Influence of Movement Dynamics on Walleye Harvest Management in Intermixed Fisheries in a Chain of Lakes

Seth J. Herbst\textsuperscript{1}, Bryan S. Stevens, and Daniel B. Hayes

Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, Room 13 Natural Resources Bldg. East Lansing, Michigan, 48824, USA

Patrick A. Hanchin

Michigan Department of Natural Resources – Fisheries Research Station, 96 Grant Street, Charlevoix, Michigan 49720, USA

Email addresses: Herbsts1@michigan.gov (S.J. Herbst), Steve563@msu.edu (B.S. Stevens),
Hayesdan@msu.edu (D.B. Hayes), HanchinP@michigan.gov (P.A. Hanchin)

Telephone: (920) 540-4199 (S.J. Herbst), (419) 565-4621 (B.S. Stevens), (517) 432-3781 (D.B. Hayes),
(231) 547-2914 (P.A. Hanchin)

\textsuperscript{1}Current address: Michigan Department of Natural Resources – Fisheries Division, 525 W. Allegan Street, Lansing, Michigan 48933
Abstract.— Fish populations that exhibit movement patterns present challenges to fishery management. In the Inland Waterway in Michigan’s northern Lower Peninsula, monitoring of Walleye *Sander vitreus* populations and harvest management is difficult because of seasonal intermixing among interconnected lakes and the presence of both tribal subsistence fishing and recreational-angling fisheries that occur during discrete time periods. We used stochastic simulation to determine the influence of movement and harvest dynamics on the performance of harvest management targets for Walleye in our study system. After accounting for post-spawn movement and harvest dynamics, our results indicated that population-specific exploitation rates on average did not exceed the target rates ($u = 0.35$) that are mandated in the waterway. We did, however, determine that some areas are at risk because they experienced population-specific exploitation rates that surpassed the target. We also determined that the interplay between movement and uncertain population and harvest dynamics will likely determine the ability of management to meet currently accepted harvest targets on average over time, as well as the risk of exceeding harvest targets each year. Our findings are broadly applicable for mobile species inhabiting lake-chains and highlight that it is critical for managers to gain an understanding of movement as well as harvest dynamics because both are imperative for understanding how these dynamics influence harvest management performance. As such, we recommend that managers of Walleye populations in other waterways implement tagging studies and harvest monitoring programs to gain an understanding of movement rates and harvest dynamics. An understanding of movement and harvest dynamics along with the stochastic simulation framework we used provides a better understanding of complex system dynamics and leads to informed harvest management decisions.
Introduction

Many harvested fish species exhibit seasonal movements that result in complex intermixing of populations. Such intermixing creates challenges for managers tasked with determining catch limits and implementing harvest management strategies (Ying et al. 2011; Molton et al. 2012; Brenden et al. 2015). For example, studies have illustrated that the risk of overexploitation can exceed desirable levels when harvesting intermixed stocks unless management strategies explicitly account for movement and the spatial ecology of the species being harvested (Morishima and Henry 1999; Ames 2004; Hutchinson 2008). Movement studies can therefore be highly informative for harvest management by describing the magnitude and seasonality of movement patterns (Rasmussen et al. 2002; Wang et al. 2007; Herbst et al. 2016). Such information is often unavailable to inform management of mixed-stock harvests in inland systems, however, and management therefore commonly proceeds under the assumption that fish stocks from interconnected waterbodies are isolated and discrete populations (Patrick Hanchin, Michigan Department of Natural Resources, personal communication). While this pragmatic simplifying assumption is common for inland fisheries management, the associated risks of ignoring movement and the implications for harvest management are often poorly understood.

Walleye Sander Vitreus are an economic and culturally important species that occupy interconnected, inland lake-chain systems throughout the upper Great Lakes region (Schmalz et al. 2011). Walleye harvest management in treaty-ceded territories of the northern Great Lakes often consists of harvest that is shared between two distinct fisheries, with tribal subsistence harvest occurring on spawning grounds and recreational angling harvest occurring after the spawning season (e.g., Rasmussen et al. 2002; Herbst et al. 2016). Moreover, co-management of these fisheries among sovereign tribal nations and states is often guided by target reference
points that specify maximum desirable exploitation rates for subsistence and angling harvests, where harvest targets are believed to be biologically sustainable and pose a low risk of overexploitation for Walleye in the Great Lakes region (e.g., Staggs et al. 1990; U.S. v. Michigan 2007; Schueller et al. 2008). In the Great Lakes region such management policies for Walleye populations are often legally mandated through the results of past litigation and the legal negotiations that followed.

The Inland Waterway of northern Michigan (hereafter the waterway; Fig. 1) is an example of a lake-chain system within the 1836 treaty-ceded territory that supports both subsistence and recreational Walleye fisheries. Management of Walleye populations in the waterway is based on a federally mandated agreement between the state of Michigan and Native American Tribes referred to as the 2007 Inland Consent Decree (U.S. v. Michigan 2007). Within the agreement lakes are managed as individual closed populations irrespective of their connectivity to other waterbodies within the waterway. Walleye populations at individual sites within the waterway experience tribal subsistence harvest that occurs as a pulse fishery during the spawning season (late-March through April), whereas the recreational fishery harvests intermixed populations during the state-regulated angling season that occurs later in the year and over a much longer duration (i.e., late-April through mid-March of the next calendar year).

Under the 2007 Inland Consent Decree, the target maximum exploitation rate of 0.35 (i.e., $u \leq 0.35$) is partially allocated to the tribal subsistence fishery ($u_s \leq 0.10$) and the recreational angling fishery ($u_a \leq 0.25$). While the biological sustainability of this mandated exploitation rate has never been evaluated due to data limitations (e.g., limited stock-recruitment information; but see Tsehaye et al. 2016), the legally negotiated and agreed upon maximum exploitation rate of 0.35
was based on findings from previously published harvest simulations for Walleye in northern Wisconsin that suggested $u \leq 0.35$ had a low risk of overexploitation (Beard et al. 2003).

Despite the common occurrence of legally mandated maximum exploitation rates for Walleye populations in the Great Lakes region, understanding of performance for Walleye harvest management strategies in the waterway and similar systems is complicated by a high degree of uncertainty surrounding population and harvest dynamics. While Walleye populations at individual sites within interconnected systems are often assumed to be closed to movement and stock intermixing, recent studies demonstrated that populations within the waterway exhibit asymmetrical post-spawn movements and spawning site-fidelity (Herbst et al. 2016). Such movements result in seasonal intermixing of spawning stocks after the spawning period (Herbst et al. 2016). Thus, subsistence and angling exploitation at the same spatial locations remove individuals from different groups of fish, and the implications of movement for Walleye harvest management in this and similar systems are poorly understood. Moreover, there is also uncertainty regarding the realized exploitation rates being experienced by local spawning populations under current regulatory mechanisms, and no data exist to rigorously estimate population-specific subsistence exploitation rates. Similarly, angling harvest regulations are intended to result in $u_a \leq 0.25$, yet realized angling exploitation rates were only recently estimated, and determined to be variable among sites within the waterway (Herbst et al. 2016). The combination of asymmetric inter-lake movements and uncertain implementation of existing target exploitation rates therefore creates concern among fishery managers as to the risks of current harvest management, and the ability of management to achieve the legally mandated maximum exploitation rates that are currently in place.
Thus, the purpose of our study was to determine the implications of movements and uncertain system dynamics on harvest management for Walleye populations in the waterway, and provide advice to managers in light of these complexities. Specifically, our objective was to determine the effects of post-spawn intermixing and uncertain population and harvest dynamics on the ability to achieve target exploitation rates for spawning Walleye populations within the waterway. While this study is evaluating performance of management that is specific to northern Michigan, similar systems exist across the upper Great Lakes region for Walleye and other valuable species. Thus we address long-standing issues of concern for management of intermixed populations that are broadly relevant to other lake-chain systems.

**Methods**

**Study area**

Michigan’s Inland Waterway is an interconnected chain of lakes located in the northern Lower Peninsula consisting of four lakes (Burt, Crooked, Mullett, and Pickerel) interconnected by a series of rivers and smaller tributaries (Figure 1). The Cheboygan Lock and Dam on the Cheboygan River, and the Alverno Dam on the Black River located at the northern portion of the Inland Waterway, restrict fish passage and are considered closed to emigration to Lake Huron or further upstream within the Black River (Figure 1). The lakes and rivers of the waterway are oligotrophic, provide various levels of suitable Walleye spawning substrate and prey resources, and range from 4.4 km$^2$ (Pickerel Lake) to 70.4 km$^2$ (Burt Lake) in total size (Hanchin et al. 2005a; Hanchin et al. 2005b).

**General approach**
We used simple deterministic calculations to determine the influence of movements on area-specific exploitation rates that would be expected if maximum exploitation rates were achieved perfectly within the waterway (i.e., $u_s = 0.10$, $u_a = 0.25$). These calculations used area-specific initial abundances (described below) and estimates of mean post-spawn movement rates (described below and by Herbst et al. 2016) to determine the change in abundance that would be expected between summer and spawning periods as a function of post-spawn movements. Consequently, these abundances and the harvests they produced were used to calculate the relative differences in area-specific exploitation rates that would be expected when such post-spawn movement occurred, as compared to the area-specific exploitation rates when no inter-lake movement occurred (and under which $u = 0.35$).

In addition to the deterministic calculations, we used stochastic simulation to assess the ability of management to achieve target exploitation rates for Walleye populations in the presence of inter-lake movements and uncertainty about population and harvest dynamics. We developed a set of simulation scenarios that started with potential values for the unknown subsistence exploitation rate (three levels) and movement scenarios (two levels). Within each scenario subsistence exploitation rates were held at fixed values for across all sites, where these rates determined harvest experienced by spawning populations at each site within the waterway. In contrast, implementation uncertainty affected the angling exploitation rates experienced by spawning-stock aggregates on summer feeding grounds throughout the waterway (described below), where distributions of angling exploitation rates were consistent with area-specific estimates for fish on summer grounds described recently (Herbst et al. 2016). Moreover, all harvest simulations were replicated over two movement scenarios: 1) closed populations with no movements among sites, and 2) asymmetrical post-spawn movements with distributions of post-
spawn movement and spawning-site fidelity parameters estimated for Walleye populations within the waterway (Herbst et al. 2016). Because recruitment dynamics for lakes in this system are poorly understood, our baseline simulation model assumed recruitment that produced steady-state dynamics for each spawning population (i.e., recruits = deaths). However, performance of management may be dependent upon stock-recruitment dynamics (Deroba and Bence 2008), and thus we conducted a sensitivity analysis to determine robustness of our conclusions to plausible stock-recruitment relationships by replicating all simulations with three plausible forms of a Ricker model developed for Walleye populations in the Great Lakes region (using parameter estimates from Tsehaye et al. (2016)). Thus, a total of 24 distinct simulation scenarios were used to evaluate the ability of management to achieve target exploitation rates in the presence of uncertain population and harvest dynamics, and robustness of conclusions to such uncertainties.

Simulated Population and Harvest Dynamics

We simulated population and harvest dynamics for Walleye spawning within the Inland Waterway using forward population projections (Figure 2). We simulated each scenario for 1,000 replications, each with a 50-year population projection to ensure that transient dynamics in the initial years did not obscure the long-term performance of management. For each population projection we initiated simulations in year $t = 1$ by starting lake-specific spawner abundances at values equal to mark-recapture (M-R) estimates of abundance from a field study conducted within the waterway in 2011 (estimated via the Lincoln-Peterson estimator with the Chapman modification using mark-recapture, Michigan Department of Natural Resources unpublished data). The forward projection model then assumed that subsistence harvest removed individuals from spawning populations at each site $i$ ($N_{spawn,i,t}$) in each year $t$, after which the remaining
individuals at each site \((N_{\text{post-subistence},i,t})\) exhibited post-spawn movements onto summer
feeding grounds. Once on summer feeding grounds, all fish summering at a given area \(j\)
experienced area-specific natural and angling mortality identically irrespective of which
spawning population they originated from. Fish that survived angling and natural mortality over
the summer at site \(j\) exhibited spawning-site fidelity and returned to their previous spawning
location to spawn in year \(t+1\) (with rate \(\psi_i\) for populations spawning at site \(i\)) or remained on
their summer foraging grounds and joined the spawning population at site \(j\) in year \(t+1\) (with rate
\(1 - \psi_i\) for all \(i\)). New recruits were also added to each population when \(t > 1\), and thus the total
spawning population available for spearing harvest at site \(i\) in future years was the number of
surviving individuals minus loses due to emigration, plus gains due to immigration and
recruitment. Age-structure was not included in our simulation model because information about
age and growth for Walleye populations in the Inland Waterway are not available.

For each site the abundance of spawners and the subsistence fishing mortality rate
determined the number of fish harvested via tribal subsistence fishing that occurred on the
spawning grounds:

\[
N_{\text{post-subistence},i,t} = N_{\text{spawn},i,t} e^{-F_s},
\]

where \(F_s\) is the instantaneous subsistence fishing mortality rate and \(e^{-F_s}\) is the fraction of the
spawning population that survives subsistence harvests, and thus \(N_{\text{post-subistence},i,t}\) refers to the
population of spawners remaining after tribal subsistence harvest at site \(i\) in year \(t\). We lacked
information to reliably estimate subsistence exploitation rates, so we replicated simulations over
a discrete set of values for \(F_s\) that resulted in subsistence exploitation rates of 0.05, 0.10, and 0.20
to cover a range of exploitation rates currently deemed plausible by regional fishery biologists
(i.e., from half to twice current target exploitation rates). Moreover, in our simulations \(F_s\) was
assumed to apply uniformly across all spawning sites because information about the degree of spatial heterogeneity in subsistence harvest was unavailable.

Following subsistence harvest, individuals from spawning populations at each site exhibited post-spawn movements to locations where they experienced recreational angling and natural mortality (Figure 2). For simulation scenarios with inter-lake movement we used $N_{post-sub}^{i,t}$ and estimated post-spawn movement rates (Herbst et al. 2016) to determine the abundance of fish at each feeding location $j$ that were available for recreational-angling harvest. Specifically, for each of the 1,000 simulation replicates we randomly drew a matrix of movement rates from Markov chain Monte Carlo (MCMC) samples of their joint posterior distribution (described by Herbst et al. 2016) to determine time-invariant post-spawn movement rates ($\varphi_{i\rightarrow j}$ = movement from spawning site $i$ to summer location $j$) (Table 1). Thus, the number of fish that spawned at site $i$ but then moved to site $j$ directly after spawning in year $t$ ($N_{summer,i,j,t}$) was simply the number of fish alive after subsistence harvest multiplied by inter-lake movement rates:

$$N_{summer,i,j,t} = \varphi_{i\rightarrow j}N_{post-sub}^{i,t}$$  \hspace{1cm} (2)

The total number of fish at each summer location $j$ after post-spawn movements in any given year was therefore the sum of individuals that moved into site $j$ after spawning earlier within the same year ($\sum_{i} \varphi_{i\rightarrow j}N_{post-sub}^{i,t}$). For simulation scenarios that assumed no inter-lake movement we used a diagonal matrix of movement parameters for each simulation replicate, such that $\varphi_{i\rightarrow i} = 1$ for all $i$ and $\varphi_{i\rightarrow j} = 0$ for all off-diagonal movement rates (i.e., for $i \neq j$).

After post-spawn movements, fish were removed from summer sites via year- and location-specific natural ($M_{j,t}$) and angling mortality ($F_{a,j,t}$), where realized values of these parameters varied annually as a function of site- and time-specific process variation ($\varepsilon_{j,t}$). The
number of fish from spawning population \( i \) that survived angling and natural mortality at a given summer location \( (N_{\text{survivors},i,j,t}) \) was the product of the number of fish at the site and the survival rate:

\[
N_{\text{survivors},i,j,t} = N_{\text{summer},i,j,t} e^{-Z_{j,t}},
\]

where

\[
Z_{j,t} = (F_{a,j} + M)e^{\varepsilon_{j,t}}.
\]

In this model \( Z_{j,t} \) is total realized instantaneous mortality for a given summer location and year and is equal to the sum of median angling \( (F_{a,j}) \) and natural mortality rates \( (M = 0.3) \) multiplied by a multiplicative process error \( (\varepsilon_{j,t}) \) that effectively accounted for spatial-temporal variation in mortality. For each time step within each simulation replicate we randomly drew process error terms from a normal distribution \( (\varepsilon_{j,t} \sim \text{Normal}(0, \sigma_{\varepsilon})) \), where \( \sigma_{\varepsilon} = 1.53 \) was estimated using the posterior mean calculated from MCMC samples of the process variation parameter described by Herbst et al. (2016). To account for uncertainty in area-specific angler exploitation, we randomly drew a vector of time invariant median angling mortality rates for each simulation replicate from MCMC samples of their joint posterior distribution (described by Herbst et al. 2016; Table 1).

After angling and natural mortality at summer locations in year \( t \), fish moved to spawning locations where they reproduced and experienced subsistence harvest at time \( t+1 \) (Figure 2). Fish that survived at each summer feeding location either returned to the same spawning population that they belonged to in year \( t \) or remained in place to join the spawning population in the location where they summered in the current year. Specifically, fish that spawned at site \( i \) during year \( t \) exhibited spawning-site fidelity and returned to the same spawning population at a rate of \( \psi_i \) at the start of year \( t+1 \), irrespective of where they summered in year \( t \), whereas \( 1 - \psi_i \) of fish
that spawned at site \(i\) remained to join the spawning population at their summer location in year \(t+1\). For simplicity, however, we assumed all surviving fish that did not disperse to a summer area different than their spawning location in year \(t\) (i.e., stayed at site \(i\) for all of year \(t\)) stayed to spawn at the same location in year \(t+1\). Thus, \(N_{\text{spawn},i,t+1}\) was the sum of survivors over time \(t\) that never left site \(i\) during year \(t\), fish that spawned at site \(i\) at time \(t\) but survived at another summer location and then exhibited spawning site fidelity, fish that spawned in another location at time \(t\) but survived the summer at site \(i\) and then failed to return to their previous spawning population (and thus joined the spawning population at site \(i\)), and new recruits into the spawning population at site \(i\):

\[
N_{\text{spawn},i,t+1} = N_{\text{survivors},i,i,t} + \sum_{j \neq i} N_{\text{survivors},i,j,t} \psi_i + \sum_{j \neq i} N_{\text{survivors},j,i,t} (1 - \psi_j) + R_{i,t}. \tag{5}
\]

The proportions of fish from each spawning population exhibiting spawning-site fidelity (\(\psi_i\)) was assumed constant over time, and the vector of \(\psi_i\) values for each simulation replicate was randomly drawn from MCMC samples of their joint posterior distribution (described by Herbst et al. 2016; Table 1).

We had little information about recruitment dynamics within the waterway, therefore the base model populations were projected forward using a time-specific number of recruits for each spawning population that produced steady-state dynamics (i.e., births = deaths). Specifically, the number of recruits produced by spawning population \(i\) in time \(t\) was equal to the number of fish removed through subsistence harvest at site \(i\) plus the total number of fish from population \(i\) that died on feeding grounds (natural and angling mortality) at all locations in year \(t-1\):

\[
R_{i,t} = N_{\text{spawn},i,t-1} (1 - e^{-F_t}) + \sum_j (1 - e^{-Z_{j,t-1}}) N_{\text{summer},i,j,t-1}. \tag{6}
\]

This approach to modeling recruitment was a pragmatic solution to the problem of having insufficient data to parameterize a stock recruitment model for spawning populations within the
waterway, where we therefore used a level of recruitment that balanced deaths in order to maintain spawning populations in each lake at a similar level to the initial abundances. This was desirable because our primary interest was to determine steady state implications of movement among lakes and uncertain exploitation rates (subsistence and angling) for harvest management within the system, whereas if lake-specific populations grew substantially the abundance changes could overshadow the implications of movement. However, because performance of harvest management is typically sensitive to stock-recruitment relationships, we also replicated simulations under three plausible stock-recruitment models. For these simulations we used a Ricker model where

\[ R_{i,t} = \alpha N_{pre-recruit,i,t} e^{-\beta N_{pre-recruit,i,t} + \omega_{i,t}}, \tag{7} \]

and \( N_{pre-recruit,i,t} \) is determined by equation 5 but without the addition of new recruits (\( R_{i,t} \)). Here the values of \( \alpha \) and \( \beta \), as well as the distribution of spatial-temporal variation in recruitment (\( \omega_{i,t} \sim \text{Normal}(0, \sigma_{\omega}) \)) were described via hierarchical modeling of stock-recruitment dynamics for Walleye populations in northern Wisconsin lakes by Tsehaye et al. (2016). Specifically, we considered three scenarios of productivity by replicating simulations over low, regional average, and high values of \( \alpha \) (1.643, 2.768, 6.046), whereas \( \beta \) was held at the regional average (0.049) and \( \sigma_{\omega} = 1.964/3 \) was consistent with values assumed in harvest simulations described by Tsehaye et al. (2016). Stock-recruitment parameters were held constant among all sites for all simulations because no information about spatially-heterogeneous recruitment dynamics was available for this system.

Performance metrics
We evaluated performance of harvests relative to target reference points by tracking the realized total exploitation rates for each spawning population and area. Monitoring realized total exploitation rates effectively allowed us to determine how uncertain population and harvest dynamics affected the ability to achieve target harvest rates for Walleye populations within the waterway, while accounting for the re-distribution of individuals among sites over time. For each simulation year the realized total annual exploitation rate for each spawning population was determined by dividing the total harvest from the tribal and angling fisheries (summarized by spawning population) by the spawning population abundance at each site in the beginning of the same time step. Total harvest from each spawning population \( H_{Total,i,t} \) was equal to the sum of subsistence \( H_{S,i,t} \) and angler harvest \( H_{a,i,t} \) experienced by that population, regardless of where angling mortality occurred, where area-specific angler harvests were calculated using the Baranov catch equation (Quinn and Deriso 1999). Thus,

\[
H_{Total,i,t} = H_{S,i,t} + H_{a,i,t}, \tag{8}
\]

\[
H_{S,i,t} = N_{spawn,i,t}(1 - e^{-F_s}), \tag{9}
\]

and

\[
H_{a,i,t} = \sum_j \frac{F_{a,j,t}}{Z_{j,t}} \left(1 - e^{-(Z_{j,t})}\right)N_{summer,i,j,t}. \tag{10}
\]

Similarly, to calculate area-specific realized exploitation rates for site \( j \) we divided total harvest at a site in each year (subsistence plus angling at site irrespective of source population; 

\[
N_{spawn,j,t}(1 - e^{-F_s}) + \frac{F_{a,j,t}}{Z_{j,t}} \left(1 - e^{-(Z_{j,t})}\right)\sum_i N_{summer,i,j,t}
\]

by the abundance of spawners alive at that site in the beginning of the same year \( N_{spawn,j,t} \). Although area-specific exploitation rates may be less biologically meaningful than exploitation rates experienced by spawning populations in the presence of movement, they are likely more representative of the types of
information that may be available to managers, for instance if abundance is estimated on spawning grounds and total catch estimates were available for both subsistence and angling harvests at a given site. Moreover, because we were interested in the ability of management to meet the target exploitation rate (i.e., $u \leq 0.35$) for each population in a given year, we focused summary of performance metrics to simulated distributions of harvests on the final simulation year.

Results

Deterministic calculations

Post-spawn movement resulted in spatial intermixing of individuals from each spawning population and affected the abundance, and consequently the area-specific exploitation rates of Walleye populations. Deterministic calculations showed that post-spawn movements resulted in expected changes in summer abundance ranging from a net loss of 31.7% at Pickerel Lake to a net gain of 236% in the Black River, while Burt, Mullett, and Crooked lakes changed by -3.0, 9.4, and 28.2 percent (Table 3). As such, the expected exploitation for each area changed by including post-spawn movements when $u_s = 0.10$ and $u_a = 0.25$. For example, the expected net loss of individuals from Pickerel Lake resulted in fewer individuals available for angling harvest in that lake, and therefore the realized exploitation rate for that lake was reduced by 0.07 relative to that expected with identical exploitation rates when assumed closed to post-spawn movements (Table 3). In contrast, Crooked Lake had an expected net increase in abundance during the angling season and therefore had an expected increase in area-specific exploitation rate because the increased summer abundance resulted in more fish being harvested when $u_a = 0.25$ (Table 3). Thus to achieve a system wide target angling exploitation rate of 0.25, area-specific angling
exploitation rates would need to be adjusted for each summer location to account for net losses and gains of individuals due to post-spawn movement (Table 3). For example, Mullett, Crooked Lake, and the Black River could withstand increased angling exploitations (relative to closed population target angling exploitation rates) because they were recipient locations of individuals from other spawning populations. In contrast, to achieve the target angling exploitation rate \( u_a = 0.25 \) for the waterway as a whole the target angling exploitation rates would need to be decreased in locations that had net losses (i.e., Burt and Pickerel lakes) of individuals (Table 3).

\section*{Stochastic simulations}

In the presence of uncertain population and harvest dynamics, realized area-specific and population-specific exploitation rates varied, but on average remained < 0.35. Total spawning population exploitation rates generally did not exceed the management target of \( u \leq 0.35 \) on average, even for scenarios with high realized subsistence exploitation rates (Figure 3). The exception was the Crooked Lake spawning population, which had a mean exploitation rate of 0.36 when the highest level of tribal subsistence exploitation was paired with estimated angling mortality (Figure 3). Although the mean population-specific exploitation rates were below the target, the spreads of the distributions of realized exploitation rates were quite wide, and the interquartile ranges of simulated exploitation rates often exceeded 0.35. Burt and Crooked lake spawning populations, for instance, both experienced population-specific exploitation rates that surpassed the target during approximately 20\% and 50\% of the simulations when \( u_s = 0.10 \) and 0.20, respectively (Figure 3). Thus, risks of exceeding target exploitation rates in any given year were sometimes large, despite achievement of target exploitation rates on average in simulations.
Total area-specific exploitation rates on average generally did not exceed the management target of \( u \leq 0.35 \), even for scenarios with high realized subsistence exploitation rates (Figure 3). The exception was the Mullett Lake area-specific exploitation rate that was greater than 1.0, which illustrated that this location had the greatest net gain of fish from other spawning populations. Thus, a greater number of fish are removed with a consistent realized angling exploitation rate, and when total area-specific harvest is divided by spawning abundance at Mullett Lake, the number harvested exceeded the spawning abundance. The elevated Mullett Lake area-specific \( u \) was due to the influx of fish from other sites after post-spawn movement. In contrast, other locations in the waterway had location-specific exploitation rates that were relatively close to or less than the desired exploitation rate (Figure 3), even when \( u_s = 0.20 \), indicating that for these sites area-specific exploitation rates should on average be at desirable levels in the presence of movement and uncertain population and harvest dynamics.

Post-spawn movement had a greater influence on area-specific exploitation rates under the scenarios that we simulated. In the presence of movement the population-specific and area-specific exploitation rates differed as much as 0.46 (Table 4). The difference in the two exploitation rates was greater for areas that received a large net change of individuals during the angling season, such as Mullett Lake (Table). The large discrepancy between the population-specific and the area-specific exploitation rates was caused by the redistribution and net change in the number of fish available for harvest during the angling season. The other important aspect to consider when interpreting these rates is that area- and population-specific harvest is divided by the spawning population abundance, which is assessed in the spring prior to movement. Thus, the area-specific exploitation disregards which spawning population the harvested individuals belong to, but instead simply accounts for all fish harvested in that particular area. The influence
of post-spawn movement was less pronounced in areas that had a lower overall net change in the number of fish available for harvest during the angling season (Table 4). The comparison of exploitation rates between the scenario that included and excluded movement also indicated that with movement the two exploitation rates differed, even if only slightly. However, when excluding movement the area-specific and population-specific exploitation rates were identical, as anticipated (Table 4).

The ability to achieve the target exploitation rate \( u \leq 0.35 \) for each spawning population was not substantially influenced by assumed stock-recruitment models considered. The spawning population and area-specific exploitation rates showed negligible differences on average \( \leq 0.03 \) between the steady-state and the Ricker (Table 5). The Mullett Lake area-specific exploitation rates were the exception to this pattern, however, where exploitation rates for Mullett Lake when assuming steady-state recruitment was much greater \( 0.70 \) than the same rates simulated using the Ricker models \( \text{low } \alpha = 0.31, \text{average } \alpha = 0.25, \text{high } \alpha = 0.22; \text{Table 5}. \)

**Discussion**

Stochastic simulations allowed us to achieve our goal of determining the implications of movement and uncertain system dynamics on harvest management for Walleye populations in an interconnected lake chain. The strengths and flexibility of using a simulation framework make the approach advantageous for addressing complex issues associated with incorporating spatial ecology into management strategy evaluation (Goethel et al. 2011; Molton et al. 2013; Li et al. 2014). Our approach allowed us to incorporate estimated population parameters (e.g., movement and fishing mortality rates), while also providing the flexibility to account for uncertainties in population and harvest dynamics in our study area. Simulation outputs illustrated the
implications and complexities of post-spawn movement when attempting to achieve harvest
management objectives for Walleye populations in a lake-chain system. Our approach could
greatly benefit managers in other waterways that have complex population and harvest
dynamics, similar to what was observed for our study area (Rasmussen et al. 2002; Wang et al.

We determined the implications of post-spawn movement and uncertain population
dynamics for achievement of target exploitation rates for Walleye populations in the Inland
Waterway. These results demonstrated that area-specific angling exploitation rates would need to
be adjusted away from 0.25 in order to achieve a population-specific total $u \leq 0.35$ after
accounting for asymmetrical post-spawn movements. In general, however, our stochastic
simulations showed that mean total exploitation for most spawning populations would likely be
< 0.35 under current levels of angling exploitation and post-spawn movement within the
waterway, and this result was robust across uncertain rates of subsistence exploitation and
recruitment models. Moreover, even though exploitation rates were within the desirable range on
average, there was considerable risk of a realized total $u > 0.35$ in any given year. Thus the
interplay between movement and uncertain population and harvest dynamics will likely
determine the ability of management to meet currently accepted harvest targets on average over
time, as well as the risk of exceeding harvest targets each year.

The ability to achieve total exploitation rates on average that were below the target
maximum in the presence of asymmetrical movements likely resulted from our study area having
angling mortality rates that were on the low end of what has been reported in other studies
(Baccante and Colby 2003; Schmalz et al. 2011). For instance, Schmalz et al. (2011) summarized
documented Walleye exploitation rates over a broad geographic range and reported exploitation
rates greater than 0.35 and as high as approximately 0.50. Such larger exploitation rates in Wisconsin lakes have led to the decline of adult Walleye populations in some areas (Schueller et al. 2005; Schmalz et al. 2011). As such, management concerns could arise in the future if angling exploitation rates increase to levels experienced in other locations (Baccante and Colby 2003; Schmalz et al. 2011). These results highlight the importance of continued monitoring of angling exploitation rates to ensure current harvest regulations do not result in harvests that exceed target levels.

In this study we demonstrated that achievement of target exploitation rates on average was robust to several models of recruitment dynamics, but we were limited in our ability to incorporate lake-specific recruitment based on empirical estimates of stock productivity. Determining the productive capacity of fish populations is a challenging process which often requires a relatively long time series of stock and recruitment data (Hilborn and Walters 1992). Because such data are not available for the waterway, we used multiple recruitment models and tested the sensitivity of simulated exploitation rates among models. Our steady-state recruitment model implicitly assumed variable levels of productivity among the spawning populations by setting recruitment at a value consistent with the harvest from each population. Under this model, more abundant spawning populations that currently support a greater harvest (e.g., Burt Lake spawning population) were also assumed to have a higher level of recruitment. We also used Ricker stock-recruitment models that were parameterized using results from studies of Walleye populations in Wisconsin (Tsehaye et al. 2016). We demonstrated that simulated total exploitation rates were, on average, relatively consistent among recruitment models, and most scenarios resulted in similar achievement of harvest targets. Although our sensitivity analysis used different recruitment models, the Ricker models were constrained by the assumption that
each spawning population in the waterway had the same productivity. While this may not be an 
entirely realistic portrayal of Walleye population dynamics for this study system, this assumption 
reflected the data available for model development, and a full assessment of the implications of 
spatially heterogeneous recruitment for Walleye harvest management in the waterway was 
beyond the scope of this study. Because performance of harvest policies is likely to depend on 
recruitment dynamics, however, there is a clear need to develop an understanding of spatial 
heterogeneity of Walleye population dynamics in northern Michigan. The addition of more 
realistic, spatially-heterogeneous recruitment models would thus provide managers more 
confidence in the effectiveness of current management systems by adding further realism to 
simulation-based evaluations of Walleye harvests (e.g., Schueller et al. 2008; Tsehaye et al. 
2016).

Walleye harvest management in the northern Great Lakes region is frequently dependent 
upon target exploitation rates and an understanding of the implications of such rates for 
accomplishing conservation goals. The appropriateness of current target exploitation rates is a 
concern among managers, especially with documented regional declines in Walleye populations 
(Hansen et al. 2015). As our study system illustrates, however, Walleye managers frequently 
lack the necessary information to assess adequacy of existing harvest targets because of limited 
resources and the vast number of lakes (i.e., > 10,000s) in the ceded-territory of the northern 
Great Lakes region. Tsehaye et al. (2016) recently suggested that \( u = 0.35 \) for some Walleye 
populations in northern Wisconsin would lead to their collapse, and determined that the optimal 
exploitation rate was approximately 0.20 for the average population in that region. Using 
different methods and data, Lester et al. (2014) suggested an optimal exploitation rate for 
Walleye harvest management of \( 0.75^*M \). Using the Lester et al. (2014) method, the optimal
The harvest rate for our study area would be approximately 0.23 based on the assumption that median $M = 0.3$. Results from these recent studies therefore illustrate that exploitation targets for our study system might lead to population decline, especially if stocks exhibit low productivity (Tsehaye et al. 2016). Our simulation indicated that on average management may be likely to achieve current target exploitation rates. Unfortunately, however, we lack sufficient understanding of recruitment dynamics to determine the long-term sustainability of these targets in light of recent studies suggesting 0.35 may be inappropriate.

Our simulations indicated that management will likely achieve current target exploitation rates on average that are below the target of 0.35, however, the spread of realized values suggested that exploitation rates in any given year could often exceeded this value. The wide spread of simulated exploitation rates indicates that risk of short-term overexploitation of Walleye populations is high, even if long-term performance is consistently with currently accepted management goals. The number of times our realized exploitation rates exceeded the target is much greater than the 1 in 40 occasions that has been identified as sustainable for Walleye populations in Wisconsin (Staggs et al. 1990). Because of this risk and data limitations described above, we suggest that it may be useful to consider altering current harvest regulation and exploitation-rate targets. Such actions could develop a reduced target exploitation rate that is more conservative given the complex and uncertain system dynamics that exist in this and other lake-chain systems.

Monitoring exploitation rates is often conducted through creel programs that track harvest, but interpretation of rates calculated through monitoring programs can be misleading because of seasonal intermixing. Exploitation rates for subsistence and angling fisheries are calculated as the number harvested divided by the abundance and populations are typically
assessed during the spring when distinct spawning populations are segregated by location. When post-spawn movement occurs, however, the abundance at each location during the angling season differs from the spawning assessment. As such, the post-spawn movement directly influences the area-specific angling exploitation rate because angling harvest by area is divided by the spawning abundance for that same area. The differences between our area-specific and population-specific exploitation rates indicated that the common approach of calculating exploitation rates from the angling harvest monitoring programs and assuming those rates apply to directly to the spawning populations are not appropriate when intermixing occurs. This finding supports, and provides context to the magnitude of the regional concern raised by Rasmussen et al. (2002) of setting angling harvest levels for Walleye fisheries that are based solely on spring-spawning population assessments, and therefore overlook post-spawn movements. Our results on the interpretation of exploitation rates have broad applicability because many exploited populations’ exhibit seasonal movement patterns (Rasmussen et al. 2002; Wang et al. 2007; Herbst et al. 2016). A comprehensive understanding of how movement influences the interpretation of exploitation rates will lead to managers implementing actions that are more likely to achieve conservation goals.

In summary, we used stochastic simulations to determine the harvest management implications of post-spawn movement and harvest dynamics for Walleye populations in an interconnected lake-chain in northern Michigan. After accounting for post-spawn movement and harvest dynamics, our results indicated that population-specific exploitation rates on average did not exceed the target rates ($u = 0.35$) that are mandated in the waterway. We did, however, determine that some areas are at risk because they experienced population-specific exploitation rates that surpassed the target. Therefore, we recommend that managers consider this risk of
overharvest and implement harvest monitoring programs. Such programs would inform
managers on the area-specific levels of subsistence harvest, which remains an uncertainty in the
waterway, and would monitor angler behaviors that could lead to changes in recently estimated
angling exploitation rates (Herbst et al. 2016). Movement and harvest dynamics observed in our
study area are common in other areas (Rasmussen et al. 2002; Wang et al. 2007; Molton et al.
2013). Therefore, our findings are broadly applicable and highlight that it is critical for managers
to gain an understanding of movement as well as harvest dynamics because both are imperative
for making informed decisions on harvest management. As such, we also recommend that
managers of Walleye populations in other waterways implement tagging studies to gain an
understanding of movement rates. An understanding of movement and harvest dynamics along
with the stochastic simulation framework we used provides a better understanding of complex
system dynamics and leads to informed harvest management decisions.

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Forsyth Kilijanczyk (MDNR Institute for Fisheries Research) for generating the map for the
manuscript. We also acknowledge the useful comments by anonymous reviewers. Funding for
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Fish Fund, and the Robert C. Ball and Betty A. Ball Michigan State University Fisheries and Wildlife Fellowship.

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Inferred from Tag Return and Fisheries Data. Transactions of the American Fisheries
Society 136:539-551.
Table 1: Input parameter values and summaries of distributions used to simulate population and harvest dynamics for Michigan’s Inland Waterway. The initial abundance was set using estimates from a mark-recapture study of spawning Walleye populations in the waterway conducted in 2011. Area-specific angler fishing mortality, spawning-site fidelity, and post-spawn movement rates with their associated 95% credible intervals were estimated from posterior distributions of analyses described by Herbst et al. (2016).

<table>
<thead>
<tr>
<th>Parameter inputs</th>
<th>Burt Lake</th>
<th>Mullett Lake</th>
<th>Crooked Lake</th>
<th>Pickerel Lake</th>
<th>Black River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial abundance</td>
<td>19,464 (2,682)</td>
<td>2,246 (674)</td>
<td>2,360 (465)</td>
<td>4,442 (1,132)</td>
<td>477 (54)</td>
</tr>
<tr>
<td>Fishing mortality</td>
<td>0.25 (0.20, 0.32)</td>
<td>0.18 (0.11, 0.29)</td>
<td>0.27 (0.21, 0.35)</td>
<td>0.18 (0.12, 0.25)</td>
<td>0.16 (0.01, 0.30)</td>
</tr>
<tr>
<td>Spawning-site fidelity</td>
<td>0.99 (0.97, 0.99)</td>
<td>0.58 (0.38, 0.76)</td>
<td>0.96 (0.91, 0.98)</td>
<td>0.80 (0.62, 0.92)</td>
<td>0.92 (0.85, 0.97)</td>
</tr>
<tr>
<td>Movement rates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer Location</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spawning Location</td>
<td>Burt Lake</td>
<td>Mullett Lake</td>
<td>Crooked Lake</td>
<td>Pickerel Lake</td>
<td>Black River</td>
</tr>
<tr>
<td>Burt Lake</td>
<td>0.93 (0.89, 0.96)</td>
<td>0.05 (0.03, 0.08)</td>
<td>0.01 (0.01, 0.02)</td>
<td>0.00 (0.0, 0.01)</td>
<td>0.01 (0.0, 0.04)</td>
</tr>
<tr>
<td>Mullett Lake</td>
<td>0.06 (0.02, 0.13)</td>
<td>0.55 (0.32, 0.91)</td>
<td>0.01 (0.0, 0.02)</td>
<td>0.01 (0.0, 0.03)</td>
<td>0.37 (0.03, 0.61)</td>
</tr>
<tr>
<td>Crooked Lake</td>
<td>0.06 (0.03, 0.11)</td>
<td>0.00 (0.0, 0.01)</td>
<td>0.83 (0.56, 0.91)</td>
<td>0.05 (0.03, 0.08)</td>
<td>0.06 (0.0, 0.32)</td>
</tr>
<tr>
<td>Pickerel Lake</td>
<td>0.11 (0.05, 0.17)</td>
<td>0.01 (0.0, 0.03)</td>
<td>0.19 (0.12, 0.26)</td>
<td>0.65 (0.51, 0.75)</td>
<td>0.04 (0.0, 0.18)</td>
</tr>
<tr>
<td>Black River</td>
<td>0.01 (0.0, 0.07)</td>
<td>0.43 (0.21, 0.85)</td>
<td>0.01 (0.0, 0.02)</td>
<td>0.01 (0.0, 0.03)</td>
<td>0.54 (0.11, 0.76)</td>
</tr>
</tbody>
</table>
Table 2. Symbols and descriptions of symbols used to describe simulated population and harvest dynamics for Walleye in Michigan’s Inland Waterway.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N_{\text{spawn,}i,t} )</td>
<td>No. of fish on spawning grounds and available for subsistence harvest at site ( i ) in yr. ( t )</td>
</tr>
<tr>
<td>( N_{\text{post-sub} \text{subs} \text{istence} \text{,}i,t} )</td>
<td>No. of fish remaining on spawning grounds directly after subsistence harvest at site ( i ) in yr. ( t )</td>
</tr>
<tr>
<td>( N_{\text{summer} \text{,}i,j,t} )</td>
<td>No. of fish that spawned at site ( i ) but exhibited post-spawn and post-sub-subsistence harvest movements to summer site ( j ) in yr. ( t )</td>
</tr>
<tr>
<td>( N_{\text{survivors} \text{,}i,j,t} )</td>
<td>No. of fish that spawned at site ( i ) but survived angling and natural mortality at site ( j ) in yr. ( t ) after post-spawn movement</td>
</tr>
<tr>
<td>( N_{\text{pre-recruit} \text{,}i,t} )</td>
<td>No. of fish alive and on spawning grounds at site ( i ) in yr. ( t ) prior to new recruits being added to the population for that yr.</td>
</tr>
<tr>
<td>( R_{i,t} )</td>
<td>No. of recruits added to the population of fish on spawning grounds and available for subsistence harvest at site ( i ) in yr. ( t )</td>
</tr>
<tr>
<td>( \varphi_{i \rightarrow j} )</td>
<td>Fraction of population of fish spawning at site ( i ) that exhibit post-spawn movement to site ( j )</td>
</tr>
<tr>
<td>( \psi_{i} )</td>
<td>Fraction of population of fish that spawned at site ( i ) during the current yr. that exhibit spawning-site fidelity the following yr.</td>
</tr>
<tr>
<td>( F_{s} )</td>
<td>Instantaneous subsistence fishing mortality rate</td>
</tr>
<tr>
<td>( F_{a,j} )</td>
<td>Median instantaneous angling mortality rate experienced at site ( j )</td>
</tr>
<tr>
<td>( F_{a,j,t} )</td>
<td>Realized instantaneous angling mortality rate experienced at...</td>
</tr>
</tbody>
</table>
site $j$ in yr. $t$

$M$

Median instantaneous natural mortality rate

$M_{j,t}$

Realized instantaneous natural mortality rate experienced at site $j$ in yr. $t$

$Z_{j,t}$

Realized total instantaneous mortality rate experienced at site $j$ in yr. $t$

$\alpha$

Recruits per spawner at low stock size

$\beta$

Degree of compensation

$\varepsilon_{j,t}$

Realized variation in instantaneous mortality at site $j$ in yr. $t$

$\omega_{i,t}$

Realized variation in recruitment at site $i$ in yr. $t$

$\sigma_\varepsilon$

Process error standard deviation for spatial-temporal variation in instantaneous mortality

$\sigma_\omega$

Process error standard deviation for spatial-temporal variation in recruitment
Table 3. Results of deterministic calculations used to determine the influence of post-spawn movements on expected location-specific exploitation rates, assuming maximum exploitation rates are achieved perfectly (i.e., $u_s = 0.10$, $u_a = 0.25$) at all sites within the Inland Waterway. Spawning abundance ($N$) are estimates from a mark-recapture study of spawning Walleye populations in the waterway conducted in 2011. Percent change in summer $N$ resulting for movement was calculated by location as $\left[-\left(\frac{\text{summer } N \text{ without movement}}{\text{summer } N \text{ with movement}}\right) \times 100 \right]$, where summer $N$ with movement was determined using spawning $N$ and the mean post-spawn movement rates presented in Table 1. Relative difference in exploitation ($u$) by location resulting from movement was calculated as $(\frac{\text{Total harvest with movement}}{\text{Spawning } N}) - (\frac{\text{Total harvest without movement}}{\text{Spawning } N})$.

<table>
<thead>
<tr>
<th>Location</th>
<th>Spawning N</th>
<th>% change in summer $N$ resulting from movement</th>
<th>Difference in $u$ by location resulting from movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burt</td>
<td>19,464</td>
<td>-3.0</td>
<td>-0.01</td>
</tr>
<tr>
<td>Mullett</td>
<td>2,246</td>
<td>9.4</td>
<td>0.02</td>
</tr>
<tr>
<td>Crooked</td>
<td>2,360</td>
<td>28.2</td>
<td>0.06</td>
</tr>
<tr>
<td>Pickerel</td>
<td>4,442</td>
<td>-31.7</td>
<td>-0.07</td>
</tr>
<tr>
<td>Black River</td>
<td>477</td>
<td>236.0</td>
<td>0.53</td>
</tr>
</tbody>
</table>
Table 4. Results of mean annual spawning population-specific and area-specific exploitation rates using simulated scenarios that included and excluded estimated movement rates (see Table 1). Results depict outputs from the simulated scenarios that used steady state recruitment, $u_s = 0.10$, and $u_a = \text{realized area-specific mortality rates from within the Inland Waterway.}$

<table>
<thead>
<tr>
<th>Location</th>
<th>Population-specific $u$ With movement</th>
<th>Population-specific $u$ Without movement</th>
<th>Diff in $u$ after accounting for movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burt Lake</td>
<td>0.27</td>
<td>0.28</td>
<td>0.01</td>
</tr>
<tr>
<td>Mullett Lake</td>
<td>0.24</td>
<td>0.24</td>
<td>0.00</td>
</tr>
<tr>
<td>Crooked Lake</td>
<td>0.29</td>
<td>0.28</td>
<td>-0.01</td>
</tr>
<tr>
<td>Pickerel Lake</td>
<td>0.25</td>
<td>0.23</td>
<td>-0.02</td>
</tr>
<tr>
<td>Black River</td>
<td>0.23</td>
<td>0.18</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Location</th>
<th>Area-specific $u$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burt Lake</td>
<td>0.26</td>
</tr>
<tr>
<td>Mullett Lake</td>
<td>0.70</td>
</tr>
<tr>
<td>Crooked Lake</td>
<td>0.29</td>
</tr>
<tr>
<td>Pickerel Lake</td>
<td>0.21</td>
</tr>
<tr>
<td>Black River</td>
<td>0.16</td>
</tr>
</tbody>
</table>

With movement | Without movement | Diff in $u$ after accounting for movement |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Burt Lake</td>
<td>0.26</td>
<td>0.28</td>
</tr>
<tr>
<td>Mullett Lake</td>
<td>0.70</td>
<td>0.24</td>
</tr>
<tr>
<td>Crooked Lake</td>
<td>0.29</td>
<td>0.28</td>
</tr>
<tr>
<td>Pickerel Lake</td>
<td>0.21</td>
<td>0.23</td>
</tr>
<tr>
<td>Black River</td>
<td>0.16</td>
<td>0.18</td>
</tr>
</tbody>
</table>
Table 5. Mean annual exploitation rates by spawning population and area, simulated using different assumptions for recruitment when $u_s = 0.10$ at all sites within the Inland Waterway. Steady state recruitment assumed new recruits perfectly replaced deaths (see methods). The Ricker recruitment models signified low, regional-average, and high productivities (i.e., $\alpha=1.643, 2.768, 6.046,$ respectively) and were based on Walleye populations from Wisconsin described by Tsehaye et al. (2016).

<table>
<thead>
<tr>
<th>Recruitment type</th>
<th>Burt</th>
<th>Mullet</th>
<th>Crooked</th>
<th>Pickerel</th>
<th>Black River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Steady state</td>
<td>0.27</td>
<td>0.24</td>
<td>0.29</td>
<td>0.25</td>
<td>0.23</td>
</tr>
<tr>
<td>Ricker-low</td>
<td>0.27</td>
<td>0.24</td>
<td>0.28</td>
<td>0.25</td>
<td>0.22</td>
</tr>
<tr>
<td>Ricker-Regional</td>
<td>0.28</td>
<td>0.24</td>
<td>0.27</td>
<td>0.25</td>
<td>0.23</td>
</tr>
<tr>
<td>Ricker-high</td>
<td>0.28</td>
<td>0.24</td>
<td>0.29</td>
<td>0.26</td>
<td>0.23</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Exploitation rates by area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burt</td>
</tr>
<tr>
<td>Steady state</td>
</tr>
<tr>
<td>Ricker-low</td>
</tr>
<tr>
<td>Ricker-Regional</td>
</tr>
<tr>
<td>Ricker-high</td>
</tr>
</tbody>
</table>
List of Figures

Figure 1.— Map of northern Michigan’s Inland Waterway that consists of four lakes (Burt, Crooked, Mullett, and Pickerel) and four major connecting rivers (north to south through the lakes: Cheboygan River, Black River, Indian River, and Crooked River).

Figure 2.— Conceptual diagram depicting the process for how each of the spawning populations is tracked and projected through time in the Inland Waterway using stochastic simulation. For simplicity the diagram uses the single spawning population from Burt Lake as an example. The population is subjected to tribal subsistence harvest (i.e., spearing \( u_s \)) within the spawning grounds, whereas after spawning and tribal harvest the spawning populations exhibit post-spawn movements \( \phi \) and are subjected to angling and natural mortality in summer feeding locations. The fraction of the spawning population that survives \( e^{-Z_{BL}} \) during time \( t \) then returns to spawning grounds (i.e., exhibits spawning-site fidelity \( \psi \)) or remains in the location that they resided during summer feeding. New additions represent immigrants from other spawning populations that fail to return to their previous spring spawning population. During time \( t+1 \) the spawning populations are projected forward with the addition of immigrants (fish that moved into Burt Lake but failed to exhibit spawning site fidelity) and recruitment that is specified using either steady state recruitment (i.e., recruits=deaths) or a Ricker stock-recruitment relationship. Locations abbreviations: BL = Burt Lake, ML = Mullett Lake, CL = Crooked Lake, PL = Pickerel Lake, and BR = Black River.

Figure 3.— Exploitation rates for each spawning population (left column) and location (right column) across three scenarios representing combinations of movement, tribal and angling exploitation while assuming steady state recruitment dynamics. The scenarios
represent lake-specific angling mortalities described by Herbst et al. (2016) with differing levels of tribal subsistence exploitation that ranged from 0.05 to 0.20. The red lines indicate the maximum prescribed total exploitation rate ($\nu=0.35$) for each location. Area-specific exploitation rates > 1.0 are possible because movement can increase the number of fish available for angling harvest than was originally present during spawning.
Figure 2
Figure 3