ANTICIPATING POSSIBLE EFFECTS OF ANGLER EFFORT LEVELS, WINTER SPEARING, AND CLIMATE CHANGE ON LAKE ST. CLAIR MUSKELLUNGE: A MODELING APPROACH

By

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ABSTRACT

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The current Lake St Clair Great Lakes Muskellunge (*Esox masquinongy*) (LSCM) fishery is entirely self-sustaining and dominated by a catch and release ethic. Catch rates of LSCM are among the highest of any waterbody, and "trophy fish" are relatively commonplace. The proximity of Lake St Clair to a large number of potential new Muskellunge anglers, angler interest in a winter spear fishery, and warming temperatures associated with climate change pose potential risks to the quality of this fishery. We developed an age-structured equilibrium yield model to predict the likely effects of increased angling effort, establishment of a winter spearing season, or warming temperatures on open-water catch rates of three size classes of LSCM (All fish, Legal fish > 42", Trophy fish > 50"). Our modeling indicated that the current high rate of voluntary release would largely buffer catch rates of all size classes of LSCM from substantial negative effects due to forseeable levels of increased fishing effort. Similarly, our simulation of a winter spearing fishery indicated that only high levels of spearing effort and harvest would negatively affect open-water catch rates to a degree that would be objectionable to anglers. However, the predicted catch rates of Legal and Trophy fish were highly sensitive to modeled reductions in growth due to climate warming. While our model predicts the LSCM fishery to be fairly insensitive to even substantial changes in angling effort and spearing harvest, possible effects of warming, which are difficult for fisheries managers to mitigate, could be significant.

For my family, especially Margaret, Nana, Papa, and Mitchell who allowed me the opportunity to follow this dream.

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Introduction

Lake St. Clair (LSC) has a long, rich and continuing history as a recreational Muskellunge (*Esox masquinongy*) fishery. Unlike other fisheries in which Muskellunge was a valued commercial species, commercial fishing for Muskellunge was banned in United States (U.S.) waters of LSC by around 1900 (Mike Thomas, Michigan Department of Natural Resources Fisheries Division, personal communication), and were not targeted or recorded in the Canadian commercial catch (although likely some were included in the northern pike reported catch) (Baldwin et al. 2009). This limited commercial take was likely a major factor in protecting the population from overexploitation in the late 1800s, allowing for the inception of the LSC recreational Muskellunge fishery.

Historic Lake St. Clair Muskellunge Fishery

The recreational fishery was popular by the 1880s, and consisted of both an open-water and through-the-ice hook and line fishery as well as a winter spearing fishery. The popularity of the open-water fishery grew after WWII with the increased availability of outboard motors (Mike Thomas, personal communication), and the winter spearing season was part of the winter Muskellunge fishery until 1973, at which point Muskellunge spearing was banned on LSC. Catch per unit effort (CPUE; catch per angler hour) for the open-water fishery was very low from the 1880s through at least 1960 (Williams 1961), likely similar to Muskellunge fisheries elsewhere. For example, creel reports in 1955 and 1956 indicate CPUE ranged from approximately 0.037 fish per angler hour for anglers fishing with guides to as low as 0.005 for anglers without guides (Williams 1961). Catch rates for the winter ice fishery are unknown. Before the 1970s, catch and release of legal size fish was uncommon and the majority of Lake

St. Clair Muskellunge (LSCM) greater than the minimum size limit (MSL) caught by anglers were harvested. Historic annual harvest data are scarce, but harvest has been estimated at several thousand fish per year in the 1950s, with winter spearing harvest making up a large proportion of that take (Williams 1961).

Current Lake St. Clair Muskellunge Fishery

Two factors, one cultural and one regulatory, began the shift from the historic catch and keep fishery to the current catch and release paradigm that predominates in the LSCM fishery today. The catch and release ethic began to take hold in the 1980s, increasing to almost 100% among current anglers who specifically target Muskellunge (Casselman et al. 1996; Margenau and Petchenik 2004; Kerr 2007; Kerr et al. 2009). Along with this changing angling ethic, LSCM regulations have become progressively more restrictive (Figure 1), partially as a response to the desires of Muskellunge angling groups. Minimum size limits have increased gradually from no minimum to the current 42" MSL, harvest limits have changed from an unlimited daily limit to one fish per year, and a closed season from December 15 to the 1st Saturday in June has been established. The decreased harvest resulting from these cultural and regulatory changes has resulted in the rare combination of high catch rates and relatively frequent catches of trophy fish. Recent catch rates for Muskellunge in LSC range from 0.069 to 0.117 fish per angler hour (Thomas and Haas 2004) and are among the highest Muskellunge catch rates reported for any waterbody (Kerr et al. 2009). Further, catches of fish greater than 50" fish, a commonly held trophy goal, are relatively commonplace (Mike Thomas, personal communication). The LSCM fishery is considered a success story not only because of high Muskellunge catch rates and trophy size structure, but also because this native species fishery has been sustained without the aid of stocking.

Lake St. Clair

Lake St. Clair is a large shallow lake that is part of the connecting waters between Lake Huron and Lake Erie (Figure 2). It is located near the southern extent of the native distribution of Great Lakes Muskellunge (Figure 3; Karvelis 1965). The lake has a surface area of approximately 1110 km^2, an average depth of 3m, and a maximum natural depth of 6.4m. Because of LSC's shallow bathymetry (Figure 4) and abundant areas with macrophyte growth, nearly the entire lake is favorable, and inhabited, Muskellunge habitat. Also due to its shallow bathymetry and large fetch, LSC does not thermally stratify and is the warmest of the Great Lakes or connecting waters (GLIN 2014). Average daily water temperature are within the range associated with Muskellunge growth for much of the year (Bevelhimer et al. 1985), and currently seldom exceed 25.6^{o} C (Figure 5), the temperature associated with maximum growth in Muskellunge (Scott and Crossman 1973; Bevelhimer et al. 1985). Lake St. Clair, like most of the Laurentien Great Lakes, includes both U.S.and Canadian waters (Figure 4). United States waters make up approximately one third of this area (Haas 1978).The Detroit metropolitan area bounds the U.S. shoreline of the lake, allowing easy access for large numbers of potential new anglers. In fact, four million people live within a one hour drive of LSC (Thomas and Haas 2005), and fishing effort on LSC, nearly 2,000,000 angler hours per year (Haas et al. 1985) makes up nearly one quarter of the total Michigan Great Lakes fishing effort (Jamsen 1985). Muskellunge anglers account for approximately 3% of LSC angling effort and are an active, vocal, and growing stakeholder group.

Potential Challenges to Lake St. Clair Muskellunge Fishery

The current LSCM fishery is viewed as a major fisheries management success; however, three potential factors could threaten the success of this fishery. First, the likely magnitude of effects of increased fishing effort on the LSCM fishery are unknown. Second, in addition to open-water angling, a second stakeholder group has voiced interest in re-opening the winter Muskellunge spearing season. This raises challenges for managers both in predicting the effects of a spearing season and in determining how to allocate a valuable resource between two stakeholder groups. Third, the potential effects of increased water temperatures due to Global Climate Change (GCC) on the fishery are uncertain, and to date, have not been investigated.

Increased angling effort and its associated increased fishing mortality was the first potential threat to the LSCM fishery that we identified. The proximity of LSC to nearly 4,000,000 potential anglers makes increased angling effort a distinct possibility. Anglers who specifically target LSCM have an estimated voluntary catch and release rate that approaches 100% (Kerr 2007, Thomas and Haas 2004), similar to rates found in other Muskellunge fisheries, and therefore mortality resulting from harvest is quite low. However, the effects of increased angling effort on fishing mortality may be underestimated in fisheries like the LSCM which are predominated by a catch and release ethic. While Muskellunge-specific anglers tend to practice high rates of catch and release, a recent study of Wisconsin generalist anglers revealed voluntary catch and release rates could be as low as 58% (Margenau and Petchenik 2004). Additionally, hooking mortality, while not well quantified in the literature, is a significant source of fishing mortality in this fishery that would increase with increased effort.

Resource managers are tasked not only with managing the LSCM fishery for open-water anglers, both those specifically targeting Muskellunge and generalist anglers, but also must address another stakeholder group, the Michigan Darkhouse Angling Association, whose members have argued for regulatory change allowing Muskellunge spearing through the ice on LSC. Spearing is presently allowed on most Michigan Muskellunge waters, and was historically allowed on LSC, but was banned in the U.S. waters of LSC mid 1960s. The post-spearing time period has coincided with an increase in LSCM abundance and CPUE (Mike Thomas, personal communication). While a winter spearing season would certainly increase mortality of LSCM, the magnitude of the effect is uncertain in part because both likely winter spearing effort and success are unknown. The potential spearing season on LSC not only raises challenges for managers in terms of estimating the likely biological effects of such a fishery, but also in terms of fairly allocating a valuable resource between stakeholder groups.

In addition to these potential fishery-related challenges, warmer water due to GCC could negatively affect growth rates of LSCM, a population likely already at the upper edge of its optimal temperature range. While climate predictions specifically for LSC are not described in the literature, Lofgren et al. (2002) assumed predictions for increases in average air temperature between 0.9^{o} C and 3.4^{o} C over the next 15 to 30 years for the Lake Erie basin. Two mechanisms could cause warmer water temperatures to negatively affect Muskellunge growth. Currently, LSC water temperatures seldom exceed the optimal temperature for Muskellunge growth. If climate change causes maximum summer temperatures to exceed the optimal temperatures for Muskellunge, growth rates for LSCM may decrease. Similarly, if LSCM consumption rates are governed by successful predator/prey interaction and not by metabolic limits, it is likely that increased metabolic demand for nutrients due to increased average daily water temperatures (even below optimal temperature) would not be met by consumption, and growth of LSCM would decrease. Decreased growth due to warming may cause significant changes to LSCM size structure, and result in decreased catch rates of large fish regardless of regulations or angling culture.

Challenges To Managers

While fisheries managers and stakeholders alike generally recognize the negative impacts of overfishing in commercial fishing, overfishing has not, until recently, been widely studied or implicated in fisheries dominated by recreational fishing (Lewin et al. 2006). In fact, many anglers and some managers do not believe that angling can have a significant effect on fish demographics (McPhee et al. 2002; Lewin et al. 2006). Rather, recreational fishing has often been thought of as a self-regulating system. Self-regulation theory states that as angler satisfaction declines, possibly from depleted fish populations and decreased catch rates, anglers will either choose to not fish, or to fish other waterbodies, thus allowing overexploited fish populations to recover (Hansen et al. 2000; Johnson and Carpenter 1994). Self-regulation assumes: (1) that anglers have alternatives to either fishing location or angling itself, and (2) that anglers would be willing to choose these alternatives when fish populations have been depleted. If catch is the overwhelming factor in angler satisfaction, anglers may behave in this fashion and choose alternative waterbodies or activities. If, however, angler satisfaction includes variables such as tradition, proximity, ease of access, and the act of angling, anglers may be reluctant to change either location or activity in response to decreasing catch, making self-regulation less likely than originally thought. Further, self-regulation assumes that fish populations overexploited through recreational angling have the ability to recover when fishing is reduced.

However, if commercial fishing can lower a population's resilience (Anderson et al. 2008), it seems plausible that the same would be true of a fish population that is overexploited by anglers. At the least, the violation of either of these two assumptions would lead to the possibility that self-regulation would not occur in all recreational fisheries.

Recent studies suggest that angling can cause changes in fish population demographics similar to those that have been attributed to commercial fishing. Compensatory effects such as decreased age/size at maturity and maximum size, as well as non-compensatory effects such as reduced reproductive success have been attributed to angling (Beard and Essington 2000), with the magnitude of the effect increasing with proximity to human population centers (Post et al. 2002). Examples of angling effects range from significantly decreasing the size structure of centrarchid populations in Wisconsin (Goedde and Coble 1981) to the suspected collapse of certain Canadian salmonid, percid and escocid fisheries (Post et al. 2002). However, the complexity of fisheries make it challenging to ascertain the specific circumstances in which the effects of angling on fish population demographics are likely to be negative and significant. Fish life history traits, waterbody characteristics, and angling effort and practices determine the magnitude of the effect fishing exerts on fish population demographics (Beard and Essington 2000; Post et al. 2002; Young et al. 2006), and therefore must all be considered when investigating the efficacy of fishing regulations.

Using regulations to manage the effects of angling on fisheries in the U.S. is challenging in part because the tradition of open access means that managers are often restricted to regulating which species can be targeted, when and how the fishing can occur, and the size and number of individuals that can be harvested, with little control over the number of people who participate in the fishery. Minimum size limits and bag limits are often ineffective at mitigating the effects of anglers on a fishery (Tomcko and Pierce 2005) in part due to uncertainty about (and lack of control over) factors such as angler effort levels, compliance and catch and release of fish greater than the MSL. Further, focus on angler harvest can overlook the non-harvest effects anglers have on a fishery. In particular, hooking mortality can be a major component of total fishing mortality, especially in long-lived fishes and in fisheries with high levels of catch and release (Landsman 2011).

The challenging nature of managing recreational fisheries, including the LSCM fishery, necessitates use of an evaluative tool that is flexible, cost effective, and predictive. Modeling is a tool that can not only predict possible effects of fishing and other stressors on fish population demographics (Radomski and Goeman 1996), but also help managers learn more about the fisheries they manage (Johnson 1995). Many models are flexible and can be parameterized relatively easily to investigate potential effects in a wide variety of species and waterbodies given changes in regulations, angling behavior, and environmental conditions. Management agencies often collect large quantities of data, but often are unable to fully utilize and synthesize all of this information. Models are tools that allow the pooling of these data into a predictive framework that can then provide relatively quick and economical evaluations of numerous 'what if' scenarios. For these reasons, modeling can be a critical component in a successful fishery management plan.

Objective

Our objective, which aligned well with the goals of the Michigan Department of Natural Resources Fisheries Division (MDNR), was to predict the magnitude of change to both catch rates and size composition of the LSCM fishery catch due to (1) increased angling effort, (2) establishment of a LSCM winter spearing season, including a comparison of the predicted effects of increased mortality from angling versus spearing, and (3) decreased growth due to GCC-induced warming. To accomplish our objective, we used an age-structured equilibrium yield model to investigate potential changes to the age/size structure and abundance of the LSCM population, as well as the associated change in open-water catch rates, due to increased effort, a winter spearing season, or decreased growth due to increasing average daily water temperatures. Our model predictions can be used to inform managers in the challenging work of protecting both the abundance and sized structure of fish that make LSC a unique Muskellunge fishery.

Methods

Initial Parameters Of The Age Structured Model

The model representing the LSCM fishery, allowed for (1) variable harvest modes (angling and spearing) and levels and (2) altered size at age due to warming, and was used to estimate effects on abundance and size composition of the LSCM population as well as the catch rates predicted from them. The parameters governing our LSCM model included annual recruitment (R), angling catchability (q_a), spearing catchability (q_s), angling effort (E_a), spearing effort (E_s), hooking mortality (H), voluntary release (r), minimum size limit (MSL), instantaneous natural mortality (M) and the associated value for annual natural survival (S_a), as well as the age-specific parameter selectivity (s_a) (Table 1). We estimated initial values for each of these parameters (Table 1) using various sources in the literature as described below.

The stock/recruit relationship for LSC is unknown, but there is little evidence of missing, extremely large, or extremely small year classes (Mike Thomas, personal communication) over the past decade. Therefore, we assumed annual recruitment for this model to be constant, and determined the value through an iterative process during model calibration. Angling catchability, the proportion of the population caught per unit of effort, is not known for the LSCM fishery, nor is it well described for any other Muskellunge fisheries. For this model, we set catchability, the proportion of the population caught per hour of angling effort, at 0.00000225. We calculated this value from an approximate average of a range of likely Muskellunge CPUE values (Thomas and Haas 2004; Kerr 2007; Kerr et al. 2009;) and population estimates (Cornelius and Margenau 1999) taken from the literature. Values for Muskellunge catchability for winter spearing gear are even less certain than for open-water angling gear. Therefore, we set q_s, the proportion of the population caught per hour of spearing effort, equal to angling q at 0.00000225. The most recent estimate of LSCM angling effort was reported to be 63,700 angler hours annually (Thomas and Towns 2011) and we set this as the nominal value for effort in our simulations. At present, no winter spearing season for Muskellunge exists on LSC; therefore, the nominal level for the spearing effort parameter was set at 0.0. Hooking mortality was set at 0.075 (7.5% mortality rate for released fish) which was an approximate average of the values found in the literature (Burkholder 1992; Ostrand et al. 2006; Arlinghaus et al. 2008A, 2008b; Arlinghaus et al. 2009; Landsman et al. 2011). Although data on the voluntary release of fish longer than the MSL are scarce, many have reported values greater than or equal to 0.95 for anglers targeting Muskellunge (Fayram 2003; Margenau and Petchenik 2004; Kerr 2007; Younk and Pereira 2007, Mike Thomas, personal communication). LSCM are currently subject to a 42” MSL.

Because estimates of Muskellunge natural mortality are not well estimated in the literature,we initially estimated natural mortality using the equation

$$\log M = -0.0066 - 0.279\log L_{inf} + 0.6543\log K + 0.04634\log T \qquad \text{(Equation 1; Pauly 1980)}$$

where Linf is the asymptotic length, K is the von Bertalanffy growth coefficient, and T is the average yearly water temperature. Using estimates of Linf and K for LSCM (Casselman et al. 1999), and LSC average daily water temperature data (Fisheries and Oceans Canada, unpublished data),we initially estimated instantaneous natural mortality to be 0.292. Analysis of Ontario Angler Diary data led us to set selectivity at 1.0 (fully selected) for all ages greater than age 2. Values for selectivity for cohorts age 2 and younger were calculated by dividing the proportion of the catch of each of these age groups by the expected proportion in the population in the respective age classes (Table 1).

Population Dynamics

Basic cohort dynamics were governed by the equation

$$N_{t+1,\ age+1} = N_{t,\ age}\, e^{-(F + M)} \qquad \text{(Equation 2)}$$

where F is instantaneous fishing mortality and M is instantaneous natural mortality. The sum of angling mortality (F_a) and spearing mortality (F_s) was total fishing mortality.

$$F = F_a + F_s \qquad \text{(Equation 3)}$$

We represented angling mortality as the product of angling intensity (I_a) and the proportion of LSCM vulnerable to fishing mortality (V_a).

$$F_a = I_a * V_a \qquad \text{(Equation 4)}$$

Angling intensity is a function of effort, selectivity, and catchability

$$I_a = E_a * s_a * q_a \qquad \text{(Equation 5)}$$

We calculated the proportion of LSCM vulnerable to angling as the sum of three components, hooking mortality rates on fish below the MSL limit ($HM_{<MSL}$), hooking mortality rates on fish

equal to or greater than the MSL ($HM_{>MSL}$), and angling harvest rates (h_a)

$V_a = (HM_{<MSL} + HM_{>MSL} + h_a)$ (Equation 6)

$HM_{<MSL} = (1\text{-proportion of population greater than MSL}) * H$ (Equation 7)

$HM_{>MSL} = (\text{proportion of population greater than MSL} * H * r)$ (Equation 8)

$h_a = \text{proportion of population greater than MSL} * (1 - r)$ (Equation 9)

Similar to angling mortality, we represented spearing mortality as the product of spearing intensity (I_s) and the proportion of LSCM vulnerable to spearing (V_s)

$F_s = I_s * V_s$ (Equation 10)

$I_s = E_s * q_s$ (Equation 11)

$V_s = \text{proportion of population greater than MSL}$ (Equation 12)

Because harvest limits are size based, we represented each cohort as a normal distribution with a mean length following a von Bertalanffy curve and a specified standard deviation (Fournier et al. 1998). We calculated the mean lengths at age and standard deviations for each age class, as presented in Table 2, by combining MDNR and Ontario Ministry of Natural Resources (OMNR) data along with data from the Ontario Angler Diary Program. For a given MSL (42"), we determined the proportion of a cohort above that size by integrating the normal distribution from a length of 0 inches up to the MSL using the normdist function in Excel (Table 2).

Model Calibration

We calibrated the model iteratively using three LSCM fishery metrics (size composition of the catch, total catch, and population abundance) as measures of model fit. To reduce the discrepancy between predicted and reported size composition of the catch, we adjusted three of the least well known model parameters (catchability, selectivity, and natural mortality) using the log-likelihood equation

$$L = \Sigma \text{ (Observed * Log(Predicted))} \qquad \text{(Equation 12; Sitar et al. 1999)}$$

We used Solver in Excel to minimize the log-likelihood equation by first adjusting catchability, followed by selectivity, and finally natural mortality. Adjusting catchability, in an effort to minimize the difference between predicted and reported catch, did not improve model fit. Therefore, model fitting resulted from adjusting selectivity and natural mortality only. The model parameter for recruitment, which we assumed constant for the model, was used to scale the model to target levels of total catch and population abundance.

Bioenergetics Model

We used a spreadsheet model based on the Fish Bioenergetics 3.0 model calibrated for Muskellunge to investigate potential changes in LSCM growth due to a warming climate. Bioenergetics models use inputs of growth, temperature, and diet; if any two of these factors are known, we can use the model to predict the unknown one. We parameterized the model using average daily surface water temperatures from a single location over the time of May 2000 to November 2013 (Fisheries and Oceans Canada, unpublished data), and current LSCM length at age (inches), converted to weight at age (grams; data are a subset of Angler Diary, MDNR trap net, and OMNR trap net data that included length and weight) by the following equation

$$\text{Log W} = 3.22 * \text{Log L} - 3.01 \ (p < 0.0001 \text{ and } r^2 = 0.943) \qquad \text{(Equation 13)}$$

to estimate LSCM consumption by age (grams/year).

We modeled two separate warming scenarios within the range of many common climate model predictions (increases in average daily temperatures of 1^{o} C and 3^{o} C) (Blumberg and Di

Toro 1990; Hengeveld 1990; Lofgren et al. 2002; Sousounis and Grover 2002) while keeping the model parameter consumption unchanged at the current estimated value. We assumed future decreases in duration of ice cover on LSC due to GCC to be similar to that described by Lofgren et al. (2002) for the western basin of Lake Erie. All average daily water temperatures during dates when ice cover (NOAA data) was predicted to be greater than or equal to 10% were assumed equal to 4^{o}C. All days for which total lake lake-wide ice cover averaged less than 10% were subject to increased temperatures (Figure 5). As changes in growth due to warming temperatures were modeled under the assumption that yearly consumption by LSCM would remain unchanged from the nominal value, the effects of increased temperature on energetic costs was the dominant factor evaluated.

Model Simulations

We used our age structured model to investigate potential changes in the LSCM population abundance and size structure. As absolute population abundance levels are much more uncertain than fishery catch rates, we investigated possible changes via CPUE, as is traditional, as well as its reciprocal, time required to catch one Muskellunge (TRCOM) as this measure is relevant to anglers. In our model, population abundance directly determines catch rates; therefore, catch rates (by size) can be used to infer changes to population abundance and size composition. Response of the LSCM fishery was evaluated for three size classes; fish of all size classes (All), fish longer than the 42” MSL (Legal), and fish longer than 50” (Trophy).

We modeled three distinct changes in the LSCM fishery: changes in angling effort (scenario one), establishment of a spearing season (scenario two), and changes in growth due to a warming climate (scenario three). In scenario one, we modeled changes in angling effort from zero to

254,800 (4X current effort), in steps of 31,850 angler hours (0.5X current effort). Spearing effort and mortality were zero in this simulation to reflect current LSCM regulations. In scenario two, we modeled potential effects of a LSCM winter spearing season. We used spearing harvest instead of spearing effort in this simulation due to the lack of literature on Muskellunge spearing catchability and the uncertainty over possible levels of spearing effort. Angling effort was kept at its nominal value of 63,700 angler hours, and we modeled the effects of spearing harvest on open-water catch rates from levels of spearing harvest ranging from zero (current level) to 3,000 fish per year (1.5X the most recent estimate of historic LSCM spearing harvest, 2,000 fish; Bob Haas Michigan Department of Natural Resources Fisheries Division (retired), personal communication). The challenge managers face in allocating resources led us to model a comparison of the effects of equal levels of angling and spearing mortality. In this comparison, all simulations started with angling effort at the nominal (current) level and spearing effort equal to zero. First, we increased levels of angling mortality from zero to 3000, in intervals of 250. We returned angling effort to its nominal value and increased spearing mortality as before. We then compared the effects of these equal levels of increased fishing mortality on the open-water fishery. In our third scenario, we investigated possible changes in the LSCM fishery due to potential changes in growth caused by GCC. We modeled changes in growth as predicted by our bioenergetics model relating to temperature increases of 1^{o} C and 3^{o} C. In these scenarios, all model parameters were returned to their nominal value (Table 1), and nominal values of mean size at age were replaced with sizes predicted from our bioenergetics model.

Model Sensitivity

We performed both a local and broad sensitivity analysis on several model parameters including hooking mortality, voluntary release, annual natural survival, and recruitment as these parameters had values that were among the most uncertain. Local sensitivities were defined as +/- 10% of the nominal parameter value while broad sensitivities were defined as +/- 30% of the nominal value. We calculated model sensitivity (E)

$$E = ((R_a - R_n) / R_n) / ((P_a - P_n) / P_n)$$

(Equation 14) where R_a was the model result using the altered parameter, R_n was the model result using the nominal parameter, P_a is the altered parameter value and P_n is the nominal parameter value. This form of sensitivity is known as elasticity (E) (Caswell 2000). The values for negative and positive perturbations were averaged both in the local and broad sensitivity analysis. Parameters with values for E less than 1 are considered insensitive, while parameters with values equal to 1 are linear, and those with values greater than 1 are sensitive parameters.

Results

Model Calibration

Based on Angler Diary data, the greatest proportion of reported catch was in the 33”-42” length category (Table 3). These fish are below the MSL of 42” and are therefore not vulnerable to harvest. The next greatest proportion of catch was made up of fish from 42” to 50” in length (Table 3). Fish of this length are greater than the MSL and therefore vulnerable to harvest. Small fish, those under 33” represented 21% of the total catch and at the other end, Trophy fish, those over 50” in length, made up just over 10% of the catch (Table 3). Overall, the calibrated model's predictions at equilibrium closely matched the size composition of the catch as reported in Angler Diary data (Figure 6). The model-predicted catch proportions only deviated from the observed catch substantially (greater than 25%) in 4 out of 12 length bins (Table 3). While the difference between the predicted and observed proportion of catch was noticeable for some individual length bins, these discrepancies largely disappear in the cumulative size frequency (Table 4, Figure 7). It seems likely that much of the remaining discrepancy between observed and predicted proportions is the result of variability in the observed catch due to varying year class strength, growth rates, and sampling variability, whereas model predictions are under equilibrium conditions. In all, the degree of concordance between observed and predicted catch proportions leads us to believe that the calibrated model is a reasonable representation of the LSCM fishery.

We used estimates of total population abundance and total catch to scale the model. Although creel estimate data are scarce for the LSCM fishery, we used a rough estimate of greater than 10,000 fish caught per year in U.S. waters of the lake (Mike Thomas personal communication). We derived an estimated range of total population abundance of 46,000 to 92,000 by multiplying likely density of LSCM greater than 30" (0.5 to 1.0 fish > 30"/acre; Cornelius and Margenau 1999) by the area of U.S. waters of LSC (92,000 acres). We used annual recruitment (assumed constant) to scale the model, and using an iterative process, selected a level of 20,000 fish per year (Table 1) which resulted in predicted annual catch of 12,052 fish and a total population of fish greater than 30" of 70,296 fish.

Predicted Effects of Increased Angling Effort

Predicted response of the fishery to increased angling effort varied in magnitude across the three LSCM size classes, with larger effects on catch, CPUE, and TRCOM for larger size classes of Muskellunge, especially at levels of effort greater than two times the current level (Figure 8). Predicted catch of All LSCM increased with effort nearly linearly at all modeled levels of effort.

However, the predicted response of total catch of Legal and Trophy fish became noticeably non-linear at effort levels greater than approximately120,000 (2X current) angler hours (Figure 8C). At effort levels twice the current levels, predicted CPUE for All fish only decreased from 0.189 fish per angler hour to 0.177 fish per angler hour, approximately a 6% decline (Table 5). The corresponding TRCOM estimate increased from 5.3 hours to 5.6 hours (Table 5). Even at effort levels 4 times the current level, CPUE only decreased to 0.158 and TRCOM increased only to 6.3 angler hours (Table 5), representing an approximately 17% response to the modeled 4-fold increase in angling effort. Predicted catch per unit effort of Legal LSCM responded similarly in direction, but with a slightly larger magnitude, to modeled changes in angling effort. Predicted CPUE of Legal size fish declined from 0.055 fish per angler hour to 0.048 (-12%) with a doubling of angling effort, and to 0.038 (-31%) when effort was increased 4 fold (Table 5). These results translate into nearly 2.5 more hours of fishing, from 18.2 to 20.6, needed to catch a Legal Muskellunge under a scenario of doubled effort and an even greater increase of almost 8 angling hours when modeled total effort increased to 4 times the current level (Table 5). Of the three size classes of fish, catch per unit effort of Trophy fish was most affected by increasing angler effort, and at very high levels of effort, the predicted response of CPUE for Trophy LSCM became non-linear. When angling effort was doubled, the model predicted that CPUE of Trophy LSCM would decrease from 0.0028 to 0.0023 (-15%) and would decrease disproportionately more to 0.0017 (-39%) if effort was quadrupled (Table 5). These results translated into a predicted increase in TRCOM of more than one third, from 363.6 hours to 429.9 hours at twice the current effort and a near doubling of TRCOM to 591.3 hours when effort increased 4 fold (Table 5).

Predicted Effects of a Winter Spearing Season

As the relationship between spearing effort and spearing mortality is unknown for LSC, we altered harvest, rather than effort as in the previous scenario, to predict effects of a winter spearing season on catch, CPUE, and TRCOM of the open-water angling season. The predicted effects due to a Muskellunge spearing season generally paralleled the effects of increased angling effort, with spearing harvest leading to decreased angling catch and CPUE and increased TRCOM, particularly for large fish (Figure 9). With the exception of TRCOM for Legal and Trophy fish, the response of the LSCM fishery was linear. The TRCOM for both Legal and Trophy fish began to appear non-linear as harvest approached and exceeded 2,000 fish (Figure 9B). The negative effect of a winter spearing season on open-water total catch appeared linear over all modeled levels of spearing mortality (Figure 9C). Using an historic spearing harvest estimate of 2,000 fish (Bob Haas, personal communication) as a reference point, angling CPUE of All fish was predicted to drop from 0.189 to 0.165, a 13% decline from nominal conditions (Table 6). Under this scenario, the predicted TRCOM increased only slightly from the current time of 5.3 hours to 6.1 hours (Table 6). Similarly, CPUE of Legal and Trophy fish were predicted to drop from 0.055 to 0.038 and from 0.0028 to 0.0015, respectively (Table 6). These declines were approximately 31% for Legal size fish, and 43% for Trophy Muskellunge. The time required for the average open-water angler targeting Muskellunge on LSC to land one Legal fish was predicted to increase from 18.2 hours currently to 26.3 hours if spearing harvest returned to historic levels (Table 6). An even more substantial increase in TRCOM, from 363.6 hours to 666.7 hours, was predicted to be needed for anglers to catch a Trophy fish at this level of spearing harvest (Table 6).

Comparison of Open-Water Fishing Mortality to Winter Spear Fishing Mortality

In order to compare the possible effects of angling and spearing mortality on the open-water LSCM fishery, we modeled the effects of increased fishing mortality above current estimated levels (1,066 fish per year; harvest of 175 fish and hooking mortality of 891 fish) from either spearing or increased open-water angling on the open-water Muskellunge fishery. For each form of fishing mortality (angling and spearing), we conducted simulations in which fishing mortality from the manipulated form of fishing ranged 0 to 2,000 fish above the current level of mortality. Equal levels of additional mortality, due to either angling or spearing, were predicted to have similar effects on open-water CPUE of All fish (Figure 10A). Even near the higher bounds of our simulation, the historic spearing harvest level of 2,000 fish, the predicted open-water CPUE for All LSCM only decreased from its current value of 0.189 to 0.163 (-14%) or 0.165 (-14%) due to angling or spearing mortality, respectively (Table 7). However, increased mortality due to spearing had a greater predicted effect on angling CPUE for Legal and Trophy fish than did an equal level of increased mortality from open-water anglers (Figure 10A). An increase in open-water angling mortality of 2,000 fish was predicted to reduce open-water CPUE of Legal fish from 0.055 to 0.041 (-25%), resulting in anglers requiring an extra 6.3 hours to catch a Legal Muskellunge (Table 7). However, if added mortality were due to winter spearing harvest, the model predicted that CPUE would decrease to 0.038 (-31%) and TRCOM would increase by nearly 8 hours to slightly over 26 hours (Table 7). Model predictions for Trophy fish revealed an even larger difference between the effects of equal levels of fishing or spearing mortality on open-water CPUE (Table 7). An increase in fishing mortality of 2,000 fish was predicted to decrease CPUE of Trophy fish from 0.0028 to 0.0019 (-32%) if mortality was from angling, and to 0.0015 (-46%) if mortality was due to spearing (Table 7). The corresponding TRCOM for Trophy fish increased from its current value of 363.6 hours, to 537.6 hours and 653.9 hours for mortality resulting from angling and spearing, respectively (Table 7).

Predicted Changes in Growth Due to Potential Warming Temperatures

Bioenergetics modeling of Muskellunge growth predicted slower growth and smaller size at age at all ages when average daily water temperatures were increased by either 1^{o} C or 3^{o} C (Figure 11) and average annual consumption (g/year) remained unchanged. While the impact of slowed growth due to warming temperatures on length accumulates with age, the magnitude of change on both mean length at age and asymptotic length (Linf) predicted by our bioenergetics model appears minor (Figure 11). The current Linf for LSCM is 45.2” and the bioenergetics model predicted a modest decrease in Linf of 0.86” to 44.3” in response to a 1^{o} C rise in water temperature, and somewhat larger decline of 1.70” to 42.6” in response to a 3^{o} C degree temperature increase.

Although the predicted reductions in average LSCM size may seem modest, the effect of these relatively small decreases in Linf could have substantial effects on the proportion of LSCM greater than the MSL and especially the proportion of fish greater than trophy length (Figure 12). On average, LSCM currently reach the MSL at age 8, with some fish reaching this length as young as age 4 (Figure 12A). As Linf is less than trophy length, it is only fish greater than one standard deviation above the mean that reach trophy size, typically at age 15 (although the fastest growers may reach this length by age 8) (Figure 12A). Under the 1^{o} C warming scenario, the average LSCM does not reach the MSL until age 9, with fish two standard deviations above the mean reaching the MSL by age 5 (Figure 12B). The effects were even more pronounced when

3° C warming was modeled. In this case, the average LSCM does not reach the MSL until age 12 and only fish greater than two standard deviations above the mean ever make it to trophy length (Figure 12C).

Fishery Effects of Predicted Decreased Growth Due to Warming

Although the predicted changes in mean length at age and Linf due to warming appeared fairly small, they had a substantial effect on the output of the age-structured model. Changes in response of the fishery were greater for larger warming scenarios and larger size classes of fish. In fact, predicted total catch and CPUE for All fish actually increased a negligible amount under each of the two warming simulations (Table 8). However, predicted total catch of Legal Muskellunge decreased by 38% and 58% under warming scenarios of 1° C and 3° C (Table 8). The predicted reductions in total catch of Trophy fish were even more striking, declining by 41% and 82% under the same modeled warming (Table 8). Similarly, predicted CPUE for Legal fish decreased under each warming scenario. Predicted CPUE for Legal LSCM decreased from its current value of 0.055 to 0.048 (-13%) and 0.034 (-38%), under modeled warning scenarios of 1° C and 3° C (Table 8). The decrease in CPUE was even more dramatic for Trophy LSCM. Predicted CPUE for Trophy size LSCM under current conditions was 0.0028 and was predicted to decrease to 0.0016 (-42%) and 0.0005 (-82%) under the two warming scenarios (Table 8).

The predicted TRCOM illustrates the effects of the small predicted change in average growth due to warming more clearly than does CPUE. While the model predicts that warming would have almost no effect on TRCOM for All Muskellunge, it predicted a rather substantial increase on the time needed to catch Legal and certainly on Trophy fish. Anglers who currently fish approximately 18 hours to catch a Legal fish were predicted to need an increase in effort of

2.5 hours if average daily water temperatures increase by 1^{o} C and 11 hours if the increase is 3^{o} C. Time required to land a Trophy fish was even more sensitive to increases in mean water temperature. Our model predicted that catching a Muskellunge over 50” in the current LSCM fishery would require an average of nearly 364 hours whereas an increase in daily average temperature of 1^{o}C was predicted to increase the effort needed to catch a Trophy LSCM by more than 250 hours, to 615 hours, and an increase of 3^{o}C was predicted to increase TRCOM by 1635 hours, to 1999 hours.

Model Sensitivities

We calculated both local (± 10%) and broad (± 30%) model sensitivities for four model parameters, hooking mortality, voluntary release, and annual natural survival, and recruitment using CPUE as the model output metric (Table 10). These model parameters were altered individually for both local and broad sensitivity analysis. The nominal values for voluntary release (0.95, Table 9) made a 10% or 30% increase nonsensical; therefore, only negative changes were modeled for this parameter. A similar situation arose for survival of fish greater than age one. With a nominal value of 0.85 (Table 9), we were unable to model a 30% increase in this parameter. Hooking mortality and age 1 survival were symmetric with regards to positive and negative perturbations, while annual survival of fish greater than age 1 was asymmetric in the local analysis (more sensitive to positive change), and likely would have been asymmetric in the broad sensitivity as well if modeling of this parameter had been possible.

Sensitivity varied across parameters, size classes, and local/broad. We considered sensitivity values < 1 as insensitive, values = 1 as linear, and those > 1 as sensitive. The model output CPUE was insensitive to hooking mortality across all size classes both locally and broadly with no value greater than 0.375 (Tables 10). Similarly, our model output was insensitive, in both the local and broad analysis, to the recruitment parameter (Table 10). The model was locally insensitive to changes in the voluntary release parameter for all sizes of LSCM (Table 10), but CPUE of Legal and Trophy LSCM was broadly somewhat sensitive to changes in this parameter with sensitivity values of 1.493 for Legal fish and 2.214 for Trophy fish (Table 10). Annual natural survival was the only parameter to which model output was locally and broadly sensitive across all size classes. Local model sensitivity values ranged from 7.964 for All fish to a hypersensitive value of 16.906 for Trophy LSCM (Table 10). Broad sensitivity values for annual survival were similar when considering All LSCM, 8.258, but did not increase as substantially for Legal (9.658) and Trophy fish (9.862) as did local sensitivity (Table 10).

Discussion

Successful fisheries, especially those emphasizing trophy fish, typically result from a combination of high growth and survival rates, and ample habitat to support the resulting high population abundance. Lake St. Clair's world class Muskellunge fishery is such an example. Therefore, it is not surprising that our model predictions projected the LSCM fishery to be resistant to substantial increases in open-water angling effort or increased mortality due to a proposed winter spearing season. The current LSCM fishery was predicted to be able to “absorb” substantially more fishing effort, and therefore increased mortality, from either open-water angling or winter spearing, with relatively small reductions in CPUE and TRCOM for all three size classes of fish. In contrast, relatively small reductions in natural survival rates or growth were projected to result in substantial changes to LSCM population demographics, and therefore, substantial reductions in catch rates of LSCM, particularly for Trophy fish. The reductions in predicted catch rates from either decreased growth or natural survival rates were judged to be substantial enough (greater than -20%) that they likely would have a negative effect on Muskellunge angler satisfaction (Mike Thomas, personal communication).

Relatively high levels of total annual survival, a function of natural and fishing mortality, are required for fish to grow to the age associated with trophy status (Casselman et al. 1996). The combination of abundant suitable Muskellunge habitat and high rates of catch and release by anglers likely lead to relatively high levels of total survival in LSCM. Available habitat is often a limiting factor for fish population abundance; however, LSC is dominated by shallow water with high levels of macrophyte growth, likely a contributing factor to high natural survival of LSCM. Further, the unusual bathymetry of LSC allows virtually the entire lake to support Muskellunge and the resulting high Muskellunge population abundance may be another factor mitigating the effects of angling effort. Historically, the LSCM fishery had been dominated by harvest-orientated anglers (Williams 1961); however as in many recreational fisheries, the catch and release ethic has grown tremendously among LSCM anglers over the past 50 years (Mike Thomas, personal communication), thereby minimizing the effect of fishing in the LSCM fishery.

Current estimates for LSCM growth rates are similar to those reported in many other trophy Muskellunge fisheries (Casselman et al. 1999). The predicted sensitivity of the LSCM fishery to growth rates raises concerns over those factors, such as availability of forage, and water temperature, that influence Muskellunge growth. While little is known about the diet of LSCM, the lake, like most of the southern Laurentian Great Lakes, supports an abundant forage fish community (Thomas and Haas 2004, 2012). Current LSC water temperatures are suitable for growth throughout much of the growing season, as indicated by growth parameters in our bioenergetics model. Water temperatures in LSC seldom exceed 25^{o} C (Figure 5), the optimal temperature for Muskellunge growth (Clapp and Wahl 1996). However, LSC's shallow bathymetry and lack of thermal stratification, which make nearly the entire lake appropriate Muskellunge habitat, also make the lake (and the fishery) vulnerable to climate change due to the lack of available thermal refuge.

Model Fit

Our calibrated model appeared to perform quite well predicting key features of the LSCM population and fishery. For example, our calibrated model's predicted catch of 12,052 fish corresponded well to the 2004 creel estimate of 10,909 fish (Thomas and Towns 2011). While our predicted catch size distribution generally matched that reported by anglers, our model under-predicted catch of Trophy Muskellunge by nearly 50%. Assuming that recent recruitment has been relatively constant, this sizable discrepancy suggests that selectivity for trophy fish may be higher than that of fish from smaller size groups. Our calibrated estimates of LSCM population abundance also indicated good model fit. For model scaling, we first estimated a likely range for the total abundance of LSCM in U.S. waters. To do so, we multiplied a literature-based LSCM density estimate (in units of fish > 30"/acre) by the total surface area of U.S. waters of LSC (92,000 acres). Muskellunge density estimates in the literature ranged from nearly zero to almost one fish per acre (Cornelius and Margenau, 1999). We reasoned that high catch rates of LSCM implied that the population's density is near the upper end of published density estimates (0.75 to 1 fish >30"/acre). Therefore, the population abundance range we used for scaling the model was between 69,000 and 92,000 Muskellunge greater than 30". Our calibrated model's population prediction of 70,311 fell within that range, indicating relatively good model fit. Although harvest estimates were not part of our model calibration, recent creel survey estimates of LSCM harvest (Thomas and Towns 2011) were quite close (164 fish) to our model prediction (175), further supporting our conclusion that our model was a reasonable representation of the demographics of the LSCM population.

Angling Effort

Despite statewide declines in overall fishing license sales (MDNR data), LSCM fishing effort seems to be steady to gradually increasing (Mike Thomas, personal communication). Overall, our model predicted the LSCM fishery to be very resistant to increasing levels of angling effort. However, the impact of angling on fishing mortality is not due directly to angler effort, but to the number of fish anglers actually catch, which is related to both total effort, as well as efficiency. In the past 50 years, estimated catch rates among LSCM anglers have increased from as low as 0.005 fish per angler hour in the 1950s (Williams 1961) to as high as 0.117 in 2001 (Thomas and Haas 2004) . This increase in catch rates can likely be attributed both to increased Muskellunge abundance and increased angler efficiency. While we did not specifically model increased angler efficiency, we attempted to account for the combination of potential increasing effort and efficiency by modeling levels of effort up to four times the current effort estimate. While predicted catch rates declined when the nominal level of modeled effort was doubled, it seems somewhat unlikely that most anglers would notice the predicted change in TRCOM for either All fish (-5.7%), Legal fish (-13.2%), or possibly even Trophy fish (-18.2%). While the upper limit of our modeled effort, four times the current level, seems unlikely in the near future, a combination of increasing effort and increasing efficiency resulting in this level of fishing intensity may be plausible. At this high level of fishing intensity, predicted TRCOM of All fish increased 18.9%, likely near the effect size that some anglers would begin to notice. The predicted increases in TRCOM for Legal fish (44.5%) and especially Trophy fish (62.6%) under quadrupled effort would almost certainly be noticed by Muskellunge anglers.

Spearing

Winter spearing of Muskellunge is currently not allowed on LCC; however, other waters in Michigan are open to winter spearing, making it the only state or province in North America with this unique fishery. While winter spearing effort for another popular esocid species, the northern pike (*Esox lucius*) is declining in Minnesota's ice fisheries (Pierce and Cook 2000), and likely in Michigan's ice fisheries as well (Patrick Hanchin, personal communication), there is continuing interest in this traditional method of harvest for LSCM. The relationship between spearing effort and harvest is unknown for esocid recreational fisheries; therefore, we chose to set spearing catchability (q_s) equal to angling catchability (q_a). Further, the potential future levels of effort that would occur if this fishery were opened are unknown. In order to mitigate both the uncertainty surrounding the relationship between spearing effort and harvest and the uncertainty of possible levels of spearing effort, we used a wide range of potential levels of harvest in all of our spearing simulations. We chose to model annual spearing harvest levels from the current level (zero) to 3,000, representing one and one half times the historic spearing harvest estimate from the 1960s (Bob Haas, personal communication). Given that LSC has very high Muskellunge abundance, we reasoned that opening a spearing season on the lake could result in a short term high level of participation (and harvest) due to the novelty of the fishery and the relatively high success rates that spearers might anticipate. However, the current harvest limit of one Muskellunge per year and declining statewide esocid spearing effort make it unlikely that winter spearing harvest would exceed our modeled levels.

At levels of winter harvest less than 1,000 fish per year, we projected that the effect from a winter spearing season on both the abundance and size composition of the open-water catch would be relatively small. The predicted change in open-water TRCOM of All fish resulting from a winter spearing harvest of 1,000 fish only increased 5.6%. However, the same level of mortality had much larger effects on time required to catch Legal and Trophy fish, increasing those times by 17.0% and 31.0% respectively. It seems possible that changes of this magnitude could be noticed by LSCM anglers. At winter spearing harvest levels of 2,000 fish per year, predicted open-water TRCOM increased a modest 15.1%. However, predicted increased levels of TRCOM for Legal fish (+44.5%) and Trophy fish (+79.8%) would almost certainly be met with angler dissatisfaction.

Comparison of Angling and Spearing Mortality

Fair allocation of valuable natural resources, often times between stakeholders with differing values, is a fundamental challenge for natural resource managers. The predominance of catch and release practiced by anglers who specifically target Muskellunge as compared to the by-definition harvest ethic of those who lobby for a winter spearing season would likely cause tension between LSCM stakeholder groups. Anglers who specifically target LSCM tend to discount their contribution to fishing mortality due to their high rates of catch and release (Mike Thomas, personal communication). Yet our model predicts that open-water angling in the current LSCM fishery causes the mortality of over 1,000 fish per year (175 from harvest, 891 due to hooking mortality). As analysis of the likely effects of stakeholder desires is required for fair allocation of valuable natural resources (Grimble and Wellard 1997), we used our age structured model to compare the predicted effects on the LSCM population abundance and size structure (as represented by predicted effects on the open-water fishery catch rates) from increased levels of mortality above the nominal due to either angling or spearing.

While additional spearing and angling mortality above the nominal level (1,066 fish) had nearly equal predicted effects on open-water catch rates of All fish, additional mortality from spearing had a greater predicted effect on open-water catch rates of Legal and Trophy fish than did equal levels of mortality due to angling (Figure 10). All modeled increases in mortality due to either angling or spearing resulted in linear reductions in CPUE, with greater declines associated with CPUE of Legal and Trophy fish due to mortality from spearing. Spearing resulted in a slightly smaller predicted change in open-water CPUE for All fish as compared to angling. As all spearing mortality is inflicted upon fish greater than the MSL, 58% of the LSCM catch (Table 4) is not subject to the direct effects of spearing mortality. However, as Legal and Trophy fish are subject to these direct effects, spearing mortality was predicted to have a larger effect on those size classes than was angling. At high levels of equal additional mortality (2,000 fish) above the nominal level (1,066 fish per year), spearing resulted in an increase in predicted open-water TRCOM for Legal fish 7.3% greater than the effect due to angling. The difference was even greater for Trophy fish, for which the effect of spearing on TRCOM was 321.6% larger than the effect of angling. The larger effect of spearing on Legal and Trophy fish is the result of all modeled spearing mortality being exerted on fish longer than the MSL (42”) whereas angling mortality has an effect on all fish vulnerable to angling gear (i.e., > age 1) many of which would die naturally before reaching Legal or Trophy size.

Bioenergetics

Our initial parameterization of the Muskellunge bioenergetics model, using current LSCM size at age and LSC water temperature data, returned estimates for average LSCM yearly consumption (average daily consumption summed over one year) and proportion of maximum consumption (Pval) for each age group. At this point, we faced the decision to model either no change in consumption or no change in Pval. Our bioenergetics model estimated adult LSCM (fish greater than age 5) consume prey at less than 18% of their theoretical maximum (Pmax), which implied that successful predatory encounters with forage, not metabolic limitations, govern consumption for LSCM. Therefore, we chose to first model the effects of warming under the assumption of no change in consumption. Both warming scenarios, with average daily water temperature increases of 1° C or 3° C, resulted in model predictions of decreased length at age and Linf for LSCM. As a further investigation, we modeled potential growth of LSCM under both warming scenarios assuming no change in Pval. Under these assumptions, the model predicted growth and ultimate size far greater than any known for Muskellunge. The unrealistic predictions that resulted from modeling no change in Pval supported our decision to model the effects of increased average daily water temperature while holding consumption at current estimated levels. We acknowledge, however, that warming could lead to increased forage abundance, and therefore, likely increased Muskellunge consumption. In this scenario, the negative effects predicted by our simulations may be overestimations.

Our age structured model predicted that decreased growth due to warming would have little to no effect on catch rates of All fish in the LSCM fishery. However, even relatively small reductions in growth, like those predicted by our bioenergetics model, were projected to have negative effects on catch rates of Legal and Trophy fish that anglers would be likely to recognize. Currently, the average LSCM greater than age 8 is larger than the MSL and a sizable number of fish from the upper tail of the size distribution for fish age 10 or greater are larger than the 50" trophy level. While the reductions in average growth that we predicted using the bioenergetics model seem fairly small, the effects upon the tail of the size distribution, from which trophy fish come, are substantial. Relatively small changes in predicted growth due to a 1^{o}C increase in average daily water temperature increased average age for a fish to reach the MSL by one year. Further, under this scenario, very few fish would reach trophy size until age 13. Anglers would perceive these predicted changes as longer TRCOM by 13.7% for Legal fish, and by 72.4% for Trophy fish. The predicted effects due to decreased growth from a 3^{o}C increase in water temperature were even more striking. In this scenario, LSCM did not attain legal size until approximately age 12, and very few were predicted to ever reach trophy size. Our model predicted that the time an angler would be required to fish to catch a Trophy fish would increase from 357.1 hours (currently) to nearly 2,000 hours. This catch rate would require an angler fishing one day (8 hours) per week throughout the entire open season to fish more than 9 years to catch what is currently considered a LSC trophy Muskellunge.

Sensitivity and Uncertainty of Model Parameters

Natural survival, voluntary release of fish larger than the MSL, hooking mortality, recruitment, and selectivity were relatively uncertain parameters in our model. Natural survival rates of Muskellunge are poorly known, with only a few literature estimates ranging from 75%-84% per year (Muir 1964; Casselman et al. 1996). Our initial modeling efforts used natural survival rates estimated using the Pauly equation (1980). This equation, based on a wide variety of fish species worldwide, integrates growth rate, asymptotic length and water temperature to predict survival rates, and returned an estimate of annual natural survival of 74%. However, our calibration run of the model with an annual survival rate of 74% lead to substantial mismatch of predicted and observed catch, in particular grossly under-predicting the number of large fish present. Our calibrated value of annual survival rate was 85%, which is at the upper end of the range of reported values, produced an excellent fit between predicted and observed catches, leading to our belief in its plausibility. Our modeled value of voluntary release rates, 95% for fish of Legal size, was our best synthesis of contrasting literature values between studies that focus on anglers targeting Muskellunge (Casselman et al. 1996; Margenau and Petchenik 2004; Kerr 2007; Kerr et al. 2009, Mike Thomas, personal communication), and those that represent generalist anglers who may be more likely to harvest fish above the MSL (Margenau and Petchenik 2004). Given the local insensitivity of our model to the exact values for catch and release rate, our value appears to be a reasonable approximation. Hooking mortality rates in the literature tended to be low for esocid species (Burkholder 1992; Ostrand et al. 2006; Arlinghaus et al. 2008a, 2008b; Arlinghaus et al. 2009; Landsman et al. 2011), and our value of 0.075 is an approximate average of these sources. While hooking mortality was one of our most uncertain parameters, it was also our most insensitive model parameter, with no elasticity value greater than 0.375. Muskellunge selectivity to angling gear in not well documented in the scientific literature. To estimate our value for selectivity, we divided the proportion in each age class of the catch (Ontario Angler Diary data) by the expected proportion in age class as estimated by an actuarial calculation. By this method, age three fish were 75% selected to angling gear, and therefore, we assumed all fish age three and greater to be fully selected. While the value for the recruitment parameter was uncertain in our model, the model output was relatively insensitive, both locally and broadly, to the exact value, with no value for elasticity greater than 0.923 (Table 10).

Future Direction

Future investigation into the LSCM fishery should focus not only on model parameters that are uncertain and biologically important (survival and growth), but also on parameters that inform managers' attempts at fair allocation of resources (hooking mortality), and increase model precision (selectivity). Neither component of total annual survival, natural or fishing related mortality, is known with a high degree of certainty for the LSCM fishery. Similarly, variation in individual growth rates is not well understood in general; however, as shown in our simulations, it can be of substantial importance in determining catch rates of trophy fish. The sub-lethal effects of hooking, possibly including decreased growth rates, are not well studied in the LSCM fishery. We did not consider the possible sub-lethal effects of hooking on LSCM and therefore may have underestimated the effect of angling on the fishery. Improved estimates for hooking mortality would allow managers to accurately estimate mortality due to angling in the LSCM fishery. This knowledge would likely be helpful to managers attempting to minimize conflict between open-water anglers, who often underestimate their role in fishing mortality (Mike Thomas, personal communication) and winter spearers, who by definition, understand spearing has an effect on fishing mortality. Selection to angling gear, which links angler behavior to fishing mortality, is not well estimated for recreational fisheries including the LSCM fishery but is an important component of models like ours. Improved understanding of all four areas would lead not only to improved model predictions, but also likely to better management of the LSCM fishery.

As in most trophy fisheries, total annual survival is a critical factor governing the LSCM fishery. Casselman et al. (1996) used an actuarial table to predict that a decrease in total annual survival from 82% to 80% would require nearly doubling recruitment to maintain the previous level of trophy Muskellunge. We did not perform an in depth investigation directly into the effects of decreased total mortality. However, as annual fishing mortality was predicted to be less than 1% of total annual mortality, changes in natural mortality approximate changes in total mortality in our simulations. Our model predicted that maintaining the current level of abundance of Trophy LSCM under a scenario of decreased in natural survival (from our nominal level of 85% to 83%) would need to be offset by a 55% increase in recruitment. While our model did not predict a reduction of trophy Muskellunge of the magnitude Casselman reported due to relatively small decreases in annual survival, it was hypersensitive to changes in the annual natural survival parameter.

Currently, the MIDNR surveys of LSC do not collect enough individual fish to estimate total annual survival via catch curve analysis. However, even if accurate measures of total mortality were possible, the uncertainty of fishing mortality in the LSCM fishery make estimating natural and fishing mortality a challenge. Our model predicted total annual mortality for LSCM of 20,016 fish/year. We predicted the current total annual natural survival rate of LSCM to be 84.1%, and annual natural mortality was predicted to be 18,959 fish/year, nearly 18 times the predicted value for annual fishing mortality (1,066 fish/year). Hooking mortality, the largest source of fishing mortality in the LSCM fishery, is not well studied for esocids in general, nor for LSCM. Using our calibrated model estimate of 7.5% for hooking mortality, we predicted that 866 fish would die from hooking each year, approximately five times greater than the total harvest. However, reported hooking mortality for esocids in the literature ranged as high as 30% (Beggs et al. 1980; Dubois et al. 1994), which, when modeled, predicted hooking mortality of 3,052 fish annually, decreasing total annual survival to 82.2%. Changes in mortality of this magnitude were predicted to reduce total catch by almost 2000 fish/year in the LSCM fishery. Minimizing the uncertainty surrounding fishing mortality, especially hooking mortality, in the LSCM fishery is critical to understanding the overall survival in this population.

In the current LSCM fishery, growth rates govern the size composition of the LSCM population, and therefore the size composition of the LSCM catch. The influence of forage availability, individual variation in growth, and potential sub-lethal effects of hooking influence fish growth rates and are not well understood in the LSCM fishery. The MIDNR has an ongoing forage survey for LSC; however, little is known about the diet of LSCM, making inferences about Muskellunge growth as a function of forage abundance nearly impossible. Trophy fish, by definition, are rare occurrences and come from the tail of the population size distribution. Often these individuals have experienced high rates of growth and little is known about the heritability of this important trait. Decreased growth has been reported as a likely sub-lethal effect of hooking (Klefoth et al. 2008). We did not investigate potential reduction in growth specifically due to hooking, but we modeled the effects on the fishery of small changes in growth rates. We predicted decreases in mean length at age as small as 3% could cause decreases in CPUE for Legal fish of 21% and just a 1% reduction in mean length at age could decrease CPUE of Trophy fish by 23%. As our model predicted that relatively small reductions in growth rates result in large reductions in the catch rates of Legal and Trophy fish, it is possible that we may have somewhat underestimated the population level effects of fishing on the LSCM fishery. Monitoring this highly influential factor is critical to the continued success of the fishery.

The proposed LSCM winter spearing season may be a source of conflict for stakeholder groups in the fishery. Many LSC anglers who target Muskellunge not only practice catch and release, but also have developed an anti-harvest ethic (Mike Thomas, personal communication). The winter spearing fishery is by definition a harvest fishery; however, our model predictions show that both types of fisheries would cause mortality of LSCM. Uncertainty about the rate of hooking mortality, and thereby angling mortality, make it challenging to accurately assess the impact of open-water angling. It is critical to accurately estimate the effects of existing and proposed regulations in order to fairly and transparently allocate a valuable resource.

Vulnerability to angling gear is not well known for most recreational fisheries. Our calibrated model under-predicted catch of Trophy fish by 44%. This under-prediction could be the result of higher than predicted proportion of trophy fish in the LSCM population due to variation in recruitment, growth, or survival not captured by our equilibrium model, or could result from under-estimating the vulnerability of trophy Muskellunge to angling gear. Because our model under-predicted catch of Trophy fish, it also likely under-predicted fishing mortality on these important fish. Due to this, we may have underestimated the effect of angling effort on a very important segment of the LSCM population, fish over 50".

Management Recommendations

To reduce uncertainty in natural mortality, fishing mortality, growth, and selectivity, we recommend a large scale, long-term study that would include tagging, from both fishery dependent and independent sources, as well as an increased creel survey effort. Improved estimates of total annual mortality as well as the size structure of the population and the catch, garnered from size and age data recorded from the tagged fish, would be an immediate benefit from a tagging study. The mark and recapture data would increase knowledge of total population abundance, variation in growth, and hooking mortality. Comparing recapture rates of fish originally captured by fishery independent methods to those of fish captured by anglers would improve estimates of hooking mortality. Increased creel survey effort would improve estimates of catch rates, total catch, harvest and voluntary release rates by anglers targeting Muskellunge and generalist anglers alike. The improved estimates of fishing mortality, both hooking mortality informed by the mark recapture study, and the harvest mortality from increased creel survey effort, along with improved estimates of total mortality from catch curve analysis, would improve the accuracy of annual natural mortality estimates. Age validation would be an additional benefit from a large scale mark/recapture study. Fish marked at a young age (<2) and subsequently recaptured, could be used to validate current Muskellunge aging techniques.

While a large tagging study would be challenging and expensive, we believe one answer to this challenging study is to enlist LSCM charter boat captains and Muskellunge fishing clubs as citizen scientists. Charter boats on LSC catch over 1,000 Muskellunge each year (MDNR unpublished data) and are required to record and report all caught Muskellunge. It is likely that charter captains could be trained to tag and record data from these fish relatively easily. Additionally, members from the Michigan Ontario Muskie Club have indicated that many club members would be happy to be involved in the conservation of Muskellunge through a study such as the one suggested here. Involving these two stakeholder groups in the research and conservation of LSCM would significantly increase the ability of the MIDNR to monitor and manage the LSCM fishery. A public/private partnership of this sort is not without successful precedent. The OMNR and Muskies Canada Inc. have partnered in Muskellunge conservation and research for many years.

As potential levels of effort as well as the relationship between spearing effort and harvest are highly uncertain for a potential LSCM winter spearing season, predicting harvest from such a season would be very challenging. However, it seems that a starting place for discussing ramifications of a winter spearing season would be to determine what level of reduction in open-water catch rates would be acceptable. We suggest a conservative approach to start, setting a maximum target for winter spearing harvest that would be predicted to reduce open-water catch rates of Legal fish by no more than 5% (331 Fish). To accomplish this harvest goal, managers could use a harvest quota, limit season length, or employ a license lottery. Lake St. Clair's large size makes implementing a precise harvest quota challenging and expensive. Season limits would likely be an imprecise method of regulating harvest due to the uncertainty regarding likely success rates for a novel fishery such as this one. A license lottery in combination with the current one fish per year harvest limit would ensure that Muskellunge spearing harvest did not exceed the harvest goal. Further, if successful anglers were required to report their harvest, the relationship between harvest and number of issued licenses could be estimated and used to set future license limits. The combination of increased understanding of the dynamics of the LSCM fishery and strengthened relationships between managers and angler groups could be vital in protecting the future LSCM fishery.

APPENDIX

Table 1. Initial and calibrated model parameters.

Parameter	Symbol	Initial Value	Calibrated
Recruitment	R	50000	20000
Angling Catchability	q_a	0.00000225	0.00000225
Spearing Catchability	q_s	0.00000225	0.00000225
Angling Effort (angling hours)	E_a	63700	63700
Spearing Effort (spearing hours)	E_s	0	0
Hooking Mortality	H	0.075	0.075
Voluntary Release	r	0.95	0.95
Minimum Size Limit (inches)	MSL	42	42
Instantaneous Natural Mortality	M	0.292	0.163
Annual Natural Survival	S	0.75	0.85
Age 1 Selectivity	s_1	0.0	0.0
Age 2 Selectivity	s_2	0.11	0.14
Age 2+ Selectivity	s_{2+}	1.0	1.0

Table 2. Observed mean length at age, standard deviation, and proportion of cohort greater than the 42” MSL (data from OMNR and MDNR trap net surveys, and Ontario Angler Diary).

Age	**Mean**	**STD**	**Proportion of cohort > MSL**
1	8.0	0.7	0.0
2	18.2	1.6	0.0
3	25.7	2.3	0.0
4	31.1	2.8	0.0
5	35.0	3.1	0.013
6	37.8	3.4	0.107
7	39.8	3.6	0.272
8	41.3	3.7	0.426
9	42.4	3.8	0.540
10	43.2	3.9	0.617
11	43.7	3.9	0.668
12	44.1	4.0	0.703
13	44.4	4.0	0.726
14	44.6	4.0	0.742
15	44.8	4.0	0.753
16	44.9	4.0	0.761
17	45.0	4.0	0.766
18	45.0	4.1	0.770
19	45.1	4.1	0.773
20	45.1	4.1	0.775
21	45.1	4.1	0.776
22	45.2	4.1	0.777
23	45.2	4.1	0.777
24	45.2	4.1	0.777
25	45.2	4.1	0.777
26	45.2	4.1	0.777
27	45.2	4.1	0.777
28	45.2	4.1	0.777
29	45.2	4.1	0.777
30	45.2	4.1	0.777

Table 3. Observed and model (calibrated to reflect current LSCM fishery) predicted proportion of angler catch in 3" length bins. Observed proportion is derived from Angler Diary data.

Length Bins	Observed (O)	Predicted (P)	Percent Difference ((P-O)/O)
21"-24"	0.025	0.017	-33.9
24"-27"	0.025	0.036	40.8
27"-30"	0.077	0.086	11.4
30"-33"	0.080	0.084	5.6
33"-36"	0.135	0.092	-31.9
36"-39"	0.088	0.109	23.8
39"-42"	0.153	0.129	-15.7
42"-45"	0.130	0.147	12.8
45"-48"	0.107	0.138	28.7
48"-50"	0.077	0.094	22.3
50"-54"	0.053	0.043	-18.9
> 54	0.049	0.014	-70.8

Table 4. Cumulative frequency of observed and model (calibrated to reflect current LSCM fishery) predicted proportion of angler catch in length bins. Observed proportion is derived from Angler Diary data.

Length Bins	Observed	Predicted	Percent Difference ((O-P)/O)
≤ 24"	0.026	0.028	-10.9
≤ 27"	0.051	0.064	-25.7
≤ 30"	0.128	0.140	-17.1
≤ 33"	0.208	0.234	-12.7
≤ 36"	0.342	0.326	4.8
≤ 39"	0.430	0.435	-1.0
≤ 42"	0.583	0.563	3.4
≤ 45"	0.713	0.710	0.4
≤ 48"	0.821	0.848	-3.4
≤ 50"	0.898	0.943	-5.0
≤ 54"	0.951	0.986	-3.7
All	1.0	1.0	0.0

Table 5. Predicted effects of increased levels (2X and 4X current) of angling effort (current angler effort is estimated at 63,700 angler hours) on CPUE, TRCOM, and total catch for three size classes in the open-water LSCM fishery (All represents any LSCM regardless of size, Legal is fish greater than 42”, and Trophy is fish greater than 50”).

	CPUE			**TRCOM**			**Catch**		
Size Class	**Current**	**2X**	**4X**	**Current**	**2X**	**4X**	**Current**	**2X**	**4X**
All	0.189	0.177	0.158	5.3	5.6	6.3	12,052	23,230	41,355
Legal	0.055	0.048	0.038	18.2	20.6	26.3	3,504	6,323	9,932
Trophy	0.0028	0.0023	0.0017	363.6	429.9	591.3	175	303	440

Table 6. Predicted effects of a winter spearing season on CPUE, TRCOM, and total catch for three size classes (See Table 5) in the open-water LSCM fishery. Current winter spearing harvest equals zero.

	CPUE			**TRCOM**			**Total Catch**		
Size Class	**Current**	**1000**	**2000**	**Current**	**1000**	**2000**	**Current**	**1000**	**2000**
All	0.189	0.177	0.165	5.3	5.6	6.1	12052	11301	10518
Legal	0.055	0.047	0.038	18.2	21.3	26.3	3505	2968	2421
Trophy	0.0028	0.0021	0.0015	363.6	476.2	653.9	175	136	97

Table 7. Comparison of the predicted effects of additional angling and winter spearing mortality (2000 fish/year) on CPUE and TRCOM for three size classes (See Table 5) in the open-water LSCM fishery. Values for simulations of the current fishery provided for reference.

	CPUE			TRCOM		
Size	**Current**	**Angling**	**Spearing**	**Current**	**Angling**	**Spearing**
All	0.189	0.163	0.165	5.3	6.1	6.1
Legal	0.055	0.041	0.038	18.2	24.5	26.3
Trophy	0.0028	0.0019	0.0015	363.6	537.6	653.9

Table 8. Predicted effects of decreased size at age due to increased average daily water temperature (1° C and 3° C) on CPUE, TRCOM, and total catch for three size classes (See Table 5) of LSCM.

	CPUE			TRCOM			Total Catch		
Size	**Current**	**+1° C**	**+3° C**	**Current**	**+1° C**	**+3° C**	**Current**	**+1° C**	**+3° C**
All	0.189	0.19	0.19	5.3	5.3	5.3	12052	12072	12106
Legal	0.055	0.048	0.034	18.2	20.7	29.5	3505	2158	1463
Trophy	0.0028	0.0016	0.0004	357.1	615.7	1999.4	175	103	32

Table 9. Nominal and adjusted values for parameters in the sensitivity analysis (-- values were greater than 1.0, therefore non-sensical for sensitivity analysis).

		Local		**Broad**	
Parameters	**Nominal**	**+10%**	**-10%**	**+30%**	**-30%**
Hooking Mortality	0.075	0.083	0.068	0.975	0.053
Voluntary Release Rate	0.950	--	0.855	--	0.665
Annual Natural Survival	0.850	0.935	0.765	--	0.595
Recruitment	20,000	22,000	18,000	26,000	14,000

Table 10. Local and broad sensitivities (elasticity) of CPUE for three size classes (See Table 5) of LSCM. When both positive and negative perturbations were possible, we averaged the absolute value of the result of each perturbation. Sensitivity values greater than one are insensitive, values equal to one are linear, and those greater than one are sensitive.

Parameters	**Sensitivity Type**	**All**	**Legal**	**Trophy**
Hooking Mortality (h)	Local	0.055	0.102	0.126
	Broad	0.164	0.304	0.375
Voluntary Release Rate (r)	Local	0.180	0.445	0.669
	Broad	0.608	**1.493**	**2.214**
Annual Natural Survival (S)	Local	**7.964**	**13.662**	**16.906**
	Broad	**8.258**	**9.658**	**9.862**
Recruitment (R)	Local	0.923	0.795	0.628
	Broad	0.923	0.795	0.628

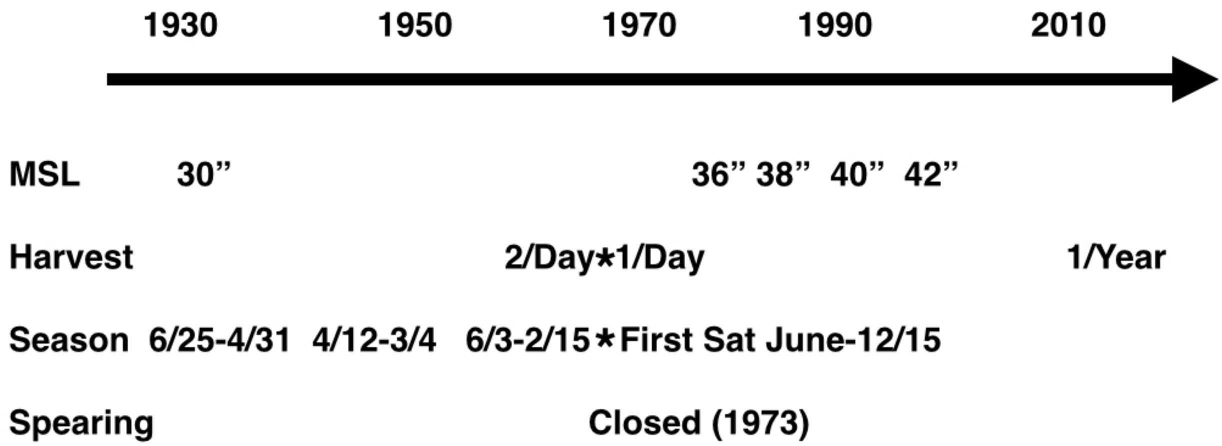

Figure 1. History of Muskellunge regulations for Lake St. Clair (* in 1968 both bag limits and season limits were rescinded for one year)

Figure 2. Geographic location of Lake St. Clair.

Figure 3. Great Lakes Muskellunge are native to the Great Lakes and St. Lawrence River watersheds (Karvelis 1965).

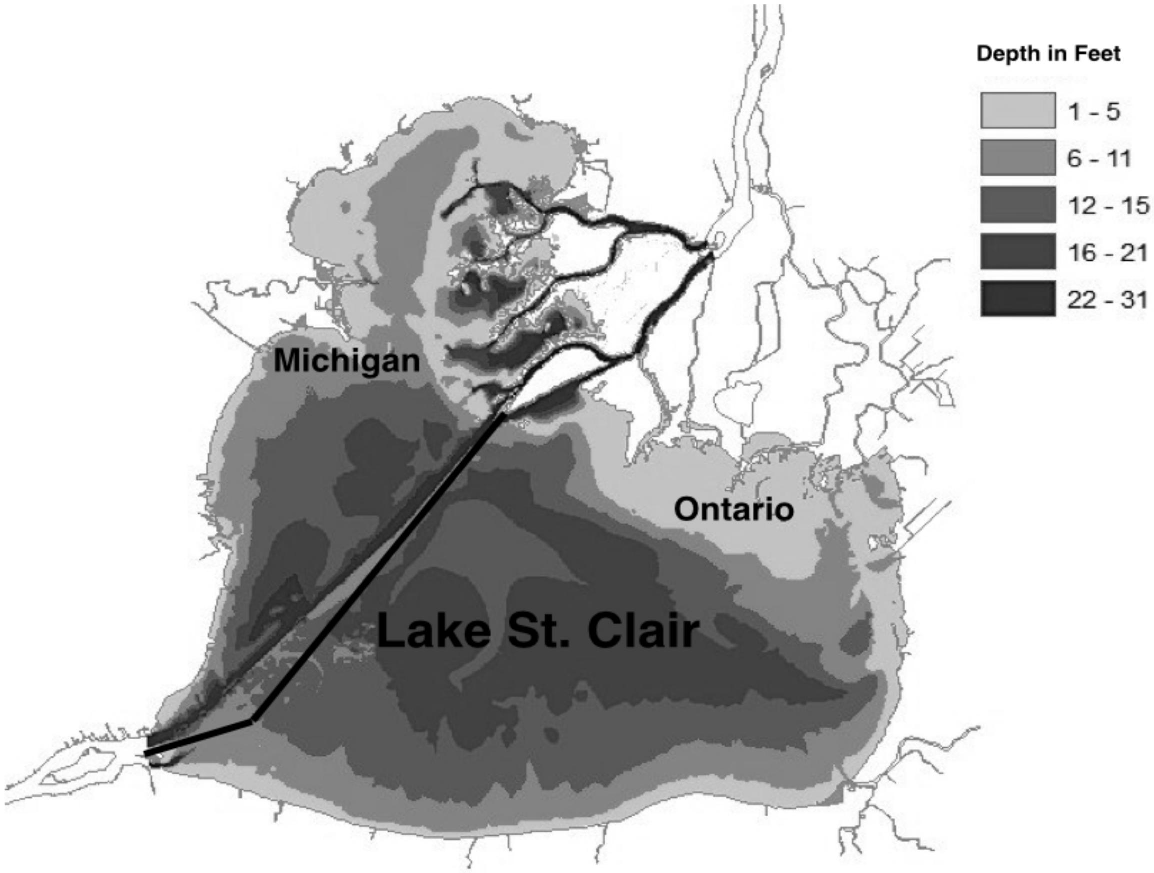

Figure 4. Bathymetry of LSC. The U.S./Ontario border is depicted with the black line.

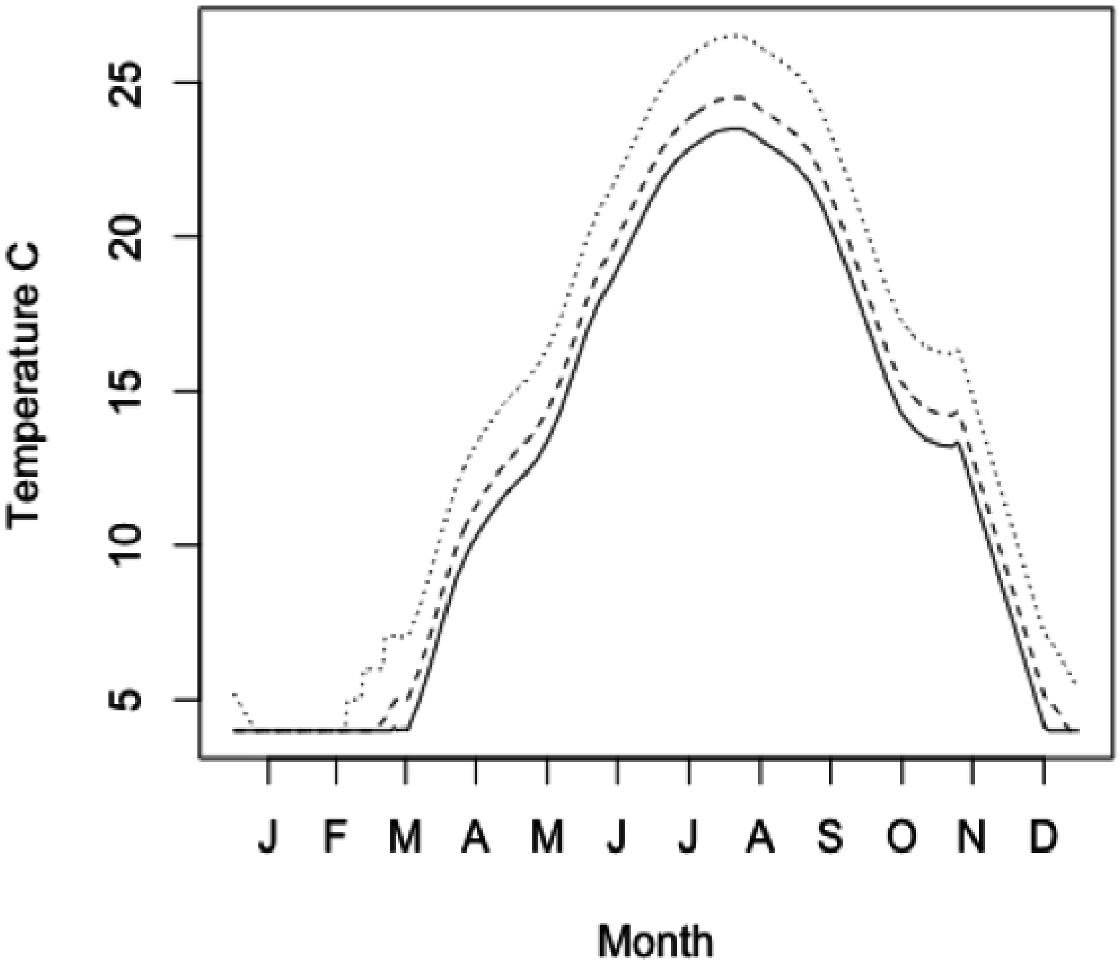

Figure 5. Average daily water temperature in LSC currently (solid line) and under warming scenarios of +1° C (dashed line) and +3° C (dotted line).

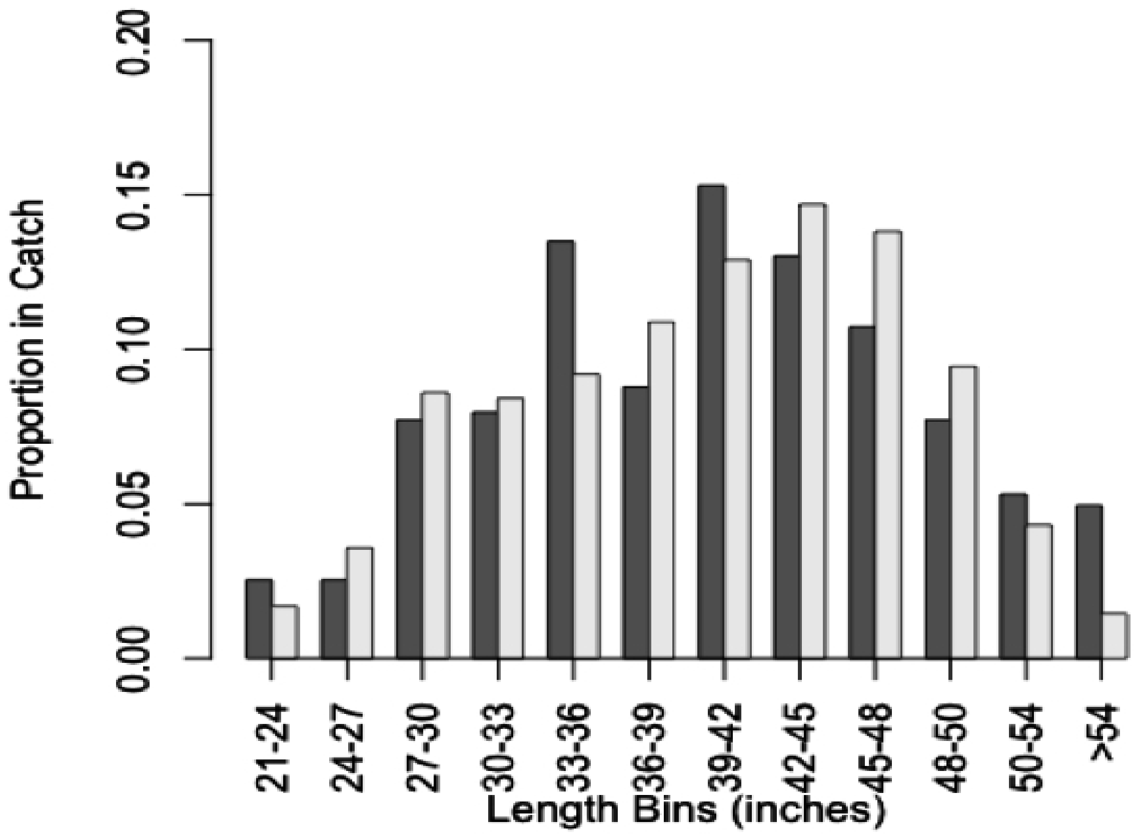

Figure 6. Comparison between observed angler catch (dark bars) from the Angler Diary program and model (calibrated to reflect current LSCM fishery) predicted catch (light bars).

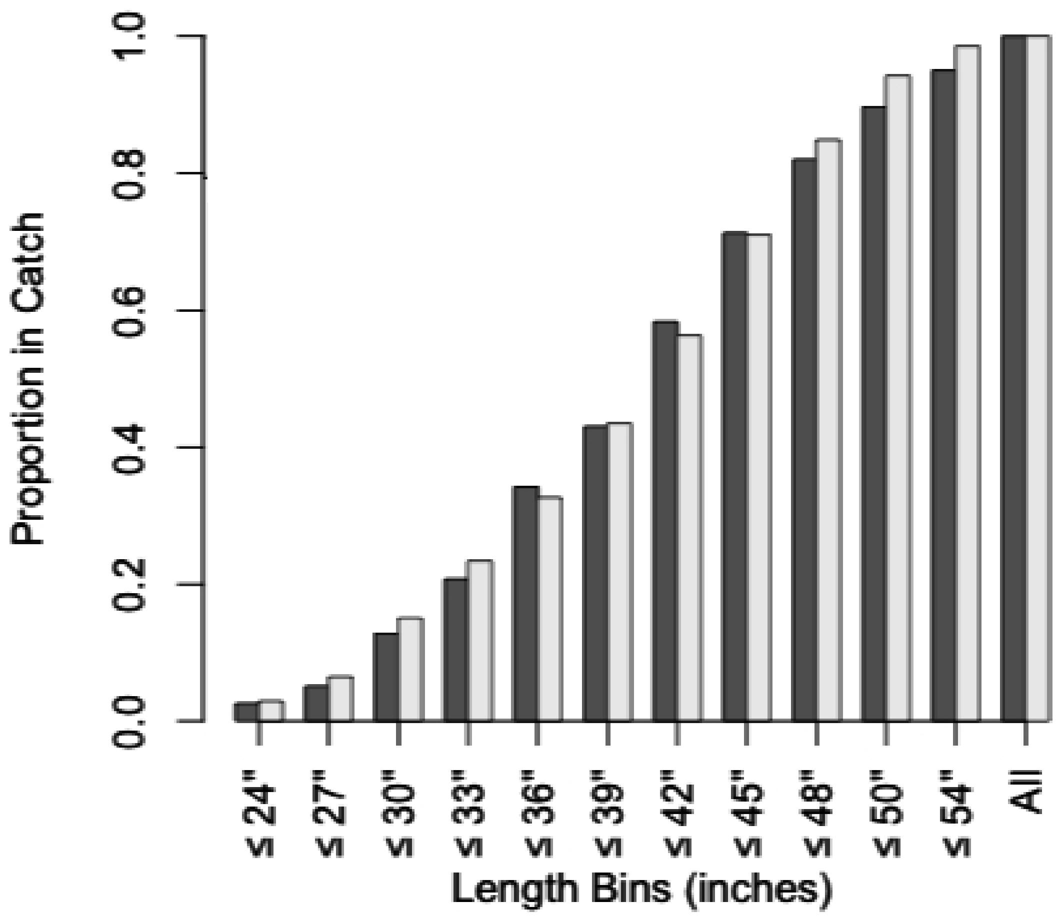

Figure 7. Cumulative frequency comparison between observed angler catch (dark bars) from the Angler Diary program and model (calibrated to reflect current LSCM fishery) predicted catch (light bars).

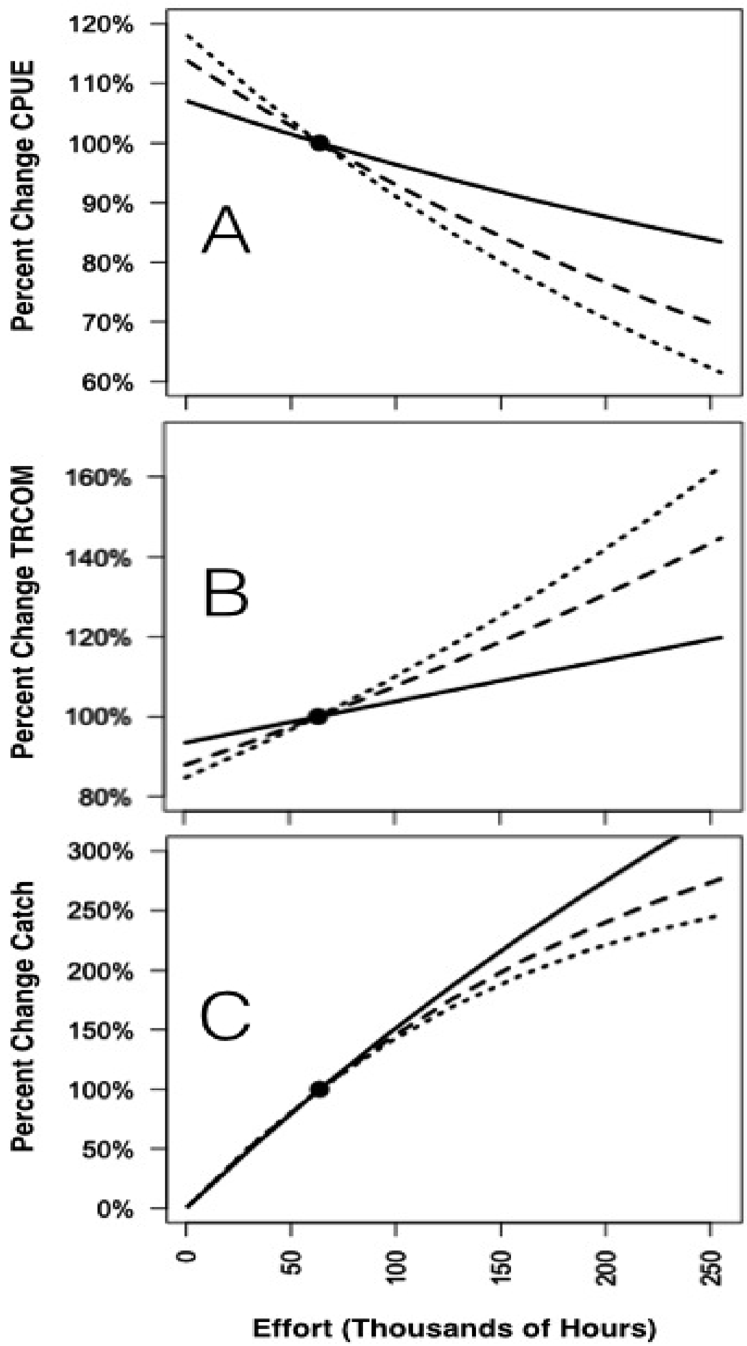

Figure 8. Predicted effect of increased angler effort on open-water CPUE, TRCOM, and total catch for three size classes (solid line is All Fish, dashed line is Legal fish, and dotted line is Trophy fish, see table 5) of LSCM. Black dots (100%) represent estimated current level of LSCM angling effort.

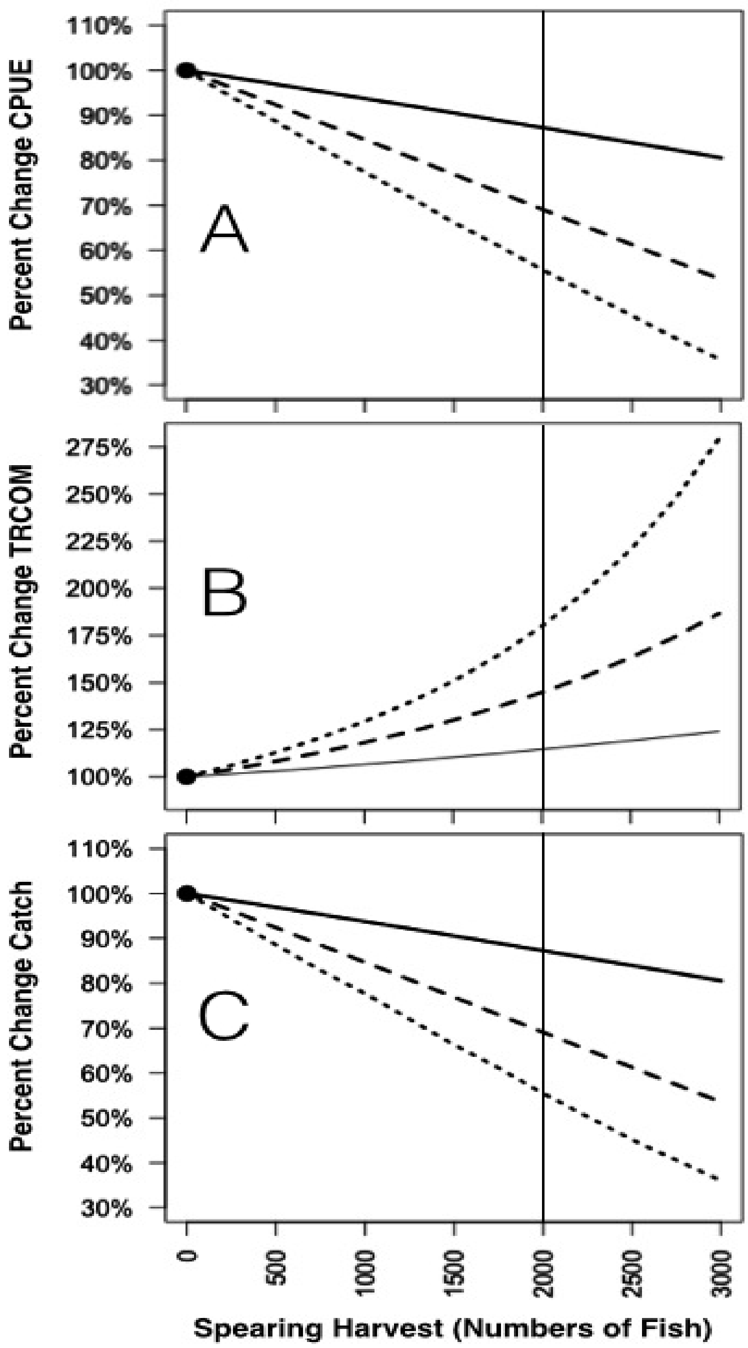

Figure 9. Predicted effect of increased spearing harvest on open-water angling CPUE, TRCOM, and total catch for three size classes (solid line is All Fish, dashed line is Legal fish, and dotted line is Trophy fish, see table 5) of LSCM. Black dots (100%) represent current LSCM spearing harvest levels (0 fish) and vertical lines represents historic LSCM spearing harvest.

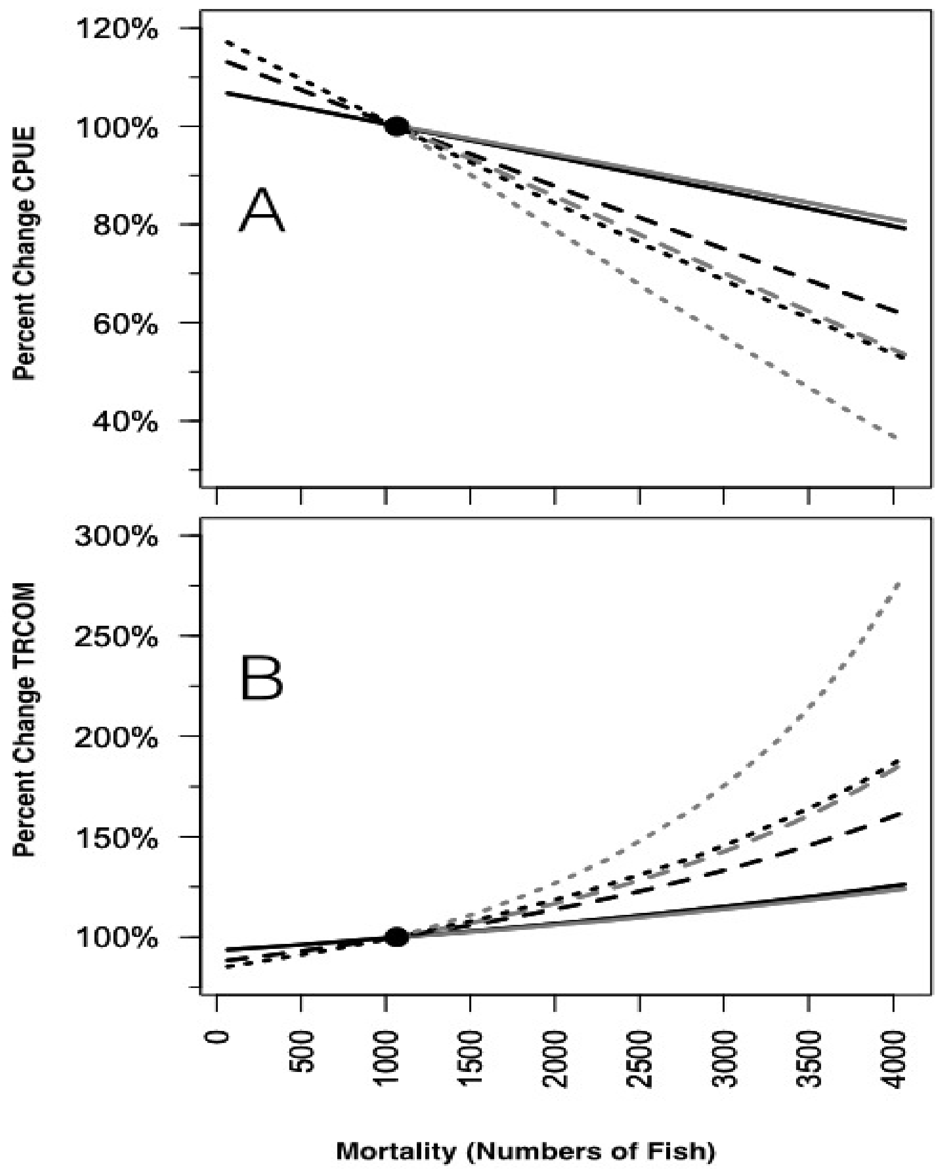

Figure 10. Comparison of the effects of increased (over current) levels of angling (dark lines) or spearing mortality (light lines) on open-water CPUE and TRCOM for three size classes (solid line is All Fish, dashed line is Legal fish, and dotted line is Trophy fish, see table 5) of LSCM. Current estimated fishing mortality of 1066 fish/year is represented by the black dot.

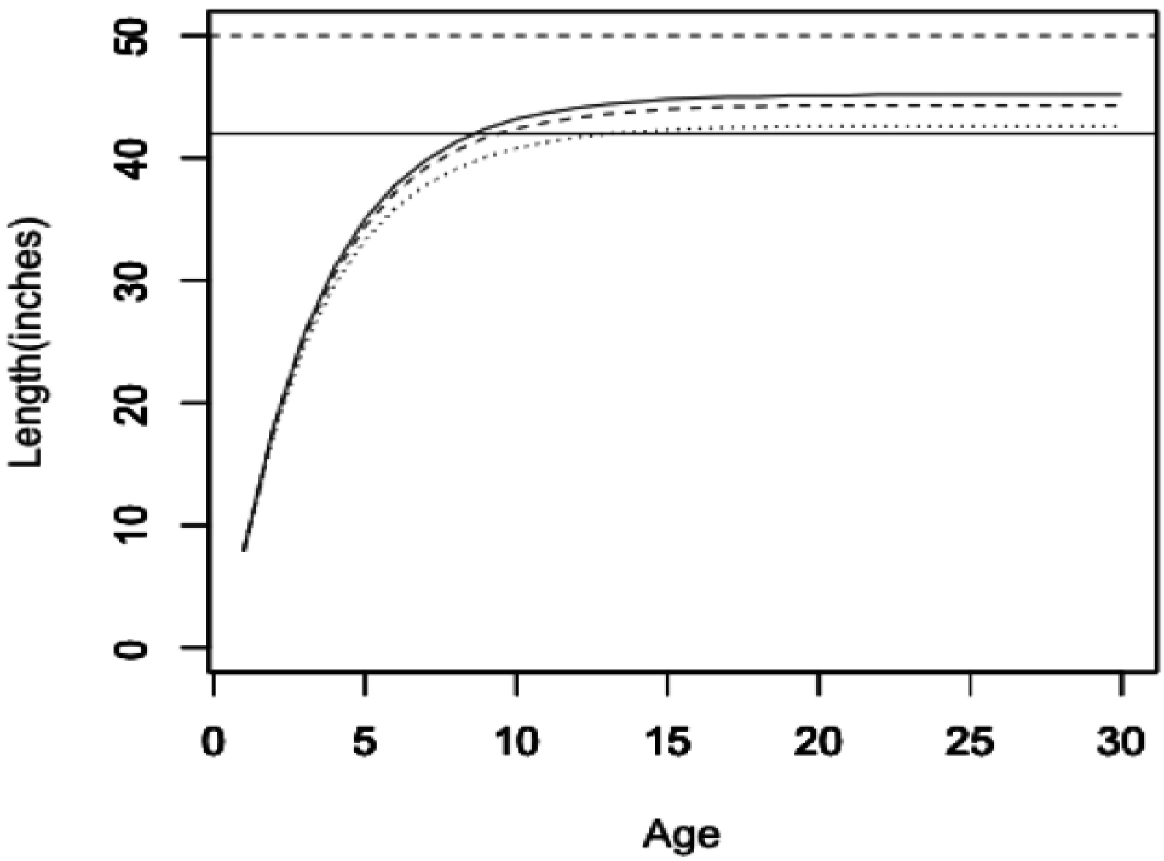

Figure 11. Current (solid line) and predicted length at age for LSCM under warming scenarios of +1° C (dashed line) and +3° C (dotted line) assuming no change in average daily consumption. Horizontal lines depict MSL (42”) and trophy length (50”).

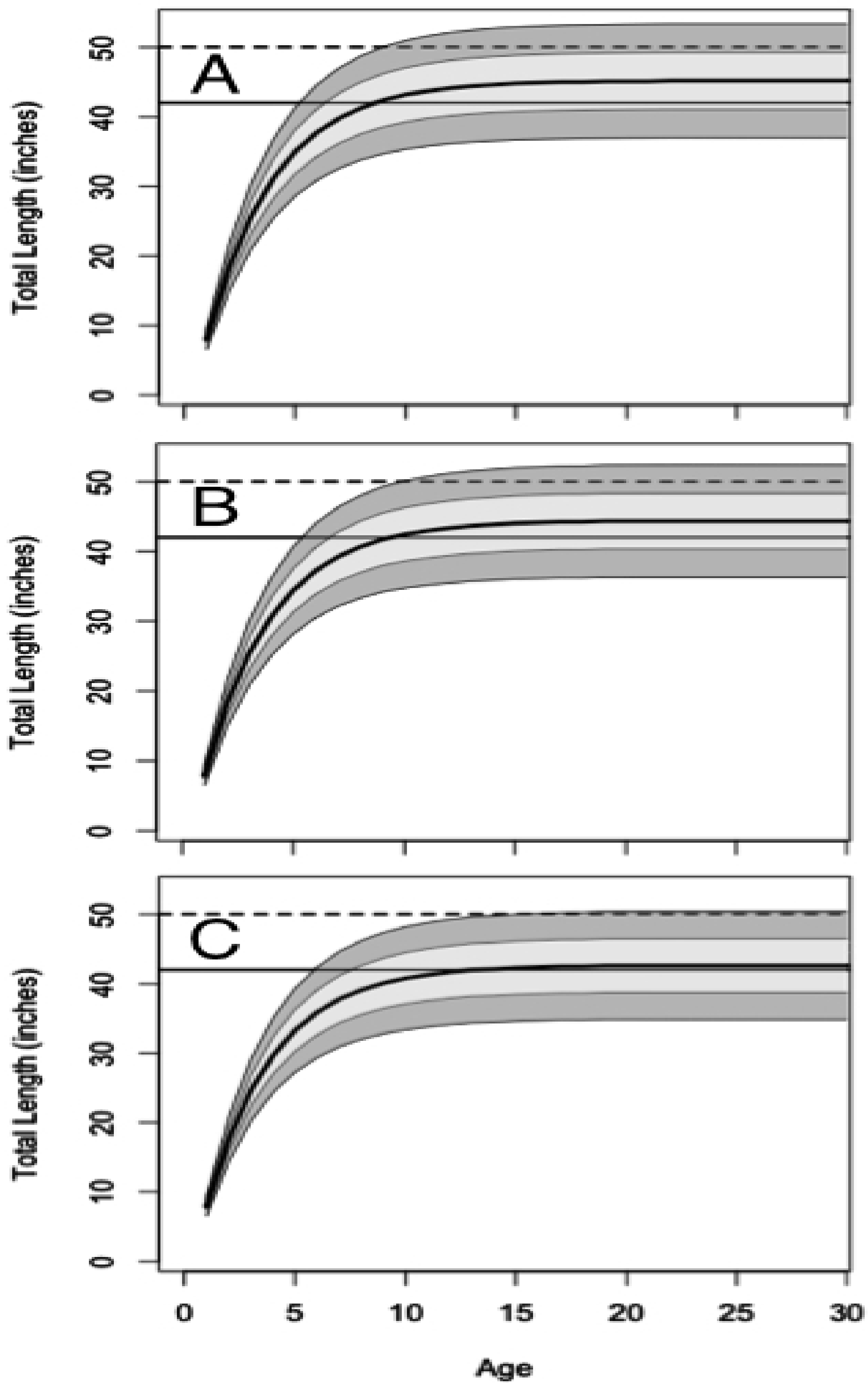

Figure 12. Predicted length at age (mean +/- one & two standard deviations) for LSCM for three temperature scenarios: current LSC temperatures (A); +1° C (B); and +3°C (C).

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