

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

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21 **Abstract.**— Fish populations that exhibit movement patterns present challenges to fishery
22 management. In the Inland Waterway in Michigan’s northern Lower Peninsula, monitoring of
23 Walleye *Sander vitreus* populations and harvest management is difficult because of seasonal
24 intermixing among interconnected lakes and the presence of both tribal subsistence fishing and
25 recreational-angling fisheries that occur during discrete time periods. We used stochastic
26 simulation to determine the influence of movement and harvest dynamics on the performance of
27 harvest management targets for Walleye in our study system. After accounting for post-spawn
28 movement and harvest dynamics, our results indicated that population-specific exploitation rates
29 on average did not exceed the target rates ($u = 0.35$) that are mandated in the waterway. We did,
30 however, determine that some areas are at risk because they experienced population-specific
31 exploitation rates that surpassed the target. We also determined that the interplay between
32 movement and uncertain population and harvest dynamics will likely determine the ability of
33 management to meet currently accepted harvest targets on average over time, as well as the risk
34 of exceeding harvest targets each year. Our findings are broadly applicable for mobile species
35 inhabiting lake-chains and highlight that it is critical for managers to gain an understanding of
36 movement as well as harvest dynamics because both are imperative for understanding how these
37 dynamics influence harvest management performance. As such, we recommend that managers of
38 Walleye populations in other waterways implement tagging studies and harvest monitoring
39 programs to gain an understanding of movement rates and harvest dynamics. An understanding
40 of movement and harvest dynamics along with the stochastic simulation framework we used
41 provides a better understanding of complex system dynamics and leads to informed harvest
42 management decisions.

43

Introduction

44
45 Many harvested fish species exhibit seasonal movements that result in complex
46 intermixing of populations. Such intermixing creates challenges for managers tasked with
47 determining catch limits and implementing harvest management strategies (Ying et al. 2011;
48 Molton et al. 2012; Brenden et al. 2015). For example, studies have illustrated that the risk of
49 overexploitation can exceed desirable levels when harvesting intermixed stocks unless
50 management strategies explicitly account for movement and the spatial ecology of the species
51 being harvested (Morishima and Henry 1999; Ames 2004; Hutchinson 2008). Movement studies
52 can therefore be highly informative for harvest management by describing the magnitude and
53 seasonality of movement patterns (Rasmussen et al. 2002; Wang et al. 2007; Herbst et al. 2016).
54 Such information is often unavailable to inform management of mixed-stock harvests in inland
55 systems, however, and management therefore commonly proceeds under the assumption that fish
56 stocks from interconnected waterbodies are isolated and discrete populations (Patrick Hanchin,
57 Michigan Department of Natural Resources, personal communication). While this pragmatic
58 simplifying assumption is common for inland fisheries management, the associated risks of
59 ignoring movement and the implications for harvest management are often poorly understood.

60 Walleye *Sander Vitreus* are an economic and culturally important species that occupy
61 interconnected, inland lake-chain systems throughout the upper Great Lakes region (Schmalz et
62 al. 2011). Walleye harvest management in treaty-ceded territories of the northern Great Lakes
63 often consists of harvest that is shared between two distinct fisheries, with tribal subsistence
64 harvest occurring on spawning grounds and recreational angling harvest occurring after the
65 spawning season (e.g., Rasmussen et al. 2002; Herbst et al. 2016). Moreover, co-management of
66 these fisheries among sovereign tribal nations and states is often guided by target reference

67 points that specify maximum desirable exploitation rates for subsistence and angling harvests,
68 where harvest targets are believed to be biologically sustainable and pose a low risk of
69 overexploitation for Walleye in the Great Lakes region (e.g., Staggs et al. 1990; U.S. v. Michigan
70 2007; Schueller et al. 2008). In the Great Lakes region such management policies for Walleye
71 populations are often legally mandated through the results of past litigation and the legal
72 negotiations that followed.

73 The Inland Waterway of northern Michigan (hereafter the waterway; Fig. 1) is an
74 example of a lake-chain system within the 1836 treaty-ceded territory that supports both
75 subsistence and recreational Walleye fisheries. Management of Walleye populations in the
76 waterway is based on a federally mandated agreement between the state of Michigan and Native
77 American Tribes referred to as the 2007 Inland Consent Decree (U.S. v. Michigan 2007). Within
78 the agreement lakes are managed as individual closed populations irrespective of their
79 connectivity to other waterbodies within the waterway. Walleye populations at individual sites
80 within the waterway experience tribal subsistence harvest that occurs as a pulse fishery during
81 the spawning season (late-March through April), whereas the recreational fishery harvests
82 intermixed populations during the state-regulated angling season that occurs later in the year and
83 over a much longer duration (i.e., late-April through mid-March of the next calendar year).
84 Under the 2007 Inland Consent Decree, the target maximum exploitation rate of 0.35 (i.e., $u \leq$
85 0.35) is partially allocated to the tribal subsistence fishery ($u_s \leq 0.10$) and the recreational angling
86 fishery ($u_a \leq 0.25$). While the biological sustainability of this mandated exploitation rate has
87 never been evaluated due to data limitations (e.g., limited stock-recruitment information; but see
88 Tsehaye et al. 2016), the legally negotiated and agreed upon maximum exploitation rate of 0.35

89 was based on findings from previously published harvest simulations for Walleye in northern
90 Wisconsin that suggested $u \leq 0.35$ had a low risk of overexploitation (Beard et al. 2003).

91 Despite the common occurrence of legally mandated maximum exploitation rates for
92 Walleye populations in the Great Lakes region, understanding of performance for Walleye
93 harvest management strategies in the waterway and similar systems is complicated by a high
94 degree of uncertainty surrounding population and harvest dynamics. While Walleye populations
95 at individual sites within interconnected systems are often assumed to be closed to movement
96 and stock intermixing, recent studies demonstrated that populations within the waterway exhibit
97 asymmetrical post-spawn movements and spawning site-fidelity (Herbst et al. 2016). Such
98 movements results in seasonal intermixing of spawning stocks after the spawning period (Herbst
99 et al. 2016). Thus, subsistence and angling exploitation at the same spatial locations remove
100 individuals from different groups of fish, and the implications of movement for Walleye harvest
101 management in this and similar systems are poorly understood. Moreover, there is also
102 uncertainty regarding the realized exploitation rates being experienced by local spawning
103 populations under current regulatory mechanisms, and no data exist to rigorously estimate
104 population-specific subsistence exploitation rates. Similarly, angling harvest regulations are
105 intended to result in $u_a \leq 0.25$, yet realized angling exploitation rates were only recently
106 estimated, and determined to be variable among sites within the waterway (Herbst et al. 2016).
107 The combination of asymmetric inter-lake movements and uncertain implementation of existing
108 target exploitation rates therefore creates concern among fishery managers as to the risks of
109 current harvest management, and the ability of management to achieve the legally mandated
110 maximum exploitation rates that are currently in place.

111

112 Thus, the purpose of our study was to determine the implications of movements and
113 uncertain system dynamics on harvest management for Walleye populations in the waterway,
114 and provide advice to managers in light of these complexities. Specifically, our objective was to
115 determine the effects of post-spawn intermixing and uncertain population and harvest dynamics
116 on the ability to achieve target exploitation rates for spawning Walleye populations within the
117 waterway. While this study is evaluating performance of management that is specific to northern
118 Michigan, similar systems exist across the upper Great Lakes region for Walleye and other
119 valuable species. Thus we address long-standing issues of concern for management of
120 intermixed populations that are broadly relevant to other lake-chain systems.

121

122

Methods

Study area

124 Michigan's Inland Waterway is an interconnected chain of lakes located in the northern
125 Lower Peninsula consisting of four lakes (Burt, Crooked, Mullett, and Pickerel) interconnected
126 by a series of rivers and smaller tributaries (Figure 1). The Cheboygan Lock and Dam on the
127 Cheboygan River, and the Alverno Dam on the Black River located at the northern portion of the
128 Inland Waterway, restrict fish passage and are considered closed to emigration to Lake Huron or
129 further upstream within the Black River (Figure 1). The lakes and rivers of the waterway are
130 oligotrophic, provide various levels of suitable Walleye spawning substrate and prey resources,
131 and range from 4.4 km² (Pickerel Lake) to 70.4 km² (Burt Lake) in total size (Hanchin et al.
132 2005a; Hanchin et al. 2005b).

133

General approach

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

145 In addition to the deterministic calculations, we used stochastic simulation to assess the
146 ability of management to achieve target exploitation rates for Walleye populations in the
147 presence of inter-lake movements and uncertainty about population and harvest dynamics. We
148 developed a set of simulation scenarios that started with potential values for the unknown
149 subsistence exploitation rate (three levels) and movement scenarios (two levels). Within each
150 scenario subsistence exploitation rates were held at fixed values for across all sites, where these
151 rates determined harvest experienced by spawning populations at each site within the waterway.
152 In contrast, implementation uncertainty affected the angling exploitation rates experienced by
153 spawning-stock aggregates on summer feeding grounds throughout the waterway (described
154 below), where distributions of angling exploitation rates were consistent with area-specific
155 estimates for fish on summer grounds described recently (Herbst et al. 2016). Moreover, all
156 harvest simulations were replicated over two movement scenarios: 1) closed populations with no
157 movements among sites, and 2) asymmetrical post-spawn movements with distributions of post-

158 spawn movement and spawning-site fidelity parameters estimated for Walleye populations
159 within the waterway (Herbst et al. 2016). Because recruitment dynamics for lakes in this system
160 are poorly understood, our baseline simulation model assumed recruitment that produced steady-
161 state dynamics for each spawning population (i.e., recruits = deaths). However, performance of
162 management may be dependent upon stock-recruitment dynamics (Deroba and Bence 2008), and
163 thus we conducted a sensitivity analysis to determine robustness of our conclusions to plausible
164 stock-recruitment relationships by replicating all simulations with three plausible forms of a
165 Ricker model developed for Walleye populations in the Great Lakes region (using parameter
166 estimates from Tsehaye et al. (2016)). Thus, a total of 24 distinct simulation scenarios were used
167 to evaluate the ability of management to achieve target exploitation rates in the presence of
168 uncertain population and harvest dynamics, and robustness of conclusions to such uncertainties.

169

170 *Simulated Population and Harvest Dynamics*

171 We simulated population and harvest dynamics for Walleye spawning within the Inland
172 Waterway using forward population projections (Figure 2). We simulated each scenario for
173 1,000 replications, each with a 50-year population projection to ensure that transient dynamics in
174 the initial years did not obscure the long-term performance of management. For each population
175 projection we initiated simulations in year $t = 1$ by starting lake-specific spawner abundances at
176 values equal to mark-recapture (M-R) estimates of abundance from a field study conducted
177 within the waterway in 2011 (estimated via the Lincoln-Peterson estimator with the Chapman
178 modification using mark-recapture, Michigan Department of Natural Resources unpublished
179 data). The forward projection model then assumed that subsistence harvest removed individuals
180 from spawning populations at each site i ($N_{spawn,i,t}$) in each year t , after which the remaining

181 individuals at each site ($N_{post-subsistence,i,t}$) exhibited post-spawn movements onto summer
 182 feeding grounds. Once on summer feeding grounds, all fish summering at a given area j
 183 experienced area-specific natural and angling mortality identically irrespective of which
 184 spawning population they originated from. Fish that survived angling and natural mortality over
 185 the summer at site j exhibited spawning-site fidelity and returned to their previous spawning
 186 location to spawn in year $t+1$ (with rate ψ_i for populations spawning at site i) or remained on
 187 their summer foraging grounds and joined the spawning population at site j in year $t+1$ (with rate
 188 $1 - \psi_i$ for all i). New recruits were also added to each population when $t > 1$, and thus the total
 189 spawning population available for spearing harvest at site i in future years was the number of
 190 surviving individuals minus losses due to emigration, plus gains due to immigration and
 191 recruitment. Age-structure was not included in our simulation model because information about
 192 age and growth for Walleye populations in the Inland Waterway are not available.

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

$$196 \quad N_{post-subsistence,i,t} = N_{spawn,i,t} e^{-F_s}, \quad (1)$$

197 where F_s is the instantaneous subsistence fishing mortality rate and e^{-F_s} is the fraction of the
 198 spawning population that survives subsistence harvests, and thus $N_{post-subsistence,i,t}$ refers to the
 199 population of spawners remaining after tribal subsistence harvest at site i in year t . We lacked
 200 information to reliably estimate subsistence exploitation rates, so we replicated simulations over
 201 a discrete set of values for F_s that resulted in subsistence exploitation rates of 0.05, 0.10, and 0.20
 202 to cover a range of exploitation rates currently deemed plausible by regional fishery biologists
 203 (i.e., from half to twice current target exploitation rates). Moreover, in our simulations F_s was

204 assumed to apply uniformly across all spawning sites because information about the degree of
205 spatial heterogeneity in subsistence harvest was unavailable.

206 Following subsistence harvest, individuals from spawning populations at each site
207 exhibited post-spawn movements to locations where they experienced recreational angling and
208 natural mortality (Figure 2). For simulation scenarios with inter-lake movement we used
209 $N_{post-subistence,i,t}$ and estimated post-spawn movement rates (Herbst et al. 2016) to determine
210 the abundance of fish at each feeding location j that were available for recreational-angling
211 harvest. Specifically, for each of the 1,000 simulation replicates we randomly drew a matrix of
212 movement rates from Markov chain Monte Carlo (MCMC) samples of their joint posterior
213 distribution (described by Herbst et al. 2016) to determine time-invariant post-spawn movement
214 rates ($\varphi_{i \rightarrow j}$ = movement from spawning site i to summer location j) (Table 1). Thus, the number
215 of fish that spawned at site i but then moved to site j directly after spawning in year t
216 ($N_{summer,i,j,t}$) was simply the number of fish alive after subsistence harvest multiplied by inter-
217 lake movement rates:

$$218 \quad N_{summer,i,j,t} = \varphi_{i \rightarrow j} N_{post-subistence,i,t}. \quad (2)$$

219 The total number of fish at each summer location j after post-spawn movements in any given
220 year was therefore the sum of individuals that moved into site j after spawning earlier within the
221 same year ($\sum_i \varphi_{i \rightarrow j} N_{post-subistence,i,t}$). For simulation scenarios that assumed no inter-lake
222 movement we used a diagonal matrix of movement parameters for each simulation replicate,
223 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 $i \neq j$).

224 After post-spawn movements, fish were removed from summer sites via year- and
225 location-specific natural ($M_{j,t}$) and angling mortality ($F_{a,j,t}$), where realized values of these
226 parameters varied annually as a function of site- and time-specific process variation ($\varepsilon_{j,t}$). The

227 number of fish from spawning population i that survived angling and natural mortality at a given
 228 summer location ($N_{survivors,i,j,t}$) was the product of the number of fish at the site and the
 229 survival rate:

$$230 \quad N_{survivors,i,j,t} = N_{summer,i,j,t} e^{-Z_{j,t}}, \quad (3)$$

231 where

$$232 \quad Z_{j,t} = (F_{a,j} + M) e^{\varepsilon_{j,t}}. \quad (4)$$

233 In this model $Z_{j,t}$ is total realized instantaneous mortality for a given summer location and year
 234 and is equal to the sum of median angling ($F_{a,j}$) and natural mortality rates ($M = 0.3$) multiplied
 235 by a multiplicative process error ($\varepsilon_{j,t}$) that effectively accounted for spatial-temporal variation in
 236 mortality. For each time step within each simulation replicate we randomly drew process error
 237 terms from a normal distribution ($\varepsilon_{j,t} \sim Normal(0, \sigma_\varepsilon)$), where $\sigma_\varepsilon = 1.53$ was estimated using
 238 the posterior mean calculated from MCMC samples of the process variation parameter described
 239 by Herbst et al. (2016). To account for uncertainty in area-specific angler exploitation, we
 240 randomly drew a vector of time invariant median angling mortality rates for each simulation
 241 replicate from MCMC samples of their joint posterior distribution (described by Herbst et al.
 242 2016; Table 1).

243 After angling and natural mortality at summer locations in year t , fish moved to spawning
 244 locations where they reproduced and experienced subsistence harvest at time $t+1$ (Figure 2). Fish
 245 that survived at each summer feeding location either returned to the same spawning population
 246 that they belonged to in year t or remained in place to join the spawning population in the
 247 location where they summered in the current year. Specifically, fish that spawned at site i during
 248 year t exhibited spawning-site fidelity and returned to the same spawning population at a rate of
 249 ψ_i at the start of year $t+1$, irrespective of where they summered in year t , whereas $1 - \psi_i$ of fish

250 that spawned at site i remained to join the spawning population at their summer location in year
 251 $t+1$. For simplicity, however, we assumed all surviving fish that did not disperse to a summer
 252 area different than their spawning location in year t (i.e., stayed at site i for all of year t) stayed to
 253 spawn at the same location in year $t+1$. Thus, $N_{spawn,i,t+1}$ was the sum of survivors over time t
 254 that never left site i during year t , fish that spawned at site i at time t but survived at another
 255 summer location and then exhibited spawning site fidelity, fish that spawned in another location
 256 at time t but survived the summer at site i and then failed to return to their previous spawning
 257 population (and thus joined the spawning population at site i), and new recruits into the spawning
 258 population at site i :

$$259 \quad N_{spawn,i,t+1} = N_{survivors,i,i,t} + \sum_{j \neq i} N_{survivors,i,j,t} \psi_i + \sum_{j \neq i} N_{survivors,j,i,t} (1 - \psi_j) + R_{i,t}. \quad (5)$$

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

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

$$270 \quad R_{i,t} = N_{spawn,i,t-1} (1 - e^{-F_s}) + \sum_j (1 - e^{-(Z_{j,t-1})}) N_{summer,i,j,t-1}. \quad (6)$$

271 This approach to modeling recruitment was a pragmatic solution to the problem of having
 272 insufficient data to parameterize a stock recruitment model for spawning populations within the

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

$$282 \quad R_{i,t} = \alpha N_{pre-recruit,i,t} e^{-\beta N_{pre-recruit,i,t} + \omega_{i,t}}, \quad (7)$$

283 and $N_{pre-recruit,i,t}$ is determined by equation 5 but without the addition of new recruits ($R_{i,t}$).
284 Here the values of α and β , as well as the distribution of spatial-temporal variation in
285 recruitment ($\omega_{i,t} \sim Normal(0, \sigma_\omega)$) were described via hierarchical modeling of stock-
286 recruitment dynamics for Walleye populations in northern Wisconsin lakes by Tsehaye et al.
287 (2016). Specifically, we considered three scenarios of productivity by replicating simulations
288 over low, regional average, and high values of α (1.643, 2.768, 6.046), whereas β was held at the
289 regional average (0.049) and $\sigma_\omega = 1.964/3$ was consistent with values assumed in harvest
290 simulations described by Tsehaye et al. (2016). Stock-recruitment parameters were held constant
291 among all sites for all simulations because no information about spatially-heterogeneous
292 recruitment dynamics was available for this system.

293

294 *Performance metrics*

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

$$307 \quad H_{Total,i,t} = H_{s,i,t} + H_{a,i,t}, \quad (8)$$

$$308 \quad H_{s,i,t} = N_{spawn,i,t}(1 - e^{-F_s}), \quad (9)$$

309 and

$$310 \quad H_{a,i,t} = \sum_j \frac{F_{a,j,t}}{Z_{j,t}} \left(1 - e^{-(Z_{j,t})}\right) N_{summer,i,j,t}. \quad (10)$$

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

313 $N_{spawn,j,t}(1 - e^{-F_s}) + \frac{F_{a,j,t}}{Z_{j,t}} \left(1 - e^{-(Z_{j,t})}\right) \sum_i N_{summer,i,j,t}$) by the abundance of spawners alive

314 at that site in the beginning of the same year ($N_{spawn,j,t}$). Although area-specific exploitation

315 rates may be less biologically meaningful than exploitation rates experienced by spawning

316 populations in the presence of movement, they are likely more representative of the types of

317 information that may be available to managers, for instance if abundance is estimated on
318 spawning grounds and total catch estimates were available for both subsistence and angling
319 harvests at a given site. Moreover, because we were interested in the ability of management to
320 meet the target exploitation rate (i.e., $u \leq 0.35$) for each population in a given year, we focused
321 summary of performance metrics to simulated distributions of harvests on the final simulation
322 year.

323

324

Results

Deterministic calculations

326 Post-spawn movement resulted in spatial intermixing of individuals from each spawning
327 population and affected the abundance, and consequently the area-specific exploitation rates of
328 Walleye populations. Deterministic calculations showed that post-spawn movements resulted in
329 expected changes in summer abundance ranging from a net loss of 31.7% at Pickerel Lake to a
330 net gain of 236% in the Black River, while Burt, Mullett, and Crooked lakes changed by -3.0,
331 9.4, and 28.2 percent (Table 3). As such, the expected exploitation for each area changed by
332 including post-spawn movements when $u_s = 0.10$ and $u_a = 0.25$. For example, the expected net
333 loss of individuals from Pickerel Lake resulted in fewer individuals available for angling harvest
334 in that lake, and therefore the realized exploitation rate for that lake was reduced by 0.07 relative
335 to that expected with identical exploitation rates when assumed closed to post-spawn movements
336 (Table 3). In contrast, Crooked Lake had an expected net increase in abundance during the
337 angling season and therefore had an expected increase in area-specific exploitation rate because
338 the increased summer abundance resulted in more fish being harvested when $u_a = 0.25$ (Table 3).
339 Thus to achieve a system wide target angling exploitation rate of 0.25, area-specific angling

340 exploitation rates would need to be adjusted for each summer location to account for net losses
341 and gains of individuals due to post-spawn movement (Table 3). For example, Mullett, Crooked
342 Lake, and the Black River could withstand increased angling exploitations (relative to closed
343 population target angling exploitation rates) because they were recipient locations of individuals
344 from other spawning populations. In contrast, to achieve the target angling exploitation rate ($u_a =$
345 0.25) for the waterway as a whole the target angling exploitation rates would need to be
346 decreased in locations that had net losses (i.e., Burt and Pickerel lakes) of individuals (Table 3).

347

348 *Stochastic simulations*

349 In the presence of uncertain population and harvest dynamics, realized area-specific and
350 population-specific exploitation rates varied, but on average remained < 0.35 . Total spawning
351 population exploitation rates generally did not exceed the management target of $u \leq 0.35$ on
352 average, even for scenarios with high realized subsistence exploitation rates (Figure 3). The
353 exception was the Crooked Lake spawning population, which had a mean exploitation rate of
354 0.36 when the highest level of tribal subsistence exploitation was paired with estimated angling
355 mortality (Figure 3). Although the mean population-specific exploitation rates were below the
356 target, the spreads of the distributions of realized exploitation rates were quite wide, and the
357 interquartile ranges of simulated exploitation rates often exceeded 0.35. Burt and Crooked lake
358 spawning populations, for instance, both experienced population-specific exploitation rates that
359 surpassed the target during approximately 20% and 50% of the simulations when $u_s = 0.10$ and
360 0.20, respectively (Figure 3). Thus, risks of exceeding target exploitation rates in any given year
361 were sometimes large, despite achievement of target exploitation rates on average in simulations.

362 Total area-specific exploitation rates on average generally did not exceed the
363 management target of $u \leq 0.35$, even for scenarios with high realized subsistence exploitation
364 rates (Figure 3). The exception was the Mullett Lake area-specific exploitation rate that was
365 greater than 1.0, which illustrated that this location had the greatest net gain of fish from other
366 spawning populations. Thus, a greater number of fish are removed with a consistent realized
367 angling exploitation rate, and when total area-specific harvest is divided by spawning abundance
368 at Mullett Lake, the number harvested exceeded the spawning abundance. The elevated Mullett
369 Lake area-specific u was due to the influx of fish from other sites after post-spawn movement. In
370 contrast, other locations in the waterway had location-specific exploitation rates that were
371 relatively close to or less than the desired exploitation rate (Figure 3), even when $u_s = 0.20$,
372 indicating that for these sites area-specific exploitation rates should on average be at desirable
373 levels in the presence of movement and uncertain population and harvest dynamics.

374 Post-spawn movement had a greater influence on area-specific exploitation rates under
375 the scenarios that we simulated. In the presence of movement the population-specific and area-
376 specific exploitation rates differed as much as 0.46 (Table 4). The difference in the two
377 exploitation rates was greater for areas that received a large net change of individuals during the
378 angling season, such as Mullett Lake (Table). The large discrepancy between the population-
379 specific and the area-specific exploitation rates was caused by the redistribution and net change
380 in the number of fish available for harvest during the angling season. The other important aspect
381 to consider when interpreting these rates is that area- and population-specific harvest is divided
382 by the spawning population abundance, which is assessed in the spring prior to movement. Thus,
383 the area-specific exploitation disregards which spawning population the harvested individuals
384 belong to, but instead simply accounts for all fish harvested in that particular area. The influence

385 of post-spawn movement was less pronounced in areas that had a lower overall net change in the
386 number of fish available for harvest during the angling season (Table 4). The comparison of
387 exploitation rates between the scenario that included and excluded movement also indicated that
388 with movement the two exploitation rates differed, even if only slightly. However, when
389 excluding movement the area-specific and population-specific exploitation rates were identical,
390 as anticipated (Table 4).

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

398

399 **Discussion**

400 Stochastic simulations allowed us to achieve our goal of determining the implications of
401 movement and uncertain system dynamics on harvest management for Walleye populations in an
402 interconnected lake chain. The strengths and flexibility of using a simulation framework make
403 the approach advantageous for addressing complex issues associated with incorporating spatial
404 ecology into management strategy evaluation (Goethel et al. 2011; Molton et al. 2013; Li et al.
405 2014). Our approach allowed us to incorporate estimated population parameters (e.g., movement
406 and fishing mortality rates), while also providing the flexibility to account for uncertainties in
407 population and harvest dynamics in our study area. Simulation outputs illustrated the

408 implications and complexities of post-spawn movement when attempting to achieve harvest
409 management objectives for Walleye populations in a lake-chain system. Our approach could
410 greatly benefit managers in other waterways that have complex population and harvest
411 dynamics, similar to what was observed for our study area (Rasmussen et al. 2002; Wang et al.
412 2007; Herbst et al. 2016).

413 We determined the implications of post-spawn movement and uncertain population
414 dynamics for achievement of target exploitation rates for Walleye populations in the Inland
415 Waterway. These results demonstrated that area-specific angling exploitation rates would need to
416 be adjusted away from 0.25 in order to achieve a population-specific total $u \leq 0.35$ after
417 accounting for asymmetrical post-spawn movements. In general, however, our stochastic
418 simulations showed that mean total exploitation for most spawning populations would likely be
419 < 0.35 under current levels of angling exploitation and post-spawn movement within the
420 waterway, and this result was robust across uncertain rates of subsistence exploitation and
421 recruitment models. Moreover, even though exploitation rates were within the desirable range on
422 average, there was considerable risk of a realized total $u > 0.35$ in any given year. Thus the
423 interplay between movement and uncertain population and harvest dynamics will likely
424 determine the ability of management to meet currently accepted harvest targets on average over
425 time, as well as the risk of exceeding harvest targets each year.

426 The ability to achieve total exploitation rates on average that were below the target
427 maximum in the presence of asymmetrical movements likely resulted from our study area having
428 angling mortality rates that were on the low end of what has been reported in other studies
429 (Baccante and Colby 2003; Schmalz et al. 2011). For instance, Schmalz et al. (2011) summarized
430 documented Walleye exploitation rates over a broad geographic range and reported exploitation

431 rates greater than 0.35 and as high as approximately 0.50. Such larger exploitation rates in
432 Wisconsin lakes have led to the decline of adult Walleye populations in some areas (Schueller et
433 al. 2005; Schmalz et al. 2011) As such, management concerns could arise in the future if angling
434 exploitation rates increase to levels experienced in other locations (Baccante and Colby 2003;
435 Schmalz et al. 2011). These results highlight the importance of continued monitoring of angling
436 exploitation rates to ensure current harvest regulations do not result in harvests that exceed target
437 levels.

438 In this study we demonstrated that achievement of target exploitation rates on average
439 was robust to several models of recruitment dynamics, but we were limited in our ability to
440 incorporate lake-specific recruitment based on empirical estimates of stock productivity.
441 Determining the productive capacity of fish populations is a challenging process which often
442 requires a relatively long time series of stock and recruitment data (Hilborn and Walters 1992).
443 Because such data are not available for the waterway, we used multiple recruitment models and
444 tested the sensitivity of simulated exploitation rates among models. Our steady-state recruitment
445 model implicitly assumed variable levels of productivity among the spawning populations by
446 setting recruitment at a value consistent with the harvest from each population. Under this model,
447 more abundant spawning populations that currently support a greater harvest (e.g., Burt Lake
448 spawning population) were also assumed to have a higher level of recruitment. We also used
449 Ricker stock-recruitment models that were parameterized using results from studies of Walleye
450 populations in Wisconsin (Tsehaye et al. 2016). We demonstrated that simulated total
451 exploitation rates were, on average, relatively consistent among recruitment models, and most
452 scenarios resulted in similar achievement of harvest targets. Although our sensitivity analysis
453 used different recruitment models, the Ricker models were constrained by the assumption that

454 each spawning population in the waterway had the same productivity. While this may not be an
455 entirely realistic portrayal of Walleye population dynamics for this study system, this assumption
456 reflected the data available for model development, and a full assessment of the implications of
457 spatially heterogeneous recruitment for Walleye harvest management in the waterway was
458 beyond the scope of this study. Because performance of harvest policies is likely to depend on
459 recruitment dynamics, however, there is a clear need to develop an understanding of spatial
460 heterogeneity of Walleye population dynamics in northern Michigan. The addition of more
461 realistic, spatially-heterogeneous recruitment models would thus provide managers more
462 confidence in the effectiveness of current management systems by adding further realism to
463 simulation-based evaluations of Walleye harvests (e.g., Schueller et al. 2008; Tsehaye et al.
464 2016).

465 Walleye harvest management in the northern Great Lakes region is frequently dependent
466 upon target exploitation rates and an understanding of the implications of such rates for
467 accomplishing conservation goals. The appropriateness of current target exploitation rates is a
468 concern among managers, especially with documented regional declines in Walleye populations
469 (Hansen et al. 2015). As our study system illustrates, however, Walleye managers frequently
470 lack the necessary information to assess adequacy of existing harvest targets because of limited
471 resources and the vast number of lakes (i.e., > 10,000s) in the ceded-territory of the northern
472 Great Lakes region. Tsehaye et al. (2016) recently suggested that $u = 0.35$ for some Walleye
473 populations in northern Wisconsin would lead to their collapse, and determined that the optimal
474 exploitation rate was approximately 0.20 for the average population in that region. Using
475 different methods and data, Lester et al. (2014) suggested an optimal exploitation rate for
476 Walleye harvest management of $0.75 * M$. Using the Lester et al. (2014) method, the optimal

477 harvest rate for our study area would be approximately 0.23 based on the assumption that median
478 $M = 0.3$. Results from these recent studies therefore illustrate that exploitation targets for our
479 study system might lead to population decline, especially if stocks exhibit low productivity
480 (Tsehaye et al. 2016). Our simulation indicated that on average management may be likely to
481 achieve current target exploitation rates. Unfortunately, however, we lack sufficient
482 understanding of recruitment dynamics to determine the long-term sustainability of these targets
483 in light of recent studies suggesting 0.35 may be inappropriate.

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

496 Monitoring exploitation rates is often conducted through creel programs that track
497 harvest, but interpretation of rates calculated through monitoring programs can be misleading
498 because of seasonal intermixing. Exploitation rates for subsistence and angling fisheries are
499 calculated as the number harvested divided by the abundance and populations are typically

500 assessed during the spring when distinct spawning populations are segregated by location. When
501 post-spawn movement occurs, however, the abundance at each location during the angling
502 season differs from the spawning assessment. As such, the post-spawn movement directly
503 influences the area-specific angling exploitation rate because angling harvest by area is divided
504 by the spawning abundance for that same area. The differences between our area-specific and
505 population-specific exploitation rates indicated that the common approach of calculating
506 exploitation rates from the angling harvest monitoring programs and assuming those rates apply
507 to directly to the spawning populations are not appropriate when intermixing occurs. This finding
508 supports, and provides context to the magnitude of the regional concern raised by Rasmussen et
509 al. (2002) of setting angling harvest levels for Walleye fisheries that are based solely on spring-
510 spawning population assessments, and therefore overlook post-spawn movements. Our results on
511 the interpretation of exploitation rates have broad applicability because many exploited
512 populations' exhibit seasonal movement patterns (Rasmussen et al. 2002; Wang et al. 2007;
513 Herbst et al. 2016). A comprehensive understanding of how movement influences the
514 interpretation of exploitation rates will lead to managers implementing actions that are more
515 likely to achieve conservation goals.

516 In summary, we used stochastic simulations to determine the harvest management
517 implications of post-spawn movement and harvest dynamics for Walleye populations in an
518 interconnected lake-chain in northern Michigan. After accounting for post-spawn movement and
519 harvest dynamics, our results indicated that population-specific exploitation rates on average did
520 not exceed the target rates ($u = 0.35$) that are mandated in the waterway. We did, however,
521 determine that some areas are at risk because they experienced population-specific exploitation
522 rates that surpassed the target. Therefore, we recommend that managers consider this risk of

523 overharvest and implement harvest monitoring programs. Such programs would inform
524 managers on the area-specific levels of subsistence harvest, which remains an uncertainty in the
525 waterway, and would monitor angler behaviors that could lead to changes in recently estimated
526 angling exploitation rates (Herbst et al. 2016). Movement and harvest dynamics observed in our
527 study area are common in other areas (Rasmussen et al. 2002; Wang et al. 2007; Molton et al.
528 2013). Therefore, our findings are broadly applicable and highlight that it is critical for managers
529 to gain an understanding of movement as well as harvest dynamics because both are imperative
530 for making informed decisions on harvest management. As such, we also recommend that
531 managers of Walleye populations in other waterways implement tagging studies to gain an
532 understanding of movement rates. An understanding of movement and harvest dynamics along
533 with the stochastic simulation framework we used provides a better understanding of complex
534 system dynamics and leads to informed harvest management decisions.

535

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633 Ying, Y., Y. Chen, L. Lin, and T. Gao. 2011. Risks of ignoring fish population spatial structure
634 in fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 68:2101-
635 2120.

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

Parameter inputs	Burt Lake	Mullett Lake	Crooked Lake	Pickerel Lake	Black River
Initial abundance	19,464 (2,682)	2,246 (674)	2,360 (465)	4,442 (1,132)	477 (54)
Fishing mortality	0.25 (0.20, 0.32)	0.18 (0.11, 0.29)	0.27 (0.21, 0.35)	0.18 (0.12, 0.25)	0.16 (0.01, 0.30)
Spawning-site fidelity	0.99 (0.97, 0.99)	0.58 (0.38, 0.76)	0.96 (0.91, 0.98)	0.80 (0.62, 0.92)	0.92 (0.85, 0.97)
Movement rates	Summer Location				
Spawning Location	Burt Lake	Mullett Lake	Crooked Lake	Pickerel Lake	Black River
Burt Lake	0.93 (0.89, 0.96)	0.05 (0.03, 0.08)	0.01 (0.01, 0.02)	0.00 (0.0, 0.01)	0.01 (0.0, 0.04)
Mullett Lake	0.06 (0.02, 0.13)	0.55 (0.32, 0.91)	0.01 (0.0, 0.02)	0.01 (0.0, 0.03)	0.37 (0.03, 0.61)
Crooked Lake	0.06 (0.03, 0.11)	0.00 (0.0, 0.01)	0.83 (0.56, 0.91)	0.05 (0.03, 0.08)	0.06 (0.0, 0.32)
Pickerel Lake	0.11 (0.05, 0.17)	0.01 (0.0, 0.03)	0.19 (0.12, 0.26)	0.65 (0.51, 0.75)	0.04 (0.0, 0.18)
Black River	0.01 (0.0, 0.07)	0.43 (0.21, 0.85)	0.01 (0.0, 0.02)	0.01 (0.0, 0.03)	0.54 (0.11, 0.76)

640

641

642 Table 2. Symbols and descriptions of symbols used to describe simulated population and harvest
 643 dynamics for Walleye in Michigan’s Inland Waterway.

Symbol	Description
$N_{spawn,i,t}$	No. of fish on spawning grounds and available for subsistence harvest at site i in yr. t
$N_{post-subistence,i,t}$	No. of fish remaining on spawning grounds directly after subsistence harvest at site i in yr. t
$N_{summer,i,j,t}$	No. of fish that spawned at site i but exhibited post-spawn and post-subistence harvest movements to summer site j in yr. t
$N_{survivors,i,j,t}$	No. of fish that spawned at site i but survived angling and natural mortality at site j in yr. t after post-spawn movement
$N_{pre-recruit,i,t}$	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.
$R_{i,t}$	No. of recruits added to the population of fish on spawning grounds and available for subsistence harvest at site i in yr. t
$\varphi_{i \rightarrow j}$	Fraction of population of fish spawning at site i that exhibit post-spawn movement to site j
ψ_i	Fraction of population of fish that spawned at site i during the current yr. that exhibit spawning-site fidelity the following yr.
F_s	Instantaneous subsistence fishing mortality rate
$F_{a,j}$	Median instantaneous angling mortality rate experienced at site j
$F_{a,j,t}$	Realized instantaneous angling mortality rate experienced at

	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
α	Recruits per spawner at low stock size
β	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
σ_ε	Process error standard deviation for spatial-temporal variation in instantaneous mortality
σ_ω	Process error standard deviation for spatial-temporal variation in recruitment

644

645

646 Table 3. Results of deterministic calculations used to determine the influence of post-spawn movements on expected location-specific
647 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
648 Waterway. Spawning abundance (N) are estimates from a mark-recapture study of spawning Walleye populations in the waterway
649 conducted in 2011. Percent change in summer N resulting for movement was calculated by location as $[-((\text{summer N without}$
650 $\text{movement}/\text{Summer N with movement}) * 100]$, where summer N with movement was determined using spawning N and the mean
651 post-spawn movement rates presented in Table 1. Relative difference in exploitation (u) by location resulting from movement was
652 calculated as $(\text{Total harvest with movement}/\text{Spawning N}) - (\text{Total harvest without movement}/\text{Spawning N})$.

Location	Spawning N	% change in summer N resulting from movement	Difference in u by location resulting from movement
Burt	19,464	-3.0	-0.01
Mullett	2,246	9.4	0.02
Crooked	2,360	28.2	0.06
Pickerel	4,442	-31.7	-0.07
Black River	477	236.0	0.53

653

654 Table 4. Results of mean annual spawning population-specific and area-specific exploitation rates using simulated scenarios that
 655 included and excluded estimated movement rates (see Table 1). Results depict outputs from the simulated scenarios that used steady
 656 state recruitment, $u_s = 0.10$, and u_a = realized area-specific mortality rates from within the Inland Waterway.

Location	With movement	Without movement	Diff in u after accounting for movement
	Population-specific u		
Burt Lake	0.27	0.28	0.01
Mullett Lake	0.24	0.24	0.00
Crooked Lake	0.29	0.28	-0.01
Pickeral Lake	0.25	0.23	-0.02
Black River	0.23	0.18	-0.05
	Area-specific u		
Burt Lake	0.26	0.28	0.02
Mullett Lake	0.70	0.24	-0.46
Crooked Lake	0.29	0.28	-0.01
Pickeral Lake	0.21	0.23	0.02
Black River	0.16	0.18	0.02

657

658

659 Table 5. Mean annual exploitation rates by spawning population and area, simulated using different assumptions for recruitment when
660 $u_s = 0.10$ at all sites within the Inland Waterway. Steady state recruitment assumed new recruits perfectly replaced deaths (see
661 methods). The Ricker recruitment models signified low, regional-average, and high productivities (i.e., $\alpha=1.643, 2.768, 6.046,$
662 respectively) and were based on Walleye populations from Wisconsin described by Tsehaye et al. (2016).

Exploitation rates by spawning population					
Recruitment type	Burt	Mullett	Crooked	Pickerel	Black River
Steady state	0.27	0.24	0.29	0.25	0.23
Ricker-low	0.27	0.24	0.28	0.25	0.22
Ricker-Regional	0.28	0.24	0.27	0.25	0.23
Ricker-high	0.28	0.24	0.29	0.26	0.23
Exploitation rates by area					
	Burt	Mullett	Crooked	Pickerel	Black River
Steady state	0.26	0.70	0.29	0.21	0.16
Ricker-low	0.34	0.31	0.30	0.19	0.15
Ricker-Regional	0.32	0.25	0.29	0.19	0.17
Ricker-high	0.33	0.22	0.30	0.19	0.18

663

664

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 (ϕ) 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 (ψ)) 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 ($u=0.35$) 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.

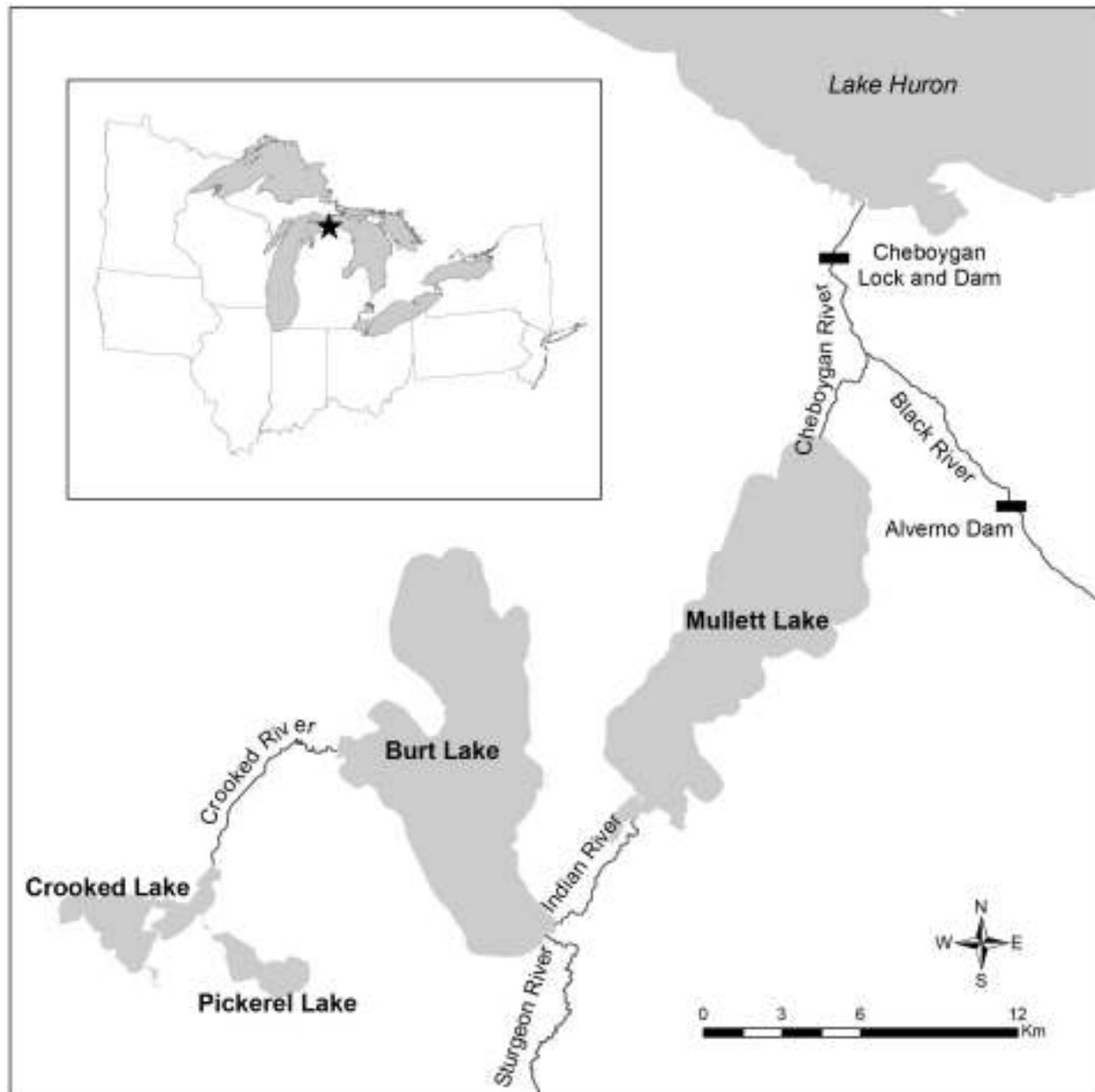


Figure 1

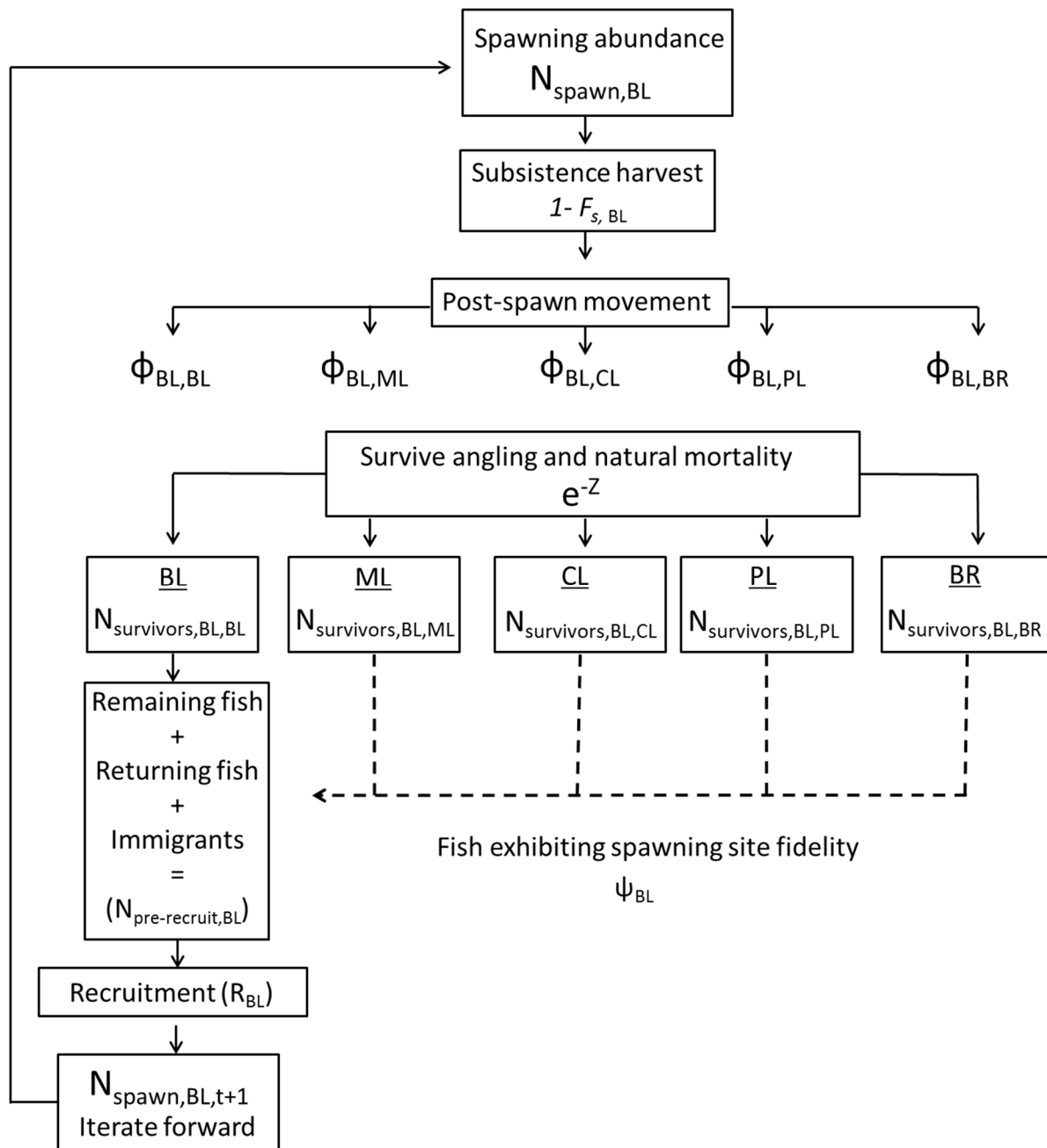


Figure 2

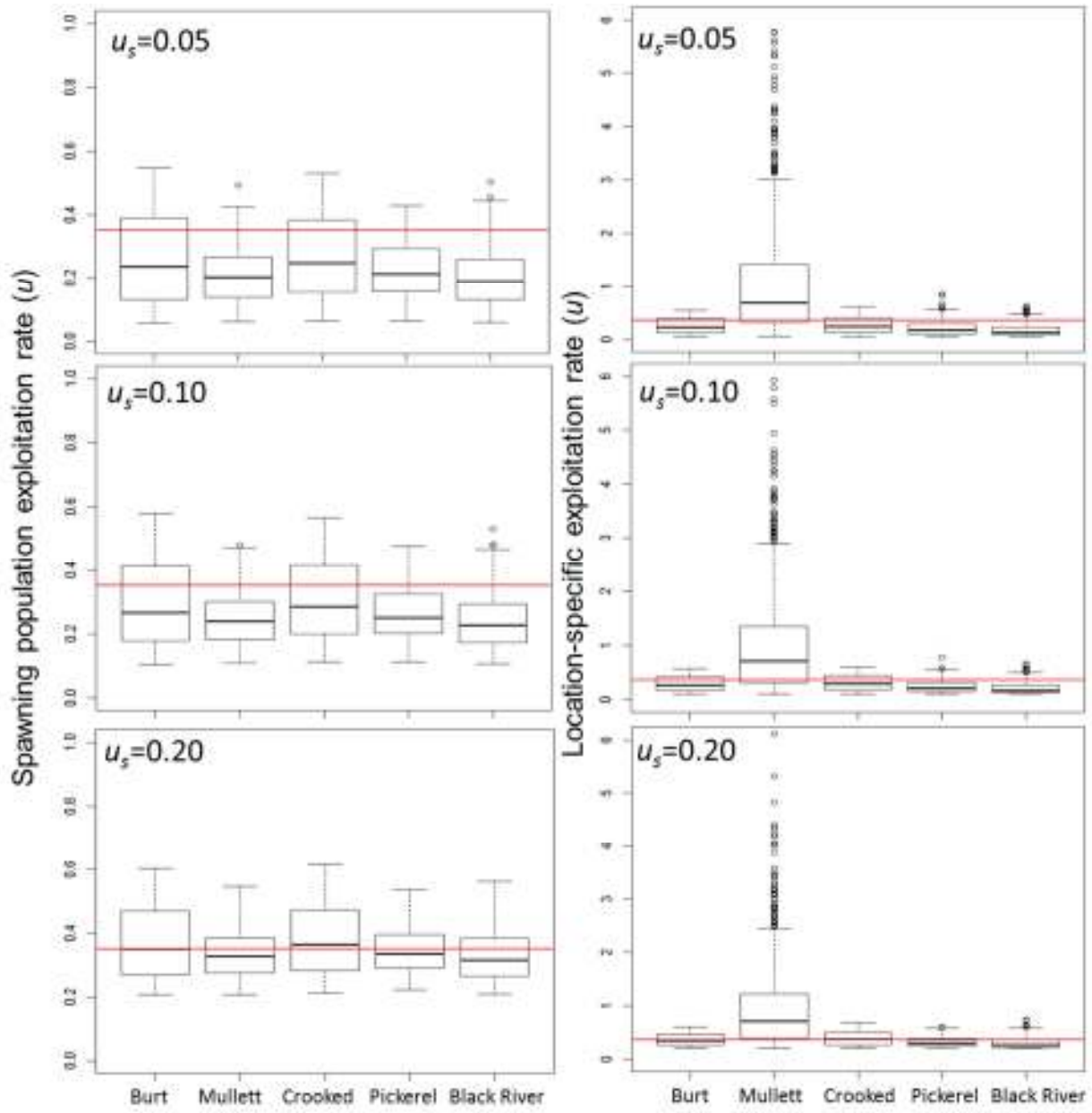


Figure 3