents a 95% confidence interval around the prediction. The blue line represents the hook and the corresponding blue ribbon represents at 95% confidence interval. The green line represents the lure and the corresponding green ribbon represents at 95% confidence interval. Total sample size was 79 fish.
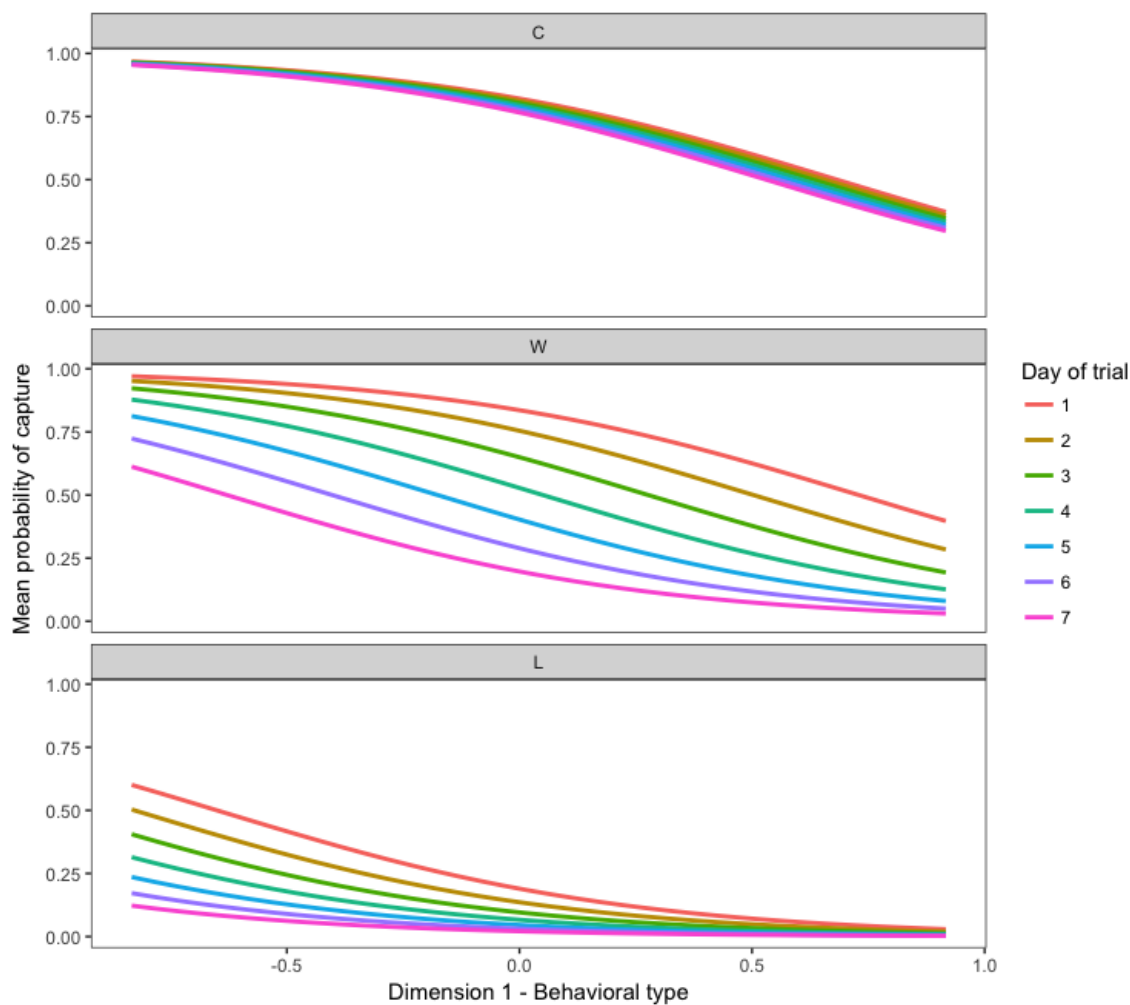
Figure 3-10

Mean probability of capture of fish each day of the 7-day trial period, across behavioral type and broken down by gear treatment. The top panel represents fish assigned the control gear, the middle panel represents fish assigned the worm gear and the bottom panel represents fish assigned the lure gear. Each line represents a unique day of the trial, from 1 to 7. Bolder fish fall between 0 and -1 on Dimension 1 (x-axis), and shy fish fall between 0 and 1 on Dimension 1. Total sample size was 79 fish.

CHAPTER 4. MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

The resiliency of recreational fisheries is an important topic to fisheries management (Arlinghaus et al. 2013; Pope et al. 2014), and there are concerns that collapsing fisheries are often masked by social and ecological functions (Post et al. 2002). The better our understanding of the social-ecological interactions and feedbacks that occur between the social and ecological components of a fishery, the better we can manage those fisheries for angler satisfaction (e.g., higher catch rates), and successful biological components (e.g., genetically diverse, self-sustaining fish populations). Results from the research in Chapter 2 and Chapter 3 suggest that the actions of humans within a social-ecological system, like recreational fisheries, may have strong effects on the behaviors exhibited by fish. Given the decline in catch rate witnessed at Lake Wanahoo for catch-and-release species (Chapter 2), and the behavioral changes we witnessed in the lab for different behavioral types (Chapter 3), we recommend several actions for consideration to effectively manage for human-induced behavioral changes.

Recommendation 1: Strategic closures and protected areas

Managers may be able to slow a regime shift from a naïve to a heavily fished fishery by employing strategies such as strategic temporary closure of certain reservoir zones to allow a refuge for fish and spaces that are devoid of angling effort. Closures may allow fish the opportunity to recover from the stress experienced from capture-related activities. Protected areas may also act as source populations of fish that successfully recovered from a refractory state post-release and returned to a vulnerable state. Given basic source-sink dynamics, the areas within a reservoir open to fishing would act as sink

populations with immigration occurring between each sub-population. Research in marine systems suggest that protected areas decrease fear in reef fish populations (Januchowski-Hartley et al. 2014), therefore we may expect a similar outcome in recreational fish populations.

Recommendation 2: Gear controls

Gear controls may also be an option to relieving angler effort. Results from our laboratory experiments suggest that initially, fish view lures with worms differently than a worm on a hook, with lure gear having a lower initial probability of capture than hook gear, independent of behavioral type (Chapter 3). The different assessment of treatments likely relates to differences in sensory cues that occur between each treatment. Like the bright, flashy coloration employed by toxic species (e.g., poison arrow frogs Dendrobatidae, monarch butterflies *Danaus plexippus*), it should be expected that flashier lures with more sensory cues available to be observed by the fish would result in stronger patterns of recognition given a stressful event (Warburton 2003). Therefore, restricting specific gear types to specific reservoir zones may increase acclimation time to certain gear, maintaining high catch rates. A gear restriction strategy may be employed by setting an initial period where gear is restricted to a certain type (e.g., fly fishing or live-bait only). Following an initial period, the season may transition to an open-gear type or artificial-only period. Limiting anglers to gear with fewer sensory cues initially may increase the longevity of high-catch rate periods like those initially observed at Lake Wanahoo (Chapter 2).

Recommendation 3: Monitoring angler-specific catchability

Managers may benefit from monitoring fish catchability (i.e., the probability of capture at a population scale) over time in addition to abundance or harvest. The results of laboratory trials conducted in Chapter 3 suggest probability of capture for both shy and bold fish may fall to low levels (i.e., 5-20%) with sustained effort. We witnessed the decline in probability of capture independent of any change in abundance in our fish population, therefore the resulting change is due to behavioral change and not mortality. Thus, monitoring abundance of a population alone does not necessarily relate to the number of fish that are vulnerable to be caught by anglers, and catchability may be a better assessment of the vulnerable population (Goetze et al. 2017). As described in Chapter 2, catchability requires an evaluation of the number of catchable fish that occur in the waterbody and a measure of the mean CPUE for anglers fishing in the waterbody. A catchability assessment could be easily accomplished by applying independent surveys of population abundance (i.e., mark-recapture, relative abundance indices) and conducting regular creel surveys that measure catch and effort. The two surveys conducted in tandem would supply additional information as to whether low catch rates are a result of behavioral changes or other factors like discard mortality. If decreasing catch rates are a result of declines in population abundance, catchability would remain stable.

Recommendation 4: Managing for limited-pressure specialized reservoirs

The relationship between body mass and catchability in our laboratory experiments (Chapter 3) suggest that large fish have a lower probability of capture,

independent of their previous experience with angling. Therefore, larger fish may have a different assessment of risk, or different foraging strategies. Managers may be able to maintain catch rates in populations with larger individuals by greatly restricting angler effort by managing fisheries through a lottery system (Cox and Walters 2002). Anglers will only be allowed to fish at the specified reservoir if their lottery number is drawn during the determined period (may be broken up into multiple periods during the fishing season). A lottery system would allow managers to control effort in a system while maintaining catch rates and therefore making it a worthwhile and sought after opportunity for anglers (e.g., lifetime lotteries to hunt bull elk in Nebraska). A rare but highly-sought fishing opportunity would likely result in the perception of high-quality fishing within the state of Nebraska. Anglers often have negative perceptions of effort control systems (Beard et al. 2003), and strategic lottery systems may help to mitigate such perceptions by providing a unique experience in exchange for the inconvenience of limited access.

Recommendation 5: Implications of opening new reservoirs

The time of year that the reservoir opens may have strong implications for catch rates. For example, the opening of Prairie Queen Lake occurred when it was still relatively cold (mean air temp for the month of 12°C) and that may have influenced both angler effort and catch rates of species like bluegill *Lepomis macrochirus*, and black crappie *Pomoxis nigromaculatus*. Additionally, by opening nearly a full month later, most the angling at Lake Wanahoo may have occurred during the bass spawning season, likely resulting in an increased catch rate but also an increased behavioral response.

Consideration of the health and behavioral variability of fish populations is critical in maintaining a sustainable fishery. In wildlife research, habitat restoration is often given supreme importance when attempting to assist in species recovery (Fahrig 1997), but often stocking is used as a fix in fisheries restoration instead of addressing issues like habitat quality (Sass et al. 2017). Instead, managers should consider increasing the complexity and diversity of underwater structure to encourage variation of behavioral types that will occupy differing components of a varied environment (Watters et al. 2003). Additionally, current stocking practices may be fueling decreased resiliency in populations by perpetually stocking and not allowing natural recruitment and population self-sufficiency to develop. Hatchery fish are less prepared to face the challenges of natural systems, such as foraging and avoiding predators, and may demonstrate more exploratory behaviors than wild individuals (Brown et al. 2013). Homogenization of behavior can also have a negative influence on the resiliency of the population, decreasing the populations ability to respond to environmental change (Conrad et al. 2011). Therefore, managers should aim to stock populations of fish with diverse behavioral types to encourage diversity among the population (Conrad et al. 2011).

Though the construction of new reservoirs is on the decline, a large percentage of existing reservoirs across the United States of America are reaching an age at which managers need to enact restoration for the fish communities (Miranda et al. 2010; Miranda and Krogman 2015; Pegg et al. 2015). Reservoir restoration will provide managers the opportunity to start fresh in both habitat, fish population structure, and management regulations. Future studies should aim to assess the trophic level effects of angling-induced behavioral change. Furthermore, an accurate estimate of the length of

the refractory period for caught-and-released individuals will aid in management

decisions regarding how best to control angling effort.

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APPENDIX
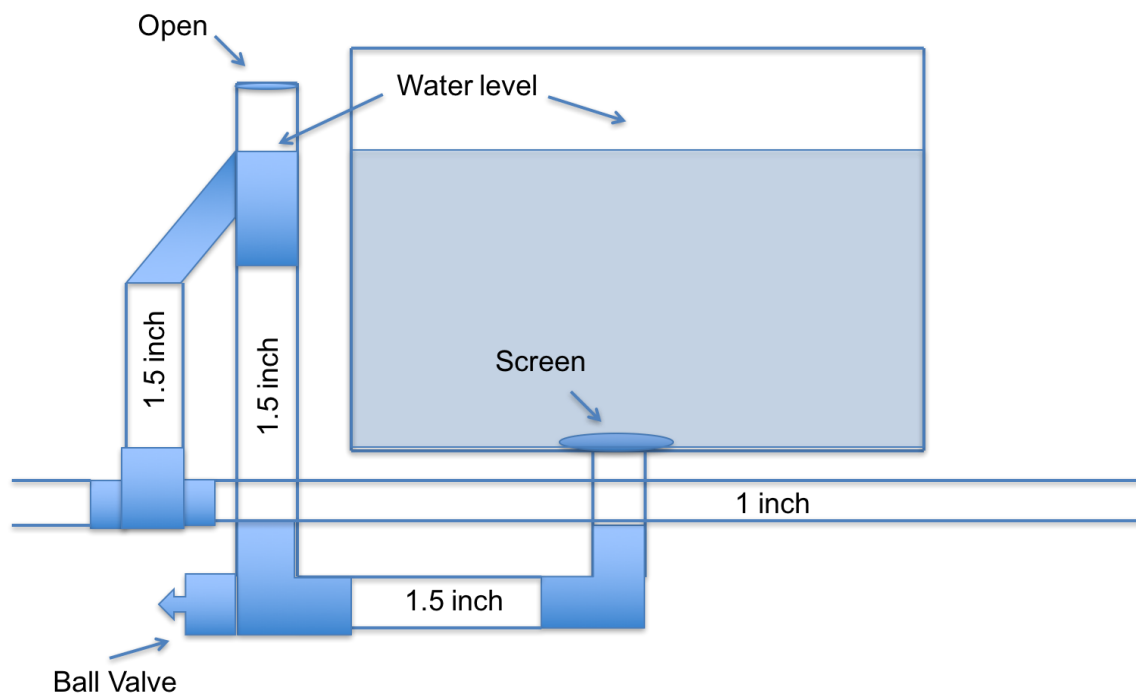
Figure A-1

Experimental tank schematic representing the basic construction of individual tanks. Ball

valves allowed for rapid flushing of the system, and external standpipes left a clear arena

for fish experiments.
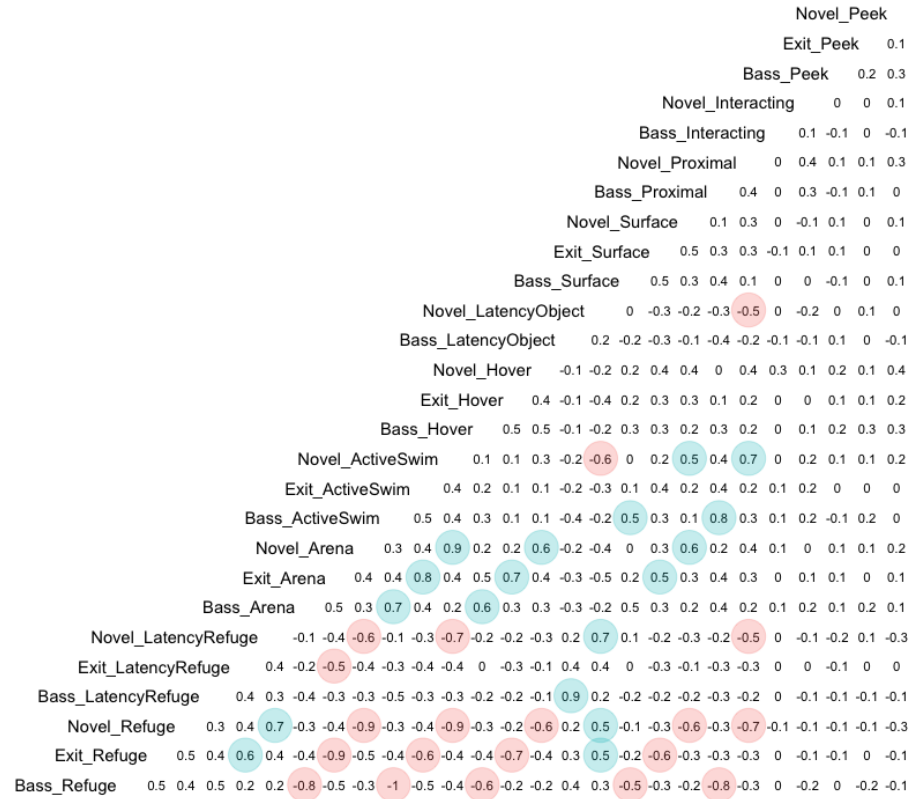
Figure A-2

Comprehensive behavioral state events measured from behavioral trials and their corresponding correlation to one another. Circles indicate a correlation of magnitude 0.5 or greater, with blue circles indicating a positive correlation and pink circles indicating a negative correlation.
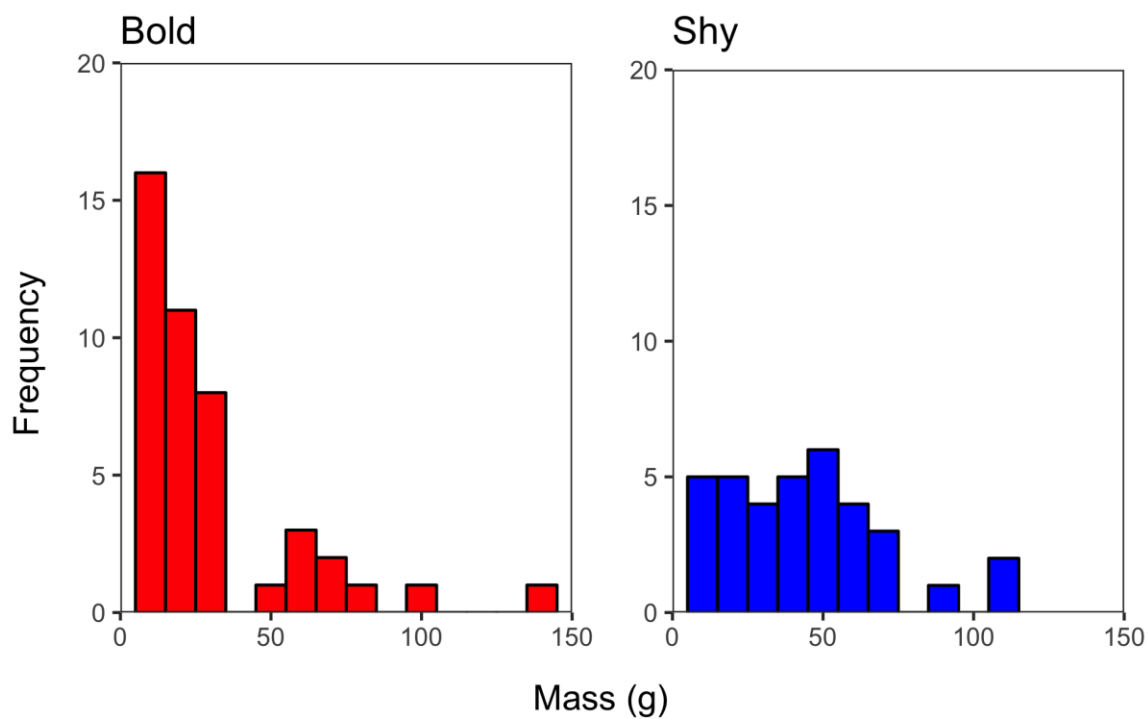
Figure A-3

Frequency of bold (red) and shy (blue) fish at varying masses (g) (n = 79).

Table A-1 – Raw data output for the catchability model of Lake Wanahoo's largemouth bass population.

Date	Effort	C	C_hi	C_lo	N	N_hi	N_lo	q	q_hi	q_lo	q_smooth	qhi_smooth	qlo_smooth	% Discard mortality
4/28/12	2866.00	7944.93	10608.59	5281.27	13452	13452	13452	0.0002061	0.0002752	0.0001370	0.0002061	0.0002752	0.0001370	0
4/29/12	1518.67	3787.12	4875.27	2698.98	13452	13452	13452	0.0001854	0.0002386	0.0001321	0.0001811	0.0002405	0.0001217	0
4/30/12	1534.67	3134.69	4287.87	1981.52	13452	13452	13452	0.0001518	0.0002077	0.0000960	0.0002728	0.0005121	0.0000760	0
5/1/12	944.00	6110.77	13841.99	0.00	13452	13452	13452	0.0004812	0.0010900	0.0000000	0.0003220	0.0005902	0.0000963	0
5/3/12	2384.00	10678.20	15165.37	6191.03	13452	13452	13452	0.0003330	0.0004729	0.0001930	0.0002861	0.0005446	0.0000701	0
5/6/12	1792.00	1062.02	1709.28	414.77	13452	13452	13452	0.0000441	0.0000709	0.0000172	0.0001449	0.0002124	0.0000774	0
5/7/12	1064.00	825.29	1336.52	314.06	13452	13452	13452	0.0000577	0.0000934	0.0000219	0.0000494	0.0000777	0.0000212	0
5/8/12	560.00	350.54	517.92	183.16	13452	13452	13452	0.0000465	0.0000688	0.0000243	0.0000549	0.0000855	0.0000242	0
5/9/12	864.00	702.35	1098.54	306.16	13452	13452	13452	0.0000604	0.0000945	0.0000263	0.0000428	0.0000687	0.0000169	0
5/10/12	944.00	272.37	542.99	1.76	13452	13452	13452	0.0000214	0.0000428	0.0000001	0.0000390	0.0000721	0.0000088	0
5/12/12	3592.00	1696.95	3812.04	0.00	13452	13452	13452	0.0000351	0.0000789	0.0000000	0.0000333	0.0000613	0.0000081	0
5/13/12	1088.00	634.19	912.93	355.45	13452	13452	13452	0.0000433	0.0000624	0.0000243	0.0000453	0.0000804	0.0000130	0
5/14/12	1136.00	877.55	1528.75	226.36	13452	13452	13452	0.0000574	0.0001000	0.0000148	0.0000774	0.0001285	0.0000263	0
5/16/12	704.00	1243.80	2111.37	376.23	13452	13452	13452	0.0001313	0.0002229	0.0000397	0.0000792	0.0001342	0.0000243	0
5/17/12	408.00	268.55	436.14	100.95	13452	13452	13452	0.0000489	0.0000795	0.0000184	0.0000748	0.0001314	0.0000194	0
5/18/12	616.00	364.60	759.34	0.00	13452	13452	13452	0.0000440	0.0000916	0.0000000	0.0000494	0.0000881	0.0000119	0
5/19/12	1000.00	742.52	1253.99	231.04	13452	13452	13452	0.0000552	0.0000932	0.0000172	0.0000404	0.0000791	0.0000057	0
5/22/12	472.00	140.52	333.20	0.00	13452	13452	13452	0.0000221	0.0000525	0.0000000	0.0000329	0.0000695	0.0000057	0
5/23/12	392.00	112.00	331.52	0.00	13452	13452	13452	0.0000212	0.0000629	0.0000000	0.0000235	0.0000651	0.0000000	0
5/24/12	312.00	113.45	335.83	0.00	13452	13452	13452	0.0000270	0.0000800	0.0000000	0.0000203	0.0000562	0.0000000	0
5/26/12	1424.00	241.57	490.62	0.00	13452	13452	13452	0.0000126	0.0000256	0.0000000	0.0000150	0.0000395	0.0000000	0
5/27/12	744.00	52.79	128.02	0.00	13452	13452	13452	0.0000053	0.0000128	0.0000000	0.0000053	0.0000128	0.0000000	0
4/28/12	2866.00	7944.93	10608.59	5281.27	12658	11597	11069	0.0002190	0.0003192	0.0001665	0.0002190	0.0003192	0.0001665	10
4/29/12	1518.67	3787.12	4875.27	2698.98	10690	10202	9932	0.0002333	0.0003147	0.0001789	0.0002215	0.0003126	0.0001630	10

4/30/12	1534.67	3134.69	4287.87	1981.52	9619	9190	8992	0.0002124	0.0003040	0.0001436	0.0004060	0.0009048	0.0001075	10
5/1/12	944.00	6110.77	13841.99	0.00	8381	6997	6997	0.0007724	0.0020957	0.0000000	0.0005801	0.0012805	0.0002761	10
5/3/12	2384.00	10678.20	15165.37	6191.03	5929	4412	3793	0.0007555	0.0014417	0.0006846	0.0005629	0.0012696	0.0002504	10
5/6/12	1792.00	1062.02	1709.28	414.77	3687	3516	3475	0.0001607	0.0002713	0.0000666	0.0003816	0.0006995	0.0002809	10
5/7/12	1064.00	825.29	1336.52	314.06	3392	3258	3227	0.0002287	0.0003855	0.0000915	0.0001952	0.0003171	0.0000876	10
5/8/12	560.00	350.54	517.92	183.16	3192	3140	3122	0.0001961	0.0002945	0.0001048	0.0002304	0.0003707	0.0001060	10
5/9/12	864.00	702.35	1098.54	306.16	3052	2942	2911	0.0002664	0.0004322	0.0001217	0.0001875	0.0003100	0.0000757	10
5/10/12	944.00	272.37	542.99	1.76	2884	2830	2829	0.0001000	0.0002033	0.0000007	0.0001813	0.0003671	0.0000408	10
5/12/12	3592.00	1696.95	3812.04	0.00	2660	2279	2279	0.0001776	0.0004658	0.0000000	0.0001803	0.0003547	0.0000524	10
5/13/12	1088.00	634.19	912.93	355.45	2215	2124	2088	0.0002631	0.0003951	0.0001564	0.0002756	0.0005297	0.0000885	10
5/14/12	1136.00	877.55	1528.75	226.36	2001	1848	1825	0.0003861	0.0007283	0.0001092	0.0005627	0.0010456	0.0002112	10
5/16/12	704.00	1243.80	2111.37	376.23	1701	1490	1452	0.0010389	0.0020135	0.0003681	0.0006290	0.0011719	0.0002192	10
5/17/12	408.00	268.55	436.14	100.95	1425	1381	1371	0.0004619	0.0007738	0.0001804	0.0006480	0.0012555	0.0001828	10
5/18/12	616.00	364.60	759.34	0.00	1335	1259	1259	0.0004434	0.0009792	0.0000000	0.0005107	0.0009789	0.0001345	10
5/19/12	1000.00	742.52	1253.99	231.04	1185	1059	1036	0.0006268	0.0011838	0.0002230	0.0004538	0.0009590	0.0000743	10
5/22/12	472.00	140.52	333.20	0.00	1022	989	989	0.0002913	0.0007139	0.0000000	0.0004034	0.0009310	0.0000743	10
5/23/12	392.00	112.00	331.52	0.00	978	944	944	0.0002923	0.0008954	0.0000000	0.0003244	0.0009353	0.0000000	10
5/24/12	312.00	113.45	335.83	0.00	933	900	900	0.0003897	0.0011966	0.0000000	0.0002919	0.0008363	0.0000000	10
5/26/12	1424.00	241.57	490.62	0.00	875	826	826	0.0001938	0.0004170	0.0000000	0.0002233	0.0006088	0.0000000	10
5/27/12	744.00	52.79	128.02	0.00	821	808	808	0.0000864	0.0002129	0.0000000	0.0000864	0.0002129	0.0000000	10
4/28/12	2866.00	7944.93	10608.59	5281.27	11069	7886	6302	0.0002505	0.0004694	0.0002924	0.0002505	0.0004694	0.0002924	30
4/29/12	1518.67	3787.12	4875.27	2698.98	5165	3703	2893	0.0004828	0.0008670	0.0006143	0.0005931	0.0018430	0.0062860	30
4/30/12	1534.67	3134.69	4287.87	1981.52	1953	666	72	0.0010460	0.0041928	0.0179513	0.0005096	0.0016866	0.0061885	30
5/1/12	944.00	6110.77	13841.99	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0003487	0.0013976	0.0059838	30
5/3/12	2384.00	10678.20	15165.37	6191.03	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/6/12	1792.00	1062.02	1709.28	414.77	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/7/12	1064.00	825.29	1336.52	314.06	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/8/12	560.00	350.54	517.92	183.16	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/9/12	864.00	702.35	1098.54	306.16	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30

5/10/12	944.00	272.37	542.99	1.76	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/12/12	3592.00	1696.95	3812.04	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/13/12	1088.00	634.19	912.93	355.45	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/14/12	1136.00	877.55	1528.75	226.36	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/16/12	704.00	1243.80	2111.37	376.23	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/17/12	408.00	268.55	436.14	100.95	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/18/12	616.00	364.60	759.34	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/19/12	1000.00	742.52	1253.99	231.04	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/22/12	472.00	140.52	333.20	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/23/12	392.00	112.00	331.52	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/24/12	312.00	113.45	335.83	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/26/12	1424.00	241.57	490.62	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30
5/27/12	744.00	52.79	128.02	0.00	0	0	0	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	0.0000000	30

Table A-2 – Raw data output for the catchability model of Prairie Queen's largemouth bass population

Date	E	C	C_hi	C_lo	N	N_hi	N_lo	q	q_hi	q_lo	q_smooth	qhi_smooth	qlo_smooth	% Discard mortality
3/31/15	244.75	235.81	361.03	110.59	11400	11400	11400	0.0000845	0.0001294	0.0000396	0.0000845	0.0001294	0.0000396	0
4/1/15	230.75	332.42	567.60	97.24	11400	11400	11400	0.0001264	0.0002158	0.0000370	0.0000980	0.0001628	0.0000332	0
4/3/15	71.50	67.75	116.67	18.83	11400	11400	11400	0.0000831	0.0001431	0.0000231	0.0001094	0.0001834	0.0000353	0
4/4/15	286.00	386.67	623.74	149.59	11400	11400	11400	0.0001186	0.0001913	0.0000459	0.0001145	0.0001776	0.0000515	0
4/5/15	299.00	483.77	676.27	291.27	11400	11400	11400	0.0001419	0.0001984	0.0000855	0.0001878	0.0002753	0.0001003	0
4/6/15	234.00	808.16	1163.98	452.34	11400	11400	11400	0.0003030	0.0004363	0.0001696	0.0002057	0.0003154	0.0000959	0
4/9/15	58.50	114.79	207.71	21.88	11400	11400	11400	0.0001721	0.0003115	0.0000328	0.0001733	0.0002796	0.0000670	0
4/10/15	39.00	19.88	40.43	-0.67	11400	11400	11400	0.0000447	0.0000909	-0.0000015	0.0001014	0.0001791	0.0000237	0
4/11/15	624.00	622.21	960.37	284.04	11400	11400	11400	0.0000875	0.0001350	0.0000399	0.0000891	0.0001496	0.0000285	0
4/12/15	351.00	540.32	892.03	188.62	11400	11400	11400	0.0001350	0.0002229	0.0000471	0.0000912	0.0001549	0.0000275	0
4/13/15	91.00	53.05	110.83	-4.73	11400	11400	11400	0.0000511	0.0001068	-0.0000046	0.0001287	0.0002252	0.0000323	0
4/15/15	65.00	148.24	256.29	40.18	11400	11400	11400	0.0002001	0.0003459	0.0000542	0.0001697	0.0003142	0.0000253	0
4/17/15	234.00	688.33	1306.63	70.02	11400	11400	11400	0.0002580	0.0004898	0.0000262	0.0002739	0.0004740	0.0000739	0
4/18/15	39.00	161.73	260.68	62.78	11400	11400	11400	0.0003638	0.0005863	0.0001412	0.0002645	0.0004387	0.0000902	0
4/21/15	6.50	12.71	17.78	7.64	11400	11400	11400	0.0001716	0.0002400	0.0001032	0.0002096	0.0003255	0.0000937	0
4/24/15	357.50	380.89	611.90	149.89	11400	11400	11400	0.0000935	0.0001501	0.0000368	0.0000988	0.0001493	0.0000484	0
4/25/15	110.50	39.64	72.63	6.66	11400	11400	11400	0.0000315	0.0000577	0.0000053	0.0000702	0.0001248	0.0000156	0
4/26/15	338.00	329.81	641.57	18.05	11400	11400	11400	0.0000856	0.0001665	0.0000047	0.0000603	0.0001079	0.0000126	0
4/29/15	169.00	122.90	191.89	53.90	11400	11400	11400	0.0000638	0.0000996	0.0000280	0.0000901	0.0001486	0.0000317	0
4/30/15	175.50	242.11	359.52	124.70	11400	11400	11400	0.0001210	0.0001797	0.0000623	0.0001210	0.0001797	0.0000623	0
3/31/15	244.75	235.81	361.03	110.59	11376	11340	11329	0.0000847	0.0001301	0.0000399	0.0000847	0.0001301	0.0000399	10
4/1/15	230.75	332.42	567.60	97.24	11296	11239	11230	0.0001275	0.0002189	0.0000375	0.0000989	0.0001648	0.0000336	10
4/3/15	71.50	67.75	116.67	18.83	11223	11211	11209	0.0000844	0.0001455	0.0000235	0.0001110	0.0001869	0.0000361	10
4/4/15	286.00	386.67	623.74	149.59	11171	11108	11093	0.0001210	0.0001963	0.0000472	0.0001173	0.0001826	0.0000532	10
4/5/15	299.00	483.77	676.27	291.27	11045	10977	10948	0.0001465	0.0002060	0.0000890	0.0001951	0.0002884	0.0001056	10

Date														
4/6/15	234.00	808.16	1163.98	452.34	10867	10751	10706	0.0003178	0.0004627	0.0001806	0.0002159	0.0003338	0.0001015	10
4/9/15	58.50	114.79	207.71	21.88	10694	10673	10671	0.0001835	0.0003327	0.0000350	0.0001830	0.0002975	0.0000713	10
4/10/15	39.00	19.88	40.43	-0.67	10669	10665	10665	0.0000478	0.0000972	-0.0000016	0.0001084	0.0001921	0.0000256	10
4/11/15	624.00	622.21	960.37	284.04	10603	10507	10479	0.0000940	0.0001465	0.0000434	0.0000965	0.0001632	0.0000313	10
4/12/15	351.00	540.32	892.03	188.62	10425	10335	10316	0.0001477	0.0002459	0.0000521	0.0000994	0.0001702	0.0000302	10
4/13/15	91.00	53.05	110.83	-4.73	10311	10300	10301	0.0000565	0.0001182	-0.0000050	0.0001420	0.0002495	0.0000358	10
4/15/15	65.00	148.24	256.29	40.18	10286	10260	10256	0.0002217	0.0003843	0.0000603	0.0001890	0.0003526	0.0000283	10
4/17/15	234.00	688.33	1306.63	70.02	10187	10057	10050	0.0002887	0.0005552	0.0000298	0.0003079	0.0005358	0.0000837	10
4/18/15	39.00	161.73	260.68	62.78	10033	10007	10001	0.0004133	0.0006679	0.0001610	0.0002992	0.0004989	0.0001028	10
4/21/15	6.50	12.71	17.78	7.64	10000	9998	9997	0.0001956	0.0002737	0.0001176	0.0002386	0.0003715	0.0001070	10
4/24/15	357.50	380.89	611.90	149.89	9959	9898	9883	0.0001070	0.0001729	0.0000424	0.0001130	0.0001711	0.0000554	10
4/25/15	110.50	39.64	72.63	6.66	9879	9872	9871	0.0000363	0.0000666	0.0000061	0.0000808	0.0001446	0.0000180	10
4/26/15	338.00	329.81	641.57	18.05	9838	9774	9772	0.0000992	0.0001942	0.0000055	0.0000700	0.0001258	0.0000148	10
4/29/15	169.00	122.90	191.89	53.90	9760	9741	9735	0.0000745	0.0001166	0.0000328	0.0001052	0.0001742	0.0000373	10
4/30/15	175.50	242.11	359.52	124.70	9711	9675	9663	0.0001421	0.0002117	0.0000735	0.0001421	0.0002117	0.0000735	10
3/31/15	244.75	235.81	361.03	110.59	11329	11221	11188	0.0000850	0.0001315	0.0000404	0.0000850	0.0001315	0.0000404	30
4/1/15	230.75	332.42	567.60	97.24	11088	10918	10889	0.0001299	0.0002253	0.0000387	0.0001007	0.0001691	0.0000345	30
4/3/15	71.50	67.75	116.67	18.83	10868	10833	10828	0.0000872	0.0001506	0.0000243	0.0001144	0.0001944	0.0000376	30
4/4/15	286.00	386.67	623.74	149.59	10712	10524	10480	0.0001262	0.0002072	0.0000499	0.0001233	0.0001937	0.0000571	30
4/5/15	299.00	483.77	676.27	291.27	10334	10132	10044	0.0001566	0.0002232	0.0000970	0.0002117	0.0003189	0.0001181	30
4/6/15	234.00	808.16	1163.98	452.34	9802	9453	9317	0.0003524	0.0005262	0.0002075	0.0002401	0.0003782	0.0001150	30
4/9/15	58.50	114.79	207.71	21.88	9282	9220	9214	0.0002114	0.0003851	0.0000406	0.0002064	0.0003414	0.0000821	30
4/10/15	39.00	19.88	40.43	-0.67	9208	9195	9196	0.0000554	0.0001127	-0.0000019	0.0001258	0.0002248	0.0000305	30
4/11/15	624.00	622.21	960.37	284.04	9009	8721	8636	0.0001107	0.0001765	0.0000527	0.0001159	0.0001996	0.0000389	30
4/12/15	351.00	540.32	892.03	188.62	8474	8206	8149	0.0001817	0.0003097	0.0000659	0.0001213	0.0002122	0.0000374	30
4/13/15	91.00	53.05	110.83	-4.73	8133	8100	8102	0.0000717	0.0001503	-0.0000064	0.0001788	0.0003180	0.0000457	30
4/15/15	65.00	148.24	256.29	40.18	8057	7980	7968	0.0002830	0.0004941	0.0000776	0.0002446	0.0004674	0.0000373	30
4/17/15	234.00	688.33	1306.63	70.02	7762	7370	7349	0.0003790	0.0007577	0.0000407	0.0004100	0.0007258	0.0001139	30

4/18/15	39.00	161.73	260.68	62.78	7300	7222	7203	0.0005681	0.0009255	0.0002235	0.0004062	0.0006878	0.0001426	30
4/21/15	6.50	12.71	17.78	7.64	7199	7194	7192	0.0002717	0.0003803	0.0001635	0.0003301	0.0005180	0.0001494	30
4/24/15	357.50	380.89	611.90	149.89	7077	6894	6849	0.0001505	0.0002483	0.0000612	0.0001582	0.0002417	0.0000779	30
4/25/15	110.50	39.64	72.63	6.66	6837	6815	6813	0.0000525	0.0000964	0.0000088	0.0001161	0.0002119	0.0000261	30
4/26/15	338.00	329.81	641.57	18.05	6714	6522	6516	0.0001453	0.0002910	0.0000082	0.0001033	0.0001881	0.0000223	30
4/29/15	169.00	122.90	191.89	53.90	6480	6422	6406	0.0001122	0.0001768	0.0000498	0.0001585	0.0002656	0.0000576	30
4/30/15	175.50	242.11	359.52	124.70	6333	6225	6188	0.0002178	0.0003291	0.0001148	0.0002178	0.0003291	0.0001148	30