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Contemporary and Historic Effects of Fishing on Largemouth Bass Populations, Using Unexploited Populations for Reference

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Jan-Michael Hessenauer, Ph.D.

University of Connecticut, 2015

ABSTRACT: Recreational fisheries represent complex coupled human and natural systems subject to intricate feedback loops. These feedback loops can affect anglers, fish populations, and the ecosystem. I studied the effects of recreational angling on Largemouth Bass *Micropterus salmoides* populations, using unexploited populations for references. Exploited populations contained significantly more individuals with low metabolic rates than unexploited populations, consistent with predictions of fisheries induced evolution. Naïve individuals from unexploited and exploited populations had equal initial angling vulnerability in standardized trials. However, individuals from exploited populations learned lure avoidance faster than unexploited individuals. The cumulative number of catch events best predicted catch rates, and many individuals from both population types were never captured suggesting social learning may be involved with learned lure avoidance. Enhanced learning may be another mechanism through which angling selection affects fish populations.

Selection from recreational angling should decrease population vulnerability to angling, and is associated with ecologically important energetic phenotypes. I evaluated whether unexploited individuals could genetically contribute to an active fishery, and thus the potential

for genetic management to restore phenotypes reduced in populations by selection from recreational angling. Parentage analysis revealed that individuals from exploited and unexploited populations contributed to an active fishery in proportion to their stocking frequency and sex ratios, suggesting that genetic management is a feasible management strategy.

To understand the current effects of recreational angling on Largemouth Bass populations I estimated the total number of catch events occurring in two lakes over two years. Catch was estimated by monitoring tournaments and from creel data collected by the Connecticut Department of Energy and Environmental Protection Inland Fisheries Division. Catch data and population size were utilized in a yield per recruit model to estimate the effects of length limits and catch-and-release mortality on population age and size structure. Modeling revealed that harvest rates estimated from creel data are likely too low for length limits to affect population structure, and even low rates of catch-and-release mortality are likely to significantly alter population structure. Creative management solutions that manage angler catch or effort are needed for high use fisheries with low harvest rates.

Contemporary and Historic Effects of Fishing on Largemouth Bass Populations, Using
Unexploited Populations for Reference

Jan-Michael Hessenauer

B.S., Michigan State University, 2008

M.S., Michigan State University, 2011

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Submitted in Partial Fulfillment of the
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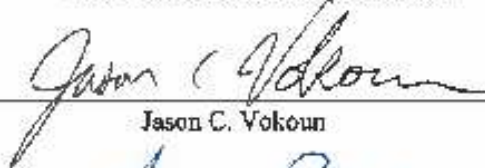
Doctor of Philosophy Dissertation

Contemporary and Historic Effects of Fishing on Largemouth Bass Populations, Using
Unexploited Populations for Reference

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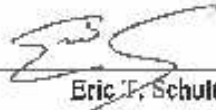
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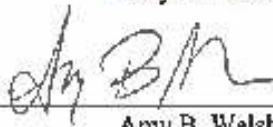
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Preface

The chapters of this dissertation are prepared as standalone manuscripts to be submitted for publication. Therefore, some repetition exists among introductory materials, methods, and cited literature.

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CHAPTER 1

Comparisons of the Resting Metabolic Rates and Angling Vulnerability of Exploited and Unexploited Populations of Largemouth Bass¹

Abstract

Recreational fishing represents a coupled human natural system subject to complex feedback processes. Non-random mortality associated with recreational fisheries has the potential to cause evolutionary changes in fish populations. Inland recreational fisheries offer unique opportunities to study fisheries induced evolution due to the ability to replicate study systems, limited gene flow among populations, and the existence of unexploited reference populations. Experimental research has demonstrated that angling vulnerability is heritable in Largemouth Bass *Micropterus salmoides*, and is correlated with elevated resting metabolic rates (RMR) and higher fitness. Therefore, over time selection from recreational angling should decrease RMR and overall population vulnerability to angling in exploited populations. I sought to quantify differences in RMR and angling vulnerability among replicated exploited and unexploited populations of Largemouth Bass. I collected age-0 Largemouth Bass from two Connecticut drinking water reservoirs unexploited by angling for almost a century, and two exploited lakes, then transported and reared them in the same pond for 10 months prior to respirometry. Field RMR of individuals from each population was quantified using intermittent-flow respirometry. Individuals from unexploited reservoirs had a significantly higher mean RMR (6%) than individuals from exploited populations. Standardized angling took place one

¹ A manuscript from this chapter has been published in the journal PLOS ONE DOI: 10.1371/journal.pone.0128336

year after respirometry trials. While no difference in initial angling vulnerability existed among fish from exploited and unexploited populations of origin, individuals from exploited populations learned lure avoidance faster than individuals from unexploited populations. Cumulative catch events, a metric which incorporates the number of opportunities individuals had to directly and indirectly experience angling, best predicted declining daily catch rates for both exploited and unexploited populations, suggesting a social learning component of learned lure avoidance. That individuals originating from exploited populations had lower RMR and lost naivety to angling quicker relative to individuals from unexploited populations is consistent with predictions of fisheries induced evolution, and may have widespread effects on ecosystem energetics as well as recreational angling quality.

Introduction

Recreational fishing is popular worldwide, accounting for an estimated 12 % of global fish harvest (Post et al. 2002; Cooke and Cowx 2004; Cooke and Cowx 2006; Lewin et al. 2006). Recreational fishing represents an excellent example of a complex coupled human and natural system (e.g. Liu et al. 2007) that includes feedback loops which effect individual fish behavior and health, angler practices and effort, fish population characteristics and ultimately the ecosystem as a whole (e.g., via trophic cascades; Carpenter et al. 1985; Carpenter & Kitchell 1993). Feedback loops associated with recreational angling can occur over multiple temporal and to some extent spatial scales (e.g. Post et al. 2002).

Selection from angling represents one potential feedback loop associated with recreational fishing. Similar to commercial fisheries, recreational fisheries are generally size selective (Alós et al. 2014a; Kuparinen and Merilä 2007; Matsumura et al. 2011), typically result

in higher population mortality rates (Allendorf et al. 2008; Law 2007), and may interrupt critical life history events (Kuparinen and Merilä 2007; Thériault et al. 2008; Alós et al. 2014a). However, the passive nature of most recreational fisheries in which a fish needs to choose to eat (or attack) the bait or lure is an important distinction (Uusi-Heikkilä et al. 2008; Alós et al. 2012). Recreational anglers also likely have more capacity to adapt terminal tackle and presentation methods to target particular sizes of fish or to intercept particular life history stages than is common in commercial fisheries. These aspects of recreational fisheries have been shown to select for behavioral phenotypes and their underlying physiological drivers (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Alós et al. 2012) as well as morphological traits such as body shape (Alós et al. 2014b). As a result, non-random mortality associated with commercial and recreational fisheries can produce selective responses in targeted populations, a phenomenon known as fisheries induced evolution (FIE).

Given the potential for FIE resulting from recreational angling, inland recreational fisheries offer opportunities to reveal both the presence and mechanisms of FIE. Multiple lakes and river systems can serve as replicate experimental units (Philipp et al. 2009), and while rare, unexploited populations still exist (Kocovsky and Carline 2001; Mueller et al. 2005; Hessenauer et al. 2014). Comparison between exploited and unexploited populations establishes a reference point for the impacts of harvest and fishing. Even in the absence of harvest, catch-and-release fisheries still have the potential to exert selective pressures as a result of unintended post-release mortality (Muoneke and Childress 1994) and decreased reproductive fitness (Philipp et al. 1997; Suski and Philipp 2004; Stein and Philipp 2014). Because multiple systems can be used as replicates, and gene flow is often limited among sites, and unexploited populations exist for

reference, research on inland recreational fisheries associated with FIE is increasing (Cooke and Cowx 2004; Uusi-Heikkilä et al. 2008; Philipp et al. 2009; Redpath et al. 2010; Post 2012).

Philipp et al. (2009) demonstrated that vulnerability to recreational angling has a heritable genetic component. This was established by developing strains of Largemouth Bass (*Micropterus salmoides*) that had high vulnerability (HV) and low vulnerability (LV) to angling through an intensive multi-generation artificial selection experiment. They demonstrated that selection from angling resulted in appreciable reductions of angling vulnerability in LV fish (Philipp et al. 2009), suggesting that selection towards decreasing vulnerability was feasible in exploited populations. Subsequent experiments demonstrated that relative to LV individuals, HV individuals exhibited a suite of correlated phenotypes including higher metabolic rates (Redpath et al. 2010), which correlated with lower rejection rates of prey (Nannini et al. 2011), and more intensive parental care and boldness (Cooke et al. 2007) resulting in higher fitness potential in the absence of angling (Sutter et al. 2012). Therefore, selection from recreational fishing acts on a suite of behavioral traits linked to underlying heritable physiological processes that collectively make some individuals more vulnerable to angling (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Alós et al. 2012). As a result Largemouth Bass, an ecologically (Carpenter et al. 1987; Mittelbach et al. 1995) and economically (US Fish and Wildlife Service 2006) important widespread sportfish, has emerged as a model species for study of FIE (Philipp et al. 1997; Cooke et al. 2007; Philipp et al. 2009; Redpath et al. 2010; Sutter et al. 2012).

Experimental evidence suggests that recreational angling should, over time, decrease the prevalence of HV phenotypes in exploited systems leading to a decrease in overall angling vulnerability (Philipp et al. 2009) and correlated phenotypes, such as metabolic rates (Redpath et al. 2010). Over the course of a single growing season (in temperate climates) angler catch rates

are known to decline (Aldrich 1939; Beukema 1970; Hackney & Linkous 1978; van Poorten & Post 2005) independent of changes in fish density associated with harvest or mortality from angling (Askey et al. 2006; Klefoth et al. 2013). Studies have associated, across several species, the decreases in population-level vulnerability to angling with behavioral modification due to individuals learning lure avoidance behaviors (Beukema 1970; Hackney & Linkous 1978; Askey et al. 2006; Kuparinen et al. 2010). Foraging arena theory represents one framework that provides a mechanistic study of the behavioral modifications of fishes in response to predation risk (Ahrens et al. 2012). Individuals of a population can be thought of as belonging to two groups, one that is currently vulnerable to angling, and another that is invulnerable to angling (Ahrens et al. 2012). The division of individuals into these two groups and the movement of individuals between these groups are a function of behavioral decisions that each individual makes, and some of these decisions have been demonstrated to have heritable components (Biro and Post 2008; Philipp et al. 2009; Klefoth et al. 2013). Therefore, selection from recreational angling may be influencing the inherent vulnerability of exploited populations, and potentially the ability of individuals within exploited populations to modify their behavior to avoid lures. Together these mechanisms may result in decreased catch rates, even if Largemouth Bass density remains unchanged.

My first objective was to examine the metabolic profiles of two exploited and unexploited populations of Largemouth Bass. I hypothesized that Largemouth Bass from exploited populations would exhibit lower metabolic rates relative to Largemouth Bass from unexploited populations, consistent with the outcomes of previous studies that used Largemouth Bass line-bred for differences in angling vulnerability (Philipp et al. 2009; Redpath et al. 2010). My second objective was to evaluate the angling vulnerability of two exploited and unexploited

populations of Largemouth Bass. I hypothesized that individuals originating from unexploited populations will have higher inherent angling vulnerability relative to individuals originating from exploited populations. Further, I hypothesize that individuals from exploited populations will modify their behavior in response to angling more quickly than individuals from unexploited populations, such that the angling vulnerability of exploited individuals will decrease more rapidly than individuals from unexploited populations.

Methods

I collected Largemouth Bass from four populations in Connecticut, USA, during fall 2012. Hemlock Reservoir (177 ha; N 41°13'2.27", W 73°17'19.78") and Easton Reservoir (198 ha; N 41°15'55.25", W 73°16'1.10") are private drinking water reservoirs and were impounded in 1914 and 1926, respectively, by the Bridgeport Hydraulic Company. Both reservoirs have been closed to angling since their construction. While some illegal shoreline angling likely occurs, both of these lakes lack public boat access and are patrolled by water company law enforcement officers; resulting in populations that have essentially been unexploited by anglers for almost a century (Hessenauer et al. 2014). In contrast, both Amos Lake (46 ha; N 41°31'1.57", W 71°58'31.14") and Gardner Lake (214 ha; N 41°30'39.66", W 73°13'38.77") support popular public Largemouth Bass fisheries, have public boat ramps, and were therefore deemed 'exploited' for the purposes of this study. All four lakes are mesotrophic, and Largemouth Bass are the dominant piscivore. Fish communities consist of Centrarchidae (primarily Bluegill *Lepomis macrochirus* and Pumpkinseed *Lepomis gibbous*) and Percidae (primarily Yellow Perch *Perca flavescens*) species. Gardner and Amos Lakes are seasonally stocked with Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss* as part of put-and-take fisheries practices, and while not stocked directly Hemlock and Easton Reservoirs

contain Brown and Rainbow trout from the downstream displacement of fish stocked upstream. Hemlock Reservoir and Amos Lake also contain populations of landlocked Alewives *Alosa pseudoharengus*. Largemouth Bass are not native to Connecticut, and are believed to have been introduced throughout the state (and region) from an upstate New York source population via Federal stocking programs in the 1850's (Whitworth 1996). It has not been management practice to stock Largemouth Bass in any lakes or reservoirs in the state since early naturalization, and no records of such stockings exist for the study lakes. All four systems experience the same climate conditions, given their similar latitude and proximity to Long Island Sound.

Age-0 Largemouth Bass were captured from widely distributed locations within each source lake via beach seining, trap netting, and boat electrofishing. Sampling occurred over approximately four weeks beginning September 25th 2012 and ending October 24th 2012. Sampling effort was consistent among the three gears in each lake. Trap netting entailed setting five trap nets over 48 h intervals, with each trap emptied each morning. Seining occurred over a two work day period (concurrent with trap netting) and night-time electrofishing completed one full lap of each lake. I chose to sample each lake with a combination of active (seining, and electrofishing) and passive (trap-netting) techniques employed with similar effort among lakes because vulnerability to sampling gears has been shown to vary with animal personality (e.g. Wilson et al. 1993; Biro and Dingemanse 2009; Carter et al. 2012). Animal personality has been linked to metabolic rate (Biro and Stamps 2008), therefore my sampling approach was designed to guard against collecting an unrepresentative sample of possible personality traits and metabolic rates. Age-0 Largemouth Bass disperse widely and randomly from their nest of origin (Hessenaar et al. 2012), suggesting that my sample is unlikely to be biased towards a small number of kin groups, and thus confounded by potential maternal effects within populations.

After capture, Largemouth Bass were transported 107, 92, 83, and 95 km from Amos, Easton, Gardner, and Hemlock, respectively, in aerated coolers to a single outdoor rearing pond at the Connecticut Department of Energy and Environmental Protection Burlington State Fish Hatchery in Burlington, Connecticut. Prior to release into the pond, individuals from each population were double tagged with population-specific batch marks including a fin clip and visual implant elastomer tag. Throughout spring and summer of 2013, the pond was stocked at regular intervals with small minnows for forage (*Pimephales promelas* and *Notemigonus crysoleucas*).

Quantification of resting metabolic rates

During fall 2013, after individuals had acclimated and been reared in the common pond for at least 10 months, I measured field resting metabolic rates (RMR) of individuals from each of the four populations. Each day, four individuals of similar size (one from each source population) were moved to a closed pen immersed in the pond and held without food for 48 h. After this 48 h period, fish were randomly assigned to respirometry chambers to measure their oxygen consumption using intermittent, flow-through respirometry (Steffensen 1989). The respirometry system, housed inside a $1.83 \times 3.05 \times 1.83$ m cargo trailer parked at the side of the pond, was identical to the system used by Redpath et al. (2010). The respirometer contained four chambers (~0.75 L total volume) immersed in a 340 L water tank. Water in the tank was aerated continuously and exchanged daily with pond water. Tank water temperatures were initially matched to pond temperatures at the time fish were placed in the respirometry chambers (mean temperature 18.5° C; range 15.0-20.4° C), and then held constant throughout each trial using a digitally controlled 250 W aquarium heater. Water flow in each chamber was controlled by two aquarium pumps. The first pump circulated water through the chamber past a fiber optic oxygen probe connected to an OXY-4 fiber optic oxygen instrument (Loligo Systems, Tjele, Denmark),

which measured variation in oxygen partial pressure. The second pump exchanged water within the respirometry chamber with aerated tank water. Pumps were automatically controlled by the AutoResp 4 software (Loligo Systems, Tjele, Denmark), which alternated between a four minute flush phase, a one minute wait phase and an 8-20 minute measurement phase (duration selected based on fish size and water temperature). The same measurement phase was applied to all four fish during a given trial, such that overall measurement lengths were not different among the four populations. Oxygen partial pressure was measured twice per second and regressed against time. The slope of the regression line comparing oxygen concentration over time was used to calculate oxygen consumption using the equation:

$$Mo_2 = \frac{k \times V \times \alpha}{m}$$

where Mo_2 is oxygen consumption ($\text{mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$), k is the slope of the regression line, V is the volume (in L) of water within the chamber (corrected for fish volume), α is the solubility of oxygen in water at the experimental temperature, and m is the mass (kg) of the fish.

Trials were initiated during the afternoon, and individuals were left undisturbed overnight in their randomly assigned chambers, resulting in a total trial length of 20-22 h. This procedure generated one data point for each fish every 13-25 min, for a total of 47- 100 data points per trial. To ensure high quality data, I limited analysis to data points generated from measurement phases resulting in oxygen consumption over time slopes with regression $r^2 > 0.90$ (Cruz-Neto and Steffensen 1997; Herrmann and Enders 2000). For each individual, I also examined a graph of oxygen consumption over total trial time to ensure that fish were not becoming active during a given measurement phase (which would manifest as a spike in oxygen consumption). Any fish that became active during multiple measurements were excluded from the dataset. After

removing fish from the chambers, background oxygen consumption rates were quantified by resuming the collection of data using empty chambers for approximately 90 minutes, generating six blank measurements. All equipment was sterilized and sensors were calibrated regularly throughout the data collection.

Analysis of resting metabolic rate data

Field RMR for each individual was defined as the six lowest observations per individual from the 47-100 data points collected during the trial, corrected for mean background oxygen consumption (Shultz et al. 2011; Blevins et al. 2013). The effect of exploitation status (exploited vs. unexploited) on log field RMR was evaluated using a mixed model analysis of covariance (ANCOVA) (Montgomery 2013). For the ANCOVA, log temperature, exploitation status, population of origin (nested within exploitation status), as well as the interaction between temperature and population of origin were treated as fixed effects. Fish identification number, respirometry tube number, and trial day were treated as random effects. This approach accounts for differences in temperature among respirometry trials and allows the variability among individuals, populations, and day of the trial to be explicitly included within the model (Wagner et al. 2006; Blevins et al. 2013). Model residuals were normally distributed (assessed by examining the normal quantile plot), and mean residuals were not significantly different among the four populations, indicating that the assumptions of the model were met. After correcting to mean temperature (18.5° C) across all trials based on the temperature vs. metabolic rate relationship defined by the ANCOVA analysis, the distribution of mean RMR among unexploited and exploited individuals were compared using a Kolmogorov-Smirnov (KS) test. Statistical analysis was conducted in JMP 11 (mixed-modeling, and residual analysis) and Program R 2.13.2 (KS test). Results were considered statistically significant when $P \leq 0.05$.

I performed a simple modeling exercise to illustrate the potential effects of different RMR for exploited and unexploited populations on ecosystem trophic dynamics. Two populations (one exploited and one unexploited) of 1,000 adult individuals were modeled, with a mean weight of 0.9 kg per individual. The exercise was limited to a growing season of 200 d, with a water temperature of 25 °C. I used the oxy-caloric multiplier of 3,800 cal·g⁻¹ O₂ (Brett and Groves 1979) to convert field RMR into calories used by each population. I assigned adults from the exploited population a RMR of 0.102 g O₂·kg⁻¹·h⁻¹ (Cech et al. 1979), and unexploited individuals a RMR 6 % higher (see results). Outcomes of this exercise were expressed in kilograms of two common prey species, Bluegill (*Lepomis macrochirus*) and Fathead Minnows (*Pimephales promelas*) based on the caloric density of those species.

Standardized angling trials

Prior to the onset of standardized angling in July 2014, a seine haul of the rearing pond (spanning the entire length and width of the pond) was conducted to determine the relative abundance of individuals originating from exploited and unexploited populations in the rearing pond. Individuals were examined and identified by their population-specific fin clips and visual implant elastomer marks. Standardized angling occurred three days per calendar week, shared among five experienced anglers, during one of four time periods randomly selected each day (07:00 - 10:00, 10:00 - 13:00, 13:00 -16:00, and 16:00 - 19:00.) To ensure that angler effort targeted the entire pond, six fishing stations were established evenly around the perimeter of the pond. Each station was marked by a stake; anglers were permitted to move around the stake, but instructed to move no further than halfway to the next stake in either direction. The starting position each day was randomly selected, and a second angler started at the position opposite the first. Anglers then proceeded around the pond in a direction (clockwise or counter-clockwise)

that was randomly selected. Three standardized lures were employed throughout the angling trials: a 5 cm F5-Rapala ® crank bait, a Mepps ® Plain Aglia size 0 inline spinner, and a 1.8 g (1/16th oz) white jig head fitted with a Mister Twister ® curly tail grub. These lures were selected because collectively they fish the entire water column, represent a variety of fishing styles and presentations, and similar lures have been used for other standardized angling studies (e.g., Philipp et al. 2009). Lures were presented in a predetermined random order and fished for five minutes of actual fishing time each at each station (i.e., when a fish was captured the five minute timer was paused for processing and data collection). When an individual was hooked, a stopwatch was started to record handling time. For each captured individual total length and weight were measured. The population of origin was determined, and the anal fin and one dorsal spine were clipped (as per Philipp et al. 2009) to facilitate the identification of recaptures. The station at which the individual was captured, and the time of day of capture were recorded and then the individual was released. Water temperature was recorded at the start and end of each angling session. Data were recorded on the weather conditions including cloud cover, air temperature, barometric pressure and humidity (the latter three downloaded from a weather station located roughly 1 km from the study site). After the conclusion of standardized angling a whole pond census was conducted by lowering the pond water level and conducting multiple whole-pond seine hauls to determine the total number of exploited and unexploited individuals remaining. A chi-square test was used to determine whether the proportions of fished and unfished individuals remaining at the conclusion of the study differed significantly from initial proportions.

Attempting to remove overt hunger as a confounding variable, the pond was liberally stocked with forage to create an *ad libitum* feeding environment during the experiment (stocking

dates: July 10th, July 31st, August 15th and September 12th). Forage included the minnow species *Pimephales promelas* and *Notemigonus crysoleucas* at the following stocking rates: 226.8 kg/ha: July 10th and July 31st, 56.8 kg/ha: August 15th and September 12th). Throughout the study period large schools of forage fishes were observed in the pond.

Analysis of angling data

Exploratory regression analyses of variation in aggregated daily catch rate (bass/hr) were used to evaluate predictors associated with environmental conditions (cloud cover, barometric pressure, humidity and max water temperature) and passage of time (angling day, cumulative number of angling hours and cumulative number of catch events). Predictor variables were regressed with catch rates one at a time, with data transformed as appropriate to ensure linearity. Because I hypothesized that both the initial angling vulnerability and the rate at which naiveté was lost (lure avoidance was learned) would differ among individuals originating from fished and unfished populations, separate regression models were fit for exploited and unexploited population. Each model included the significant predictors identified in the exploratory analyses. Prior to fitting regression models, daily catch rate was standardized for individuals originating from exploited and unexploited population (catch rate divided by relative abundance at start of the angling trials). Regression parameters calculated for exploited and unexploited individuals were compared using t-tests. Regression model assumptions were verified by visually examining the normal quantile plots for the exploited and unexploited regression models. Potential differences in length, weight or handling time were evaluated among captured individuals from exploited and unexploited populations using t-tests. Statistical analyses were performed using program JMP v. 11, maintaining an overall alpha value of 0.05 to determine

significance. Results were considered statistically significant when $P \leq 0.05$. Data are reported as mean \pm SD where appropriate.

Results

Respirometry

Respirometry trials were conducted on 30 (Amos Lake), 25 (Easton Reservoir), 25 (Gardner Lake), and 31 (Hemlock Reservoir) Largemouth Bass during fall 2013. Log transformed field RMR were normally distributed ($W = 0.99$, $P = 0.84$). Fish weight did not differ significantly across populations (Amos: 33 ± 1 g, Easton: 32 ± 2 g, Gardner: 33 ± 2 g, Hemlock: 31 ± 1 g; $F_{3,107} = 0.69$, $P = 0.56$).

Mean field RMR of Largemouth Bass from unexploited reservoirs was approximately 6% higher than that of fish from lakes open to fishing (unexploited least squares mean: $118.2 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$, exploited least squares mean: $111.6 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$; $F_{1,73} = 8.34$, $P = 0.005$, Table 1.1). Based on the modeling exercise a 6% difference in mean field RMR would require a population of 1,000 0.8 kg unexploited individuals to consume an extra 100,600,000 calories relative to a similar population of exploited individuals. This is the caloric equivalent of 86.7 kg of Bluegill (Pope et al. 2001) and 142.5 kg of Fathead Minnows (Bourret et al. 2008). Population of origin was not a significant predictor of RMR once the effect of exploitation status had been accounted for ($F_{2,75} = 1.48$, $P = 0.23$). Temperature had a significant effect on field RMR ($F_{1,444} = 118.9$, $P < 0.001$), however there was no significant temperature by population interaction ($F_{3,326} = 0.77$, $P = 0.51$) suggesting all four populations responded to the temperature range in a similar manner.

The temperature-corrected and back-transformed range of RMR observations was similar for both exploited and unexploited populations (unexploited range: 86.5-163.1 mg O₂·kg⁻¹·h⁻¹, exploited range: 79.9-156.3 mg O₂·kg⁻¹·h⁻¹; Figure 1.1). However, the groups had significantly different distributions (D= 0.26, P= 0.04) where 75 % of unexploited individuals had higher metabolic rates than the median of the exploited populations (exploited population median: 113.2 mg O₂·kg⁻¹·h⁻¹; Figure 1.2), and 71 % of exploited individuals had metabolic rates lower than the median of the unexploited populations (unexploited population median: 124.8 mg O₂·kg⁻¹·h⁻¹).

Standardized Angling

Standardized angling began on July 14th 2014 and continued until September 29th 2014, resulting in 123 captures representing 102 unique individuals (41 from exploited populations and 61 from unexploited populations). Angling resulted in a rapid decline in daily aggregate catch rates for individuals originating from both exploited and unexploited populations (Figure 1.3). The total catch closely mirrored the estimated initial abundance of fish in the pond (39% exploited, 61% unexploited).

No significant differences in length (exploited individuals mean = 176.5 ± 33.3 mm, unexploited individuals mean = 172.9 ± 30.4 mm; P = 0.59) or weight (exploited individuals mean = 84.9 ± 58.9 g, unexploited individuals mean = 79.8 ± 48.4 g; P = 0.65) existed among individuals originating from exploited or unexploited populations captured in this study. Mean handling time for all individuals was 113 ± 10 s and did not differ significantly between individuals originating from exploited and unexploited populations (P = 0.93).

Water temperature was the only significant weather-related predictor (Table 1.2) of total aggregate daily catch rate (adjusted R² = 0.12, F_{1,27} = 4.67, P = 0.04). All three predictor

variables associated with the passage of time were significant predictors of total aggregate daily catch (angling day: adjusted $R^2 = 0.48$, $F_{1,27} = 26.9$, $P < 0.0001$; cumulative angler hours: adjusted $R^2 = 0.41$, $F_{1,27} = 20.7$, $P < 0.0001$; cumulative catch events: adjusted $R^2 = 0.85$, $F_{1,27} = 159.8$, $P < 0.0001$). Because cumulative catch events explained the highest proportion of variance in aggregate daily catch rate among covariates associated with the passage of time, this index was used along with water temperature to calculate separate regression models for the corrected daily catch rates of individuals originating from exploited and unexploited populations. Models including water temperature and cumulative catch events explained a significant proportion of the variance in daily catch for individuals originating from both exploited (Catch = $17.1 - 0.29[\text{WaterTemp}] - 0.10[\text{CumulativeCatch}]$; adjusted $R^2 = 0.80$, $F_{2,26} = 55.5$, $P < 0.0001$) and unexploited (Catch = $10.6 - 0.11[\text{WaterTemp}] - 0.07[\text{CumulativeCatch}]$; adjusted $R^2 = 0.86$, $F_{2,26} = 88.0$, $P < 0.0001$) populations. The slopes associated with the cumulative catch predictor were significantly different ($t = -2.623$, $P_{\text{adjusted}} = 0.033$) between individuals originating from exploited and unexploited populations (Figure 1.4), which represents the rate at which naivety was lost, or the rate at which lure avoidance behaviors were learned among fished and unfished individuals. However, there was no significant difference for the y-intercept, which represents initial angling vulnerability ($t = 2.09$, $P_{\text{adjusted}} = 0.12$) between individuals originating from exploited and unexploited populations. These results indicate that, contrary to my hypothesis, initial vulnerability to angling was not different among totally naïve individuals from exploited and unexploited populations. However, congruent with my second hypothesis, individuals originating from exploited populations tended to lose their vulnerability to angling faster than individuals originating from unexploited populations. Water temperature was a significant predictor of daily catch for individuals originating from exploited populations, but not significant

for unexploited populations ($P = 0.07$). However, there was no significant difference in the water temperature parameters estimated from the regression models fit for individuals originating from exploited and unexploited populations ($t = -1.64$, P adjusted = 0.30). A visual examination of the normal quantile plot of model residuals revealed no substantial departures from normality indicating that model assumptions were adequately met.

The final whole pond census revealed that 155 total individuals remained at the conclusion of standardized angling, of which 65 originated from exploited populations and 90 were from unexploited populations. The final proportions of individuals originating from exploited and unexploited populations were not significantly different from the initial proportions (Chi-square: 0.68, d.f.:1, $P=0.41$), indicating that individuals originating from exploited and unexploited populations did not experience differential mortality rates over the course of the standardized angling. Of the 155 individuals remaining at the end of study period, 69 were captured at least once by angling. Twenty-seven individuals captured by angling originated from exploited populations and 42 individuals originated from unexploited populations. The majority of individuals (56%) present at the end of the standardized angling were never captured by angling. Of the individuals remaining that had never been captured by angling, 38 originated from exploited populations and 48 originated from unexploited populations which was not significantly different from expectations based on their initial abundance (Chi-square: 0.19, d.f.:1, $P = 0.66$).

Discussion

The potential for recreational angling to act as an evolutionary force is well established in theory (Cooke and Cowx 2004; Philipp et al. 2009; Alós et al. 2012; Sutter et al. 2012; Alós et al. 2014b), and this study represents a first step towards identifying outcomes of selection from

angling in wild recreationally-targeted populations using unexploited populations as references. In my study mean field RMR of Largemouth Bass from unexploited reservoirs was approximately 6 % higher than that of fish from lakes open to fishing. While individuals originating from lakes open to fishing also learned to avoid lures faster than fish from lakes closed to angling, there was no difference in naïve angling vulnerability.

For black bass (*Micropterus* spp.), selection due to angling is known to influence a range of behaviors including foraging (Nannini et al. 2011) and reproduction (Sutter et al. 2012). Angling during the vulnerable nesting stage has negative effects on the fitness of individual nest-guarding males by decreasing nest success even when removal is temporary (e.g., catch-and-release) (Kieffer et al. 1995; Philipp et al. 1997; Stein and Philipp 2014). Likewise, increased mortality rates associated with angling (e.g., purposeful harvest or post-release hooking mortality) may have selective effects on exploited populations (Allendorf et al. 2008). Therefore, the mechanism for FIE exists given that recreational angling preferentially targets individuals with a collection of heritable phenotypes, including boldness, foraging behavior, and nest defense that collectively increase angling vulnerability (Sutter et al. 2012). Previous studies suggest that Largemouth Bass populations may be evolving (or may have already evolved) towards decreased vulnerability to angling (Philipp et al. 2009). My finding, that unexploited populations contained more individuals with high metabolic rates than those from exploited populations, was predicted by the results obtained using Largemouth Bass bred for high and low angling vulnerability (Redpath et al. 2010), and supports the hypothesis that angling may be altering the distribution of metabolic rates in populations. Yet the continued presence of high metabolic rate phenotypes at low abundance in exploited populations suggests that if selective effects of angling are occurring, mitigation may be possible. Sutter et al. (2012) found that high

metabolic rate individuals had higher reproductive fitness than those with low metabolic rates. If one assumes that wild, high metabolic rate individuals also have higher fitness relative to wild low metabolic rate individuals in the absence of angling, then restricting angling during the nesting season may promote the fitness of high metabolic rate phenotypes and increase their abundance in the population. Exploring the mechanisms through which high metabolic rate phenotypes are retained in exploited populations has conservation importance, especially if future studies confirm that FIE in recreational fisheries is widespread. One explanation may be that selection has not been sufficiently strong, or occurred for a sufficient time period, to eliminate these phenotypes. Alternatively, the fitness advantage for high metabolic rate phenotypes (Sutter et al. 2012) when not captured by anglers may be sufficient to maintain these phenotypes in the population.

The disruption of food web structures may limit the recovery of exploited fish stocks (Post 2012; Fraser 2013) and my results infer that different basal prey demand may exist between unexploited and exploited populations. I performed a simple exercise to evaluate how a 6 % difference in Largemouth Bass RMR and resultant moderation of top-down predation might influence ecosystem-level trophic dynamics. Extrapolation of field RMR to a population for an entire year is difficult because of variations associated with water temperature, individual sizes, etc.; however, I assumed that the 6 % difference in RMR was maintained between exploited and unexploited individuals. This assumption requires further testing, but I make it here because the four populations I examined responded similarly to temperature. Based solely on basal metabolic demand 1,000 unexploited individuals would require 100,600,000 more calories during a 200 day season than 1,000 exploited individuals. This caloric demand is equivalent to the caloric content of 86.7 kg of Bluegill or 142.5 kg of Fathead Minnow. The effects that such

energetic differences among exploited and unexploited individuals have on a system's trophic dynamics would of course be modulated by system productivity and other factors. While this exercise is too simplistic to be quantitatively predictive, it nonetheless suggests that a 6% difference in RMR could affect biomass at lower trophic levels, thus having substantial energetic consequences at the ecosystem level.

An alternative explanation for the observed difference in RMR is that unmeasured environmental variation among the four study lakes could have driven the differences observed. Subtle differences in climatic conditions influencing the exploited and unexploited reservoirs might explain the differences in metabolic rates that I observed. All four systems are in relatively close proximity to Long Island Sound which has strong effects on local climate conditions, but the possibility of subtle differences which could impact the systems remains. I statistically tested for differences in the four populations studied here and found that population of origin was not a significant predictor of field RMR, once the effect of exploitation status had been accounted for ($F_{2,75} = 1.48$, $P = 0.23$). This finding suggests if some unmeasured environmental variation were confounding my results, it would have been distributed among the four populations in the same manner as exploitation status (i.e., similar in two lakes and the same, but different in the other two). Not surprisingly, field RMR increased with temperature ($F_{1,444} = 118.8$, $P < 0.001$), however, the interaction between temperature and population of origin was also not significant ($F_{3,326} = 0.77$, $P = 0.51$). If climatic conditions, such as temperature regime were driving differences in metabolic rates among the study populations, I hypothesized that a significant difference in the population by temperature interaction would be observed when fish were acclimated to a common environment. The lack of a significant population by temperature interaction is one indication that all four populations responded

similarly to the temperature range (15.0°-20.4° C) experienced during data collection, but I cannot equivocally rule out the possibility that unmeasured differences in climatic conditions affected metabolic rates among the source populations.

Hemlock and Easton Reservoirs had higher densities of Largemouth Bass than another exploited Connecticut population of Largemouth Bass (Hessenauer et al. 2014), but interestingly, the condition (mass-at-length) of adult fish did not differ among exploited and unexploited populations in that study (Hessenauer et al. 2014). It has been shown in mammals that net primary productivity of different environments (i.e., desert versus woodland) can lead to differences in basal metabolic rates among related species (Mueller and Diamond 2001), in which those with ample food tend to ‘idle fast’. However, the differences in fish density among the four source populations were most likely related to exploitation status, given the physiographic proximity and general similarity of the waterbodies, and may present an alternate mechanism of how fishing could alter metabolic rates among exploited and unexploited populations such that a reduction in density from fishing could ‘release’ primary production and promote higher metabolic rates. However, in the present study higher density unexploited populations had higher metabolic rates than exploited populations. Therefore, my findings are more congruent with the mechanism of selection from angling on a suite of correlated behavioral phenotypes and their underlying physiological processes (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Alós et al. 2012).

Maternal effects are another possible explanation of the differences that I observed in RMR. Research has indicated that female Three-Spined Stickleback *Gasterosteus aculeatus* can transfer environmental information via their eggs, resulting in higher metabolic rates in high predation (stressful) environments (Giesing et al. 2011). In the current study, angling represents

an additional predation stress which differed among parents of my test subjects, and the finding of higher metabolic rates in unexploited populations runs contrary to those observed in stickleback. Maternal effects, classically controlled, require breeding in a common environment and testing of F2 individuals. Such an experiment would be needed to determine whether maternal effects could explain some or all of the differences in RMR observed. However, such an experiment would be difficult to implement with a large sample of Largemouth Bass and researchers would need to carefully monitor the influence of unwanted selection (e.g., adaptation to captivity Christie et al. (2012)) given the size at maturity and the reproductive biology of Largemouth Bass.

The current study represents a snapshot of energetic differences among two unexploited and two exploited populations of Largemouth Bass. Changes in angler behavior may alter the strength and perhaps direction of selection on the RMR of Largemouth Bass populations. Recently, many recreational fisheries in North America have experienced a shift towards catch-and-release practices rather than harvest, where large portions of fish (approaching 100 % in some cases) are released following capture (Quinn 1996; Cooke and Cowx 2004; Bartholomew and Bohnsack 2005). If one assumes that harvest-oriented recreational fisheries exert greater (or different) selective forces than catch-and-release angling, then selection on traits that are potentially affected by fishing may be changing. For example, catch-and-release practices may have relaxed selection on boldness or foraging behaviors by reducing the probability of mortality associated with angling. Even with reduced mortality rates, catch-and-release angling has potential to cause selective effects on individuals through the disruption of reproductive behavior (Kieffer et al. 1995; Philipp et al. 1997; Stein and Philipp 2014), or unintentional post-release mortality, and may select for individuals that can learn lure avoidance (Askey et al. 2006;

discussion below). Given that high metabolic rate phenotypes are known to be more vulnerable to angling (Redpath et al. 2010), future studies should seek to quantify the metabolic rates of individuals originating from an unexploited source population exposed to various angling treatments (e.g., catch-and-release, various levels of annual harvest, no angling during spawn, etc.) and intensities over multiple generations. Such a study would inform scientists about the relative strength of selection of different angler behaviors. Continued monitoring of these populations after angling ceased could be used to evaluate recovery rates. Such an experiment could reveal whether changes in management would be likely to elicit population-level phenotype recovery.

Standardized angling of naïve individuals originating from exploited and unexploited populations resulted in a rapid loss of naivety to angling for individuals from both exploited and unexploited population types. My analysis revealed that individuals originating from exploited and unexploited populations were initially equally vulnerable to angling; however, individuals originating from exploited populations lost their naivety to angling at a faster rate than individuals from unexploited populations. Researchers and managers have long documented rapid declines in catch rates when previously closed populations are opened to recreational angling (e.g., Goedde & Coble 1981) and that catch rates are typically higher in unfished populations (Philipp et al. 2015). The results of this study indicate that both of these phenomena are likely predominately attributed to naivety of individuals. However, because learning ability is known to be a heritable trait in fishes (Huntingford & Wright 1992), that individuals originating from fished populations lost their naivety to angling faster than individuals from unfished populations fits well the hypothesis that recreational angling can drive fisheries-induced evolution (Philipp et al. 2009; Philipp et al. 2015). Specifically, I hypothesize that recreational

fishing selects for individuals that can learn lure avoidance behaviors quickly and elude to a greater extent the potential mortality and fitness consequences of capture.

Learned lure avoidance behaviors have been linked to seasonal decreases in catch rates for Rainbow Trout, *Oncorhynchus mykiss*, in an intensive catch-and-release scenario (Askey et al. 2006). Likewise, decreases in the future vulnerability of individuals to angling after being previously captured has been demonstrated for several fishes including Largemouth Bass (Hackney & Linkous 1978) and Carp, *Cyprinus carpio*, (Beukema 1970). Field studies suggest that fish may modify their behavior in response to fishing pressure, which is likely associated with learned lure avoidance (Alós et al. 2014). In addition to learning through direct experience, fishes are capable of social learning (Brown & Laland 2003). Brown & Laland (2003) defined social learning as the ability of individuals to acquire new behavior or information about their environment by observing or interacting with other individuals. In my study I emphasize cumulative catch events, a metric which accounts for the possibility of social learning by integrating the passage of time and the number of opportunities individuals had to experience angling either directly or indirectly (e.g., observe another individual captured). Cumulative catch events better explained catch rates than either the number of days since angling began or the cumulative number of angler hours, which suggests the existence of a social learning component of learned lure avoidance behavior in Largemouth Bass. Indeed, that individuals originating from both unexploited and exploited populations avoided lures at such high rates (i.e., capture rates near zero once initial naivety to angling was lost), despite less than half of the individuals having been captured by the conclusion of angling, indicates a social learning component to the rapid acquisition of lure avoidance behavior. Previous studies on fishes have demonstrated rapid rates of social learning in response to predation risk (Vilhunén et al. 2005; Manassa et al. 2013),

and a study on Arctic Char, *Salvelinus alpinus*, found that a relatively small number of predator-experienced individuals can alter the behavior of a large number of predator naïve individuals (Vilhunen et al. 2005). It is possible however, that some (or all) of the fish which remained uncaptured were simply more predisposed as individuals to avoid angling, without need of social learning, and further experimentation is needed to determine the role of social learning in learned lure avoidance.

Recreational angling for Largemouth Bass, especially with recent increases in catch-and-release practices (e.g., Quinn 1996; Cooke & Cowx 2004), represents a potentially novel evolutionary scenario selecting for learned lure avoidance behavior. Kelley & Magurran (2003) predicted differences in learning ability among populations experiencing different predation risks, such that high risk populations would be better adapted for social learning than low risk populations. In the present study, angling represents a predation-like risk and individuals originating from fished populations learned lure avoidance behaviors more quickly than those originating from unfished populations, consistent with the predictions of Kelley & Magurran (2003). Catch-and-release events represent a negative stimulus associated with negative reproductive fitness (Philipp et al. 1997; Suski et al. 2003) and physiological effects (Cooke et al. 2002); however, mortality for many recreational catch-and-release fisheries can be quite low (Cooke et al. 2002). Therefore, in contrast to a primarily harvest-based fishery where mistakes (being captured) are often lethal leaving little opportunity for learning, catch-and-release events provide the opportunity for individuals to learn because catch-and-release is usually not lethal. Individuals that learn quickly are better able to avoid future negative effects of angling and may therefore accrue fitness advantages.

Largemouth Bass are generally not vulnerable to the gear used by anglers in the wild until they reach 250 mm in total length (Dotson et al. 2013), and all individuals that were angled during this study were collected at age-0 well below this size (largest individual collected at 142 mm). Therefore, I assume that no individuals in this study had any direct experience with angling in the wild and the faster rate at which individuals originating from exploited populations lost their naivety to angling must be associated with information that they received prior to translocation to the study pond. This information could include observations of angling events on larger fish in their natal environments, genetic differences in learning ability, or maternal effects. I collected large numbers of Largemouth Bass from locations distributed throughout each source lake, using multiple gears. My angling trials occurred nearly two years after capture from the wild, with no angling in the interim, which is longer than the memory of Largemouth Bass trained in a shuttle box to avoid electric shock (Coble et al. 1985). Maternal effects are possible, but unlikely as discussed above. Therefore, genetic differences in the learning ability of individuals originating from fished populations in this study seem to be the most likely explanation for their apparent enhanced ability to learn to behaviorally avoid lures, but I cannot fully rule out social learning in their natal environments or maternal effects. Further research is needed to conclusively determine whether the differences in learning ability for exploited and unexploited populations observed in this study is a heritable trait under selection from recreational fishing, or rather embedded in phenotypic plasticity somehow activated in the natal environment.

Another potential explanation is that my findings are explained by differences in animal personality. Wilson et al. (1993) demonstrated that a shy-bold continuum existed in Pumpkinseed Sunfish, *Lepomis gibbosus*, such that some individuals were more likely to explore

a novel environment. Similarly, "bold" Smallmouth Bass, *M. dolomieu*, are more likely to begin foraging after a simulated predator attack than "shy" Smallmouth Bass (Smith et al. 2009). Therefore, given that activity levels (Alós et al. 2012) and personality type (Biro and Post 2008; Wilson et al. 2011; Sutter et al. 2012) are related to angling vulnerability, it is possible that my results represent different abundances of personalities among fished and unfished populations. However, if this explanation alone were true, I would expect that the intercept (initial inherent angling vulnerability) of the equations for individuals originating from exploited and unexploited populations would be significantly different. In my study the intercepts were not significantly different, rather the slopes were different suggesting that individuals originating from exploited populations lost naivety to angling more rapidly than individuals originating from unexploited populations.

It is also possible that individual condition or energetic status contributed to the differences in learned lure avoidance observed within this study. I confirmed that individuals originating from unfished populations had higher RMR than individuals originating from fished populations and therefore require more calories to meet basal metabolic demand. In the current study, the pond was regularly stocked with forage fishes to create an *ad libitum* feeding environment during standardized angling, and indeed no differences in length or weight were observed among individuals originating from fished and unfished populations suggesting that differences in catch rate were not driven by hunger alone. Finally, similar to previous studies (e.g., Askey et al. 2006), my study likely exaggerated the rate of learning, because I used the same three lures throughout the angling trials to ensure standardization, and intensive angling occurred in a small environment with high fish density (density at the conclusion of the angling trial: 3875 individuals/ha).

Comparisons to unexploited reference populations facilitated a straightforward detection of RMR differences and differences in learning ability consistent with the predictions of FIE in wild exploited Largemouth Bass populations. In exploited populations, the ability of individuals to learn lure avoidance behaviors both directly and indirectly, and reduced caloric demand represent important feedback processes in the coupled human and natural system represented by recreational angling. This feedback process manifests in an ‘arms race’ between anglers and fish populations, whereby anglers develop and deploy novel lures and techniques in an effort to overcome reductions in angling vulnerability associated with learned lure avoidance behaviors and energetics associated with selection from recreational angling. This arms race has the potential to have far reaching consequences on both fish and angler populations as well as the ecosystem as a whole. It is unknown, but possible, that behavioral modification to avoid lures may come with a caloric opportunity cost associated with less effective foraging. Also, avoidance behaviors and decreased caloric demand may result in decreased catch rates for anglers, and therefore decreases in angler satisfaction and perhaps shifts in angler effort towards other species or populations easier to catch (Askey et al. 2006), creating challenges for environmental managers tasked with setting regulations. Differences in learning ability (e.g., Coble et al. 1985) and memory (e.g., Beukema 1970; Coble et al. 1985; Kuparinen et al. 2010) are known to exist among fish taxa. Future research is needed to understand the extent to which learned lure avoidance behaviors are retained across multiple fishing seasons, the relative contribution of direct and indirect experience to learned lure avoidance behavior, and how these factors vary among different fish taxa. Periodic closures of fisheries have been shown to decrease fish wariness and therefore increase catch rates (Januchowski-Hartley et al. 2014), which may have the additional benefit relaxing selection for reduced RMR.

Future study should involve the controlled breeding of individuals from unexploited reference populations, and could conclusively determine that the patterns that I observed in RMR and lure avoidance behavior resulted from selection by angling alone. If FIE is occurring, it is likely that similar differences could be found throughout the range of Largemouth Bass, and similar outcomes may be expected in other marine and inland recreational fisheries, especially if individuals exhibit variation in behavior that makes some more vulnerable to angling relative to others. Eikeset et al. (2013) presented a model developed for Atlantic Cod *Gadus morhua* that predicted evolutionary change, even with low fishing mortality, and concluded that management to avoid FIE was unfeasible. Establishing the extent to which FIE has occurred or is occurring in populations subject to recreational fishing, and the patterns of change in population-level distributions of phenotypes associated with FIE seems the next step. Learning whether or not these changes are altering trophic dynamics or represent a problem for fisheries sustainability and quality is critical for the future management of recreational fisheries and the aquatic ecosystems within which they reside.

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Table 1.1. Table of main effects for the analysis of covariance (ANCOVA), quantifying the effects of temperature, exploitation status and population on the resting metabolic rate of 4 populations of Largemouth Bass. Table includes numerator degrees of freedom (DF), denominator degrees of freedom (DFden), f-statistic (F), and p-value (P). Population was nested within exploitation status to account for the fact that there were two populations each from the exploited and unexploited treatments.

Source	DF	DFden	F	P
Temperature	1	444	119	<0.001
Exploitation Status	1	73	8.34	0.005
Population (Exp Stat)	2	75	1.48	0.235
Pop*Temp	3	326	0.77	0.510

Table 1.2. Predictor variables, their associated F statistics, p-values and the amount of variation in total aggregate catch per unit effort of individuals originating from exploited and unexploited populations explained. Variables include water temperature, air pressure, cloud cover, percent humidity, angling day, cumulative effort in hours, and cumulative catch events.

	Variable	Fstat [†]	P	R ²
Weather	Water Temp	4.67	0.04	0.12
	Air Pressure	1.4	0.27	0.03
	Cloud Cover	1.8	0.19	0.05
	Humidity	0.47	0.5	0.01
Time	Exp. Day	26.9	<0.0001	0.48
	C. Effort	20.7	<0.0001	0.41
	C. Catch	159.8	<0.0001	0.85

[†] all F statistics are associated with 1 and 27 degrees of freedom.

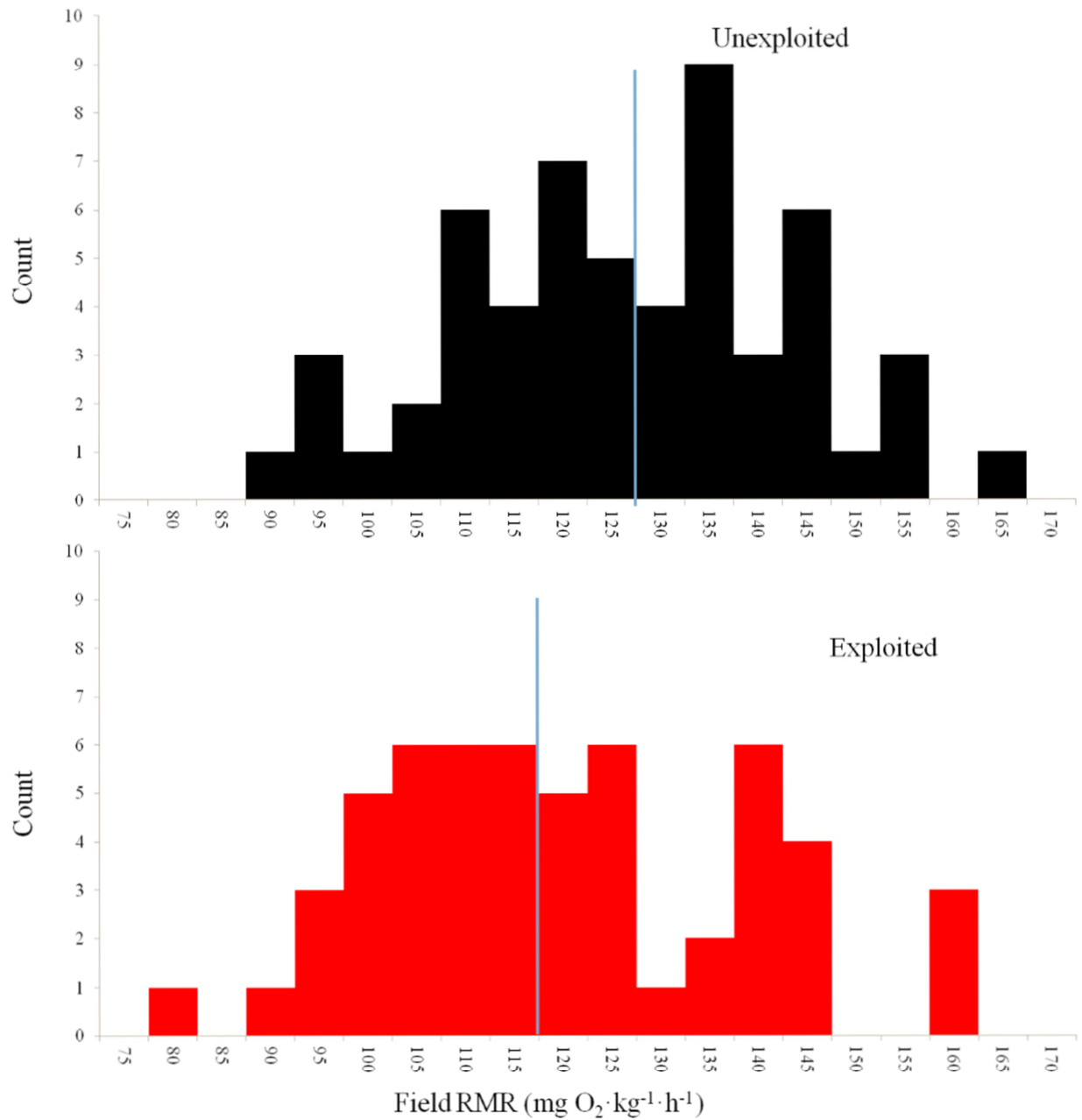


Figure 1.1. Histogram of field resting metabolic rates of unexploited populations (black bars) and exploited populations (red bars) of Largemouth Bass raised in a common environment. X-axis values represent the starting value of each bin. Vertical reference line represents the median of each population.

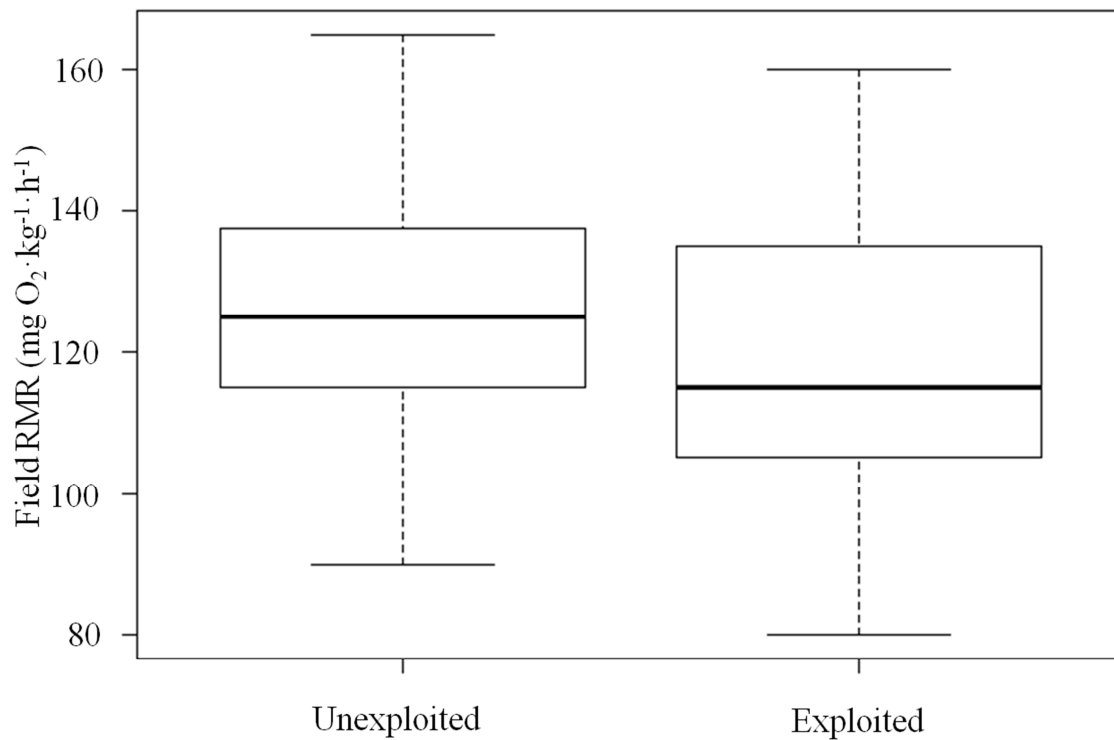


Figure 1.2. Boxplot of field resting metabolic rates of unexploited and exploited populations of Largemouth Bass raised in a common environment. The horizontal black line represents the population median, the top and bottom of each box represent the 75th and 25th quartiles respectively, and the whiskers represent the range of 95% of all observations.

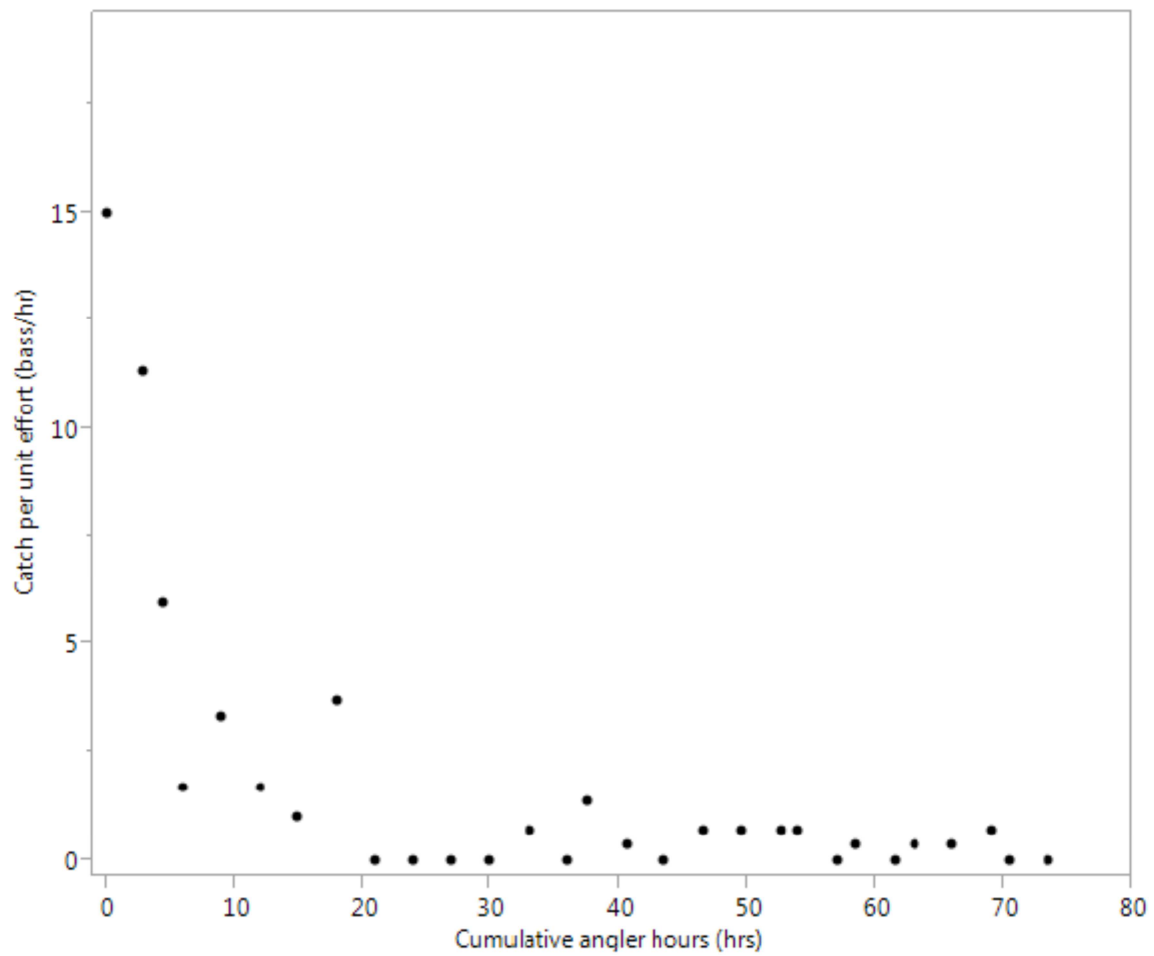


Figure 1.3. Overall aggregated catch per unit effort (bass/hr) of individuals originating from fished and unfished population types plotted against cumulative angler effort, in hours, of standardized fishing.

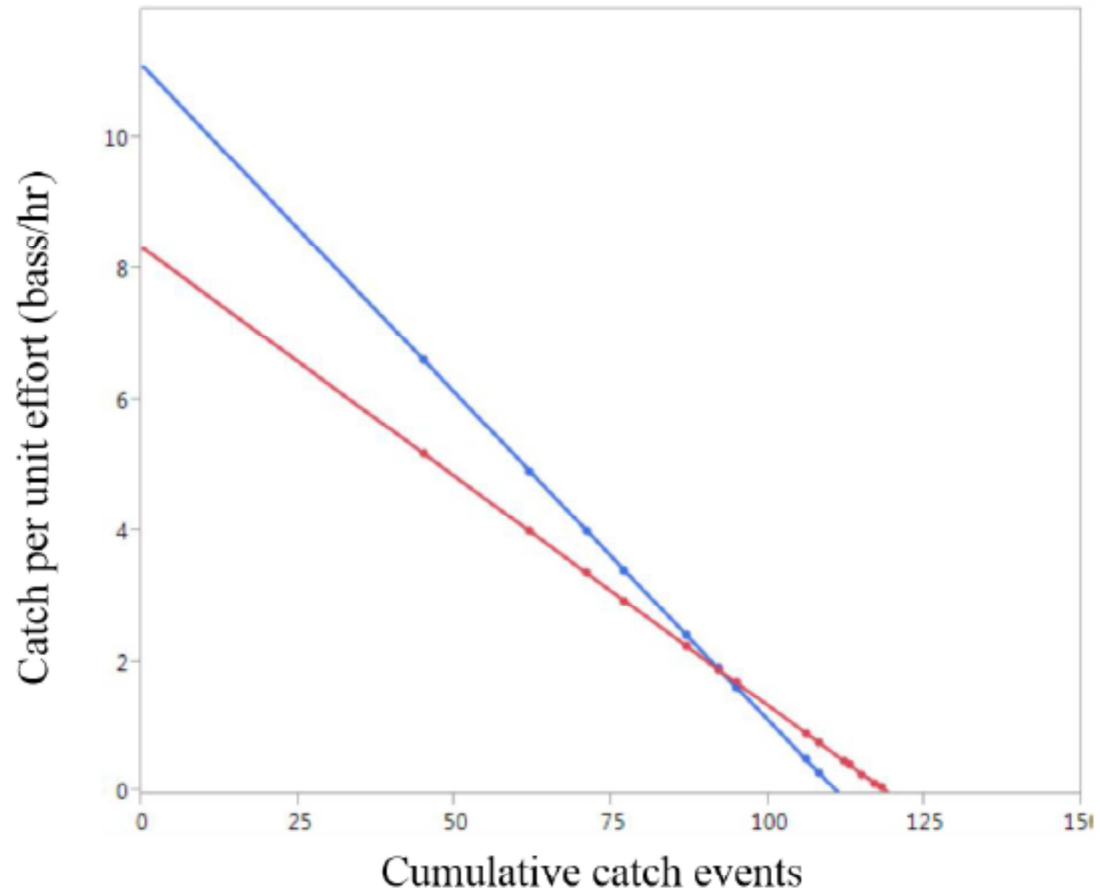


Figure 1.4. Predicted catch per unit effort for individuals originating from fished (blue line) and unfished (red line) populations at the average temperature (20.7 degrees Celsius) of angling trials as a function of cumulative catch events.

CHAPTER 2

Can Largemouth Bass Transplanted from an Unexploited Population Genetically Contribute to an Active Fishery? A Test Case for Genetic Management of Exploited Fish Populations

Abstract

Recreational fishing is one of the most popular outdoor activities in the world, resulting in substantial effects on recreational fish stocks. Recent studies have found that recreational angling can drive fisheries induced evolution, resulting in changes in the size, behavior and physiology of exploited recreational stocks. Traditional management of recreational fisheries may be unable to mitigate these changes, especially with the rise of catch-and-release practices for many fisheries. This study explores the potential to genetically manage exploited fisheries by introducing individuals from unexploited populations as a means to mitigate selection from recreational angling. I stocked 77 individuals from an unexploited population and 79 individuals from an exploited population into an active fishery and evaluated the extent to which the unexploited individuals contributed to fall age-0 recruits relative to the stocked exploited individuals. A genetic sample was taken from all stocked individuals and used to conduct a parentage analysis of subsequent age-0 recruits. Fifty-four percent of age-0 bass sampled with reliable parentage were determined to be hybrids of stocked and resident parents. Individuals from exploited and unexploited populations contributed to my age-0 sample in proportion to their initial abundance. No sex-biased contribution was detected between the exploited and unexploited individuals stocked into the pond although the largest females contributed the most to my age-0 sample. No difference in the condition of age-0 recruits was detected between individuals from stocked parents vs. resident parents. I conclude that individuals from

unexploited populations can successfully reproduce in an exploited system and genetic management may be a feasible management option to mitigate the effects of recreational fisheries induced evolution.

Introduction

Recreational fishing is among the most popular outdoor activities worldwide, contributing substantially to the exploitation of global fish stocks (Cooke and Cowx 2004; Lewin et al. 2006). Concerns about the evolutionary effects of recreational angling and the management implications of those effects have increased. Recent studies attributed differences in size, behavior and physiology of fish species to evolutionary impacts of recreational angling (Uusi-Heikkilä et al. 2008; Matsumura et al. 2011; Alós et al. 2014a, 2014b; Chapter 1). For example, a modelling study found that recreational fishing may deplete high-activity phenotypes because highly active fish are more likely to encounter and be captured by recreational anglers (Alós et al. 2012).

Largemouth Bass *Micropterus salmoides* are a popular North American sportfish (USFWS 2011), and have become established as a model species for the study of recreational fisheries induced evolution (e.g., Philipp et al. 2009; Redpath et al. 2010; Sutter et al. 2012; Nannini et al. 2011; Chapter 1). This is partly because male bass are vulnerable to angling while guarding their nest (Kieffer et al. 1995; Philipp et al. 1997; Suski and Philipp 2004). Even temporarily removing a male bass from the nest by angling has been associated with negative reproductive fitness (Kieffer et al. 1995; Philipp et al. 1997; Suski and Philipp 2004; Stein and Philipp 2015), providing a clear mechanism for fisheries induced evolution. Philipp et al. (2009) demonstrated that vulnerability to recreational angling is a heritable trait by conducting multi-generation artificial selection on Largemouth Bass based on the number of times individuals

were captured by experimental angling. Further studies on the lines developed by Philipp et al. (2009) revealed that selection from recreational angling acts on a suite of behavioral (Cooke et al. 2007; Sutter et al. 2012; Nannini et al. 2011), physiological (Cooke et al. 2007; Redpath et al. 2010), and reproductive traits (Cooke et al. 2007; Sutter et al. 2012) of Largemouth Bass. Individuals bred for high angling vulnerability had higher metabolic rates (Redpath et al. 2010), and higher reproductive success (Sutter et al. 2012). I studied wild populations and confirmed that exploited populations of Largemouth Bass contained significantly more individuals with lower metabolic rates than unexploited populations (Chapter 1), consistent with the findings of Redpath et al. (2010) and the predictions of Philipp et al. (2009). Therefore, it is reasonable to predict that one outcome of fisheries induced evolution on exploited recreational populations is a decrease in population-wide vulnerability to angling.

Decreases in population vulnerability to angling represent a challenge faced by managers of recreational fisheries who seek to maintain ecosystem function, high angler catch rates, and attendant angler satisfaction. Because selection reduces angling vulnerability and not necessarily fish density, declines in traditional indices such as angling catch per unit effort may not reliably predict changes in population abundance (Askey et al. 2006; Klefoth et al. 2013). Selection from angling is also correlated with fish energetics (Redpath et al. 2010; Chapter 1); therefore, selection for reduced vulnerability may have ecosystem level consequences. Largemouth Bass are considered ecologically important because they are the primary piscivorous predator in many water bodies and therefore have a propensity to control biomass at lower trophic levels (e.g., Carpenter et al. 1987; Mittelbach et al. 1995). Thus, decreased angling vulnerability and correlated phenotypes such as metabolic rates may relax control of lower trophic levels, which could potentially contribute to the stunting of prey species.

Traditional management options may not be effective at restoring catch rates, if angler catch or satisfaction has declined in a fishery due to decrease vulnerability to angling through its inherent selection. Management tools typically include reductions in allowable harvest, or efforts to direct harvest at particular portions of the population e.g., length limits (Radomski et al. 2001; Lewin et al. 2006; Gwinn et al. 2015). These actions may not mitigate the evolutionary effects of recreational angling for several reasons. Recent trends towards increased catch-and-release angling (Quinn 1996; Cooke and Cowx 2004; Bartholomew and Bohnsack 2005) may reduce the ability of harvest-oriented regulations from affecting selection on exploited populations. Nonetheless, evolutionary consequences are possible from catch-and-release angling. Catch-and-release angling increases population mortality rate through accidental discard mortality, can select for decreased age-at-maturation (Allendorf et al. 2008), and may interrupt Largemouth Bass life-history events (Kieffer et al. 1995; Philipp et al. 1997; Suski and Philipp 2004; Stein and Philipp 2015). Additionally, high vulnerability phenotypes may have been substantially reduced or eliminated from the population due to selection by recreational angling (Philipp et al. 2009), causing population recovery once selection has relaxed to be slow or improbable. Under this scenario, novel approaches may be needed to effectively manage recreational fisheries.

The concept of ‘genetic rescue’ (Tallmon et al. 2004; Hedrick et al. 2011), where a small number of migrants are introgressed into a population to improve population fitness (Mills and Allendorf 1996; Tallmon et al. 2004), has shown promise for the management of imperiled populations (Whiteley et al. 2015). For example, improvements in genetic diversity and demographic rebound were observed for the Florida panther (*Puma concolor coryi*) after the introduction of a small number of panthers from the Texas subspecies (*P. c. stanleyana*; Johnson

et al. 2010). A similar technique, whereby individuals from an unfished population are introduced into a population deemed in need of management, might have the potential to mitigate the effects of fisheries induced evolution. This ‘genetic management’ could potentially increase the presence of high vulnerability phenotypes, those most desired by anglers, as well as ecologically important behavioral and physiological phenotypes that are associated with high angling vulnerability. Importantly, successful genetic management could also reintroduce the underlying genetic basis of angling vulnerability to a population where genetic diversity has been reduced by selection from angling, similar to demographic and fitness improvements associated with ‘genetic rescue’.

Genetic management has already occurred at large spatial scales in several southern states where Largemouth Bass and Florida Bass *M. floridanus* have been widely introgressed (Philipp et al. 1983) in an effort to increase the size and growth of bass for anglers (e.g., Forshage and Fries 1995; Williams et al. 1998). Some studies have reported success in producing large fish desired by anglers (e.g., Myers and Allen 2005; Lutz-Carrillo et al. 2006), but others have found no relationship between fish condition and phenotype (Allen et al. 2009). These actions have provided a large-scale experiment demonstrating that genetic introgression is feasible. However, the purposeful hybridization of different species or strains has in some cases been associated with negative fitness consequences (e.g. Philipp et al. 2002), resulting in heavy criticism of the purposeful mixing of stocks (Philipp 1991; Cooke et al. 2001; Philipp et al. 2002; Cooke and Philipp 2006). Likewise, the hybridization of two locally adapted Largemouth Bass populations has been shown to result in negative physiological effects (Cooke et al. 2001; Cooke and Philipp 2006) including higher susceptibility to disease (Goldberg et al. 2005), which could translate to lower overall fitness. Therefore, the ideal source population for genetic management would be

adapted to a similar environment as the population targeted for management, to reduce the possibility of negative fitness consequences.

For genetic management to be a viable strategy, introduced individuals from the unexploited population must be able to reproduce successfully in an exploited environment, i.e. not be harvested by anglers at a high rate or sufficiently stressed by translocation into a novel environment or by catch-and-release angling that they do not breed. Reproductive success of stocked individuals is potentially problematic because not only are unexploited individuals expected to be genetically more vulnerable to angling (Philipp et al. 2009), but unexploited fish are also naïve to angling. Recent research suggests that naivety may account for the majority of the differences in catch rates among exploited and unexploited populations (Chapter 1). Additionally, if unexploited individuals succeed in spawning, resultant hybrid offspring must not have a fitness disadvantage, when compared to non-hybrid offspring, or any utility of the management action will be short-lived in the population.

I conducted a case study as a first step to evaluate the potential of genetic management using translocated naïve to angling individuals, which if successful has promise to improve population characteristics in heavily fished waterbodies. Individuals from an unexploited population and exploited population (to serve as a basis for comparison) were captured and translocated to an active fishery. Tissue samples from age-0 bass were collected after the spawn to assess rates of hybridization. The condition of hybrid age-0 offspring was estimated and compared to the condition of resident age-0 offspring to assess potential differences in fitness. This case study had three primary objectives. The first was to assess the relative genetic contribution of translocated naïve individuals from and unexploited populations to the genetic contribution of translocated angling-exposed individuals from an exploited population when both

are supplementally stocked prior to the spawn into an active fishery. I hypothesized that sex-biased contribution would occur from the unexploited population because nest-guarding males are more likely to be exposed to angling and are expected to be more vulnerable to angling than females (Cooke et al. 2007; Philipp et al. 2009; Sutter et al. 2012). Conversely, I hypothesized that there would be a relatively equal contribution between male and female individuals translocated from the exploited population, because nest-guarding males likely had previous experience with angling and were also expected to be less vulnerable to angling as a result of selection (Cooke et al. 2007; Philipp et al. 2009; Sutter et al. 2012). My second objective was to evaluate whether physical characteristics of stocked parents, e.g. size, sex, etc. were predictive of reproductive contribution to the age-0 population, in order to provide managers with information about what sex and size of fish would be best suited for genetic management of Largemouth Bass. I hypothesized that the largest male and female individuals would have the greatest contribution to age-0 individuals, because large males tend to receive more eggs in their nest and are therefore thought to contribute more to recruitment (Philipp et al. 1997; Parkos et al. 2011). Finally, I evaluated whether age-0 individuals of hybrid origin (i.e., offspring derived from crosses between the stocked and resident parents) had significantly different condition when compared to resident age-0 individuals. I hypothesized that there would be no difference in condition among hybrid and resident individuals because lakes of origin of the translocated individuals are geographically close to the system in which they were stocked and experience similar climate.

Methods

Study sites

This study was conducted in the State of Connecticut, USA (Figure 2.1). Largemouth Bass were introduced to Connecticut in the mid-nineteenth century as part of Federal stocking programs from a single upstate New York source population (Whitworth 1996). Adult fish were collected from unexploited Hemlock Reservoir, hereafter Hemlock, and exploited Mansfield Hollow Reservoir, hereafter Mansfield. Hessenauer et al. (2014a) describes the population characteristics of these systems. Briefly, Hemlock is a 176.8 ha drinking water reservoir built in 1914 that has been closed to fishing since its construction, is patrolled by water company law enforcement personnel, and has no public access, therefore I deemed it unexploited. Mansfield is a 186.2 ha flood control reservoir with a large public boat launch and a popular black bass tournament fishery (Edwards et al. 2004a, 2004b). Hemlock and Mansfield individuals were stocked into Bigelow Pond (hereafter Bigelow), a 9.8 ha popular fishing pond with boat ramp, located within the Bigelow Hollow State Park. During 2013, an estimated 5,500 anglers-hours were directed at Bigelow Pond during the open water season, representing 560 angler-hours per ha (Davis and Leonard 2014).

Population Survey and Collection of Stocked Individuals

I estimated the population size of adult Largemouth Bass in Bigelow Pond using a multi-lap, mark-recapture boat electrofishing survey in fall 2012. Individuals were marked using fin clips and given a colored visual-implant elastomer tag with a unique color for each day of sampling. The visual implant elastomer tags were used to ensure that recaptures represented fish previously captured on different sampling days. Population size was estimated using the Schnabel method.

In spring 2013, adult individuals (over 200 mm total length) were collected from Hemlock and Mansfield. Individuals were measured to the nearest mm total length and weighed

to the nearest g. Sex of individuals was estimated in the field using the methods of Benz and Jacobs (1986). Individuals were given population-specific fin clips, which were preserved in 100% ethanol for genetic analysis. Individuals were transported from their population of origin in aerated stocking tanks and released through the ice into Bigelow.

Collection of age-0 individuals

Beginning in late June 2013, I targeted age-0 Largemouth Bass in Bigelow using a combination of sampling gears. Dumont and Lutz-Carrillo (2011) confirmed that age-0 cohorts are suitable for estimating rates of genetic introgression for Largemouth Bass. In June, July and August, age-0 individuals were sampled by beach seining. To ensure that seine hauls were spread throughout the pond, the pond's shoreline was divided into 10 zones of roughly equal length. For each sampling period, the first zone was randomly chosen and sampled in the first suitable location. Sampling then proceeded with every other zone in a randomly chosen direction (clockwise or counter clockwise), resulting in five total zones sampled each day. Largemouth Bass are known to disperse widely and randomly from their nest of origin (Hessenauer et al. 2012); therefore, my sampling design should have ensured a representative sample of age-0 individuals. During August, September and October I also targeted age-0 Largemouth Bass by conducting complete laps of the pond's shoreline using boat electrofishing. All age-0 individuals were measured to the nearest mm total length and the nearest g for weight. A small five-by-five mm fin clip was collected from all age-0 fish captured by both gears and preserved in 100% ethanol. If the age of a sampled individual was in question, i.e. for particularly large individuals, I also collected scales to confirm age-0 status. Scales were cleaned, pressed between two glass slides, and photographed using an Olympus QColor 3 digital camera mounted on an Olympus SZ61 dissecting scope. Photographs were independently

examined by two experienced scale readers, and any discrepancies were examined jointly after comparison of ages. I sampled a total of 330 age-0 individuals from Bigelow during the summer of 2013. A total sample size of 226 confirmed age-0 individuals were genotyped for genetic analysis.

Genetic Analysis

DNA was extracted from tissue samples of stocked adult Hemlock (N= 77), Mansfield (N=79), and age-0 (N= 226) Largemouth Bass using the Qiagen DNeasy (Qiagen) extraction kit following the manufacturer's specifications. Extracted DNA was quantified using a NanoDrop Lite (Thermo Scientific) and diluted to a standard concentration of 25 ng/μl. Polymerase chain reactions were conducted for ten microsatellite loci (Table 2.1) in 10 μl reaction volumes using 50 ng of template DNA, 1X GoTaq Flexi buffer (Promega), 1-2 mM MgCl₂ (Table 2.1), 0.2 mM dNTPS (Promega), 0.2 mM fluorescently labeled forward primer, 0.2 mM unlabeled reverse primer, and 0.25 U of Taq polymerase (Promega). Samples were visualized on a Beckman Coulter GeXP Genetic Analysis System. Ten percent of samples were amplified and visualized again as an error check. Only one error was detected, therefore error rates for all loci were conservatively set to 1% for subsequent analysis.

Multi-locus genotype data of all individuals were analyzed using program MICRO-CHECKER (van Oosterhaut et al. 2004) to check for and correct data entry and scoring errors. I checked for the presence of null alleles and scoring errors associated with stuttering on a subset of the data (stocked adults only) using the program MICRO-CHECKER to avoid over-estimation of errors associated with anticipated family structure.

Parentage analysis was conducted using the programs COLONY (Wang 2004) and PARENTE (Cercueil et al. 2002). Both programs seek to assign offspring to male and female parents based on the compatibility of their multi-locus genotypes while permitting some level of genotyping error. COLONY settings were based on the author's recommendations and Largemouth Bass life history. I assumed that males and females were polygamous, and that mating was random. Error rates for all loci were set at 1%, and I assumed that at least one true parent was included among the candidates for maternity and paternity. Four independent runs of COLONY, and an independent run of PARENTE was conducted. Maternity and paternity assignments of age-0 individuals were considered valid when concordance occurred over multiple runs of COLONY, and PARENTE identified the same individual as the most probable parent. Conversely an individual was assumed to have a resident Bigelow maternity or paternity with high confidence if they were not assigned in any run of COLONY or PARENTE. In order to evaluate hybridization as conservatively as possible, individuals were only considered hybrids (or not hybrids) if assigned with high confidence to two parents. However, a valid assignment to a stocked parent (regardless of whether assignment to a second parent was valid) was used to compare contributions of Hemlock and Mansfield parents and the characteristics of successful parents as described below.

Data analysis

Length and weight data were used to calculate relative weight (W_r ; Wege and Anderson 1978) of all stocked parents. Fish size is known to affect the reproductive success of male Largemouth Bass (Philipp et al. 1997; Parkos et al. 2011) and female size can affect egg quantity and quality (reviewed in Hixon et al. 2014). I tested for normality and then differences in the length and weight of Hemlock and Mansfield parents, using two sample t tests. Relative weight

is not normally distributed and was therefore assessed using a Mann-Whitney U test. I tested whether the sex ratio of stocked parents from Hemlock and Mansfield differed from 1:1 as well as from each other using Chi-square tests.

I conducted a series of Chi-square tests to determine the proportional contribution of stocked Hemlock and Mansfield individuals to the age-0 population. The first Chi-square test evaluated whether the number of age-0 individuals assigned to stocked parents conformed with the expected frequencies based on the total number of individuals from each population that were stocked into the pond. Next I conducted two separate Chi-square tests (one for Hemlock and Mansfield) to evaluate whether sex biased contribution to age-0 populations had occurred. Sex biased contribution was evaluated by testing whether the number of age-0 individuals assigned to stocked mothers and fathers occurred at the expected frequencies given the initial stocking number and sex ratios for each population.

A generalized linear modeling approach was used to evaluate the contribution of individual stocked parents to my age-0 sample. The number of age-0 recruits was the response variable, whereas parental characteristics including sex, population of origin, parental weight-class, and interactions were entered as predictor variables. Non-significant terms were then dropped from the final model. Weight-class was defined by dividing individuals into four groups based on the quartiles of the weight distribution of all stocked parents. I fit two models to the data in R using the *glm* function. The first model assumed a Poisson error distribution and used a log-link function. I also modeled the data using a negative binomial distribution and a log-link function to evaluate if over-dispersion of the data significantly violated the assumptions of the Poisson model.

The condition of individual age-0 fish assigned with high confidence to two parents was assessed as the residual value of that individual from a regression line (Jakob et al. 1996) fit using the log transformed length as a predictor variable and log transformed weight as a response variable pooled for all sampled age-0 individuals across the sampling period. Age-0 condition was then assessed using a mixed-model analysis. Age-0 condition was the response variable; hybrid status, sample date, and the interaction between hybrid status and sample date were entered as fixed effects. Hybrid status is a categorical variable which recorded whether the age-0 individual was the result of a Hemlock X Bigelow cross, a Mansfield X Bigelow cross, or a Hemlock X Mansfield cross. Hybrid status does not split offspring into different classes depending on the sex of the stocked parent, i.e., age-0 offspring with a Hemlock mother and Bigelow father, and an age-0 offspring with a Bigelow mother and Hemlock father are both treated as Hemlock X Bigelow crosses. A preliminary analysis of the data that distinguished among populations and sexes was not significant and was therefore collapsed into the more general hybrid classification described above. Sample date was a categorical variable used to account for any variation associated with offspring condition related to the date of collection. The interaction of hybrid status and sample date was used to evaluate whether the condition of hybrid classes responded differently over the sampling period.

For individuals assigned with high confidence to two parents I assessed whether or not random intermixing occurred among the three populations (resident and stocked Hemlock and Mansfield) present in Bigelow Pond. Random mating was assessed by determining whether the number of offspring assigned to a hybrid class (as defined above) was congruent with the expected number of offspring in each class based on the composition of the adult population using a chi-square test. The probability of each offspring class was calculated by multiplying the

proportion of the total population represented by each stocked population (e.g., resident individuals = 0.62 of total population; probability of Bigelow X Bigelow cross: $0.62 * 0.62 = 0.38$). Probabilities of each cross were standardized by summing the probability of all crosses and then dividing the individual probability of each cross by the summed probability. The expected number of offspring for each cross type was calculated by multiplying the total number of offspring assigned with high confidence to two parents and the standardized probability of each cross type.

Results

The population size of Bigelow Pond was an estimated 254 (95% CI: 190-385) individuals over 200 mm in total length. I stocked 156 individuals into Bigelow pond, resulting in a final population that contained approximately 40% stocked individuals. In total I stocked 77 individuals from Hemlock (34 males, 43 females) and 79 individuals from Mansfield (58 males, 21 females). Stocked Hemlock individuals did not statistically differ from a 1:1 expected sex ratio (Table 2.2, Chi-square = 1.05, df = 1, P = 0.31), but Mansfield individuals did statistically differ from a 1:1 sex ratio (Table 2, Chi-square = 17.3, df = 1, P < 0.001). Females from both populations were larger than their male counterparts for both length and weight (Table 2.2; Hemlock, length: $t = 3.75$, df = 75, $p < 0.001$, weight: $t = 4.1$, df = 70, $P < 0.001$; Mansfield, length: $t = 3.74$, df = 77, $P < 0.001$, weight: $t = 4.77$, df = 77, $P < 0.001$). However, relative weight did not differ significantly among males and females for either Hemlock or Mansfield (Table 2.2; Hemlock: $W = 685$, $P = 0.79$; Mansfield: $W = 705$, $P = 0.23$). The sex ratio of stocked Hemlock and Mansfield individuals differed significantly from each other (Chi-square = 9.73, df = 1, $P = 0.002$). Hemlock females were significantly longer (Table 2.2; $t = 2.26$, df = 53, $P = 0.03$), but not heavier (Table 2.2; $t = 0.96$, df = 52, $P = 0.34$) than Mansfield females.

Hemlock females had significantly lower relative weight than Mansfield females (Table 2.2; $W = 221$, $P = 0.03$). Hemlock males were significantly longer (Table 2.2; $t = 4.3$, $df = 99$, $P < 0.001$) and heavier (Table 2.2; $t = 4.04$, $df = 95$, $P < 0.001$) than Mansfield males, but there was no significant difference in relative weight (Table 2.2; $W = 221$, $P = 0.06$).

A total of 94 unique age-0 individuals were determined to have a stocked Mansfield or Hemlock parent (Table 2.2; representing 99 total parentage assignments, five fish were assigned to two stocked parents). These 94 individuals were used to assess whether sex biased contribution existed among stocked Hemlock and Mansfield fish, and whether characteristics of stocked parents were predictive of contribution to the age-0 sample. Of the 99 parentage assignments, 56 assignments were made to stocked Hemlock individuals and 43 assignments were made to stocked Mansfield individuals, which did not differ from their expected contribution based on their stocking ratio (Chi-square = 2.59, $df = 1$, $P = 0.11$). Similarly, there was no difference in the sex-specific contribution rates of stocked Mansfield and Hemlock individuals relative to their expected contribution based on stocking proportions (Table 2.2; males: Chi-square = 0.08, $df = 1$, $P = 0.77$, females: Chi-square = 2.15, $df = 1$, $P = 0.14$).

General linear modeling revealed that my data were over dispersed; therefore the negative binomial distribution model was used to evaluate the characteristics of successful stocked individuals. I found a significant effect of sex on the number of recruits, with males contributing fewer recruits ($P = 0.001$), but population of origin ($P = 0.10$) and weight class ($P = 0.19$) were not significant predictors of the number of age-0 recruits of an individual. There was a significant interaction between sex and weight class ($P = 0.03$) such that the heaviest female weight class contributed the most age-0 recruits to my sample (Figure 2.2). The contribution of individual stocked parents from Mansfield and Hemlock ranged between one and nine age-0

recruits (mean = 1.3 age-0) for males and one and eight age-0 recruits (mean = 1.9 age-0) for females.

A significant relationship was detected for log-transformed length and weight data of age-0 individuals ($F_{1,114} = 941.1$, $P < 0.001$, $R^2 = 0.89$). Individuals sampled during the first summer sampling period ($N=50$, June 29th 2013) were excluded from this length-weight regression because most individuals approached the lower tolerance of the scale used in the field, and therefore accurate weights could not be determined. In order to calculate hybridization as conservatively as possible, an additional 68 individuals were not assigned a hybrid status because there was low confidence in at least one of their parentage assignments resulting in a final sample size of 108 hybrid classifications (Table 2.3). Among these 108 individuals, hybridization of stocked Hemlock and Mansfield individuals into the Bigelow population was estimated at 54% (58 out of 108 offspring). Analysis of variance analysis revealed that hybrid status significantly predicted age-0 condition ($F_{3,90} = 3.4$, $P = 0.02$). Sampling period was a significant predictor ($F_{4,90} = 5.9$, $P < 0.001$), but there was no significant interaction among hybrid classification and sampling period ($F_{10,90} = 1.2$, $P = 0.31$) suggesting that there was no differences among hybrid classifications across sampling periods.

Among the 108 age-0 individuals assigned with high confidence to two parents there was evidence of non-random mating among the stocked individuals (Chi-square = 31.7, $df = 5$, $P < 0.001$). Hemlock X Hemlock, and Mansfield X Mansfield crosses occurred less frequently than expected based on the adult population composition (Table 2.4). Hemlock X Bigelow crosses occurred more frequently than expected based on adult population composition (Table 2.4).

Discussion

The stocking of exploited and unexploited, naïve Largemouth Bass into an active fishery resulted in substantial hybridization with the resident Largemouth Bass population. Of offspring assigned with high confidence to two parents ($N = 108$; Table 2.3), 54% were the result of hybridization between a stocked and resident parent. Mating among resident and stocked fish was apparently non-random, as fewer Hemlock X Hemlock and Mansfield X Mansfield individuals were observed than expected, and more Hemlock X Bigelow hybrids were observed than expected. I detected no difference in hybridization rate among stocked naïve and presumably angling-experienced individuals. Stocked females contributed more recruits than stocked males for both populations, but contrary to my first hypothesis - that the contribution from Hemlock parents would be sex biased - I detected no sex biased contribution for either population. Therefore this result suggests that recreational angling occurring prior to and during the nesting period did not disproportionately affect the ability of naïve males from an unexploited population to contribute to age-0 samples when compared to males originating from an active fishery. Replication of this study with additional unexploited and exploited populations is needed in order to confirm that unexploited and naïve individuals can genetically contribute to an active fishery.

Parent sex and an interaction between parent sex and parent weight-class were predictive of parental contribution to the age-0 sample; specifically the heaviest class of females had the greatest contribution to my age-0 sample (Figure 2.2). This finding partly conforms to my hypothesis that the largest females would have the highest contribution, but I did not find evidence that male size was associated with recruitment. Parent population and parent weight alone were not predictive of contribution to the age-0 sample. My finding that male size was not

a significant predictor of contribution to the age-0 sample for stocked populations is surprising because larger individuals typically receive more eggs in their nest from female bass (Philipp et al. 1997) and are therefore thought to contribute more to age-0 population recruitment (Parkos et al. 2011). For male Largemouth Bass bred for differential angling vulnerability, the largest high-vulnerability males had the greatest contribution to age-0 populations (Sutter et al. 2012).

Previous studies on the contribution of male black bass to age-0 populations have documented that a small number of males contribute disproportionately to age-0 samples. Gross and Kapuscinski (1997) reported that 20% of successful male Smallmouth Bass (*M. dolomieu*) contributed 54% of fall age-0 samples. Similarly, Parkos et al. (2011) found that the majority of fall age-0 Largemouth Bass in small Illinois ponds were contributed by just one or two broods from each pond. In the present study, contribution among stocked males from Hemlock and Mansfield to my age-0 sample was relatively uniform and not related to male size. Only three individuals contributed more than a single age-0 individual, representing 30% of the age-0 sample (2, 9 and 4 age-0 recruits contributed) with paternal assignments. Hessenauer et al. (2014b) also found relatively uniform contribution of male Largemouth Bass to age-0 samples (their range: 1-4 age-0/per nest), perhaps indicating that disproportionate contribution by some males in previous studies represents variation associated with study systems and species studied. Further investigation of factors associated with the contribution of individual male bass is warranted. This study is novel in that I was also able to assess the contribution of individual female bass. Six females (23% of contributing females) contributed 60% of the total maternal assignments. In contrast to males, the contribution of females was significantly related to size. However, only the heaviest 25% of females contributed significantly more than other weight

classes. These findings suggest that managers wishing to implement genetic management may be best served by stocking large females if possible.

I found a significant difference in condition among hybrid and pure resident age-0 individuals, such that Hemlock X Bigelow hybrids had higher condition than other hybrid classes (Table 2.3). Similar or better condition is an indication of similar fitness among hybrid individuals when compared to pure Bigelow individuals. Previous studies have noted that introgression among locally adapted Largemouth Bass strains can result in poorer physiological performance when introgressed F1 offspring are compared to pure strain offspring (Cooke et al. 2001; Cooke and Philipp 2006). These data suggest that genetic management could be a feasible management strategy if source populations are carefully matched to populations in need of management, because hybrid individuals had similar condition to pure resident age-0 individuals.

This case study provides a strong starting point for genetic management of heavily fished sportfish populations in freshwater lakes, but additional research is needed to evaluate the success and potential population level consequences of such management actions. I demonstrate that individuals naïve to angling from an unexploited population are able to successfully and significantly contribute to age-0 populations and therefore contribute genetically to an active fishery. These individuals therefore have the potential to contribute phenotypes including high angling vulnerability and high metabolic rates that may have been lost due to selection from recreational angling. These phenotypes have the potential to increase angler satisfaction and restore the ability of sportfish species such as Largemouth Bass to exert top-down control on forage fish species (e.g. Mittelbach et al. 1995). Additional research determining whether offspring descended from unexploited individuals demonstrate phenotypes associated with high angling vulnerability e.g., high metabolic rates (Redpath et al. 2010; Chapter 1) is critically

important. Evaluating the timescales over which genetic management actions remain effective and monitoring for unforeseen consequences is also important. Recreational angling is expected to continue to select against the phenotypes associated with high angling vulnerability (Philipp et al. 2009), potentially decreasing the effectiveness of a single genetic management action over time. Likewise, outbreeding depression may occur - defined as the disruption of locally adapted alleles or gene complexes (Templeton 1996; Frankham 1999) that can reduce fitness of individuals if the original populations were locally adapted. Outbreeding depression may be likely if the stocked individuals were moved from a system with vastly different environmental conditions (Philipp et al. 2002). Therefore, a long-term study that monitored the presence of introgressed individuals over multiple generations would be informative, especially because outbreeding depression may become more pronounced in the F2 generation. For example, Goldberg et al. (2005) found that F2 hybrids of Wisconsin and Illinois Largemouth Bass populations were more susceptible to Largemouth Bass Virus. Additionally, evaluating the stocking rates at which genetic management could be effective is important. In the current study, 54% of genotyped age-0 individuals were hybrids, with stocked individuals representing 40% of the total population. Such a large-scale stocking rate would likely not be feasible for a larger system and could potentially have deleterious effects on the source population (see discussion below). I chose to utilize a relatively high stocking rate in this case study because I was unsure if naïve to angling individuals from an unexploited population could persist and reproduce in a waterbody fished prior to and during the spawn. However, given the apparent non-random mating occurring among stocked and resident individuals it is possible that a reduced stocking rate could still produce measureable hybridization rates. Future studies should evaluate the costs

and benefits of various stocking rates for achieving management objectives, while documenting potential negative population level effects.

I also encourage consideration and dialog about the ethics associated with genetic management strategies. The movement of individuals from one population to another is not something that should be done without considering potential effects to both populations. The present study occurred outside of the native range of Largemouth Bass where the source population is an unexploited drinking water reservoir characterized by high density of large individuals relative to other Connecticut populations (Hessenauer et al. 2014a). Relatively few unexploited Largemouth Bass populations remain, with fewer still described in the literature (e.g., Mueller et al. 2005; Hessenauer et al. 2014a). Care must be taken to avoid negative effects on these rare yet important populations, i.e. removing so many individuals to be stocked elsewhere that the term “unexploited” no longer applies to the population. However, the potential for unexploited populations to serve as brood stock for new hatchery program targeting genetic management of exploited populations provides increased incentive for managers to identify, describe and protect these populations. Similar to traditional supplemental stocking of populations, genetic management has the potential to permanently alter both the donor and source population which may positively or negatively affect one or both populations. Therefore, care must be taken when selecting candidate and source populations.

In conclusion, the present case study suggests that the stocking of unexploited individuals into an exploited system results in genetic hybridization, allowing for the infusion of genetic material that may have been lost over time in response to recreational fisheries induced evolution. Reintroducing genetic diversity associated with high-vulnerability phenotypes could be used as a strategy to mitigate the effects of recreational fisheries induced evolution, especially

if traditional harvest based management is unlikely to succeed in the face of high catch-and-release rates and subsequent low levels of harvest.

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Table 2.1. Microsatellite loci used for parentage analysis including number of alleles, heterozygosity observed, heterozygosity expected for stocked parents. PCR conditions including annealing temperature (°C), MgCl₂ concentrations and original reference.

Locus	Alleles	Ho	He	Annealing T	MgCl ₂	Reference
MiSaTPW011	12	0.82	0.842	60	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW012	12	0.81	0.871	60	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW020	4	0.266	0.264	55	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW038	16	0.793	0.833	60	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW047	10	0.801	0.819	60	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW055	8	0.659	0.679	50	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW068	12	0.699	0.742	55	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW107	53	0.888	0.945	60	1.5	Lutz-Carrillo et al. (2008)
MiSaTPW173	24	0.678	0.794	60	2	Lutz-Carrillo et al. (2008)
Lma21	12	0.827	0.856	50	1	Colbourne et al. (1996)

Table 2.2. Characteristics of stocked Hemlock (unexploited) and Mansfield (exploited) individuals into Bigelow including number of individuals stocked (N), number of offspring assigned (Noff), average length in mm, average weight in g and average relative weight (Wr). Values reported as mean (SE) where appropriate.

	Hemlock		Mansfield	
	Males	Females	Males	Females
N	34	43	58	21
Noff	22	34	28	15
Length	402 (6.99)	442 (8.90)	362 (6.02)	409 (11.3)
Weight	921 (44.1)	1273 (85.7)	688 (37.0)	1140 (107)
Wr	99.1 (0.18)	98.8 (0.37)	99.5 (0.22)	100.1 (0.19)

Table 2.3. The number of offspring (N) assigned to three hybrid classes as well as the number of offspring assigned to pure Bigelow parentage and the mean (SE) condition (Cond) of those classes. Letters denote statistical significance based on the honest significant difference test.

	Hybrid Classification			
	Hemlock X Bigelow	Mansfield X Bigelow	Hemlock X Mansfield	Bigelow X Bigelow
N	34	24	5	45
Cond	0.066 (0.040) ^a	0.033 (0.056) ^{a,b}	-0.16 (0.15) ^{a,b}	-0.054 (0.024) ^b

Table 2.4. Chi square analysis of observed (Obs. Offspring) and expected (Exp. Offspring) of each cross type based on the proportion of parental parents in the adult population. Probability of cross (Prob. Of Cross) and standardized probability of cross (Std. Prob. of Cross) are given along with Chi-square value (Chi-sq).

Cross	Prob. of Cross	Std. Prob. of Cross	Exp. Offspring	Obs. Offspring	Chi-sq
Bigelow X Bigelow	0.38	0.53	57	45	2.5
Hemlock X Bigelow	0.12	0.16	17	34	16.2
Mansfield X Bigelow	0.12	0.16	18	24	2.2
Hemlock X Mansfield	0.04	0.05	5	5	0.0
Hemlock X Hemlock	0.04	0.05	5	0	5.2
Mansfield X Mansfield	0.04	0.05	6	0	5.5

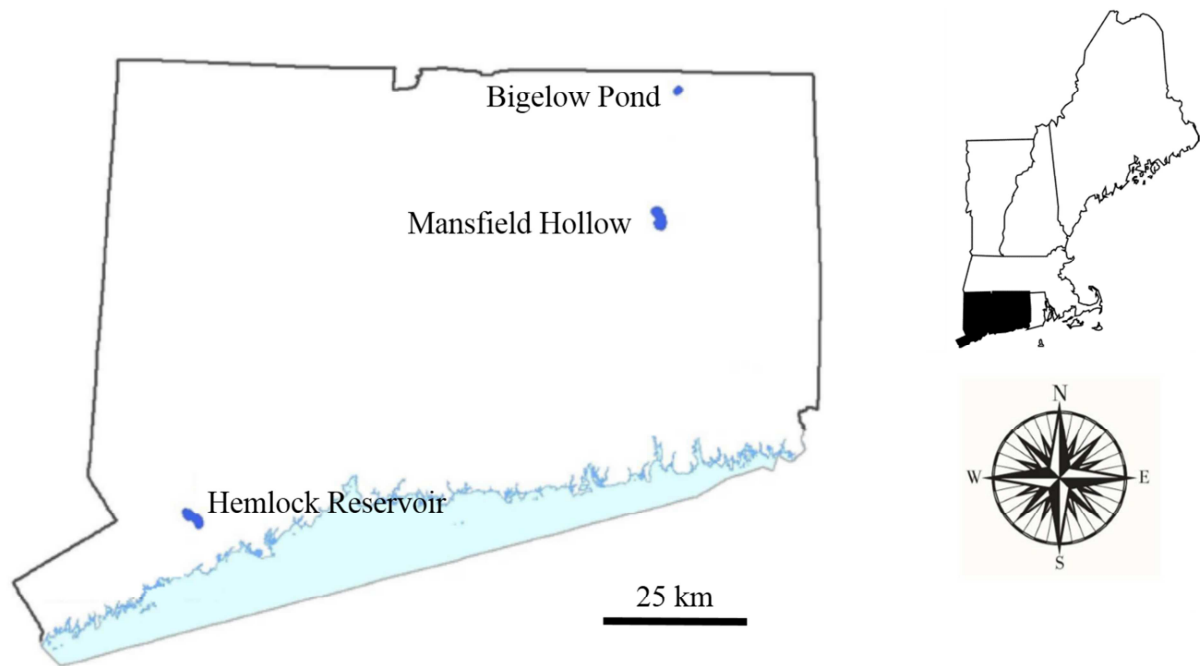


Figure 2.1. Study sites including unexploited Hemlock Reservoir, exploited Mansfield Hollow Reservoir, and exploited Bigelow Pond located within the state of Connecticut, USA.

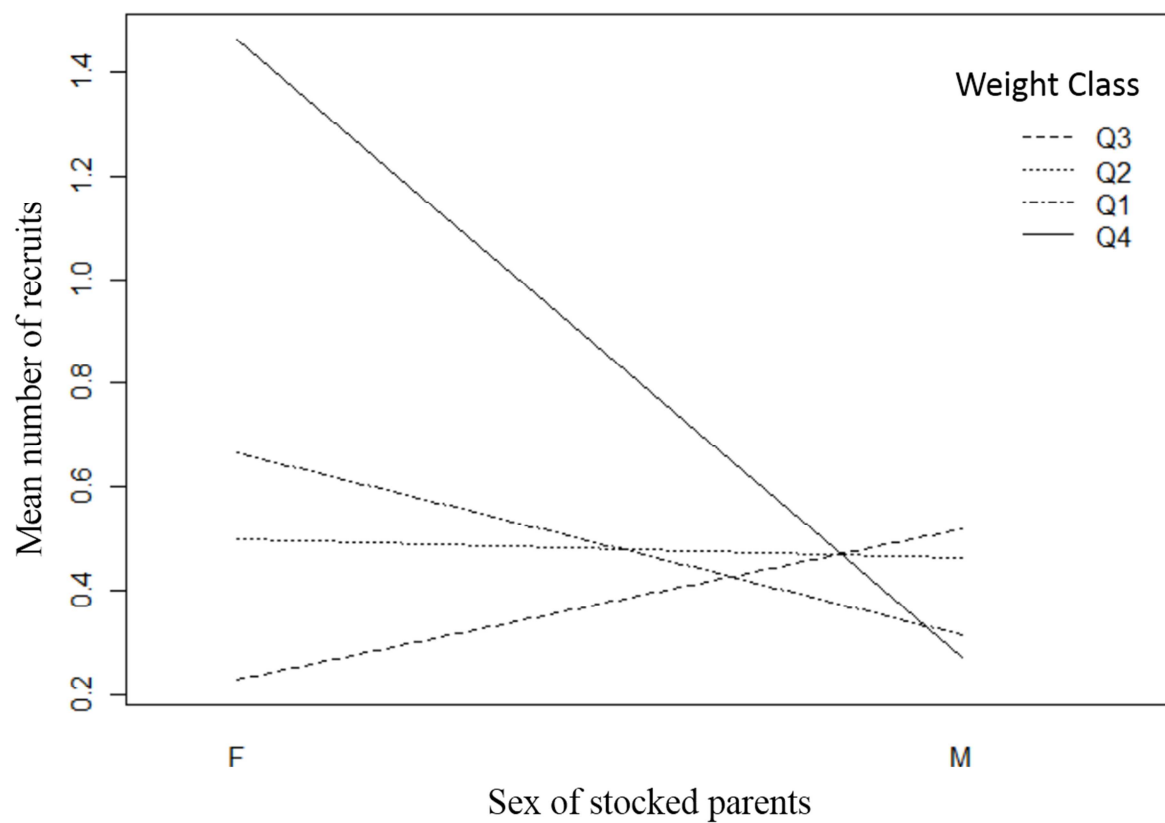


Figure 2.2. Interaction plot showing the mean number of recruits for parental sex and weight class of stocked Hemlock and Mansfield individuals. Weight class refers to the population quartile of stocked parents.

CHAPTER 3

The Catch-and-Release Era: Population Effects of Length Regulations and Catch-and-Release Mortality in High Use Fisheries

Abstract

Catch-and-release (CR) is not a new concept in recreational fisheries. However, recently CR trends have increased and spread globally. Some fisheries have entered a new era of fisheries management: the catch-and-release era, defined by fisheries in which unintentional mortality associated with CR represents the largest component of total fishing mortality. I sought to evaluate the utility of length limits and the effects of CR mortality on population age and size structure of two high-use Connecticut fisheries by characterizing the total number of Largemouth Bass *Micropterus salmoides* catch events in two lakes over two years. Catch events were estimated by monitoring Largemouth Bass tournaments and from creel surveys conducted by Connecticut Department of Energy and Environmental Protection Inland Fisheries Division. In both lakes across both years, catch events exceeded estimated population size by a factor of two to three. The percentage of capture events resulting in harvest was low across lakes and years ranging from 0-1.8%. A yield per recruit model was utilized to evaluate the harvest probability at which 346 and 406 mm length limits no longer alter population age and size structure, across a range of catch to population size ratios. The same model was used to evaluate the CR mortality rate at changes in population age and size structure occurs due to CR mortality. At observed catch event to population size ratios for both lakes over both years, model results indicate that current harvest rates were less than the harvest rates needed to significantly affect age and size structure. Using CR mortality rates estimated from tournament monitoring, both lakes approached or exceeded the CR mortality rate at which significant effects on age and size

structure are expected. Even low rates of CR mortality can alter population size structure in high-use fisheries by compounding over multiple catch events over multiple seasons, reducing the probability that individuals survive to old ages, and hence large sizes. Traditional management tools such as length limits may not be effective in the catch-and-release era. Creative new management solutions will be needed to manage fisheries in the catch-and-release era.

Introduction

The concept of catch-and-release (CR) is not new; in the 1930's Lee Wulff suggested in his *Handbook of Freshwater Fishing* that "game fish are too valuable to be captured only once", and the first scientific study of CR mortality concluded that hooking mortality of immature trout was low (Westerman 1932). Quinn (1989) reported that CR could "recycle" fish and improve fishing quality in some situations. Since that time, trends in voluntary CR angling have increased and spread globally (e.g., Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007; Thomé-Souza et al. 2014; Gupta et al. 2015; Lennox et al. 2015; Taylor et al. 2015). For some fisheries, CR rates approach 100% (Quinn 1996; Cooke and Cowx 2004; Bartholomew and Bohnsack 2005), such that many recreational fisheries are now dominated by CR practices. The popularity of CR in these fisheries is ushering in a new era in recreational fisheries: the catch-and-release era. The catch-and-release era is characterized by fisheries in which unintentional mortality associated with the hooking and handling of fish that are released represents the majority of population-wide fishing mortality. Catch-and-release may be implemented voluntarily as a conservation practice by anglers seeking to reduce their impact on fish populations; releasing an individual alive allows it to survive, continue to grow and perhaps be captured again in the future (Quinn 1996; Cooke and Suski 2005; Arlinghaus et al. 2007). In

some fisheries, CR may be mandated by regulations (Quinn 1996; Arlinghaus et al. 2007). The catch-and-release era represents a significant challenge for the management of recreational fisheries because most commonly implemented management tools were designed to reduce or redirect harvest, e.g. length and slot limits (Radomski et al. 2001; Wilde et al. 2003; Lewin et al. 2006). Such tools may be increasingly, if not already, obsolete for fisheries where most fishing mortality occurs unintentionally (e.g., Pollock and Pine 2007), reducing the number of tools managers have to respond to ecological or social challenges associated with recreational fishing.

Catch-and-release mortality varies substantially among species and is related to a wide range of factors including angler gear, fishing depth, water temperature, fish condition, and reproductive status as well as complex interactions among these factors (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Cooke and Suski 2005; Gingerich et al. 2007; Hühn and Arlinghaus 2011). For the purposes of this chapter, I define CR mortality as unintentional mortality in angled fishes intended to be released by the angler either voluntarily or in accordance with regulations. These mortalities are associated with hooking and handling injuries as well as mortality resulting from physiological stresses incurred during a catch event. A fundamental challenge for fisheries managers is that, unlike harvest mortality which can be directly observed (e.g., from creel surveys) and is commonly estimated using tagging studies and other well established quantitative methods (Kerns et al. 20212), CR mortality goes largely unobserved. However, an increasing body of literature provides recommendations for the study and quantification of CR mortality (Cooke and Schramm 2007; Pollock and Pine 2007). Delayed mortality can occur as a result of a CR event hours or days after the actual catch event, compounding the challenge of estimating CR mortality rates (Muoneke and Childress 1994; Pollock and Pine 2007).

Recognition of the potential population and management importance of CR mortality is increasing (e.g., Coggins et al. 2007; Pollock and Pine 2007; Kerns et al. 2012). Many studies provide valuable estimates of the CR mortality rate of fish species over a variety of conditions (e.g., Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011). Attention has also been given to best practices, methods, and gear to reduce CR mortality rates (e.g., Cooke and Suski 2005; Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011; Bergmann et al. 2014; Lennox et al. 2015); however, a holistic understanding of the effects of CR mortality and its potential population level effects is generally lacking. Kerns et al. (2012) reported that in their experience many fisheries professionals consider high CR mortality as bad, and low CR mortality as not of management concern. Few studies have attempted to estimate the population level effects of CR mortality (Pine and Pollock 2007; Kerns et al. 2012). However, among studies that quantitatively assessed population-level effects of CR mortality, even low rates of CR mortality may provide substantial contribution to overall fishing related mortality under the right circumstances (Bartholomew and Bohnsack 2005; Mueller and Taylor 2006; Coggins et al. 2007; Hühn and Arlinghaus 2011). Water temperature is consistently identified as an important factor in determining CR mortality rates, with warmer water associated with higher CR mortality (Muoneke and Childress 1994; Edwards et al. 2004a; Gingerich et al. 2007; Hühn and Arlinghaus 2011; Danylchuck et al. 2014). The relationship between water temperature and CR mortality across taxa is a concern because global climate change is expected to increase water temperatures (e.g., Ficke et al. 2007; Trumpickas et al. 2009) potentially leading to higher rates of CR mortality, and thereby increasing the potential for CR mortality to affect populations. Increases in CR mortality rate associated with climate change and continuing trends in angler behavior for some fisheries towards CR practices represent an urgent need to

evaluate whether or not harvest based regulations such as length limits are still relevant, and under what conditions CR mortality can influence recreational fish stocks.

I sought to generate a complete-as-possible representation of the Largemouth Bass *Micropterus salmoides* recreational fisheries in two lakes over two open water fishing seasons addressing three primary objectives. My first objective was to estimate the total number of catch events that occurred in each lake each season. Such data are rarely available, but important to understand the potential magnitude of CR mortality. My second objective used this data in a yield per recruit modelling approach to estimate the harvest rate at which length limit regulations no longer significantly affected population size and age structure under a variety of scenarios. Finally, I estimated the CR mortality rate at which CR mortality alone was expected to significantly alter population size and age structure compared to an unexploited fishery under a variety of model scenarios.

Methods

In order to understand the potential for harvest regulations and CR mortality to affect population size and age structure, a detailed estimate of the total number of catch events was needed. I attempted to estimate the total number of catch events for two Connecticut Lakes, Mansfield Hollow Reservoir (hereafter Mansfield, 186 ha; N 41°46'6.53", W 72°10'31.73") and Gardner Lake (hereafter Gardner, 214 ha; N 41°30'39.66", W 73°13'38.77") for two open water fishing seasons each. Both lakes are mesotrophic systems and popular Largemouth Bass fisheries (Edwards et al. 2004a, 2004b); having averaged over 30 small club tournaments per year since 2000 (CTDEEP unpublished data). Population size was estimated for both lakes during the first year of monitoring using a multi-lap mark-recapture electrofishing survey. I used a two staged approach to estimate the total number of fish captured by anglers in both lakes for

two-open water fishing seasons each. Capture events were estimated by monitoring Largemouth Bass tournaments and creel surveys.

The monitoring of Largemouth Bass tournaments provided a direct observation of catch events occurring in each lake. The State of Connecticut requires that organized fishing tournaments obtain free permits, and publically publishes tournament schedules online, which facilitated my efforts to monitor each tournament. At each tournament, I made contact with the tournament director and asked him or her to allow me to examine each fish after normal weigh-in and tournament activities had been completed. After anglers had completed their weigh-in procedure, fish were brought in bags typically containing lake water and were placed in covered plastic laundry baskets immersed in the lake to await processing. For processing, the entire laundry basket containing fish was moved to a large cooler full of lake water. All fish were measured to the nearest mm total length, examined for clips from previous tournaments (see below), examined for status (alive or dead) and injuries associated with angling such as hook wounds, bleeding, lesions, bruising, etc., and given fin clips that designated the fish as a tournament captured individual. Fish that had never been previously captured by tournament anglers received both a right ventral or pectoral clip (depending on which fishing season) and a dorsal spine clip. Half spine clips starting at the anterior end and proceeding in the posterior direction (one clip at each tournament) were used during the first season of monitoring at each lake, and full spine clips, leaving a small nub of spine remaining, starting at the posterior and proceeding in the anterior direction were used during the second season of monitoring. Fish were then released back into the lake. Each angler was also asked how many tournament legal fish (>305 mm) had been captured but culled out prior to the weigh in. Anglers often reported

culling out a range of fish (e.g. 10-12 fish culled); to ensure that total catch estimates were as conservative as possible, I always used the low end of the range for catch estimates.

Initial CR mortality for tournament captured fish was estimated as the proportion of fish that were dead when I examined them compared to the total number of fish captured. I estimated the effect of factors hypothesized *a priori* to be associated with initial mortality using a logistic regression framework. The status of individual fish at each tournament was coded as 0 for fish that were alive and 1 for mortalities and entered into the model as the response variable. Fish length, number of previous tournament captures, water temperature, water surface conditions (i.e., level of wave action), weather conditions (i.e., clear, overcast, etc.), wind conditions, tournament regulations (number of fish permitted for capture), lake and year were entered as predictor variables. Non-significant parameters were dropped from the final model. While this study did not directly estimate delayed mortality, I used a logistic regression framework to evaluate factors associated with the probability of an individual being injured during a tournament capture event under the assumption that individual injury was related to delayed mortality. Injury was a binary response variable coded as 0 for uninjured and 1 when an injury was present for each individual. The same predictor variables for mortality were used, and non-significant variables were dropped from the model.

The Connecticut Department of Energy and Environmental Protection (CTDEEP) conducted standardized random roving creel surveys at Mansfield and Gardner for both years in which I monitored tournaments. Surveys are stratified by weekdays and weekend/holidays, and also by season (Spring: 3rd Saturday in April- June 15th, Summer: June 16th – September 15th, Fall: September 16th – October 31st). Sampling effort was divided in order to sample each weekend day and two weekdays during each week. Survey start times were randomly chosen.

Creel agents conduct instantaneous counts of anglers to estimate angler effort and incomplete trip angler interviews are conducted to determine catch rates. Creel data were expanded to estimate angler effort using the equation:

$$E_d = F_d \times A_d$$

where E_d is the effort on day d , F_d is the number of fishable hours on day d , and A_d is the number of anglers counted on day d (Lockwood et al. 1999). These estimates of effort were expanded to their strata using the equation:

$$E_p = \frac{D_p}{m_p} \sum_{d=1}^{m_p} E_d$$

where E_p is the effort for strata p , D_p is the number of days in strata p , and m_p is the number of days sampled in strata p (Lockwood et al. 1999). Variance for each strata containing more than one sample day was calculated using the equation (Lockwood et al. 1999):

$$\widehat{Var}(E_p) = \left(\frac{D_p}{m_p} \right)^2 \left[\frac{\sum_{d=1}^{m_p} E_d^2 - \frac{(\sum_{d=1}^{m_p} E_d)^2}{m_p}}{m_p(m_p - 1)} \right]$$

Catch (and harvest) rates were calculated from incomplete-trip interviews using the equations:

$$\bar{R}_p = \frac{\sum_{i=1}^{k_p} \frac{c_{pi}}{h_{pi}}}{k_p}$$

where \bar{R}_p is the catch (or harvest) rate for strata p , c_{pi} is the catch (or harvest) of target species by angler i during strata p , h_{pi} is the hours fished by angler i during period p , and k_p is the total number of anglers interviewed during period p (Lockwood et al. 1999). The variance in catch (or harvest) rate for strata with more than one sample were calculated using the equation (Lockwood et al. 1999):

$$\widehat{R}_p = \frac{\sum_{i=1}^{k_p} \left(\frac{c_{pi}}{h_{pi}}\right)^2 - \frac{\left(\sum_{i=1}^{k_p} \left(\frac{c_{pi}}{h_{pi}}\right)\right)^2}{k_p}}{k_p(k_p - 1)}$$

Total catch was estimated by multiplying effort by catch rate for each strata and then summing across all strata. Similarly, total harvest was calculated for each strata and summed across all strata to estimate total harvest.

Catch events from tournaments including the number of fish weighed in and the total number of fish reported culled were subtracted from the estimated number of fish captured from creel expansion to generate a complete estimate of the number of catch events occurring within a given fishing season for each lake. The total catch was compared with the total population size to estimate the fraction of the total stock captured, or the average number of times that catchable sized fish were actually captured within a given fishing season.

Total catch events and total harvest were used to estimate the effects of length limits and CR mortality on population age and size structure using the yield per recruit model developed by Allen et al. (2009) and modified for Largemouth Bass by Dotson et al. (2013):

$$l_{fa} = l_{fa-1}S_a(1 - UV_{a-1})(1 - (U_0V'_{a-1} - UV_{a-1})D)$$

where l_{fa} represents the probability of a recruit surviving to age a , S_a is the natural survival rate corrected for length, U is the fraction of the stock harvest annually, U_0 is the ratio of catch events to population size, V_a is the vulnerability schedule for harvest, V'_a is the vulnerability schedule for capture, and D is the catch-and-release mortality rate. Formulae for calculation of S_a , V_a and V'_a are described in Dotson et al. (2013). This model breaks mortality probability into three discrete components: natural mortality $l_{fa-1}S_a$, mortality due to harvest $(1 - UV_{a-1})$, and mortality due to CR $(1 - (U_0V'_{a-1} - UV_{a-1})D)$ (Allen et al. 2009; Dotson et al. 2013). I parameterized the

model (Table 3.1) to a “typical” Connecticut Largemouth Bass population, represented by Mansfield. Population characteristics for Mansfield were described in Hessenauer et al. (2014). Recruitment was modeled using a Beverton and Holt stock recruit curve with a Goodyear (1980) compensation ratio of 15 (as per Dotson et al. 2013). Growth was modeled using a von Bertalanffy growth model, with growth parameters (i.e., k , L_{∞} , t_0) estimated by Hessenauer et al. (2014) for Mansfield. Natural survival rate was estimated as 1 - natural mortality; natural mortality was estimated by averaging the mortality rates of Largemouth Bass from two unexploited Connecticut populations (Hessenauer et al. 2014) that I assumed represented the natural mortality rates of Connecticut populations. All modeled individuals were female, and the number of individuals at a given age was determined by multiplying the number (1000) of age-1 recruits by the survivorship probability (l_{fa}). An age-length key developed by Hessenauer et al. (2014) for Mansfield was applied to convert age structure into size structure. While this model is fundamentally deterministic, I incorporated natural stochasticity and uncertainty in the model parameter estimates by running the model 10,000 times, each time randomly selecting the starting parameters from a normal distribution with the mean and variance of each parameter estimated from field data.

In order to evaluate the ability of length limit regulations to alter population age and size structure at various rates of harvest and for various catch to population size ratios (U_0), I altered the vulnerability schedule for harvest (V_a) to represent a 356 mm (14 inch) and a 406 mm (16 inch) minimum length, while CR mortality rate was fixed at 5%. To maintain comparability across model runs, harvest rates were standardized to represent the probability of harvest of a single catch event. At a given catch event to population size ratio, harvest probability was increased until the distribution of age and length obtained under the regulation scenario were

significantly different ($P < 0.05$) than the distribution of age and length obtained from a scenario with no minimum length ($V_a = V_a'$), as assessed using a Kolmogorov-Smirnov (KS) test. A significant KS test indicated that the age and size structure obtained using the modeled length limit was significantly different from the age and size structure obtained under the no minimum length scenario, and hence that the regulation had an effect on size and age structure. To characterize model uncertainty, I also estimated the harvest probability at which the regulations significantly affected size and age structure with 90% and 99% probability ($P < 0.1$ and $P < 0.01$, respectively).

I also used the model to evaluate the CR mortality rate (D) at which significant reductions in population age and size structure would be expected for a given catch to population size ratio (U_0), in the absence of harvest. Similar to my evaluation of regulations, I assessed the effect of CR mortality in two ways: first, by comparing the distribution of ages and lengths at a fixed catch to population size ratio but varying CR mortality rate. Within each run the distribution of ages and lengths under a given CR mortality rate were compared with the distribution of ages and lengths under a very low (0.001) CR mortality rate using a KS test. A significant KS test ($P < 0.05$) indicated that CR mortality would be expected to cause significant decreases in population age and length structure. I also evaluated the effect of CR mortality by calculating proportional size distributions (PSD; Guy et al. 2007), proportional size distribution of preferred (PSD-P), and the proportional size distribution of memorable (PSD-M) sized fish using 20 cm as stock sized, 30 cm as quality sized, 38 cm as preferred sized, and 51 cm as memorable sized (Anderson 1980). PSD values were compared among model scenarios to evaluate changes associated with CR mortality. To characterize model uncertainty, I also estimated the CR mortality rate at which significant effects on size and age structure were

expected with 90% and 99% probability ($P < 0.1$ and $P < 0.01$, respectively). Model sensitivity to input parameters was assessed by evaluating changes in population size structure based on the extreme high and low ranges of input variables.

Results

In close collaboration with CTDEEP, I monitored a total of 106 Largemouth Bass tournaments at Mansfield (2012 & 2013) and Gardner (2013 & 2014). I directly observed 4,617 capture events at both lakes (Table 3.2; Mansfield two year total: 1,852, Gardner two year total: 2,765). The population size of Largemouth Bass over 250 mm was 3,100 for Mansfield and 2,800 for Gardner (Table 3.2). Within a single year between 20% and 50% of all individuals over 250 mm were weighed-in at tournaments in both lakes, and many individuals were captured multiple times (Figure 3.2). Tournament anglers reported capturing, but culling out an additional 3,312 individuals (Table 3.2; Mansfield two year total: 1,377, Gardner two year total: 1,935), indicating that the total proportion of individuals captured by tournament anglers (number of fish weighed-in and culled out) across lakes and years ranged from 51 to 87%. Overall, initial weigh-in mortality rates were very low (Table 3.2) ranging from 1% in Gardner 2014, to 3% in Mansfield 2013. Fishing-related injury rates were slightly higher than mortality rates (Table 3.2) ranging from 2% in Gardner 2013, to 5% in Mansfield 2012 and Gardner 2014. Three significant predictor variables were associated with tournament mortality probability. Fish size was significantly related to tournament mortality, such that larger fish were less likely to be mortalities than smaller fish (Wald Chi-square = 7.5, $df = 1$, $P = 0.006$). Water temperature was also significantly related to tournament mortality rate, with higher water temperatures being associated with higher mortality rates (Wald Chi-square = 19.8, $df = 1$, $P < 0.0001$). Finally, tournament regulations were related with significant mortality rates (Wald Chi-square = 19.4, df

= 4, $P = 0.0006$). Five variables were associated with increased tournament injury probability. I found a significant difference among lakes (Wald Chi-square = 4.05, $df = 1$, $P = 0.04$), such that Mansfield had higher injury rates. There was also a significant difference among years (Wald Chi-square = 11.5, $df = 2$, $P = 0.003$). High wind conditions were positively associated with injury rates (Wald Chi-square = 9.4, $df = 3$, $P = 0.02$). Likewise larger fish were more likely to be injured than smaller fish (Wald Chi-square = 6.6, $df = 1$, $P = 0.01$). Water temperature was also significantly related with injury rates such that higher water temperature increased injury rates (Wald Chi-square = 9.7, $df = 1$, $P = 0.002$).

Creel surveys conducted by CTDEEP revealed low harvest rates in both lakes across both years. The estimated number of harvested fish ranged from 0-99, with creel agents observing only nine total harvested Largemouth Bass (Table 3.2) across lakes and years. The probability that a single non-tournament capture event would result in harvest ranged from 0 to 1.8% across lakes and years. Substantial numbers of CR events were reported to creel agents (Table 3.2) ranging from a low of 4,400 in Mansfield 2013 and a high of 5,500 in Gardner 2013. In both lakes across both years, the number of fish captured by non-tournament anglers exceeded the total estimated population size by a factor of 1.4 (Mansfield 2013) to 2.0 (Gardner 2013). When tournament and non-tournament captures were combined, the total number of catch events exceeded the population size of each lake across years by a factor of 2.0 to 3.0. This suggests that every catchable fish in these two populations was captured between 2 and 3 times each. If one conservatively assumes that catch and release mortality rates were 2% (my average initial tournament mortality rate was 2%, not accounting for discard mortality), then the number of fish that died as a result of CR was higher than the number of fish purposefully harvested in all lakes across all years of study.

I modeled the harvest probability of an individual capture event at which a 356 mm and 406 mm minimum length significantly affected population size and age structure for a typical Connecticut Largemouth Bass population. As the ratio of catch events to population size increased, the harvest probability needed for a 356 mm and 406 mm length limit to significantly alter age and size structure declined (Figure 3.2). Catch-and-release mortality has the potential to significantly affect age and size structure of Largemouth Bass populations. When the number of catch events equaled or exceeded the population size, CR mortality rates of over 10% were predicted to significantly affect population age and size structure (Figure 3.3). At the catch events to population size ratios I observed in Gardner (max 3.0) and Mansfield (max 2.0), the model predicted that CR mortality rates would significantly affect size and age structure at relatively low rates (5% and 3%, respectively). At a given catch event to population size ratio, increasing CR mortality resulted in declines of large individuals by decreasing the probability that fish survive to old ages and hence large sizes (Figure 3.4). As a result of the loss of old, large individuals, proportional size distributions declined across all model scenarios (Table 3.3). Declines in proportional size distributions were especially stark for preferred (5-70% decline across model scenarios) and memorable sized (11-95% decline across model scenarios) fish. Model sensitivity analysis revealed that parameters associated with natural mortality had the largest effect on model outcomes. These parameters included the natural mortality rate, but also von Bertalanffy growth parameters t_o and k . This is because the model assumes higher rates of natural mortality for small fish (Allen et al. 2009; Dotson et al. 2013), so faster growth reduced exposure to high natural mortality rates associated with small sizes.

Discussion

My effort to characterize the total number of catch events that occurred in two lakes over two consecutive fishing seasons revealed a surprising number of catch events in both populations over both years. The number of catch events exceeded the estimated population size by a factor of two to three for both lakes studied (Table 3.2), suggesting that each catchable size individual was captured an average of two or three times within a single open water fishing season depending on the lake and year. Recreational bass fishing has been described as “commodity intensive serious leisure”, whereby many anglers invest heavily in equipment, technology and information to improve catch rates (Yoder 1997), and the ability of anglers to catch a surprisingly large proportion of catchable individuals speaks to the seriousness, specialization, and sophistication of bass anglers. While both of these lakes are indeed popular tournament lakes (Edwards et al. 2004a, 2004b), they are not exceptional compared to other Connecticut lakes in terms of number of tournaments or fishing effort (CTDEEP unpublished data). Therefore it seems likely that the catch event to population size ratios that I observed are possible, if not common, in other northern North American Largemouth Bass populations.

I evaluated factors associated with weigh-in mortality of Largemouth Bass at tournaments to gain insight into factors associated with CR mortality in general. Overall initial tournament mortality was low, ranging from 1% of fish weighed-in for Gardner in 2014 to 3% of fish weighed-in for Mansfield in 2013. Water temperature was positively associated with the mortality of Largemouth Bass captured in tournaments, such that increased water temperature increased the probability of mortality. Conversely, fish size was negatively associated with weigh-in mortality, such that small individuals had a greater probability of mortality than large individuals. Injury rates were positively associated with water temperature, fish size, and wind

speed, suggesting that these factors may increase the risk of delayed mortality. Increased water temperature is known to increase mortality probability associated with CR across a variety of fish taxa (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Edwards et al. 2004a; Cooke and Suski 2005; Gingerich et al. 2007; Hühn and Arlinghaus 2011; Danylchuck et al. 2014). In contrast to previous studies conducted on Largemouth Bass (Edwards et al. 2004a) and reviews conducted across fish taxa (Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011), I found that length was significantly related to mortality and injury probability. Edwards et al. (2004b) concluded that the impacts of tournaments were low on Gardner and Mansfield primarily because initial and delayed mortality rates were low for black bass species. Studies since Edwards et al. (2004b) have determined that low CR mortality can be influential under the right circumstances (Bartholomew and Bohnsack 2005; Mueller and Taylor 2006; Coggins et al. 2007; Hühn and Arlinghaus 2011) and I found that low CR mortality rates can have important population consequences if individuals are repeatedly exposed to CR events. Allen et al. (2004) suggested that tournaments have the potential to influence population size structure and abundance when the number of fish captured in tournaments exceeded the number of fish harvested by a factor of three, providing a useful metric for managers to evaluate the potential for tournaments to influence population age and size structure. Estimating the total catch event to population size ratio gives managers a complete sense of the potential for CR mortality to influence population age and size structure.

Many individuals were captured in multiple tournaments over the two year monitoring period in each lake (Figure 3.1). However, I did not detect a significant relationship between the number of times an individual fish had been captured over the two year monitoring period and the probability of mortality or injury. One explanation is that the probability of mortality

associated with a given capture event is independent of previous capture events. Independent probability of mortality among capture events is significant because most models that include a CR mortality parameter, including the one that I used, assume that mortality probability is equal for all capture events. Such models would substantially underestimate CR mortality if the probability of mortality for a given capture event were increased by previous capture events.

Tournament fishing and CR fishing in general is associated with numerous sub-lethal physiological stressors (Plumb et al. 1998; Cooke et al. 2002; Suski et al. 2003; Suski et al. 2004; Suski et al. 2006), such that the effect of repeated captures is likely highly dependent on the time between captures, which may vary substantially (e.g., Cline et al. 2012). The current study did not mark fish as individuals and therefore time duration between capture events could not be assessed. Additional research determining the relationship between CR mortality and number of capture events would be particularly relevant for the management of high-use fisheries with high CR rates.

The modeling exercise that I conducted predicted that as the catch event to population size ratio increased from 0.25 to 4.0, the probability of an individual capture event resulting in harvest at which a 356 mm length limit significantly altered age and size structure decreased from 0.64 to 0.07. For a 406 mm length limits to significantly affect age and size structure over the same range of catch event to population size ratios, the harvest probability of an individual capture event at which significant changes in age and size structure were expected declined from 0.44 to 0.05. The observed harvest probability of an individual non-tournament capture was estimated from the creel data to range from 0 (Gardner 2014) to 1.8% (Gardner 2013), substantially lower than the rates at which length limits were predicted to affect size and age structure for all catch to population size ratios. Therefore, I conclude that length limits are

unlikely to affect population size and age structure in Mansfield and Gardner, given the low rates of harvest observed.

Based on the simulated model scenarios, I predicted that significant effects on population size and age structure would occur as a result of CR mortality. As the ratio of catch events to population size increased from 0.25 to 4.0, the catch and release mortality rate at which significant changes were expected decreased from 0.35 to 0.03. Based on the observed catch rate to population size ratios for Gardner and Mansfield, the model predicted that a catch-and-release mortality rate ranging from 3-5% would likely alter population size and age structure in each lake. Initial mortality rates for fish captured in tournaments ranged from 1-3% across lakes and years. This study did not quantify delayed mortality rates directly, but Edwards et al. (2004a) found delayed mortality rates averaging 1% for bass tournaments on the same populations. Therefore, if the estimated 2-4% total CR mortality rate from tournaments are applied to all catch events for each population, the total CR mortality may be at or approaching the range at which population effects on age and size structure would be expected. Cooke et al. (2002; their table 2) reviewed hooking mortality rates for Largemouth Bass, reporting a broad range of mortality rates (0-76.9%) across a variety of habitat types and conditions. I expect the effects of CR mortality will vary substantially across systems, regions and over time.

Catch-and-release mortality influences a population's size and age structure by reducing the probability that recruits will survive to old ages and hence large sizes (Figure 3.4). Therefore, the changes in size structure observed between model runs with low CR mortality and model runs with high CR mortality are driven by declines in the oldest, largest fish. This effect is clearly observed across all model scenarios: increasing CR mortality resulted in reduced proportional size distributions (Table 3.3), especially for preferred and memorable sized fish.

This model result is important because large individuals are typically the most sought after by anglers (Dotson et al. 2013), and are desired by managers because of their ecological significance to the population, e.g., high fecundity, high offspring quality (e.g., Hixon et al. 2014). For managers interested in establishing or maintaining trophy fisheries, substantial effects of CR mortality can occur at lower rates than needed to alter the population size and age structure as a whole. For example, when the catch to population size ratio is 1.0, an increase in CR mortality from less than 1% to 2% is not predicted to affect overall population size structure, (Figure 3.3) but is predicted to reduce the yield of memorable sized and larger individuals from 28 to 21 per 1000 recruits, a reduction of 25%. Therefore assuming that the opportunity for an angler to capture a memorable sized fish is related to angler effort and fish abundance alone, CR mortality reduces the abundance of memorable sized individuals by 25%, requiring an increase in effort by anglers to maintain similar numbers of memorable sized fish captured.

Over the two years that I closely monitored two Connecticut Largemouth Bass populations, the catch events of individual fish exceeded the population size by two times or more, and few of those catch events resulted in the purposeful harvest of Largemouth Bass. This result has several important management implications. First, harvest rates in these systems are low enough that length limits are not expected to affect population size and age structure. While I did not model more complicated regulation scenarios e.g., protected slots, etc., it seems unlikely that any regulation seeking to direct or reduce harvest effort at particular portions of the population could be successful when so few fish are harvested. If one conservatively assumes that CR mortality was 2% for all lakes and years that I studied, CR mortality would exceed harvest mortality for each lake and year, indicating that these systems truly have entered the “catch-and-release era”. In practice this means that a manager of one of these systems has lost

the ability to use harvest-based regulations such as length limits, the most commonly implemented tool in the fisheries management toolbox, to exert change on these populations. I do not advocate for the abolition of regulations seeking to direct or reduce harvest in the catch-and-release era, as such regulations provide a valuable safeguard against changes in angler behavior (i.e., back towards harvest-based practices), and may have an important social basis; however, harvest-based regulations are unlikely to promote the achievement of management goals for some fisheries.

Management to reduce CR mortality rates is a worthy goal. Some studies have found that the use of lures reduces hooking mortality rates relative to the use of live bait across fish taxa (Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011), and therefore, some jurisdictions ban the use of live bait to reduce mortality rates (Wilde et al. 2003). Research has attempted to establish “best practices” for the handling of many species in order to reduce mortality rates associated with angling (e.g., Cooke and Suski 2005). Many North American fisheries agencies provide recommendations to anglers regarding CR practices, though substantially different and occasionally contradictory recommendations were often given (Pelletier et al. 2007). I strongly advocate that anglers follow best practice guidelines in an effort to reduce mortality and improve the welfare of individuals captured by anglers. However, the ability of best practices or regulations to significantly improve population characteristics will depend on the life history of the species (Cooke and Schramm 2007) and likely the catch to population size ratio of the fishery of interest. Given the low rates of mortality that I observed at Largemouth Bass tournaments it seems that for some species, like Largemouth Bass there is little room for additional improvement. Therefore, for some species and systems where the catch event to population size ratio is high and CR mortality rates are already low, management

seeking to reduce CR mortality further, using regulations such as gear restrictions, may not be effective in preventing effects of CR mortality on age and size structure. Creative management techniques capable of managing either the success of anglers, the amount of angler effort, or the target population size are needed.

Gear regulations could be enacted in an effort to influence the vulnerability of fish to angling. Many recreationally valuable fish species are piscivorous, and therefore a direct relationship exists between their gape size and the size of prey that can be captured and consumed (Werner 1974). Capitalizing on this relationship, Wilde et al. (2003) demonstrated that large lures capture large fish relative to small lures, and suggested that restrictions on lure length could be utilized to reinforce minimum length limits. Cerdà et al. (2010) reported that increasing hook size decreased catch rates overall but not the total weight of fish captured for marine recreational fisheries. Importantly, Cerdà et al. (2010) reported that sport fish angler associations favored restricting allowable hook sizes because it promoted catch of larger and more valued species. In the catch-and-release era, gear restrictions could be enforced to reduce the captures of small fish, thereby reducing the catch event to population size ratio of a fishery, as well as the number of life time CR events individuals are exposed to. Such a regulation could reduce the opportunity for CR mortality to negatively affect population age and size structure.

The management of fishing effort could also be advantageously used to reduce the effects of CR mortality on fish populations. The management of fishing effort is a daunting task that will require creative solutions in an era where managers are seeking to retain and recruit anglers. This study and others have found that CR mortality rates are related to water temperature (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Edwards et al. 2004a; Cooke and Suski 2005; Gingerich et al. 2007; Hühn and Arlinghaus 2011; Danylchuck et al. 2014),

indicating that reducing effort during the warmest months of the year may have utility for reducing CR mortality (Edwards et al. 2004b, Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011). Alternatively, seasonal closures aimed at reducing effort could be lined up to co-occur during periods of high vulnerability or high importance to the population under management, e.g., during the spawning season (Kwak and Henry 1995; Cooke and Suski 2005). Finally, managers could strive to direct angler effort at particular populations within a region, in an effort to reduce effort at other populations in a region (Martin and Pope 2011). Populations targeted for increased effort could be chosen based on their characteristics, e.g., high productivity, large population size, the reputation of the fishery, or other management efforts such as stocking.

Improving the precision and accuracy of commonly collected fishery statistics should always be a goal of researchers and managers to increase understanding of the effects of recreational fishing on fish populations. In the catch-and-release era, improving precision of fishery parameters is especially important; in this study the catch event to population size ratio is a metric critical for estimating the effect of both harvest regulations and CR mortality on population size and age structure. This approach illustrates the opportunity for even low rates of CR mortality to compound across multiple capture events over multiple seasons to reduce the probability that an individual survives to an old age and large size, and has utility across a wide variety of recreationally targeted taxa. The catch event to population size ratio is a metric based on two notoriously imprecise fishery parameters: the number of catch events and the population size. In the current study, considerable variation in the possible true catch event to population size ratio existed across lakes and years (Table 3.2), resulting from considerable uncertainty associated with the population size and the total number of catch events. Therefore, management

in the catch-and-release era will need to be increasingly data-intensive in order to reduce uncertainty of critical parameters such as the number of catch events and population size.

In summary, the management of recreational fisheries in the catch-and-release era will require an increased understanding of the ratio of catch events to population size for a system, rates of CR mortality, and factors associated with CR mortality. Research and action to address these issues is needed, as CR mortality rates are expected to rise in response to climate change. Thirty-five years ago, slot limits and size structure ratios like PSD rose quickly to meet the challenges of recreational fisheries management. Today, the ubiquity of catch-and-release practices for some fisheries poses a challenge to the management of those recreational fisheries. A similar period of creativity, experimentation, and collaboration among researchers and managers is once again required to respond to the rise of highly efficient, species-specific fishing tactics and catch-and-release practices against a backdrop of a rapidly changing aquatic environment.

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Table 3.1. Population parameters to evaluate the effects of harvest regulations and CR mortality rates.

Parameter	Value	Definition	Reference
Linf	415	Asymptotic length	Hessenauer et al. (2014)
K	0.42	Growth coefficient	Hessenauer et al. (2014)
to	-0.61	Age at size-0	Hessenauer et al. (2014)
Z	0.37	Instantaneous mortality rate	Hessenauer et al. (2014)
50% V. Catch	250	Size at 50% vulnerability to catch	Dotson et al. (2013)
50% V. Harv	356, 406	Size at 50% vulnerability to harvest	
Ro	1000	Number of age-0 recruits	Dotson et al. (2013)
CR	15	Compensation ratio	Dotson et al. (2013)
Wmat	0.86	Weight at maturity	Dotson et al. (2013)

Table. 3.2. Summary statistics for two years of intensive monitoring at Gardner and Mansfield Lakes including a population estimate with 95% confidence interval (Pop Est), the number of tournaments monitored (N Tourn), the number of fish weighed in in tournaments (T Weigh-in), the number of fish reported culled by tournament anglers (T culled), the percentage of initial tournament mortalities (T mort), the percentage of tournament fish observed to be injured (T Injury), estimated number of fish captured and released with 95% confidence interval from creel surveys (Creel CR), estimated number of fish harvested with 95% confidence interval from creel surveys (Creel Harv), estimated total catch of Largemouth Bass (Est Tot Catch), and the catch to population size ratio with possible range based on variation associated with the population and catch estimates (Catch to Pop).

	Mansfield		Gardner	
	2012	2013	2013	2014
Pop Est	3100 (2100-4100)		2800 (1800-3800)	
N Tourn	24	21	31	30
T Weigh-in	958	894	1368	1397
T culled	634	743	1069	866
T Mort	2%	3%	2%	1%
T Injury	5%	4%	2%	5%
Creel CR	4600 (3400 - 5800)	4400 (3200 - 5600)	5500 (3900-7100)	4600 (3200-6000)
Creel Harv†	76 (5 - 150)	68 (1 - 200)	99 (3-260)	0
Est Tot Catch	6268	6105	8036	6863
Catch to Pop	2 [1.2 - 3.6]	2 [1.2 - 3.5]	2.9 [1.7 - 5.4]	2.5 [1.4 - 4.6]

†95% confidence intervals for harvest overlapped zero for all years. Therefore, the lower bound

was set as the number of harvest events observed by creel agents.

Table 3.3. Predicted proportional size distribution under three catch event to population size ratios (U_o), for four different catch-and-release mortality rates (D). Percent decline from the lowest catch-and-release mortality rate given in parentheses for each catch event to population size ratio.

U_o	D	PSD	PSD-P	PSD-M
1.0	0.001	37.5	13.4	1.9
	0.020	36.5 (3%)	12.7 (5%)	1.7 (11%)
	0.050	34.8 (7%)	11.3 (16%)	1.4 (26%)
	0.100	32.2 (14%)	9 (33%)	0.8 (58%)
2.0	0.001	37.5	13.4	1.9
	0.020	35.3 (6%)	11.7 (13%)	1.5 (21%)
	0.050	32.2 (14%)	9 (33%)	0.8 (58%)
	0.100	27.6 (26%)	5.9 (56%)	0.4 (79%)
3.0	0.001	37.1	13.2	1.9
	0.020	34.1 (8%)	10.6 (20%)	1.2 (37%)
	0.050	29.7 (20%)	7.1 (46%)	0.6 (68%)
	0.100	23.9 (36%)	3.9 (70%)	0.1 (95%)

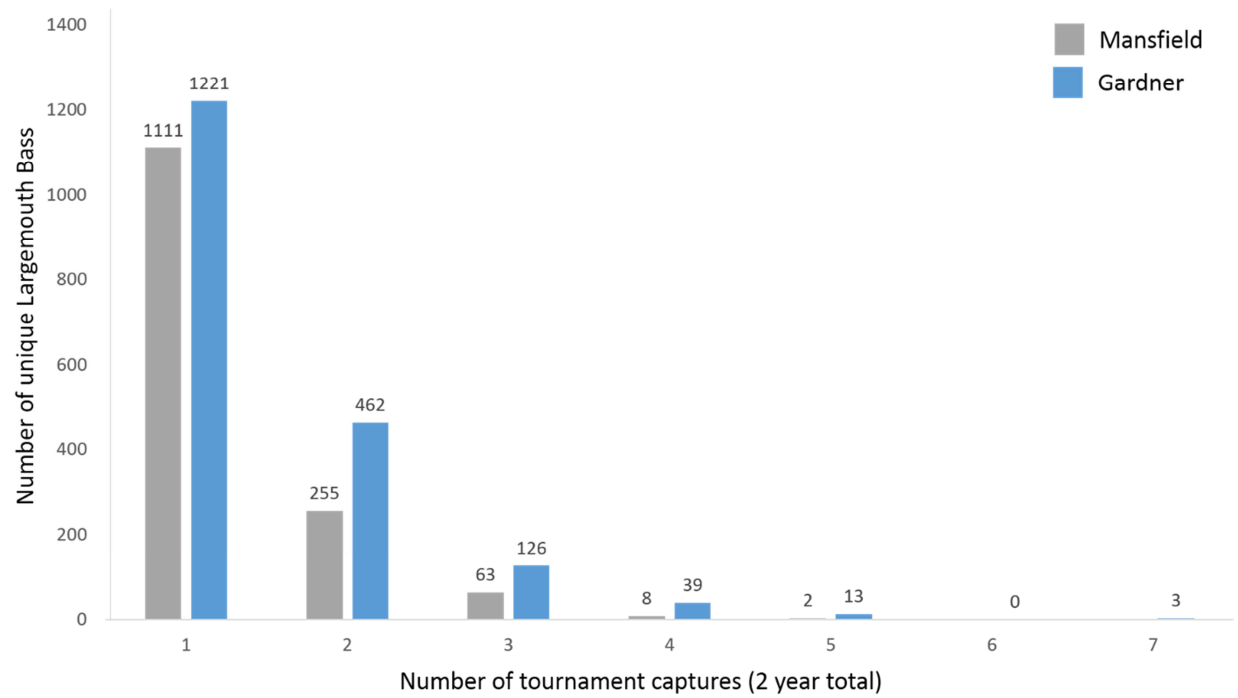


Figure 3.1. Capture histories of Largemouth Bass captured by tournament anglers in Mansfield Hollow Reservoir (Grey) and Gardner Lake (Blue).

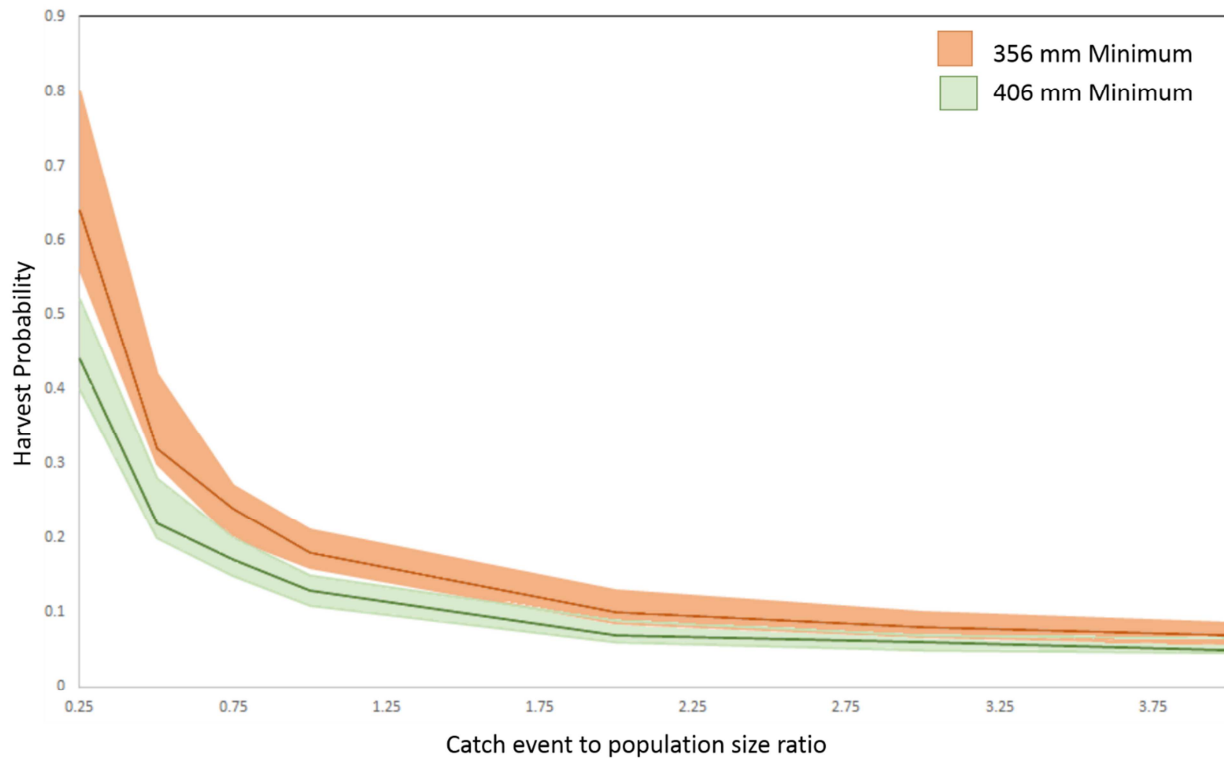


Figure 3.2. The harvest probability at which 356 mm and 406 mm minimum lengths are expected to affect population size and age structure with 95% probability (solid lines) given a catch to population size ratio. Shaded regions represent the harvest probability at which regulations will affect size and age structure with between 90 and 99% probability. Area below each curve represent harvest probabilities at which regulations are not expected to significantly affect size and age structure.

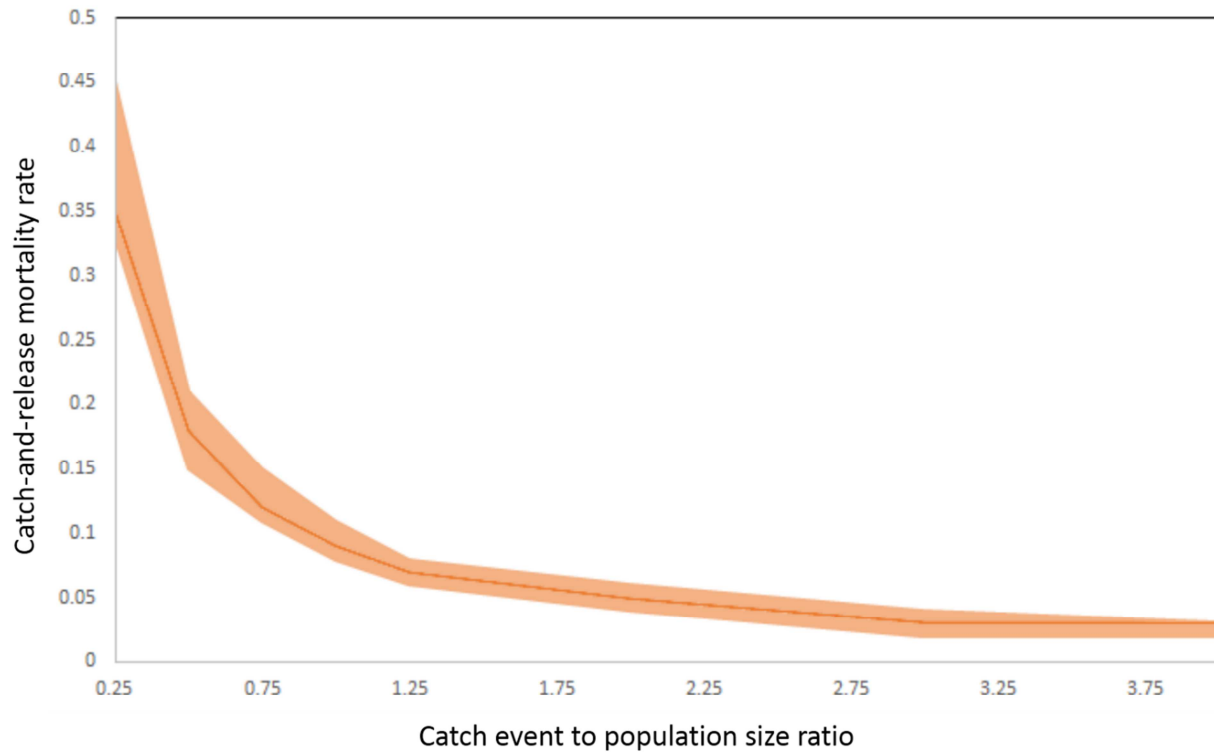


Figure 3.3. Catch-and-release mortality rate expected to significantly alter population age and size structure with 95% probability (solid line) for a given catch event to population size structure ratio. Shaded region represents the catch-and-release mortality rate expected to affect size and age structure with 90-99% probability. Area above the curve represents catch-and-release mortality rates that are expected to significantly affect age and size structure.

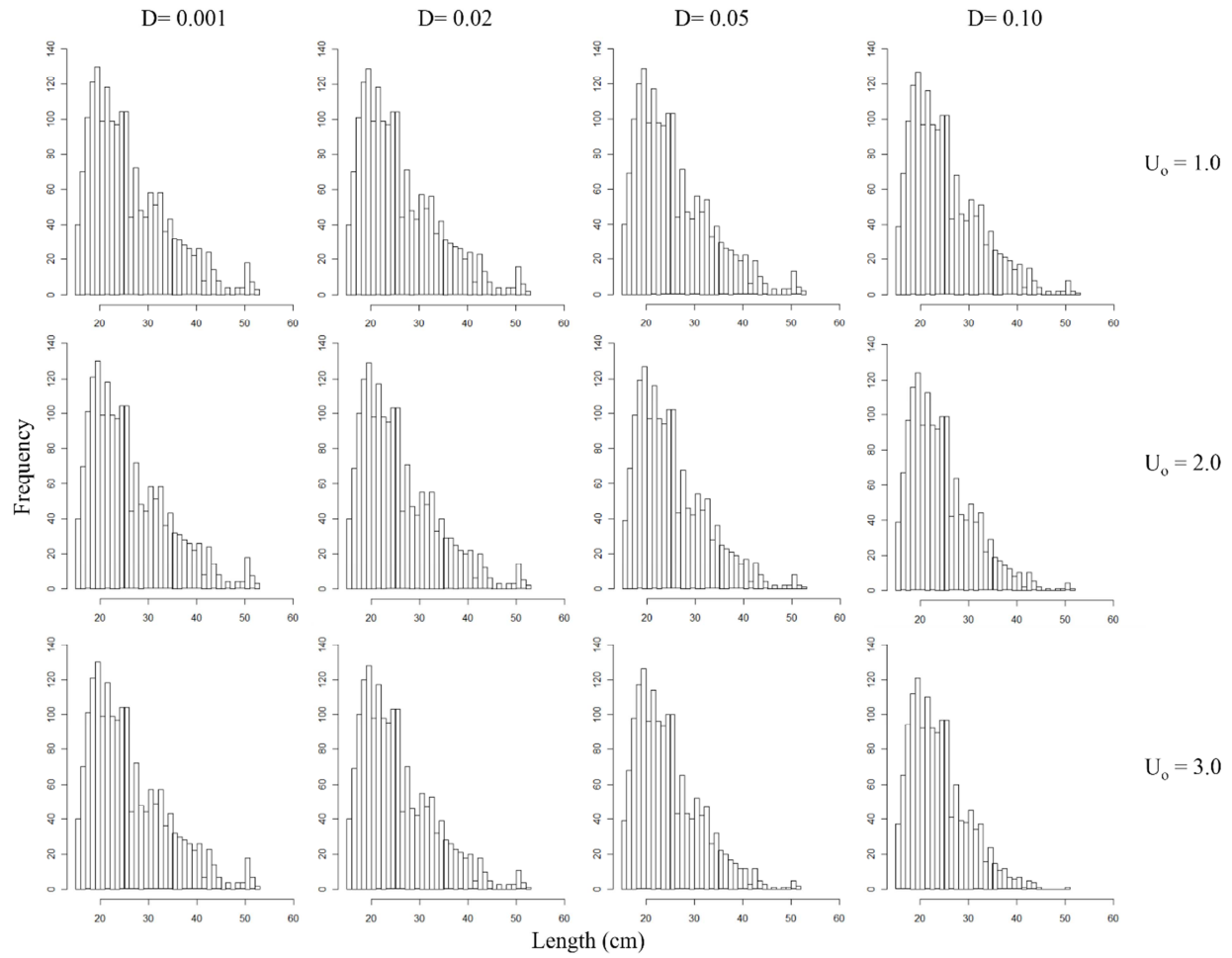


Figure 3.4. Changes in population size structure resulting from four different levels of catch-and-release mortality rates (D) modeled under three different catch event to population size ratios (U_o).