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# Long-Term Mark–Recapture Data to Assess Muskellunge Population Characteristics: Application to Two Illinois Reservoirs

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23 **Abstract**

24 Accurate estimates of growth and mortality are important for management of recreational  
25 fisheries. Accurate age estimates often require the sacrifice of fish, thus assessments of growth  
26 and mortality rates of trophy fishes such as Muskellunge *Esox masquinongy* often lack sufficient  
27 data. Mark-recapture history can be used as a non-lethal alternative to estimate growth and  
28 mortality in fishes. To determine the utility of this approach, we used data from a 17-year  
29 Muskellunge mark-recapture program conducted on two Illinois reservoirs (Kinkaid Lake and  
30 North Spring Lake). von Bertalanffy parameter estimates by sex, lake, and tag type (passive  
31 integrated transponder, and T-bar anchor tags) were obtained using a novel modification of the  
32 Fabens growth model and compared to von Bertalanffy growth estimates using known- or scale-  
33 aged fish. Mortality was calculated using both age- and length-based methods. Fabens growth  
34 model estimates of asymptotic length ( $L_{\infty}$ ) and growth coefficient ( $K$ ) were within 6% ( $\leq 62$  mm)  
35 and 23% ( $\leq 0.11$ ) of corresponding von Bertalanffy growth model parameter estimates from  
36 known- or scale-aged fish by lake and sex. Provided that all sizes of fish are sampled, four years  
37 of mark-recapture data with  $> 100$  recaptures were found to be sufficient to produce reliable  
38 parameter estimates. Growth parameters differed between male fish tagged with passive  
39 integrated transponder or T-bar anchor tags, but did not differ by tag type for females.  
40 Differences in Muskellunge growth and mortality rates between the two study lakes suggest that  
41 changing from a regionally-applied minimum length limit to lake-specific minimum length limits  
42 may be warranted. Our results highlight the feasibility of mark-recapture data as a non-lethal  
43 technique to estimate population-specific growth and mortality rates for Muskellunge and the  
44 potential value of this approach in facilitating lake-specific Muskellunge management.

45           Understanding population characteristics, such as growth and mortality, and the factors  
46 that influence them are important for the management and conservation of fish populations  
47 (Beverton and Holt 1957). In particular, accurate estimates of these vital rates are required to set  
48 biologically sound fisheries regulations, and reliably assess population responses to exploitation  
49 (Beverton and Holt 1957; Casselman 2007; Pardo et al. 2013) and environmental conditions  
50 (Munkittrick and Dixon 1989). Sparse or inaccurate length-at-age data may lead to spurious  
51 estimates of growth and mortality (DeVries and Frie 1996; Pardo et al. 2013). Obtaining  
52 accurate age data often requires sacrificing individuals and excising calcified structures for age  
53 estimation (e.g., otoliths, vertebrae, cleithra; Campana and Neilson 1985; Casselman 1990;  
54 DeVries and Frie 1996; Maceina et al. 2007). However, sacrificing individuals may be  
55 problematic for species with low population densities such as imperiled or trophy species where  
56 harvest of individuals (for science or recreation) can be detrimental to the population (Allan et al.  
57 2005; Dunton et al. 2016). These scenarios often leave biologists and managers tasked with  
58 managing fish populations in data-limited situations (Pikitch et al. 2004; Dunton et al. 2016).

59           Management decisions for populations of Muskellunge *Esox masquinongy* are frequently  
60 data-limited because the species is difficult to sample, typically occurs at low densities, and is  
61 long-lived (Graff 1986; Strand 1986; Casselman et al. 1999). Despite inherent limitations for  
62 estimating Muskellunge population characteristics, some Muskellunge age and growth studies  
63 have been published (Casselman and Crossman 1986; Casselman et al. 1999; Faust et al. 2015);  
64 these studies used cleithra to estimate age and von Bertalanffy growth parameters (asymptotic  
65 length ( $L_{\infty}$ ), growth coefficient ( $K$ ), and theoretical time at length zero ( $t_0$ )), using back  
66 calculated estimates of length-at-age. However, while cleithra age estimates are assumed to  
67 provide the most accurate and precise age estimates for Muskellunge, they have not been

68 validated as an ageing structure (Harrison and Hadley 1979; Casselman and Crossman 1986;  
69 Casselman 1990). Furthermore, removal of the cleithra requires sacrificing fish, which is  
70 problematic because sacrificing a sufficient number of individuals within a water body to  
71 estimate growth and mortality rates is inconsistent with the strong catch-and-release ethic of  
72 Muskellunge anglers and trophy-fishery status (Margenau and Petchenik 2004; Brenden et al.  
73 2006a; Faust et al. 2015). To combat these issues, cleithra used in these studies were archived  
74 across multiple years from angler-caught trophy individuals (often from taxidermists) and  
75 agency survey mortalities (Casselman and Crossman 1986; Casselman et al. 1999; Faust et al.  
76 2015). Cleithra samples obtained in this manner may not represent the growth rate of the  
77 majority of fish in a population because they are trophy individuals, and anglers may  
78 preferentially harvest large individuals (Faust et al. 2015). Furthermore, previous research  
79 indicates growth rate of Northern Pike *Esox lucius*, which are closely related to Muskellunge,  
80 caught by anglers differs from fish sampled during electrofishing surveys (Crane et al. 2015).  
81 Due to the small number of cleithra typically archived from a given water body, growth is often  
82 estimated at coarser spatial (lake-district or regional) scales (Casselman and Crossman 1986;  
83 Faust et al. 2015). Consequently, archived cleithra studies rarely provide estimates of mortality  
84 rates for Muskellunge from a specific water body due to sample size constraints and because  
85 samples are archived across multiple years. Thus, lake-specific assessment of how changing  
86 environmental conditions, catch and release mortality, angler harvest attitudes, or other factors  
87 that may affect a particular Muskellunge population typically is not possible.

88         Limited data on Muskellunge growth and mortality rates at a water-body specific scale  
89 has often lead to management strategies at a regional or statewide scale. One approach to  
90 combat uncertainties in water-body specific growth and mortality rates is to enforce a high

91 minimum length limit at a regional scale. While this management strategy limits harvest of a  
92 large proportion of individuals in the waterbodies throughout the region and helps ensure higher  
93 survival rates to sexual maturity and trophy sizes (Casselman 2007), it could potentially result in  
94 reduced growth rates due to increased density (Lorenzen and Enberg 2002; Gilbert and Sass  
95 2016). Muskellunge anglers typically support these regulations because of their tendency to  
96 practice catch-and-release fishing, even when exceptional trophies are caught (Margenau and  
97 Petchenik 2004). However, some anglers may want the opportunity to harvest a trophy  
98 individual (Margenau and Petchenik 2004), but cannot in lakes where minimum length limits  
99 exceed Muskellunge growth potential. Therefore, there is a need for methods to non-lethally  
100 obtain growth and mortality estimates that are water-body specific to tailor management to each  
101 water body's Muskellunge population.

102 Non-lethal ageing structures (e.g., scales and fin rays) have been investigated as an  
103 alternative to cleithra for age estimation in Muskellunge to develop growth models for  
104 populations at a water-body specific scale because significantly more age data can be obtained  
105 (Johnson 1971; Harrison and Hadley 1979; Fitzgerald et al. 1997; Brenden et al. 2006a; Brenden  
106 et al. 2006b). However, multiple studies caution the use of scales or fin rays to age Muskellunge  
107 due to their tendency to be inaccurate, especially with increasing fish age (Johnson 1971;  
108 Brenden et al. 2006a). Specifically, scale age estimates may only be reliable up to age-4 in many  
109 Muskellunge populations (Fitzgerald et al. 1997), and fin rays up to age-10 (Johnson 1971;  
110 Brenden et al. 2006a), but ongoing research suggests that modern viewing techniques may  
111 improve precision and accuracy of fin ray age estimates for fish > age-10 (D.P. Crane,  
112 unpublished data). Thus, use of non-lethal ageing structures does not eliminate the need to

113 sacrifice large, old individuals to obtain reliable estimates of growth and mortality rates (Brenden  
114 et al. 2006a).

115         Marking and recapturing stocked individuals is another non-lethal technique to estimate  
116 fish growth and mortality rates, but has rarely been applied to Muskellunge. Marking individuals  
117 with fin clips or physical tags (e.g., T-bar anchor tags) have been used in many fish species to  
118 estimate population size (Frohnauer et al. 2007), exploitation (Pierce et al. 1995), fish movement  
119 (Diana et al. 1977), growth (Paragamian and Beamesderfer 2003; Hamel et al. 2014a; Hamel et  
120 al. 2014b), and mortality (Pine et al. 2003). Fin clipping, along with other physical markings,  
121 have been used to evaluate age estimates derived from bony structures and assess growth rate of  
122 recaptured fish and individuals belonging to the same year class (Johnson 1971). However,  
123 estimating growth rates with these methods is limited because distinguishing these marks can be  
124 problematic in old fish due to regeneration resulting in loss of the mark or decreased confidence  
125 in distinguishing a mark (McNeil and Crossman 1979; Nielsen 1992), and naturally reproduced  
126 individuals are often not represented as these marks are typically applied to individuals at the  
127 time of stocking. Physical tags such as individually numbered T-bar anchor tags or passive  
128 integrated transponder (PIT) tags can be applied to both stocked and naturally reproduced  
129 individuals (Nielsen 1992), allowing identification of individual fish, and having sufficient short-  
130 and long-term retention rates in juvenile and adult Muskellunge (Younk et al. 2010; Rude et al.  
131 2011). Numerous studies have used PIT and T-bar tags to evaluate population sizes of  
132 Muskellunge (Wahl and Stein 1993; Frohnauer et al. 2007). However, growth rate estimates  
133 have been limited to annual growth rates of a fish over the course of a study, rather than over the  
134 lifespan of a fish in a population (Frohnauer et al. 2007).



135 Measures of growth over longer time periods, such as von Bertalanffy growth parameters  
136 ( $L_{\infty}$ , and  $K$ ), are important to obtain for Muskellunge management because they are used for  
137 setting minimum length limits ( $L_{\infty}$ ; Casselman 2007) and may aid in estimating specific  
138 components of mortality (both  $L_{\infty}$ , and  $K$ ; Beverton and Holt 1956; Pauly 1980). von  
139 Bertalanffy growth parameters can be obtained with the Fabens growth model (FGM) using only  
140 mark-recapture data even when age is unknown (Fabens 1965). Despite the potential utility of  
141 the FGM, it remains under-utilized by fisheries scientists; most applications of the FGM have  
142 been for marine invertebrates (Frazer et al. 1990), and testudines (Kennett 1996; Schmid and  
143 Witzell 1997). Recently, the FGM has been demonstrated to be a powerful approach for using  
144 mark-recapture data to elucidate population characteristics of imperiled fish species such as  
145 sturgeons (Paragamian and Beamesderfer 2003; Hamel et al. 2014a; Hamel et al. 2014b) for  
146 which limited population demographic data hinders informed management. These studies used  
147 the FGM to assess growth of Shovelnose Sturgeon *Scaphirhynchus platyrhynchus* (Hamel et al.  
148 2014b) and to evaluate age estimates derived from multiple hard-part structures in Shovelnose  
149 Sturgeon and White Sturgeon *Acipenser transmontanus* (Paragamian and Beamesderfer 2003;  
150 Hamel et al. 2014a). However, despite the common practice of biologists and managers in  
151 marking and recapturing Muskellunge, we are unaware of any published studies that have  
152 applied the FGM to mark-recapture datasets to evaluate Muskellunge population characteristics.

153 The primary objective of this study was to assess the accuracy and precision of von  
154 Bertalanffy growth model parameters estimated by the FGM using long-term mark-recapture  
155 datasets for Muskellunge from two Illinois, USA reservoirs with distinct environmental  
156 characteristics (Kinkaid Lake and North Spring Lake). Model estimates of  $L_{\infty}$ , and  $K$  were  
157 compared with corresponding parameter estimates derived from von Bertalanffy growth models

158 developed using known-age and scale-aged fish. We also sought to estimate the number of  
159 recapture events and years of mark-recapture data needed to precisely estimate von Bertalanffy  
160 growth model parameters for these populations. Furthermore, to illustrate how lake-specific  
161 mark-recapture data may inform management of Muskellunge populations, we estimated  
162 mortality using von Bertalanffy estimates derived from the FGM and its predicted ages of  
163 marked and recaptured individuals and assessed differences in growth and mortality rates  
164 between sexes within each reservoir and within sexes between the two lakes. Our results  
165 highlight the feasibility of mark-recapture data as a non-lethal technique to estimate population-  
166 specific growth and mortality characteristics for Muskellunge and the potential value of this  
167 approach in facilitating lake-specific Muskellunge management.

168

## 169 **Methods**

### 170 **Study Sites**

171 Kinkaid Lake (KL) is a 1113-ha reservoir located in Jackson County in southern Illinois  
172 (37°47'50"N, 89°25'55"W) and was created in 1968 by impoundment of Kinkaid Creek.  
173 Kinkaid Lake has an average depth of 12 m and maximum depth of 24 m. North Spring Lake  
174 (NSL) is a 234-ha spring-fed, formerly connected floodplain lake of the Illinois River and is  
175 located in Tazewell County in central Illinois (40°28'13"N, 89°51'46"W). North Spring Lake  
176 was isolated from the Illinois River by construction of levees in 1916 and has an average depth  
177 of 0.88 m and maximum depth of 3 m. Both lakes are important Muskellunge fisheries in  
178 Illinois, as evidenced by the proportion of the total annual statewide catch of Muskellunge  
179 determined from angler creel reports (21% and 6% of reported Muskellunge catch statewide  
180 occurs in KL and NSL, respectively; Illinois Department of Natural Resources 2010). North

181 Spring Lake also serves as the brood stock lake for Illinois' Muskellunge rearing and stocking  
182 program. Recreational fishing regulations for Muskellunge in both lakes consist of a 1219 mm  
183 (48 in) minimum length limit with a bag and possession limit of one fish. The lakes receive  
184 supplemental stocking of juvenile Muskellunge (~275 mm total length) on an annual basis (KL;  
185 2000 individuals) or every third year (NSL; 1700 individuals). Natural reproduction may  
186 contribute a small proportion to the population in each lake (Rude et al. 2014).

187

## 188 **Field Methods**

189 Muskellunge were collected annually from 1999-2016 during a 1-2 week period each  
190 spring (late February to mid-April depending on lake-specific water temperatures) using 1.22 m  
191 x 1.83 m frame trap nets (15.24-m lead, 25.4-mm mesh bar measure). Nets were set at 12-18  
192 fixed locations throughout each lake during each year. All fish were removed from nets daily.  
193 Total length of each captured Muskellunge was measured (nearest mm) and sex was determined  
194 for each fish based on the shape of the urogenital papilla (Lebeau and Pageau 1989; Rude et al.  
195 2011; Rude et al. 2014). Upon initial capture, each fish was implanted with a DESTRON 125-  
196 kHz PIT tag (12.0 x 2.1 mm; Destron Fearing, South St. Paul, Minnesota) in the dorsal  
197 musculature (below the dorsal fin). Age-0 Muskellunge stocked into KL during 2004 and 2005  
198 were implanted with a PIT tag immediately prior to stocking and thus represented known-age  
199 individuals. Fish captured in KL were also tagged with an algicide-treated, individually  
200 numbered, 76-mm T-bar anchor tag (Floy Tag and Manufacturing, Inc., Seattle, Washington;  
201 product FD-68B) affixed through the dorsal pterygiophores. A scale was removed from  
202 individuals collected in NSL for ageing. Successful implantation of a functional PIT tag was  
203 confirmed in the field by scanning the fish with a portable handheld tag reader before fish were

204 released. Individuals captured during 2000–2016 were scanned to determine presence or  
205 absence of a functioning PIT tag. Fish bearing neither a PIT tag nor a T-bar anchor tag were  
206 tagged as described above and released, and T-bar anchor tag and PIT tag numbers were  
207 recorded for recaptured individuals. Recapture histories were compiled for individual fish for  
208 the duration of the study in each lake. T-bar anchor tags and PIT tags were used to identify  
209 recaptured individuals in KL, whereas only PIT tags were used for this purpose in NSL (T-bar  
210 anchor tags were not applied to fish in NSL). Recapture histories included sex and length at each  
211 encounter, and any fish exhibiting negative growth between recapture events (likely due to small  
212 errors in length measurements) were assumed to have not changed in length.

213

#### 214 **Growth Estimation**

215 Growth of Muskellunge was assessed by developing von Bertalanffy models using long-  
216 term mark-recapture data with the FGM that was modified to incorporate the effect of a given  
217 variable (lake, sex, and tag type) on von Bertalanffy growth parameters (Kimura 2008). Tag  
218 type was included as a variable in the FGM comparisons because previous research by Rude et  
219 al. (2011) indicated that retention rates of PIT and T-bar tags differ in adult Muskellunge. Tag-  
220 specific retention rates may affect FGM parameter estimates because time between recapture  
221 events is an integral component of the FGM. The modified Fabens model was:

$$R_{ij} = M_{ij} + (L_{\infty(j)} - M_{ij})(1 - e^{-K_j \Delta t_{ij}})$$

222 where  $R_{ij}$  is the length-at-recapture of the  $i$ th individual of the  $j$ th variable,  $M_{ij}$  is the length of the  
223  $i$ th individual of the  $j$ th variable at the previous time of capture,  $L_{\infty(j)}$  is the maximum length of  
224 the average fish of the  $j$ th variable,  $K_j$  is the growth coefficient of the  $j$ th variable, and  $\Delta t_{ij}$  is the

225 time between marking and recapture events for the  $i$ th fish of the  $j$ th variable. Incorporation of  
226 the effects of a given variable on von Bertalanffy growth parameters was achieved by using:

$$L_{\infty(j)} = L_{\infty(0)} + \text{variable} \cdot \Delta L_{\infty(1)}$$

$$K_j = K_0 + \text{variable} \cdot \Delta K_{(1)}$$

227 where *variable* is a “dummy variable” as used in Draper and Smith (1981) and Kimura (2008) in  
228 which 0 defines the set of von Bertalanffy growth parameters, and 1 defines the change in the set  
229 of von Bertalanffy growth parameters (e.g., 0 for male, 1 for female). A nonlinear mixed-effects  
230 model (Lindstrom and Bates 1990) was used to derive maximum likelihood estimates of each  
231 parameter and to test whether differences in von Bertalanffy growth parameters due to a given  
232 variable were significantly different from zero. Each recaptured individual was represented as an  
233 independent observation, and dependence among measurements from individuals recaptured  
234 multiple times were accounted for by specifying each fish as a normally distributed random  
235 effect.

236 To determine if the FGM can provide reliable estimates of growth of mark-recaptured  
237 fish, data from known-age (PIT tagged at stocking) individuals from KL were used to estimate  
238 growth parameters from a traditional von Bertalanffy growth model:

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)})$$

239 where  $L_t$  is Muskellunge length at age  $t$ ,  $L_{\infty}$  is the asymptotic length,  $K$  is the instantaneous rate at  
240 which  $L_t$  approaches  $L_{\infty}$ , and  $t_0$  is the hypothetical age of Muskellunge at zero length (Ricker  
241 1975). Because known age fish were not available for NSL, parameter estimates for the  
242 traditional von Bertalanffy growth model were estimated using a combination of information  
243 based on scale-based age estimates for young fish and the subsequent recapture history of those  
244 fish. If an individual was aged with a scale and subsequently recaptured in future years, an age

245 was assigned based on its time at large and scale age. For example, if a fish was collected and  
246 tagged in 2003 and estimated to be age-3 during that year based on scale annuli counts and was  
247 later recaptured in 2010, it was assigned as age-10 upon recapture. Scale ages of individuals  
248 only up to age-4 were used in this analysis because Muskellunge scale age estimates decline in  
249 accuracy after age-4 (Fitzgerald et al. 1997; Brenden et al. 2006a), the low sample size of age 5-8  
250 fish, and no fish  $> 9$  were aged solely from viewing scale annuli. Therefore, if an individual was  
251 aged with a scale and subsequently recaptured in future years, an age was assigned based on its  
252 time at large and scale age. For example, if a fish was collected and tagged in 2003 and  
253 estimated to be age-3 during that year based on scale annuli counts and was later recaptured in  
254 2010, it was assigned as age-10 upon recapture. Similar to the FGM, a non-linear mixed-effects  
255 model (Lindstrom and Bates 1990) was used to derive maximum likelihood estimates of each  
256 parameter, and each scale-aged individual was represented as an independent observation, and  
257 dependence among measurements from individuals used multiple times were accounted for by  
258 specifying each fish as a normally distributed random effect. Statistical comparisons of  
259 parameter estimates between the FGM and von Bertalanffy models were not obtained; however,  
260 95% confidence intervals were provided as a baseline to determine if differences existed.

261 To illustrate the potential importance of lake-specific population characteristics for  
262 Muskellunge management, the aforementioned FGM methods were used to determine whether  
263 growth (parameter estimates) differed between sexes within each lake, and between lakes within  
264 a given sex. Furthermore, the models were run by tag type for each sex (PIT or T-bar; KL fish  
265 only) to assess the potential influence of differing retention rates between tag types on FGM  
266 parameter estimates. Additionally, annual FGM were run with each year of mark-recapture data  
267 consecutively from first year of mark-recapture data to the final year of study (17 years) for each

268 lake and by sex (and both tag types for KL fish only) to estimate of number of marked and  
269 recaptured individuals and the number of years of mark-recapture data needed to provide stable  
270 estimates of  $K$  and  $L_{\infty}$  (within two standard errors of parameter estimates from the final model  
271 that was developed using data from all years). A  $P$ -value of  $\leq 0.05$  was considered significant  
272 for all statistical tests, and all statistical analyses were performed using SAS 9.2 (SAS Institute,  
273 Inc. Cary, NC).

274

### 275 **Mortality Estimation**

276 Weighted catch curves were developed to estimate instantaneous and annual mortality  
277 rates using predicted ages derived from the FGM for fish from each lake (Robson and Chapman  
278 1961). The FGM does not include an estimate of  $t_0$  needed to predict an age for an individual  
279 fish. Therefore,  $t_0$  was derived in SAS by using the high correlation among von Bertalanffy  
280 parameters to predict  $t_0$  (Pilling et al. 2002). Then, age ( $t$ ) of a fish of a given size was predicted  
281 through reformulation of the von Bertalanffy equation (Kirkwood 1983):

$$t = t_0 - \log_e[(1 - L_t/L_{\infty})/K]$$

282 An age was derived for all recapture events throughout a fish's life, and any fractional predicted  
283 ages were rounded to the nearest integer. An instantaneous mortality rate was calculated for the  
284 entire duration of the study for each lake by sex. Differences in instantaneous mortality rates  
285 were compared by sex within each lake and within sexes between lakes using a homogeneity of  
286 slopes test (test for interaction with ANCOVA). A  $P$ -value of  $\leq 0.05$  was considered significant  
287 for all statistical tests.

288 In addition to using predicted ages of fish for estimating mortality, von Bertalanffy  
289 parameters from the FGM were used to estimate annual mortality using the (Beverton and Holt  
290 1956) length-based mortality equation:

$$Z = \frac{K(L_{\infty} - \bar{L})}{(\bar{L} - L_c)}$$

291 where  $K$  and  $L_{\infty}$  are von Bertalanffy parameters derived from the FGM,  $L_c$  is the smallest size at  
292 which fish are fully vulnerable to the gear, and  $\bar{L}$  is the mean length of fish greater than  $L_c$ .  
293 Length frequency distributions were calculated and used to estimate  $L_c$  and  $\bar{L}$  values within each  
294 lake. The Beverton-Holt length-based mortality equation was applied to both sexes in each lake  
295 using all years of data. Beverton-Holt mortality rate estimates were compared qualitatively  
296 between sexes and lakes and to mortality rates among models derived from weighted catch  
297 curves.

298

## 299 **Results**

300 A total of 1762 male and 1012 female Muskellunge were collected from Kinkaid Lake,  
301 and a total of 2674 male and 1330 female were collected from North Spring Lake. A total of 355  
302 male, and 199 female fish were recaptured in KL, resulting in 554 male and 260 female recapture  
303 events (some fish were recaptured multiple times). A total of 313 male, and 171 female fish  
304 were recaptured in NSL, resulting in 807 male and 294 female fish recapture events (Table 1).  
305 Mean total lengths of male and female fish from KL were 872 and 972 mm, and ranged from  
306 415-1082 mm and 413-1269 mm, respectively. Mean total lengths of male and female fish from  
307 NSL were 790 and 859 mm, and ranged from 448-1044 mm and 451-1168 mm, respectively  
308 (Figure 1).



309 von Bertalanffy parameter estimates from the FGM developed from mark-recapture  
310 histories of fish from KL and NSL were similar to parameter estimates from von Bertalanffy  
311 growth models developed using known-age individuals from KL and scale-aged individuals from  
312 NSL (Table 1, Figure 2). Estimates of  $L_{\infty}$  from mark-recapture data and known- and scale-aged  
313 fish were within the 95% confidence intervals for  $L_{\infty}$  estimated using FGM, except for NSL  
314 female fish. Estimates of  $L_{\infty}$  derived from FGM were  $\leq 6\%$  ( $\leq 62$  mm) greater than  
315 corresponding estimates of  $L_{\infty}$  from known-age or scale-aged fish. Estimates of  $K$  from known-  
316 and scale-aged fish were within the 95% confidence intervals for FGM estimates of  $K$  for males  
317 from both lakes, but not for females. Estimates of  $K$  from FGM were  $\leq 14\%$  ( $\leq 0.09$ ) less for  
318 male fish and  $\leq 23\%$  ( $\leq 0.11$ ) less for females compared to estimates of  $K$  for known-age or  
319 scale-aged fish (Table 1). Graphical representations of both model types indicated similar  
320 growth curves between models for both males and females collected from KL (Figure 2).  
321 However, ages of young Muskellunge from NSL were systematically overestimated by the FGM  
322 compared to scale-based von Bertalanffy models (Figure 2).

323 Fabens growth model parameter estimates for KL fish differed between sexes ( $L_{\infty}$ :  $t_{552} =$   
324 26.04,  $P < 0.0001$ ;  $K$ :  $t_{552} = 6.87$ ,  $P < 0.0001$ ); females had greater  $L_{\infty}$  and lower  $K$  estimates  
325 compared to males (Table 1, Figure 2). Similarly, growth model parameters differed between  
326 sexes for fish from NSL ( $L_{\infty}$ :  $t_{482} = 18.49$ ,  $P < 0.0001$ ;  $K$ :  $t_{482} = 4.69$ ,  $P < 0.0001$ ; Table 1, Figure  
327 2). Significant differences in FGM parameter estimates were detected between lakes for male  
328 fish ( $L_{\infty}$ :  $t_{663} = 12.38$ ,  $P < 0.0001$ ;  $K$ :  $t_{663} = 8.13$ ,  $P < 0.0001$ );  $L_{\infty}$  and  $K$  were greater for fish from  
329 KL compared to NSL. Estimated  $K$  was significantly higher for female fish from KL compared  
330 to NSL, whereas estimated  $L_{\infty}$  for females did not differ between lakes ( $L_{\infty}$ :  $t_{370} = 1.00$ ,  $P =$   
331 0.3179;  $K$ :  $t_{370} = 5.45$ ,  $P < 0.0001$ ; Table 1, Figure 2). Estimates of  $L_{\infty}$  for male fish from KL did

332 not differ based on tag type (PIT: 949.7, T-bar anchor: 957.2;  $t_{654} = 1.75$ ,  $P = 0.0814$ ); however,  
333 estimated  $K$  values for males differed by tag type (PIT: 0.5086, T-bar anchor: 0.4639;  $t_{654} = 2.02$ ,  
334  $P = 0.0442$ ; Figure 3). Both  $L_{\infty}$  (PIT: 1090.5, T-bar anchor: 1122.5;  $t_{369} = 2.32$ ,  $P = 0.0208$ ) and  
335  $K$  (PIT: 0.3753, T-bar anchor: 0.2989;  $t_{369} = 2.80$ ,  $P = 0.0054$ ) estimates for female fish from KL  
336 differed based on tag type (Figure 3). Parameter estimates of  $K$  and  $L_{\infty}$  for males from KL fell  
337 within two standard errors of the final model (all years) parameters after 4 years and 134 and 126  
338 recapture events for PIT and T-bar tags, respectively (Figure 4). Similarly, parameter estimates  
339 of  $K$  and  $L_{\infty}$  for females from KL fell within two standard errors of the final model parameters  
340 after 4 years and 67 and 56 recapture events for PIT and T-bar tags, respectively (Figure 5).  
341 Parameter estimates for both male and female fish from NSL were within two standard errors of  
342 the final model parameters at 7 years and 573 and 227 recapture events for males and females,  
343 respectively (Figure 6).

344 Predicted ages from the FGM applied to KL fish ranged from age 1-16 for males, and 1-  
345 18 for females. Predicted ages from the FGM for NSL ranged from 2-26 for males, and 2-16 for  
346 females. Muskellunge fully recruited to the gear at age-5 for both sexes in KL, and fully  
347 recruited to the gear at age-7 for males and age-6 for females in NSL. Instantaneous mortality  
348 rates derived from weighted catch curves for male and female fish from KL were 0.456 and  
349 0.367, respectively (annual mortality rate of 36.6% and 30.7%) and did not differ between sexes  
350 ( $F = 0.86$ ,  $P = 0.3631$ ; Figure 7). Instantaneous mortality rates differed between sexes in NSL ( $F$   
351  $= 21.57$ ,  $P < 0.0001$ ; male: 0.302, female: 0.471; annual mortality 26.1% and 37.6%; Figure 7).  
352 Instantaneous mortality rates differed between lakes for male ( $F = 26.65$ ,  $P < 0.0001$ ), but not  
353 female fish ( $F = 0.66$ ,  $P = 0.4257$ ), with lower estimated mortality rates in male fish from NSL  
354 (Figure 7). The Beverton-Holt length-based mortality equation required an estimate of the

355 smallest size at which fish were fully vulnerable to the gear ( $L_c$ ), and the mean size of fish  
356 greater than  $L_c$  ( $\bar{L}$  value). In KL  $L_c$  values were determined as 750 mm for males and 800 mm  
357 for females, and in NSL,  $L_c$  values were determined as 650 mm for males and 700 mm for  
358 females. The mean lengths of fish greater than  $L_c$  ( $\bar{L}$  values) in KL were 882 mm for males and  
359 984 mm for females; NSL fish  $\bar{L}$  values were 798 mm for males and 872 mm for females.  
360 Instantaneous mortality rates derived from the Beverton-Holt length-based equation were 0.259,  
361 and 0.230 (annual mortality 22.9% and 20.3%) for male and female fish from KL. Instantaneous  
362 mortality rates for male and female fish from NSL were 0.256 and 0.335 (annual mortality  
363 22.5% and 28.5%), respectively.

364

## 365 **Discussion**

366 The FGM incorporating mark-recapture data for Muskellunge produced similar growth  
367 curves and parameter estimates to von Bertalanffy growth models developed for known-age and  
368 scale-aged fish. Parameter estimates from the FGM for KL fish were nearly identical to known-  
369 age von Bertalanffy parameter estimates, which is consistent with previous research examining  
370 the utility of the FGM compared to traditional von Bertalanffy growth models (Wang 1998).  
371 Consistency of FGM growth parameter estimates with those obtained from traditional von  
372 Bertalanffy growth models for known-age fish from KL demonstrates that mark-recapture data  
373 can be used to generate accurate predictions of length-at-age for Muskellunge populations.  
374 However, the FGM for male and female fish from NSL resulted in apparent underestimation of  
375 length for fish ages 2-5. Lack of tagging small individuals < age-3 in NSL may have led to  
376 reduced model accuracy for young fish from this lake. In contrast, the KL FGM included mark-  
377 recapture data from known-age individuals (< age-4) which likely improved model estimates of

378 growth for fish < age-4 in this lake (Frazer et al. 1990; Wang 1998). Removal of small or large  
379 individuals within a mark-recapture dataset can result in changes in parameter estimates (Frazer  
380 et al. 1990). Our results highlight the importance of tagging and recapturing a broad range of  
381 fish sizes and ages (potentially including some age-0 at stocking) to obtain accurate and precise  
382 growth parameter estimates.

383 Muskellunge growth was sexually dimorphic in each lake with males approaching their  
384 estimated lake-specific asymptotic lengths at a faster rate and having a smaller asymptotic length  
385 relative to females, which is consistent with previous research on Muskellunge populations  
386 throughout their geographic range (Casselman and Crossman 1986; Casselman et al. 1999;  
387 Brenden et al. 2006a; Kapuscinski et al. 2007; Faust et al. 2015). Furthermore, estimates of  
388 growth coefficients for Muskellunge in this study were greater than reported for populations  
389 from northern waters of Muskellunge range (Canada and upper Midwest and northeast, USA;  $K$   
390 values < 0.25 for both sexes (Casselman and Crossman 1986; Casselman 2007; Kapuscinski et  
391 al. 2007; Faust et al. 2015), but similar to populations (Virginia, USA) from similar latitudes ( $K$   
392 values 0.30-0.50 for both sexes (Brenden et al. 2006a). Conversely, estimated asymptotic length  
393 of male and female fish in both northern and southern populations are substantially higher than  
394 our study (Johnson 1971; Brewer 1980; Casselman and Crossman 1986; Casselman et al. 1999;  
395 Brenden et al. 2006a; Kapuscinski et al. 2007; Faust et al. 2015). Reduced asymptotic length and  
396 growth potential in our fish compared to other populations may be attributed to multiple factors  
397 such as genetic strain performance at differing temperatures and latitudinal differences in  
398 temperature and length of growing season, or differences in prey base (Clapp and Wahl 1996), as  
399 these factors are some of the most important factors driving differences in individual growth  
400 rates among populations (Fry 1971). Previous research by both Younk and Strand (1992) and

401 Wolter et al. (2012) revealed that different genetic strains of Muskellunge exhibited different  
402 growth rates within the same lakes.

403         Similar to our FGM methods to evaluate growth, our age- and length-based methods to  
404 estimate mortality provided the opportunity to evaluate differences in mortality between  
405 populations and lakes. Similarity between FGM and known-age von Bertalanffy growth curves  
406 for KL fish suggest that our assigned predicted ages and subsequent weighted catch curve  
407 mortality estimates were plausible. However, both mortality estimators may have been biased to  
408 some degree. Using predicted ages from the FGM due to limited availability (in KL) or lack (in  
409 NSL) of known-age fish may have led to potential error in mortality rate estimates. Probable  
410 overestimation of age for young individuals using the FGM for fish from NSL was likely  
411 responsible for predicted age ranges of fish extending beyond typical maximum age for  
412 Muskellunge at latitudes comparable to Illinois (Brenden et al. 2006a). Inaccuracy of length-  
413 based age estimates derived from the FGM may have affected mortality rate estimates. Bias in  
414 estimated mortality rates using predicted ages from the FGM may have been particularly  
415 prominent in male fish from NSL due to inherent uncertainty of length-based age predictions for  
416 fish at or near  $L_{\infty}$ . Our results highlight the importance of tagging a broad size range of  
417 individuals to reduce bias in estimates of mortality rate derived from length-based age estimation  
418 from FGM. Beverton-Holt length-based mortality estimates may also have been biased; this  
419 estimator is particularly sensitive to the size of fish that are first fully vulnerable to sampling gear  
420 ( $L_c$ ). Error in estimated  $L_c$  can result in mortality rate errors (Pauly and Morgan 1987; Ehrhardt  
421 and Ault 1992). Potential biases aside, mortality estimates were similar in KL compared to NSL  
422 using both methods; an average mortality rate combining both methods resulted in annual  
423 mortality estimates of approximately 25-30% in KL and 25-35% in NSL (Beverton-Holt annual

424 mortality estimates were approximately two thirds of that of the catch curve method). Annual  
425 mortality rates estimated from scale-aged fish from NSL were 44.9% for male and 44.2% for  
426 female fish. Although estimates of mortality are limited for Muskellunge populations,  
427 Casselman et al. (1996) estimated annual mortality at 8-22% in waters of Canada, Minnesota and  
428 Wisconsin, and Brenden et al. (2006b) estimated annual mortality in the New River, Virginia to  
429 be 32%.

430 Differences in estimated von Bertalanffy growth parameters and mortality rates between  
431 KL and NSL Muskellunge populations illustrate the potential utility of the Fabens approach for  
432 revealing differences between water-bodies that would likely be undetected using cleithra  
433 obtained from a limited number of fish sampled at a regional scale. A combination of lake-  
434 specific abiotic and biotic factors likely influenced the differences in growth and mortality rates  
435 between KL and NSL. Differences in genetic stocks are not the underlying cause for observed  
436 differences in growth and mortality rates between lakes because Muskellunge in each lake are of  
437 the same genetic stock (NSL serves as the brood stock lake for Illinois' Muskellunge rearing and  
438 stocking program). Numerous abiotic factors, such as lake depth and surface area, can result in  
439 differences in growth rates among populations (Simonson 2008; Griffiths 2013). Differences in  
440 water temperature regimes, extent of optimal thermal habitat for Muskellunge growth, or  
441 differences in forage fish base between KL and NSL may also have contributed to differences in  
442 growth and mortality rate estimates between these two lakes (W.E. Herndon and S.C. Hirst,  
443 Illinois Department of Natural Resources, unpublished data). Differences in Muskellunge  
444 density between KL and NSL may also have contributed to differences in growth and mortality  
445 rate estimates between these populations. High density may limit individual growth rate in fish  
446 (Lorenzen and Enberg 2002), and density-dependent growth has been suggested for Muskellunge

447 (Gilbert and Sass 2016) and Northern Pike (Margenau et al. 1998) populations. Although precise  
448 Muskellunge density estimates in each lake are unknown, results from netting data (fish/net  
449 night) and angler creel surveys (fish/angler hour) suggest that Muskellunge density may be  
450 higher in NSL than in KL (Illinois Department of Natural Resources 2010; W.E. Herndon, and  
451 S.C. Hirst, Illinois Department of Natural Resources, unpublished data), although net or angler  
452 catch rate data have not been validated as an index of Muskellunge density.

453

#### 454 **Management Implications**

455 This study provides new techniques to evaluate population characteristics of  
456 Muskellunge using mark-recapture data. Application of the FGM and its parameter estimates  
457 and predicted ages facilitated lake-specific growth and mortality estimates to determine if  
458 populations differed between lakes. More specifically, the FGM produced estimates of von  
459 Bertalanffy parameters comparable to fish of known-age (and scale-aged), facilitating use of the  
460 FGM to compare growth between populations. Both age- and length-based methods also  
461 produced estimates of mortality that could be compared among populations. However, we  
462 acknowledge that potential errors and biases associated with these methods may exist, but use of  
463 non-lethal mark-recapture data instead of methods that require sacrificing individuals may  
464 preclude some of the associated biases with the provided techniques in this paper. Potential  
465 biases and errors aside, these methods provide a potential ‘tool kit’ for Muskellunge biologists to  
466 facilitate analyses of Muskellunge population characteristics using mark-recapture datasets.

467 Using mark-recapture data and these methods as a ‘tool kit’ to estimate population  
468 characteristics may be more advantageous than traditional methods because substantially larger  
469 sample sizes can be obtained, and they do not require sacrificing individuals for age estimation.

470 Muskellunge of all sizes can be tagged (Younk et al. 2010; Rude et al. 2011), and subsequently  
471 the entire population can be represented with mark-recapture data; whereas, growth estimates  
472 from cleithra may only represent trophy individuals (Faust et al. 2015). We also acknowledge  
473 that mark-recapture datasets used in this study are likely unique in sample size and duration  
474 (years) compared to many other Muskellunge mark-recapture datasets. However, we found that  
475 smaller sample sizes and years of mark-recapture data can be used to derive similar parameter  
476 estimates. Sample sizes of < 100 fish and 4 years of mark-recapture data may be sufficient to  
477 produce reliable growth parameter estimates in situations similar to the KL dataset where a broad  
478 range of fish sizes were tagged and recaptured. Conversely, increased sample sizes (> 500) and  
479 years of mark-recapture data (7) may be required in situations similar to the NSL dataset where  
480 only adult Muskellunge were tagged, because under-represented or missing length groups may  
481 influence FGM parameter estimates (Frazer et al. 1990; Wang 1998). Thus, our results highlight  
482 the importance of marking and recapturing a broad range of fish sizes when using this technique  
483 to estimate growth parameters. Individually numbered T-bar anchor tags may also be used to  
484 estimate growth parameters as we found little difference in FGM parameter estimates derived  
485 from PIT tag and T-bar anchor tag datasets. However, we caution the use of only T-bar anchor  
486 tags because long-term data may be reduced as a result of decreased retention rates over  
487 time (Rude et al. 2011), but in data-poor situations T-bar anchor tags facilitate the use of angler-  
488 recorded data.

489 For Muskellunge management, using mark-recapture data may reduce data-limited  
490 situations when managing a population. Estimates of  $L_{\infty}$  from the FGM may be useful for setting  
491 minimum length limits tailored to differences in Muskellunge growth potential among lakes  
492 (Casselman 2007), along with providing required information for estimating annual mortality



493 using length-based methods (Beverton and Holt 1956; Pauly 1980; Pauly and Morgan 1987;  
494 Ehrhardt and Ault 1992). For example, results of the FGM applied to Muskellunge populations  
495 in NSL and KL suggest that the current 1219 mm (48 in) minimum length limit may exceed the  
496 biological growth potential of Muskellunge in NSL but not in KL; no fish > 1219 mm were  
497 collected during this study and anglers have only caught two fish > 1143 mm (45 in) in NSL  
498 from 1989-2010, whereas numerous fish > 1219 mm were sampled in this study and have been  
499 caught by anglers from 1992-2010 in KL (Illinois Department of Natural Resources 2010).  
500 Based on Casselman (2007), using the lower 99% confidence interval bound of  $L_{\infty}$ , to set the  
501 minimum length limit would result in a 1016 mm (40 in) length limit for NSL, which should  
502 increase the opportunity for anglers to potentially harvest a trophy individual. Even if harvest of  
503 trophy fish did not substantially increase under a reduced minimum length limit due to the catch  
504 and release ethic of many Muskellunge anglers (Margenau and Petchenik 2004), setting  
505 minimum length limits in accordance with lake-specific Muskellunge growth potential could be  
506 used to provide anglers with an indication of a total length that could be considered  
507 representative of a trophy fish for a particular lake or set of lakes.

508 In addition to the methods described in this study, mark-recapture data can also be used  
509 to determine population size and provide estimates of mortality (Pine et al. 2003). Therefore,  
510 Muskellunge biologists can design mark-recapture studies that may allow them to estimate  
511 growth using the FGM, estimate mortality using a catch-curve approach incorporating predicted  
512 ages, length-based methods, and mark-recapture models, while also incorporating fish population  
513 size estimates. These data may provide Muskellunge biologists with lake-specific population  
514 characteristics needed to set effective length regulations based on individual lake growth  
515 potential (Casselman 2007; Faust et al. 2015). Furthermore, these data may provide the ability to

516 assess changes in the population in respect to changes in angler attitude (i.e., fishing pressure),  
517 catch and release mortality, exploitation, fish density, and environmental conditions (Beverton  
518 and Holt 1957; Munkittrick and Dixon 1989; Casselman et al. 1996; Margenau and Petchenik  
519 2004; Margenau 2007; Gilbert and Sass 2016). Therefore, application of the mark-recapture data  
520 and the techniques described in this study ultimately may lead to improved management of  
521 Muskellunge fisheries.

522

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737 Table 1. Summary of von Bertalanffy parameter estimates of asymptotic length ( $L_\infty$ ), growth  
738 coefficient ( $K$ ) and theoretical time at length zero ( $t_0$ ) derived from the Fabens growth model  
739 using mark-recapture data, and from known-age fish from Kinkaid Lake (KL) and scale-aged  
740 fish from North Spring Lake (NSL) by sex. Values associated with parameter estimates are the  
741 range of upper and lower 95% confidence intervals. Sample size (n) is the number of recapture  
742 events used in a given model. Note ( $t_0$ ) is not calculated in the Fabens growth model and is  
743 assumed to be zero.

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Model	Fabens			von Bertalanffy			
	n	$L_\infty$	$K$	n	$L_\infty$	$K$	$t_0$
KL Male	554	948.3 ± 5.7	0.5189 ± 0.03	73	937.7 ± 18.6	0.6004 ± 0.06	0.059 ± 0.05
KL Female	260	1088.8 ± 9.2	0.3974 ± 0.02	48	1043.9 ± 34.3	0.5001 ± 0.06	0.029 ± 0.07
NSL Male	807	903.7 ± 6.7	0.3599 ± 0.03	1399	900.5 ± 5.4	0.3867 ± 0.01	-0.507 ± 0.10
NSL Female	294	1080.3 ± 17.6	0.2771 ± 0.02	583	1018.7 ± 11.5	0.3601 ± 0.02	-0.436 ± 0.10

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752 Figure 1. Length frequency distributions of Muskellunge collected from 1999-2016 for each  
753 lake: male fish from Kinkaid Lake (A), and North Spring Lake (C), and female fish from  
754 Kinkaid Lake (B) and North Spring Lake (D).

755  
756 Figure 2. Fabens growth model and von Bertalanffy growth model curves from (A) Kinkaid  
757 Lake and (B) North Spring Lake. Solid lines represent the Fabens growth models, and dashed  
758 lines represent the von Bertalanffy growth function. Black lines and gray lines represent male  
759 and female fish, respectively. Black and gray dots represent length-at-age and standard deviation  
760 of known-age individuals by sex from (A) Kinkaid Lake, and black and gray dots represent  
761 length-at-age and standard deviation of scale-aged individuals by sex from (B) North Spring  
762 Lake.

763  
764 Figure 3. Fabens growth model growth curves from Kinkaid Lake fish by tag type and sex.  
765 Black and gray lines represent male and female fish, respectively. Solid and dashed lines  
766 represent PIT tagged and T-bar anchor tagged individuals, respectively.

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768 Figure 4. Annual von Bertalanffy parameter estimates of the growth coefficient ( $K$ ) (A), and  
769 asymptotic length ( $L_{\infty}$ ) (B) derived from the Fabens growth model for male fish from Kinkaid  
770 Lake by tag type with each successive year of mark-recapture data. Black and gray dots  
771 represent PIT tagged and T-bar anchor tagged individuals, respectively. Error bars represent

772 standard errors of parameter estimates. Black and gray numbers (by tag type) above each year  
773 represent the number of total recapture events used to estimate parameters.

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775 Figure 5. Annual von Bertalanffy parameter estimates of the growth coefficient ( $K$ ) (**A**), and  
776 asymptotic length ( $L_{\infty}$ ) (**B**) derived from the Fabens growth model for female fish from Kinkaid  
777 Lake by tag type with each successive year of mark-recapture data. Black and gray dots  
778 represent PIT tagged and T-bar anchor tagged individuals, respectively. Error bars represent  
779 standard errors of parameter estimates. Black and gray numbers (by tag type) above each year  
780 represent the number of total recapture events used to estimate parameters.

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782 Figure 6. Annual von Bertalanffy parameter estimates of the growth coefficient ( $K$ ) (**A**), and  
783 asymptotic length ( $L_{\infty}$ ) (**B**) derived from the Fabens growth model for fish from North Spring  
784 Lake by sex with each successive year of mark-recapture data. Black and gray dots represent  
785 male and female fish, respectively. Error bars represent standard errors of parameter estimates.  
786 Black and gray numbers (by sex) above each year represent the number of total recapture events  
787 used to estimate parameters.

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789 Figure 7. Weighted catch curves of male (**A**, **C**) fish from Kinkaid Lake and North Spring Lake,  
790 and female fish (**B**, **D**) fish from each lake, respectively. The natural log of the number of  
791 predicted age fish derived from the Fabens growth model were plotted as a function of age for  
792 Kinkaid Lake, and North Spring Lake fish. Note x-axis range differs among figures.















