

1 Fishing regulations, sexual dimorphism, and the life history of harvest

2 Running head: Harvest life history

3 Lyndsie S. Wszola¹, Zachary S. Feiner^{2,3}, Christopher J. Chizinski⁴, J.B. Poletto⁴, and J.P.

4 DeLong¹

5 Corresponding Author: Lyndsie Wszola

6 406 Manter Hall

7 1101 T St

8 Lincoln, NE, 68588, USA

9 Lyndsie.Wszola@huskers.unl.edu

10

11

12 1. School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE, USA

13 2. Office of Applied Science, Wisconsin Department of Natural Resources, Madison, WI,

14 USA

15 3. Center for Limnology, University of Wisconsin-Madison, Madison, WI, USA

16 4. School of Natural Resources, University of Nebraska Lincoln, Lincoln, NE, USA

17

18 **ABSTRACT**

19 Freshwater recreational fisheries regulations are a vital tool for achieving social and ecological
20 fisheries objectives. However, angler behavior and fish biology may interact to influence
21 regulation efficacy in unexpected ways. We combined models of fish growth and angler behavior
22 to explore how angler behavior interacts with fish life history to shape the probability of fish
23 harvest given capture across ages, life-stages, and sexes of walleye (*Sander vitreus*). Compared
24 to females, males grew more quickly as juveniles, matured earlier, and reached smaller
25 maximum sizes. Male walleye were therefore vulnerable to harvest for more of their
26 reproductive lives than females because males spent more time at sizes where anglers were very
27 likely to harvest them. We suggest that restricting harvest of large individuals in sexually-
28 dimorphic species may favor the survival of large, reproductive-aged females. Moreover, we
29 show that combining models of fish growth and harvester behavior can provide insights into how
30 harvest affects fish with complex life histories over the course of their lives.

31 **KEYWORDS:** fisheries regulations, freshwater fisheries, recreational fisheries, sexual
32 dimorphism, slot limits, walleye

33

34

35

36

37

38

39 INTRODUCTION

40 Harvest regulations facilitate social and ecological objectives by shaping the distribution
41 of harvest mortality among life-stages and sexes of harvested populations. Freshwater
42 recreational fisheries managers (hereafter “fisheries managers”) pursue population management
43 goals with the aid of anglers. This strategy is complicated by the fact that fish age, life-stage, sex,
44 and other traits can be highly cryptic. Anglers seek fish that they often do not see until the animal
45 has been landed, at which point survival is already reduced by handling (Bartholomew and
46 Bohnsack 2005). Fish also typically lack the kind of secondary sexual characteristics that denote
47 sex, age, and reproductive status to an untrained observer, though exceptions like spawning
48 colors and behaviors may be apparent to anglers.

49 Effective regulations describe biologically meaningful traits of harvest-legal and harvest-
50 illegal individuals to a regulation-adherent user base (Ainsworth et al. 2012; Johnston et al. 2018;
51 Ahrens et al. 2020). The primary tools available to fisheries managers for managing the effects
52 of harvest on population age, sex, and life-stage structure are combined bag and length limits.
53 Bag limits specify how many fish may be harvested per day and length limits specify what
54 lengths those fish may be. Length, however, has a complex relationship with fish physiology and
55 population ecology (Arlinghaus et al. 2010; Gwinn et al. 2015). Fish growth is influenced by
56 diverse factors including population density, maternal effects, predation, and environmental
57 variation (Shaw et al. 2018; Thorson 2020). Many fish consequently exhibit indeterminate
58 growth and plasticity in age or size at maturity (Charnov et al. 2001). The resulting fish length is
59 often directly related to fecundity (Barneche et al. 2018), making it an important determinant of a
60 fish’s value to the fishery. Thus, the consequences of removing a fish at a given length may be

61 quite different across systems depending on a population's underlying life history and
62 interactions with its environment.

63 The question of how to craft effective harvest regulations for freshwater recreational
64 fisheries is further complicated by angler social dynamics (Arlinghaus et al. 2016, 2017).
65 Harvesters acting within the bounds of regulations may exhibit completely legal behaviors with
66 unexpected biological consequences (Aas et al. 2000; Post et al. 2003). For example, though
67 largemouth bass (*Micropterus salmoides*) regulations are frequently designed to facilitate legal
68 harvest, most anglers release captured bass due to a lasting catch-and-release ethic that
69 developed in response to past over-exploitation (Myers et al. 2008; Kerns et al. 2015; Long et al
70 2015). In contrast, "rough fish" species like gars (*Lepisosteidae*) and buffalofishes (*Ictiobus* spp.)
71 that were not historically targeted by recreational anglers are experiencing an unexpected
72 increase in fishing mortality as bowfishing and spearfishing become more popular (Quinn 2010;
73 Scarneccchia and Schooley 2020; Lackmann et al. 2021).

74 Variation in anglers' responses to regulations may affect the distribution of mortality
75 within fish populations in subtle ways. Stewardship ethics and enlightened self-interest may
76 drive anglers to self-impose minimum and maximum length limits on their harvest in addition to
77 official length regulations (Chizinski et al. 2014; Kaemingk et al. 2020). Anglers motivated by
78 eating their catch may preferentially harvest larger fish (Hunt et al. 2002; Feiner et al. 2021;
79 Roop et al. 2021). Conversely, anglers may voluntarily release very large fish because they are
80 wary of bioaccumulated toxins or perceive releasing large individuals to be a form of resource
81 stewardship (Fayram 2003; Reitz and Travnichek 2006). Furthermore, length and bag limits may
82 interact to shape angler perceptions and behavior. When a bag limit is reduced, anglers may
83 respond by changing fishing locations or harvest decisions, redistributing mortality risk across

84 landscapes and within populations (Beard et al. 2003; Woodward et al. 2003; Fayram and
85 Schmalz 2006; Feiner et al. 2021).

86 Angler responses to harvest regulations demonstrate that regulations may communicate
87 expectations of angler experience and behavior in ways not yet understood. To craft socially and
88 ecologically effective regulations, we must therefore ask how angler behavior within varying
89 harvest regulations affects the distribution of harvest mortality among ages, life-stages, and sexes
90 of harvested populations. Understanding the total distribution of mortality requires a joint
91 understanding of catch, harvest, and post-release processes, each a complex dynamic unto itself.
92 We therefore focus on a step in the fishing process where the interaction between fish biology,
93 regulations, and angler harvest decisions is uniquely observable. Herein, we combine fish
94 monitoring data with harvest surveys to ask how angler decisions under varying regulations
95 interact with fish life history to shape the probability of fish harvest given capture, hereafter
96 “retention probability.”

97 MATERIALS AND METHODS

98 *Study system*

99 We used data from an intensively studied walleye (*Sander vitreus*) fishery to evaluate the
100 hypothesis that angler harvest selectivity interacts with regulations and fish life history to shape
101 the distribution of retention probability across ages, life-stages, and sexes of a population.
102 Walleye are widely studied and harvested in recreational, subsistence, and commercial fisheries
103 across their native range in Canada, the United States, and Tribal waters (Bozek et al. 2011).
104 Previous investigations of walleye angler behavior have demonstrated that retention probability
105 increases as a function of fish length up to a point after which it asymptotes or even declines

106 (Kaemingk et al. 2020). The extent to which this voluntary release of large fish is reflected
107 across different regulation types has not been intensively examined, nor has the impact of within-
108 regulation angler behavior on patterns of fish mortality.

109 In addition to their social importance, walleye life history makes them an excellent
110 species for evaluating the interacting effects of regulations, angler decisions, and fish biology.
111 Female walleye grow more slowly, mature later, and ultimately reach larger sizes than males
112 (Henderson et al. 2003). This life history is adaptive for a broadcast-spawning fish where female
113 fitness increases as a function of body mass and male fitness is more strongly affected by how
114 quickly males can begin reproducing (Hayden et al. 2018). Managers frequently use length-based
115 regulations to facilitate female walleye survival to maturity, making walleye ideal for examining
116 the ecological effects of angler behavior and regulations (Quist et al. 2010; Haglund et al. 2016).

117 We modeled walleye life history and angler harvest decisions using data from the Leech
118 Lake, MN, USA walleye fishery. Leech Lake is located within the Chippewa National Forest and
119 much of it is within the Leech Lake Indian Reservation. Leech Lake is accordingly managed by
120 treaty agreement between the Minnesota Department of Natural Resources and the Leech Lake
121 Band of Ojibwe. It comprises approximately 41,662 hectares with a maximum depth of 46
122 meters. The lake supports a diverse fish community including warm-water species like bluegill
123 (*Lepomis macrochirus*) and largemouth bass, as well as large cool-water predators including
124 walleye, muskellunge (*Esox masquinongy*), and northern pike (*Esox lucius*).

125 **Walleye sampling**

126 We extracted walleye length, age, sex, and life-stage (juvenile or adult) data from the
127 annual Leech Lake walleye fall gillnet survey including study years 1990-2019. Walleye were

128 sampled via experimental gill net array annually in the first two weeks of September using 77-m
129 long gill nets with 5 different mesh sizes: 1.91 cm, 2.54 cm, 3.18 cm, 3.81 cm, and 5.08 cm in
130 panels with stretch length of 15.25 m. Surveyors conducted 36 roughly 24-hour net sets most
131 years. Walleye were measured to total length, weighed, aged using otoliths, and evaluated for sex
132 and sexual maturity via internal examination. More comprehensive descriptions of the Leech
133 Lake system and annual walleye survey may be found in the Leech Lake 2016-2020 Fisheries
134 Management Plan (Ward 2015, supplemental).

135 ***Creel sampling***

136 Creel surveys recording numbers of fish caught as well as lengths of harvested and
137 released fish were performed in years 2008-2011, 2014, and 2019. A creel survey is a social
138 survey of anglers intended to assess angler objectives, demographics, and harvest (Pollock 1994;
139 Nieman et al., 2021). Creel clerks intercepted anglers using a clustered access point survey
140 design stratified by times of expected angler usage (weekends, holidays, etc.). Creel clerks
141 interviewed anglers at the conclusion of their fishing trip to assess numbers and lengths of fish
142 caught, harvested, and released. Harvested fish were measured by creel clerks and lengths of
143 released fish were self-reported by anglers. Angler intercept surveys conducted on the day of a
144 fishing trip have long been prized for their high-resolution insights into angler effort and catch
145 characteristics (Malvestuto 1978; Robson and Jones 1989; Newman et al. 1997; Ditton and Hunt
146 2001; Kozfkay and Dillon 2011; Chizinski et al. 2014; Shaw et al. 2019; Gundelund et al. 2021;
147 Johnston et al. 2021; Trudeau et al. 2021). Additional information about creel methods and
148 results may be found in the comprehensive Leech Lake Creel Report (Stevens and Ward 2014,
149 supplemental).

150 The Leech Lake creel data includes three regulation periods between the years 2008-2020,
151 creating the opportunity to observe how anglers make harvest decisions within varying
152 regulation structures. Regulation periods one and two were protected slot limits and regulation
153 period three allowed harvest of any sized walleye but restricted the number of large fish that
154 could be harvested:

155 1. 2005-2013: Fish less than 18" (45.72 cm) may be kept. All fish from 18-26" (45.72-66.04
156 cm) must be immediately released. One fish over 26" (66.04 cm) allowed in possession.
157 Possession limit four.

158 2. 2014-2018: Fish less than 20" (50.8 cm) may be kept. All fish from 20-26" (50.8-66.04
159 cm) must be immediately released. One fish over 26" (66.04 cm) allowed in possession.
160 Possession limit four.

161 3. 2019-Present: Fish less than 20" (50.8 cm) may be kept. Only one fish over 20" (50.8
162 cm) allowed in possession. Possession limit four.

163 We classified the small size bins (<18" or <20") that allowed a larger number of fish (zero to
164 four) to be harvested as "small liberal" bins, the protected slots in which fish must be released as
165 "illegal," and the large size bins in which one fish could be harvested (>26" or >20") as "large
166 restricted."

167 ***Analysis***

168 *Walleye growth and life history*

169 We modeled walleye life history using a sexually dimorphic extension of the biphasic
170 growth model (Lester et al. 2004;2014). The biphasic model corrects the tendency of other
171 models to ignore differences in energy allocation between adults and juveniles by relating

172 growth across the fish's life cycle to observable life history traits. The model predicts fish length
 173 L as a function of fish age t , sex s , linear juvenile growth rate h , unitless gonadosomatic index g
 174 (gonad mass expressed as a fraction of somatic mass), age at 50% probability of maturing $T50$,
 175 and τ , a temporal offset reflecting the effect of early environmental conditions on juvenile
 176 growth. Juvenile length $L_{js}(t)$ is modeled as a linear function of age because juveniles dedicate
 177 all energy exceeding maintenance to somatic growth,

178 (1.1)
$$L_{js}(t) = h_s(t - \tau_s).$$

179
 180 Adult length $L_{As}(t)$ is modeled as an asymptotic function of age defined by asymptotic length
 181 L_∞ , growth coefficient k , and t_0 , the hypothetical age at which length = 0,

182 (1.2)
$$L_{As}(t) = L_\infty(1 - e^{-k_s(t - t_0s)}),$$

183 where

184 (1.3)
$$L_\infty = \frac{3h_s}{g_s},$$

185 (1.4)
$$k_s = \ln\left(1 + \frac{g_s}{3}\right),$$

186 and

187 (1.5)
$$t_0s = T50_s + \frac{\ln(1 - g_s(T50_s - \tau_s)/3)}{\ln\left(1 + \frac{g_s}{3}\right)}.$$

188 The shape of a fish's growth trajectory over its lifespan is determined by g and h . For any given
 189 h , individuals with a smaller g exhibit faster somatic growth as adults because they devote
 190 relatively more energy to somatic growth than to reproduction, whereas individuals with a larger
 191 g devote more energy to reproduction and thus exhibit slower somatic growth as adults.

192 We estimated $T50$ for males and females using a hierarchical Bayesian model where life
 193 stage (A for adulthood) was predicted as a logistic function of age (t) with sex-specific intercepts
 194 (θ_{0s}) and effects of age (θ_{1s}),

195 (2.1)
$$A \sim B(\theta_s)$$

196 (2.2)
$$\theta_s = \frac{1}{1 + \exp(-(\theta_{0s} + \theta_{1s}t))}.$$

197

198 We extracted sex-specific estimates of $T50$, the age at which 50% of a cohort was
 199 predicted to be mature (i.e. we set equation 2.2 = 0.5 and solved for t) and used them in place of
 200 individual age at maturation to model sex and stage-specific biphasic length and mass growth
 201 using a hierarchical Bayesian approach (per Wilson et al. 2018). The model describes fish length
 202 (L) of each gillnet-sampled fish as a random variable drawn from a normal distribution with
 203 mean μ_L , and coefficient of variation cv_L ,

204 (3.1)
$$L \sim N(\mu_L, cv_L).$$

205 The distribution mean μ_L was determined by the juvenile growth function for individuals
 206 with ages less than their sex-specific $T50$ and by the adult growth function for individuals with
 207 ages greater than or equal to their sex-specific $T50$.

208 (3.2)
$$\mu_L = \begin{cases} t < T50_s, & L_J(t) \\ t \geq T50_s, & L_A(t). \end{cases}$$

209 We then modeled mass (M) as a power function of length where an individual's mass was
 210 predicted by mass allometric constant a_s and exponent b_s .

211 (3.3)
$$M = a_s L^{b_s}$$

212 As above, all growth and life history parameters varied by sex to capture the effect of
213 sexual dimorphism on lifelong growth and maturation patterns. Mass was considered a random
214 variable drawn from a normal distribution ($N()$) with parameters mass mean μ_M and mass
215 precision τ_M .

216 (3.4)
$$M \sim N(\mu_M, \tau_M)$$

217 All priors for the maturation and biphasic growth models are described in Table 3.

218 *Modeling harvest*

219 Creel surveys frequently include only lengths of harvested fish, making it difficult to
220 assess why anglers harvest some fish and release others. The Leech Lake creel survey, in
221 contrast, included information on both harvested and released fish across three different
222 regulation periods, allowing us to parse the relationship between regulations, fish size, and angler
223 decision-making. We modeled harvest as a binomial ($B()$) dependent variable (1 = harvested, 0 =
224 released) that varied as a function of fish length (L) with intercepts (p_{0r}) and effects of fish
225 length (p_{1r}) for each regulation set-size bin combination (r).

226 (4.1)
$$H \sim B(p_r)$$

227 (4.2)
$$p_r(L) = \frac{1}{1 + \exp(-(p_{0r} + p_{1r}L))}$$

228 We evaluated the effect of fish length on retention probability by calculating the
229 difference between the length bin minimum and the fish's length. For example, under regulation
230 set 1 (18-26 inch \approx 46-66 cm protected slot), a fish with length equal to 50 cm would be in the
231 illegal bin with bin length equal to 4.28 cm. Expressing fish length as the difference between
232 total length and the length bin minimum rather than raw total length allowed us to predict
233 retention probability within each regulation-bin combination using the bin length minimum as
234 the intercept, rather than 0, facilitating easier comparison among regulation size bins. Further

235 information on the bin length calculations is available in the supplemental material and all priors
236 for the harvest model are described in Table 4.

237 We fit all models using a Markov Chain Monte Carlo (MCMC) algorithm in the Nimble
238 R package (R Core Team 2016; de Valpine et al., 2017), estimated parameter means and 95%
239 credible intervals using 10,000 draws from the joint posterior distributions, and confirmed
240 convergence using convergence plots. Nimble uses a syntax very similar to the BUGS language,
241 but provides a much faster MCMC implementation than older samplers via an R interface to a
242 novel C++ compiler. We estimated retention probability for males and females across their
243 lifespans by predicting length at age for males and females based on the growth model, then
244 predicting the retention probability for each predicted length. All model code and data are
245 available in the supplemental material.

246 **RESULTS**

247 We used 8,688 walleye samples from the Leech Lake gillnet database including 4,717
248 females and 3,945 males (Table 1). The gillnet sample included 3,851 mature fish, 4,772
249 immature fish, and 6 fish unidentified to sex or life-stage. The mean length of gillnet-sampled
250 fish was 39 cm ($sd = 11$ cm) and the mean age of gillnet-sampled fish was 4 years ($sd = 3$ years).
251 Mean mass of gillnet-sampled fish was 661 g ($sd = 557$ g). Males were on average younger than
252 females and had smaller average lengths and masses than females as both juveniles and adults
253 (Table 1). We extracted 212,990 walleye harvest and release records from the creel database.
254 Overall, 38% of captured fish were retained (Table 2). Fish captured in the small liberal size bins
255 were most likely to be retained (55-57% harvested). Fish in the large restricted size bins were
256 retained at comparatively low rates (18% in the protected slot regulations and 5% in the “one
257 over 20 inch” regulation). Fish in the illegal size bins also were harvested at low rates (5-10%).

258 Males matured at younger ages than females per the sexually dimorphic maturation
259 model (Table 3, Figure 1). Mean age at 50% maturity was 2.59 years for males (2.5% CI = 2.54,
260 97.5% CI = 2.64) and 3.93 years for females (2.5% CI = 3.87, 97.5% CI = 3.99). The life history
261 differences between males and females also were apparent in the growth model (Table 4, Figure
262 2). Males grew faster as juveniles than females, at a rate of 7.57 cm per year (2.5% CI = 7.45
263 cm/year, 97.5% CI = 7.70 cm/year) compared to females' 6.79 cm per year (2.5% CI = 6.70
264 cm/year, 97.5% CI = 6.88 cm/year). The model also estimated a higher gonadal-somatic index
265 for males (0.36, 2.5% CI = 0.35, 97.5% CI = 0.37) than females (0.24, 2.5% CI = 0.23, 97.5% CI
266 = 0.25). When biphasic model parameters were translated into "von Bertalanffy" growth model
267 parameters, males expressed faster growth k growth coefficients and smaller asymptotic lengths.
268 Male k was 0.11 (2.5% CI = 0.11, 97.5% CI = 0.12) whereas female k = 0.08 (2.5% CI = 0.07,
269 97.5% CI = 0.08). Though they grew faster as juveniles, males approached smaller asymptotic
270 lengths (63.39 cm, 2.5% CI = 62.23 cm, 97.5% CI = 64.62 cm) than females (84.08 cm, 2.5% CI
271 = 81.76 cm, 97.5% CI = 86.51 cm).

272 In all regulation regimes, retention probability in the small liberal size bin was relatively
273 high (55-57%) and increased as a function of fish length (Tables 5-6, Figure 3). Retention
274 probability in the large restricted bins was relatively low across regulations, but especially in the
275 "1 over 20 inches" regulation. The interaction between walleye life history, regulations, and
276 angler behavior shaped fishes' retention probability at different sexes, ages, and life-stages
277 (Figure 4). Overall, males were more likely to be retained than females under all three
278 regulations because they grew slightly faster to harvestable size, but their smaller size at age as
279 adults ensured they stayed within the small liberal size bins for most of their lives. For example,
280 a six-year-old female walleye would be on average 52 cm and harvested in 5% (2.5% CI = 4%,

281 97.5% CI = 5%) of capture events under the “one over 20 inches” regulation whereas a six-year-
282 old male walleye would be on average only 46 cm but have a 48% (2.5% CI = 42%, 97.5% CI =
283 54%) retention probability. Assuming that walleye survived to the system maximum of 20 years,
284 males and females also experienced different stage-specific and average retention probabilities.
285 Under all three regulations, female retention probability was lower for adults than for juveniles,
286 but juvenile male retention probability was similar to that of adult males (Table 6). Males were
287 additionally more likely to be harvested given capture over the full span of their life cycle than
288 females were (Figure 4).

289 **DISCUSSION**

290 Harvest regulations are an essential tool for managing the distribution of harvest
291 mortality in fish populations and for communicating with anglers. However, angler behavior and
292 fish biology ultimately control the demographic impacts of fishing. We set out to ask how angler
293 behavior in the context of varying regulations affected the distribution of retention probability
294 across ages, life-stages, and sexes of a species with well-known sexual dimorphism in life
295 history. We confirmed the widely reported sexual dimorphism in growth and maturation among
296 male and female walleye (Henderson et al. 2003; Venturelli et al. 2010). Males grew faster as
297 juveniles, matured earlier and at smaller sizes, and reached smaller overall sizes than did
298 females. Our observation that males grew slightly (~1 cm/year) faster than females as juveniles
299 contrasts with previous evidence that males and females have similar juvenile growth rates
300 (Bozek et al. 2011), but the extent to which this difference is biologically significant is unclear.

301 We found that retention probability in the large restricted size bins of all three regulations
302 was always relatively low compared to that of the small liberal size bins and that the “1 over 20
303 inches” regulation produced much lower large restricted retention probabilities than did the slot

304 limits. There are several plausible explanations for the frequent release of large walleye. Anglers
305 could be voluntarily imposing minimum and maximum length limits on their catch, as has been
306 previously observed for anglers targeting walleye (Chizinski et al. 2014; Kaemingk et al. 2020).
307 Such a pattern would add to previous evidence that anglers perceive releasing very small or very
308 large fish to be an element of good resource stewardship (Uphoff and Schoenebeck 2012; Cooke
309 et al. 2013). It is further possible that the angler release of large restricted fish resulted from
310 anglers catching a large fish early in their trip and releasing all subsequent very large catches as
311 they were legally required to do while seeking to fill their remaining bag limit of small liberal
312 fish. Conversely, anglers may have been releasing large fish because they were waiting on a
313 trophy-sized individual in the large restricted size bins and did not want to “waste” their large
314 restricted allocation.

315 The observation that the “1 over 20 inches” regulation resulted in much lower retention
316 probabilities in the large restricted size bin than did the slot regulations likely resulted from the
317 regulations interacting with the size structure of the walleye population. Large restricted fish
318 composed a much larger percentage of the total catch in the “1 over 20 inches” regulation (34%)
319 than in either slot regulation (1.5% in both slot regulations). This likely occurred because the
320 large restricted size bin in the “1 over 20 inches” regulation contained a larger range of lengths
321 and included more small and intermediate lengths. Smaller lengths would have corresponded to
322 younger, and thus more abundant, fish. However, anglers could only retain one large restricted
323 fish under all three regulations. It is therefore logical that anglers allowed to harvest only one
324 large fish would retain a much smaller percentage of the more-frequently caught “1 over 20
325 inches” large fish than the less-frequently caught slot regulation large fish. A similar process was
326 likely at play in the small liberal size bins of the two slot regulations. Anglers fishing under the

327 18-26 inch \approx 46-66 cm protected slot limit were more likely to harvest 17-18 inch (43-46 cm)
328 fish than were anglers in the 20-26 inch slot \approx 51-66 cm limit despite being allowed to harvest up
329 to four fish in both regulations. This pattern is indicative of an angler population that still wanted
330 to fill their quota of food-sized fish, and thus adjusted their behavior to harvest more 18-inch fish
331 when they were the largest available in the size bin. Similar shifts in angler behavior have been
332 previously noted when regulations tighten the number or size range of fish available for legal
333 harvest (Feiner et al. 2021). Put simply, anglers redistributed the same total amount of fish
334 retention over the size bins stipulated by regulations.

335 We found that retention probability increased as a function of fish length in small liberal
336 size bins under all three regulations whereas the relationship between fish length and retention
337 probability in the large restricted size bins varied among regulations. Though retention
338 probability declined slightly as a function of fish length in the large restricted size bin of the
339 protected slot regulations, it increased slightly as a function of fish length in the large restricted
340 size bin of the “1-over 20 inches” regulation. One potential explanation for this apparent shift in
341 behavior is that anglers interpreted the new regulation as a sign that the population was doing
342 well. If this was the case, they might perceive harvest of large fish to be more in keeping with
343 stewardship ethics than it would have been during the protected slot periods. It is also possible
344 that being exposed to a more continuous distribution of legally harvestable fish sizes resulted in a
345 behavior where anglers simply sought to harvest the largest legal individuals in both size bins.
346 Ultimately, the differences in retention probability and its relationship to size across size bins
347 and regulations suggests that when the size allocation structure of a regulation changes without
348 changing the bag limit, anglers will respond by shifting their harvest behavior relative to fish size
349 such that they still meet their harvest objectives. Such a redistribution of harvest suggests that

350 changing regulation size bins without changing bag limits is more likely to redistribute harvest
351 mortality across age, sex, and life-stage groups than to holistically increase or decrease it.

352 Angler behavior within regulations interacted with walleye sexual dimorphism to shape
353 the distribution of retention probability across ages, life-stages, and sexes. Males grew to smaller
354 sizes and were slower to exit the small liberal size bins where retention probability was greatest,
355 exposing them to increased retention probability for much of their lives. This result is
356 commensurate with previous findings that male walleye are more likely to be harvested than
357 females due to variation in size and behavior between sexes (Spirk 2012; Myers et al. 2014;
358 Koupal et al. 2015; Bade et al. 2019). In addition to anticipated differences in retention
359 probability among males and females, we also found evidence that retention probability is
360 distributed asymmetrically among ages and life-stages for both sexes. Females were subject to
361 their highest retention probability right around the size and age of maturity because retention
362 probability increased as a function of fish length in the small liberal size bins. This period of
363 increased retention probability extended further into adulthood under the 20-26 inch \approx 51-66 cm
364 protected slot and the “1 over 20 inches” regulations than under the 18-26 inch \approx 46-66 cm
365 protected slot regulation. Females over age five were much more likely to be released than
366 harvested under all three harvest regulations, but especially under the 18-26 inch \approx 46-66 cm
367 protected slot regulation. Females therefore experienced a sharp decline in their retention
368 probability after they matured, whereas male retention probability was similar for adults and
369 juveniles. This outcome is likely good news from a management perspective. Recruitment in
370 broadcast-spawning fish like walleye is often driven by the number of large egg-producing
371 females in the population. Walleye recruitment in particular may be improved by decreasing the
372 mortality rate of large females in good body condition (Hixon et al. 2014; Shaw et al. 2018;

373 Feiner et al. 2019). Concentrating harvest on males and juvenile females may therefore create
374 satisfying harvest experiences for anglers who simultaneously act as good stewards of the
375 fishery.

376 We focused here on how fish life history and angler behavior interact to shape retention
377 probability because it is an important first step toward a holistic model of fish and angler
378 dynamics. Such a holistic model of linked fish and angler dynamics will require information on
379 population age and size distributions and the effects of size on capture probability, retention
380 probability, and discard mortality. Though we cannot make direct inferences about the
381 distribution of harvest mortality in the population without this additional information, the
382 concentration of retention probability around the age and size of female maturation has the
383 potential to affect recruitment, size distribution, and age distribution. Concentrating harvest on
384 large female juveniles could limit recruitment or prevent fish from reaching the large sizes where
385 their fecundity is the greatest. However, the harvest refuge provided by angler behavior and
386 regulations means that mature females will likely have relatively high survival and reduced
387 competition for food from other walleye (De Roos et al. 2008). Predators of adult walleye (e.g.,
388 northern pike and muskellunge) are gape-limited, so surviving to large size also reduces natural
389 mortality (Nilsson and Bronmark 2000; Kapuscinski et al. 2012).

390 The combination of size-dependent fecundity, high juvenile mortality, and low adult
391 mortality often induces biomass compensation or overcompensation responses (Allen et al 1998).
392 When a smaller number of large adult fish experience high survival and lower competition, they
393 convert prey directly into new juveniles, often much more efficiently than would a larger number
394 of smaller adults (Ohlberger et al. 2011; Lester et al. 2014). A harvest and natural mortality
395 structure that reduces mortality as females reach large size and reproductive age may therefore

396 be conducive to creating high reproductive output and recruitment to fishable size. In applied
397 terms, this means that size-selective walleye anglers who harvest small fish and release very
398 large fish may protect very large females and limit their competition for resources. Beyond
399 walleye fisheries, our findings demonstrate that the effects of sexual dimorphism and other life
400 history complexity on regulation efficacy are likely to be wide-ranging and worthy of study.

401 The varying responses of anglers to regulations demonstrate that more in-depth
402 examinations of angler decisions in the context of varying regulations will likely prove
403 scientifically interesting and practically important. In particular, as social norms surrounding
404 recreational fishing and fish harvest change (e.g., Solomon et al. 2020), understanding the social
405 mechanisms motivating angler harvest decisions will be essential to anticipating the biological
406 impacts of recreational fishing. Unfortunately, the Leech Lake data did not include such a
407 longitudinal survey of angler demographics or opinions, but it is promising that many current
408 creel programs (Lynch et al. 2021) are collecting such social data. As with any project using data
409 collected over many years, investigators seeking to replicate our approach should proceed with
410 caution. The Leech Lake monitoring program is remarkably consistent and well-resourced due to
411 the lake's great social and ecological importance. Additionally, the access point intercept design
412 used to conduct the Leech Lake creel program has been shown to result in minimal bias of
413 observed caught and released fish size structure (Malvestuto 1978; Robson and Jones 1989;
414 Newman et al. 1997; Ditton and Hunt 2001; Kozfkay and Dillon 2011; Chizinski et al. 2014;
415 Shaw et al. 2019; Gundelund et al. 2021; Johnston et al. 2021; Trudeau et al. 2021). However, it
416 is always possible for recall bias to be introduced when interviewers must rely on angler recall of
417 released fish sizes and anglers may sometimes exaggerate the size of the "one that got away."
418 The Leech Lake Fisheries Management plan shows that walleye gillnet catch per unit effort was

similar in all years during which creel surveys were conducted (Ward 2015). Though the biomass of adult females increased in the population during the creel survey, overall growth trajectories did not differ, suggesting that retention probability per age, the quantity of greatest interest to this study, should be unaffected by changes in population structure. Changes in the fish population status and size structure could also change anglers' catch composition and thus the interpretation of their retention decisions. Future efforts to combine harvest and ecological models should therefore consider the potential independent and interactive effects of fish and angler sampling biases when matching data and models to research questions. One challenge to implementing effective regulations is the issue of regulation compliance. We observed some harvest within the illegal size bins under both slot regulations, indicating that some anglers intentionally or unintentionally failed to abide by the regulation. This result suggests that future efforts to model the ecological effects of fishing should account for the possibility of illegal harvest and that regulation planning should incorporate expected compliance rates in the decision process.

We examined how patterns of angler behavior within the context of varying regulations affected the distribution of retention probability across ages, stages, and sexes of a well-studied walleye population. We found that anglers tended to harvest larger fish in smaller size bins, but released most fish in larger size bins. The apparently voluntary release of large fish suggests that freshwater recreational fisheries will benefit from understanding and engaging a user base attentive to both science-based regulations and their own internal conservation values. In particular, it will likely be valuable to understand what drives the release of large fish. Is it simply adherence to regulations, gambling on a bigger trophy fish, or an effort on the part of anglers to conserve fisheries? Additionally, our finding that angler behavior within regulations

442 drove the distribution of retention across ages, life-stages, and sexes demonstrates that human
443 social behavior interacts with underlying patterns of ecology and evolution to shape the
444 consequences of harvest. Freshwater fisheries are facing an era of rapid social and environmental
445 change. Integrating the long freshwater recreational fisheries tradition of exceptional social
446 science with emerging models of fish ecology and evolution will empower researchers,
447 managers, and anglers to face a dynamic future as collaborators working for the good of the
448 fisheries we all value.

449 **ACKNOWLEDGEMENTS**

450 We thank the Minnesota Department of Natural Resources and the Leech Lake fisheries
451 biologists, particularly C. Pedersen, for kindly sharing their data. We further thank the editor and
452 three reviewers whose kind feedback greatly improved the manuscript. LSW was supported by
453 the National Science Foundation National Research Traineeship program. This material is based
454 upon work supported by the National Science Foundation under Grant No. DGE-1735362. Any
455 opinions, findings, and conclusions or recommendations expressed in this material are those of
456 the author(s) and do not necessarily reflect the views of the National Science Foundation. ZSF
457 was supported by the US Fish and Wildlife Service Federal Aid in Sport Fish Restoration
458 Program and the Wisconsin Department of Natural Resources, project F-95-P. Finally, LSW
459 thanks PWB for insights into the ecology of Leech Lake.

460 **COMPETING INTERESTS STATEMENT**

461 The authors declare there are no competing interests.

462

463

464 **CONTRIBUTORS' STATEMENT**

465 LSW, ZSF, CJC, JBP, and JPD contributed to conceptualization of the work. JPD provided
466 resources. LSW curated data, developed the methodology, conducted the formal analysis, wrote
467 the original draft, and reviewed and edited subsequent drafts. ZSF, CJC, JBP, and JPD
468 contributed to writing the manuscript via review and editing.

469 **FUNDING STATEMENT**

470 LSW was supported by the National Science Foundation National Research Traineeship
471 program. This material is based upon work supported by the National Science Foundation under
472 Grant No. DGE-1735362. ZSF was supported by the US Fish and Wildlife Service Federal Aid
473 in Sport Fish Restoration Program and the Wisconsin Department of Natural Resources, project
474 F-95-P.

475 **DATA AVAILABILITY STATEMENT**

476 All data and code are available in the supplementary materials:

477 https://osf.io/6sjfd/?view_only=d35def61bb134f79854d2b7c39430443

478 **REFERENCES**

479 Aas, Ø., W. Haider, & Hunt, L. (2000). Angler Responses to Potential Harvest Regulations in a
480 Norwegian Sport Fishery: A Conjoint-Based Choice Modeling Approach. *North
481 American Journal of Fisheries Management* 20, 940–950.

482 Ahrens, R. N. M., Allen, M. S., Walters, C. & Arlinghaus, R. (2020). Saving large fish through
483 harvest slots outperforms the classical minimum-length limit when the aim is to achieve
484 multiple harvest and catch-related fisheries objectives. *Fish and Fisheries* 21, 483–510.

485 Ainsworth, C. H., Morzaria-Luna, H. N., Kaplan, I. C., Levin, P. S. & Fulton, E. A. (2012). Full
486 compliance with harvest regulations yields ecological benefits: Northern Gulf of
487 California case study. *Journal of Applied Ecology* 49, 63–72.

488 Allen, M. S., Miranda, L. E., & Brock, R. E. (1998). Implications of compensatory and additive
489 mortality to the management of selected sportfish populations. *Lakes & Reservoirs:
490 Science, Policy and Management for Sustainable Use* 3, 67–79.

491 Arlinghaus, R., Alós, J., Beardmore, B., Daedlow, K., Dorow, M., Fujitani, M., Hühn, D., Haider,
492 W., Hunt, L. M., Johnson, B. M., Johnston, F., Klefth, T., Matsumura, S., Monk, C.,
493 Pagel, T., Post, J. R., Rapp, T., Riepe, C., Ward, H., & Wolter, C. (2017). Understanding
494 and Managing Freshwater Recreational Fisheries as Complex Adaptive Social-Ecological
495 Systems. *Reviews in Fisheries Science & Aquaculture* 25, 1–41.

496 Arlinghaus, R., Lorenzen, K., Johnson, B. M., Cooke, S. J., & Cowx, I. G. (2016). Management
497 of freshwater fisheries: addressing habitat, people and fishes. *Freshwater Fisheries
498 Ecology*, 1st edition. John Wiley & Sons Ltd.

499 Arlinghaus, R., Matsumura, S., & Dieckmann, U. (2010). The conservation and fishery benefits
500 of protecting large pike (*Esox lucius L.*) by harvest regulations in recreational fishing.
501 *Biological Conservation* 143, 1444–1459.

502 Bade, A. P., Binder, T. R., Faust, M. D., Vandergoot, C. S., Hartman, T. J., Kraus, R. T.,
503 Krueger, C. C., & Ludsin, S. A. (2019). Sex-based differences in spawning behavior
504 account for male-biased harvest in Lake Erie walleye (*Sander vitreus*). *Canadian Journal
505 of Fisheries and Aquatic Sciences* 76, 2003–2012.

506 Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-
507 energy output increases disproportionately with body size. *Science* 360, 642–645.

508 Bartholomew, A. and Bohnsack, J.A. (2005). A review of catch-and-release angling mortality
509 with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15, 129–
510 154.

511 Beard, T. D., Cox, S. P., & Carpenter, S. R. (2003). Impacts of Daily Bag Limit Reductions on
512 Angler Effort in Wisconsin Walleye Lakes. *North American Journal of Fisheries
513 Management* 23, 1283–1293.

514 Bozek, M., Baccante, D., & Lester, N. (2011). Walleye and Sauger Life History. Pages 233–301.

515 Charnov, E. L., Turner, T. F., & Winemiller, K. O. (2001). Reproductive constraints and the
516 evolution of life histories with indeterminate growth. *Proceedings of the National
517 Academy of Sciences* 98, 9460–9464.

518 Chizinski, C. J., Martin, D. R., Hurley, K. L., & Pope, K. L. (2014). Self-imposed length limits
519 in recreational fisheries. *Fisheries Research* 155, 83–89.

520 Cooke, S. J., Suski, C. D., Arlinghaus, R., & Danylchuk, A. J. (2013). Voluntary institutions and
521 behaviours as alternatives to formal regulations in recreational fisheries management.
522 *Fish and Fisheries* 14, 439–457.

523 De Roos, A. M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., &
524 Persson, L. (2008). Simplifying a physiologically structured population model to a stage-
525 structured biomass model. *Theoretical Population Biology* 73, 47–62.

526 Ditton, R.B., & Hunt, K.M. (2001). Combining creel intercept and mail survey
527 methods to understand the human dimensions of local freshwater fisheries. *Fisheries
528 Management and Ecology* 8, 295–301.

529 Fayram, A. H. (2003). A Comparison of Regulatory and Voluntary Release of Muskellunge and
530 Walleyes in Northern Wisconsin. *North American Journal of Fisheries Management* 23,
531 619–624.

532 Fayram, A. H., & Schmalz, P. J. (2006). Evaluation of a Modified Bag Limit for Walleyes in
533 Wisconsin: Effects of Decreased Angler Effort and Lake Selection. *North American
534 Journal of Fisheries Management* 26, 606–611.

535 Feiner, Z., Latzka, A., & Wolter, M. (2021). What to Exploit When You're Exploiting: Angling
536 Rates and Size Selection Responses to Changing Bag Limits. In Harvest of Fish and

Wildlife: New Paradigms for Sustainable Management. CRC Press. Pope and Powell, editors.

Feiner, Z.S., Shaw, S.L., & Sass, G.G. (2019). Influences of female body condition on recruitment success of walleye (*Sander vitreus*) in Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 76, 2131-2144.

Gundelund, C., Venturelli, P., Hartill, B.W., Hyder, K., Olesen, H.J., & Skov, C. (2021). Evaluation of a citizen science platform for collecting fisheries data from coastal sea trout anglers. *Canadian Journal of Fisheries and Aquatic Sciences* 78, 1576-1585.

Gwinn, D. C., Allen, M. S., Johnston, F. D., Brown, P., Todd, C. R. & Arlinghaus, R. (2015). Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries* 16, 259–281.

Haglund, J. M., Isermann, D. A., & Sass, G. G. (2016). Walleye Population and Fishery Responses after Elimination of Legal Harvest on Escanaba Lake, Wisconsin. *North American Journal of Fisheries Management* 36, 1315–1324.

Hayden, T. A., Binder, T. R., Holbrook, C. M., Vandergoot, C. S., Fielder, D. G., Cooke, S. J., Dettmers, J. M., & Krueger, C. C. (2018). Spawning site fidelity and apparent annual survival of walleye (*Sander vitreus*) differ between a Lake Huron and Lake Erie tributary. *Ecology of Freshwater Fish* 27, 339–349.

Henderson, B. A., Collins, N., Morgan, G. E., & Vaillancourt, A. 2003. Sexual size dimorphism of walleye (*Stizostedion vitreum vitreum*). *Canadian Journal of Fisheries and Aquatic Sciences*, 1345–1352.

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71, 2171–2185.

Hunt, L., Haider, W., & Armstrong, K. (2002). Understanding the Fish Harvesting Decisions by Anglers. *Human Dimensions of Wildlife* 7, 75–89.

Johnston, F. D., Allen, M. S., Beardmore, B., Riepe, C., Pagel, T., Hühn, D., & Arlinghaus, R. (2018). How ecological processes shape the outcomes of stock enhancement and harvest regulations in recreational fisheries. *Ecological Applications* 28, 2033–2054.

Johnston, F.D., Simmons, S., van Poorten, B., & Venturelli, P. (2021). Comparative analyses with conventional surveys reveal the potential for an angler app to contribute to recreational fisheries monitoring. *Canadian Journal of Fisheries and Aquatic Sciences* e-First <https://doi.org/10.1139/cjfas-2021-0026>.

Kapuscinski, K. L., Farrell, J. M., & Murry B. A. (2012). Feeding Strategies and Diets of Young-of-the-Year Muskellunge from Two Large River Ecosystems. *North American Journal of Fisheries Management* 32, 635–647.

Kaemingk, M.A., Hurley, K.L., Chizinski, C.J. & Pope, K.L. (2020). Harvest–release decisions in recreational fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 77, 194–201.

Kerns, J. A., Allen, M. S., Dotson, J. R., & Hightower, J. E. (2015). Estimating Regional Fishing Mortality for Freshwater Systems: a Florida Largemouth Bass Example. *North American Journal of Fisheries Management* 35, 681–689.

Kozfkay, J.R., & Dillon, J.C. (2011). Creel survey methods to assess catch, loss, and capture frequency of white sturgeon in the Snake River, Idaho. *North American Journal of Fisheries Management* 30, 221-229.

582 Koupal, K. D., Katt, J. D., Schoenebeck, C. W., & Eifert, B. E. (2015). Sex-specific Changes in
583 Walleye Abundance, Size Structure and Harvest Following Implementation of Regulation
584 to Protect Broodstock. *Journal of Fish and Wildlife Management* 6, 448–455.

585 Lackmann, A. R., Kratz, B. J., Bielak-Lackmann, E. S., Jacobson, R. I., Sauer, D. J., Andrews,
586 A. H., Butler, M. G., & Clark, M. E. (2021). Long-lived population demographics in a
587 declining, vulnerable fishery - bigmouth buffalo (*Ictiobus cyprinellus*) of Jamestown
588 Reservoir, North Dakota. *Canadian Journal of Fisheries and Aquatic Sciences*:cjfas-
589 2020-0485.

590 Lester, N. P., Shuter, B. J., & Abrams, P. A. (2004). Interpreting the von Bertalanffy model of
591 somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of*
592 *London. Series B: Biological Sciences* 271, 1625–1631.

593 Lester, N. P., Shuter, B. J., Venturelli, P., & Nadeau, D. (2014). Life-history plasticity and
594 sustainable exploitation: a theory of growth compensation applied to walleye
595 management. *Ecological Applications* 24, 38–54.

596 Long, J. M., Allen, M. S., Porak, W. F., & Suski, C. D. (2015). A Historical Perspective of Black
597 Bass Management in the United States. *American Fisheries Society Symposium* 82, 99–
598 122.

599 Lynch, A.J., N.A. Sievert, H. S. Embke, A. M. Robertson, B. J. E. Myers, M. S. Allen, Z. S.
600 Feiner, F. Hoogakker, S. Knoche, R.M. Krogman, S.R. Midway, C.L. Nieman, C.P.
601 Paukert, K. L. Pope, M.W. Rogers, L.S. Wszola, T. D. Beard, Jr. (2021). The U.S. Inland
602 Creel and Angler Survey Catalog (CreelCat): Development, Applications, and
603 Opportunities. *Fisheries* 46, 574-583.

604 Malvestuto, S.P, Davies, W.D., & Shelton, W.L. (1978). An evaluation of the roving creel
605 survey with nonuniform probability sampling. *Transactions of the American Fisheries*
606 *Society* 107, 255-262.

607 Myers, R. A., Smith, M. W., Hoenig, J. M., Kmiecik, N., Luehring, M. A., Drake, M. T.,
608 Schmalz, P. J., & Sass, G. G. (2014). Size- and Sex-Specific Capture and Harvest
609 Selectivity of Walleyes from Tagging Studies. *Transactions of the American Fisheries*
610 *Society* 143, 438–450.

611 Myers, R., Taylor, J., Allen, M., & Bonvechio, T. F. (2008). Temporal Trends in Voluntary
612 Release of Largemouth Bass. *North American Journal of Fisheries Management* 28,
613 428–433.

614 Newman, S.P., Rasmussen, P.W., & Andrews, L.M. (1997). Comparison of a stratified,
615 instantaneous count creel survey with a complete mandatory creel census on Escanaba
616 Lake, Wisconsin. *North American Journal of Fisheries Management*, 17, 321-330.

617 Nilsson, P. A., & Bronmark, C. (2000). Prey vulnerability to a gape-size limited predator:
618 behavioural and morphological impacts on northern pike piscivory. *Oikos* 88, 539–546.

619 Nieman, C.L., Iwiski, C., Lynch, A.J., Sass, G.G., Solomon, C.T., Trudeau, A., & van Poorten,
620 B. (2021). Creel Surveys for Social-Ecological-Systems Focused Fisheries Management.
621 *Reviews in Fisheries Science & Aquaculture*. DOI: 10.1080/23308249.2020.1869696.

622 Ohlberger, J., Langangen, Ø., Edeline, E., Claessen, D., Winfield, I. J., Stenseth, N., &
623 Vøllestad, L. A. (2011). Stage-specific biomass overcompensation by juveniles in
624 response to increased adult mortality in a wild fish population. *Ecology* 92, 2175–2182.

625 Pollock, K.H., Jones, C.M., & Brown, T.L. (1994). Angler survey methods and their applications
626 in fisheries management. The American Fisheries Society, Bethesda, MD.

For personal use only. This Just-IN manuscript is the accepted manuscript prior to copy editing and page composition. It may differ from the final official version of record.

627 Post, J. R., Mushens, C., Paul, A., & Sullivan, M. (2003). Assessment of Alternative Harvest
628 Regulations for Sustaining Recreational Fisheries: Model Development and Application
629 to Bull Trout. *North American Journal of Fisheries Management* 23, 22–34.

630 Quinn, J. W. (2010). A Survey of Bowfishing Tournaments in Arkansas. *North American*
631 *Journal of Fisheries Management* 30, 1376–1384.

632 Quist, M. C., Stephen, J. L., Lynott, S. T., Goeckler, J. M., & Schultz, R. D. (2010). Exploitation
633 of walleye in a Great Plains reservoir: harvest patterns and management scenarios.
634 *Fisheries Management and Ecology* 17, 522–531.

635 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
636 Statistical Computing, Vienna, Austria.

637 Reitz, R. A., & Travnichek, V. H. (2006). Examining the Relationship between Species
638 Preference and Catfish Angler Demographics, Angling Behavior, & Management
639 Opinions:7.

640 Robson, D., & Jones, C.M. (1989). The theoretical basis of an access site angler survey design.
641 *Biometrics* 45, 83–98.

642 Roop, H. J., Poudyal, N. C., & Jennings, C. A. (2021). Fishing preferences, angling behavior, &
643 attitudes toward management: a comparison between White and Nonwhite anglers.
644 *Human Dimensions of Wildlife* 26, 84–89.

645 Scarneccchia, D. L., & Schooley, J. D. (2020). Bowfishing in the United States: History, Status,
646 Ecological Impact, and a Need for Management. *Transactions of the Kansas Academy of*
647 *Science* 123, 3–4.

648 Shaw, S. L., Sass, G. G., & VanDeHey. J. A. (2018). Maternal effects better predict walleye
649 recruitment in Escanaba Lake, Wisconsin, 1957–2015: implications for regulations.
650 *Canadian Journal of Fisheries and Aquatic Sciences* 75, 2320–2331.

651 Shaw, S.L., Sass, G.G., & Eslinger, L.D. (2019). Effects of angler harvest on adult muskellunge
652 growth and survival in Escanaba Lake, Wisconsin, 1956–2016. (2019). *North American*
653 *Journal of Fisheries Management* 39, 124–134.

654 Solomon, C.T., Dassow, C.J., Iwicki, C.M., Jensen, O.P., Jones, S.E., Sass, G.G., Trudeau, A.,
655 van Poorten, B.T., & Whittaker, D. (2020). Frontiers in modelling social–ecological
656 dynamics of recreational fisheries: A review and synthesis. *Fish and Fisheries* 21, 973–
657 991.

658 Spirk, P.J. (2012). Effects of length limits on sexually size dimorphic fishes. MS Thesis.
659 University of Nebraska-Lincoln.

660 Stevens, T., & Ward, M. (2014). Completion Report for Summer Creel Survey Report for Leech
661 Lake 2014. F13AF00322 R29G60F29RP31.

662 Thorson, J. T. (2020). Predicting recruitment density dependence and intrinsic growth rate for all
663 fishes worldwide using a data-integrated life-history model. *Fish and Fisheries* 21, 237–
664 251.

665 Trudeau, A., Dassow, C.J., Iwicki, C.M., Jones, S.E., Sass, G.G., Solomon, C.T., van Poorten,
666 B.T., & Jensen, O.P. (2021). Estimating fishing effort across the landscape: A spatially
667 extensive approach using models to integrate multiple data sources. *Fisheries Research*
668 233.

669 Uphoff, C. S., & Schoenebeck, C. W. (2012). Quantifying inter-population variability in yellow
670 perch sexual size dimorphism. *Journal of Freshwater Ecology* 27, 507–516.

671 de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Temple Lang, D., & Bodik, R.
672 (2017). Programming with models: writing statistical algorithms for general model

673 structures with NIMBLE. *Journal of Computational and Graphical Statistics* 26, 403–
674 417.

675 Venturelli, P. A., Lester, N. P., Marshall, T. R., & Shuter, B. J. (2010). Consistent patterns of
676 maturity and density-dependent growth among populations of walleye (*Sander vitreus*):
677 application of the growing degree-day metric. *Canadian Journal of Fisheries and Aquatic
678 Sciences* 67, 1057–1067.

679 Ward, M. 2015. Fisheries Management Plan for Leech Lake 2016 - 2020. Page 39. Minnesota
680 Department of Natural Resources.

681 Wilson, K. L., Honsey, A. E., Moe, B., & Venturelli, P. (2018). Growing the biphasic
682 framework: Techniques and recommendations for fitting emerging growth models.
683 *Methods in Ecology and Evolution* 9, 822–833.

684 Woodward, R. T., & Griffin, W. L. (2003). Size and Bag Limits in Recreational Fisheries:
685 Theoretical and Empirical Analysis. *Marine Resource Economics* 18, 239–262.

686

687 **TABLES AND FIGURES**

Table 1: Numbers, life-stages, sexes, lengths, and ages of gillnetted walleye in Leech Lake, MN, USA from 1990-2019.

Sex	Stage	N	Mean length (cm)	SD Length (cm)	Mean age (years)	SD Age (years)	Mean mass (g)	SD mass (g)
Female	Juvenile	2903	33	8	2	1	356	245
Female	Adult	1798	53	7	6	2	1386	541
Female	NA	16	30	11	2	2	295	327
Male	Juvenile	1863	29	5	1	1	209	121
Male	Adult	2053	45	6	5	3	855	357
Male	NA	29	32	8	2	1	295	187
NA	NA	6	22	5	1	1	NA	NA

688

689

690

Table 2: Numbers, mean lengths, proportions kept, and lengths of kept and released walleye from creel surveys at Leech Lake, MN, USA. In the slot regulations, small liberal size bins refer to lengths below the lower boundary of the protected slot, illegal size bins contain the lengths within the protected slot, and large restricted size bins contain the lengths larger than the upper bound of the protected slot. In the “1 over 20 inches” regulation, the small liberal size bin contains lengths below 20 inches and the large restricted size bin contains lengths greater than or equal to 20 inches \approx 51 cm.

Years effective	Regulation	Bin	N	Mean length (cm)	SD length (cm)	% kept	Mean kept length (cm)	SD kept length (cm)	Mean released length (cm)	SD released length (cm)
2005-2013	18-26” protected slot	Small liberal	71040	36	6	57	39	4	33	7
	18-26” protected slot	Illegal	47579	55	5	18	51	5	56	5
	18-26” protected slot	Large restricted	1800	69	3	18	69	4	69	3
2014-2018	20-26” protected slot	Small liberal	40120	37	7	55	40	4	35	8
	20-26” protected slot	Illegal	19771	57	4	5	56	4	57	4
	20-26” protected slot	Large restricted	884	69	3	18	69	4	69	3
2019-	1 over 20”	Small liberal	20993	37	7	55	40	4	35	8
2020	1 over 20”	Large restricted	10803	57	5	5	58	6	57	5

691

692

693

694

Table 3: Maturation model parameter means, priors, and 95% credible intervals of walleye from Leech Lake, MN, USA. All priors are normally distributed and specified as $N(\text{mean}, \text{precision})$.

Parameter	Mean	2.5% CI	97.5% CI	Prior
$\theta_0 F$ Female Intercept	-7.65	-8.14	-7.20	$N(0, 0.0001)$
$\theta_0 M$ Male Intercept	-6.18	-6.60	-5.77	$N(0, 0.0001)$
$\theta_1 F$ Female effect of age	1.95	1.83	2.07	$N(0, 0.0001)$
$\theta_0 M$ Male effect of age	2.39	2.23	2.56	$N(0, 0.0001)$
$T50_F$	3.93	3.87	3.99	NA
$T50_M$	2.59	2.54	2.64	NA

695

696

697

Table 4: Sexually dimorphic biphasic growth model parameter means, priors, and 95% credible intervals for walleye from Leech Lake, MN, USA. Priors specified with brackets are bounded within the brackets. All normally-distributed priors are specified as $N(\text{mean}, \text{precision})$, uniform priors are specified as $U(\text{minimum}, \text{maximum})$, and gamma-distributed priors are specified as $G(\text{shape}, \text{scale})$.

Parameter	Mean	2.5% CI	97.5% CI	Prior
a_F Female mass multiplier	0.0057	0.0054	0.0061	$N(0, 0.001)$
a_M Male mass multiplier	0.0047	0.0043	0.0052	$N(0, 0.001)$
b_F Female mass exponent	3.1139	3.1000	3.1272	$N(3, 0.01)[0, 001, \infty]$
b_M Male mass exponent	3.1678	3.1458	3.1904	$N(3, 0.01)[0, 001, \infty]$
g_F Female GSI	0.2422	0.2330	0.2516	$U(0.001, 3/(T50_F - \tau_F))$
g_M Male GSI	0.3584	0.3469	0.3697	$U(0.001, 3/(T50_M - \tau_M))$
h_F Female linear growth rate	6.7885	6.6977	6.8797	$N(7, 0.01)[0.001, \infty]$
h_M Male linear growth rate	7.5744	7.4453	7.7007	$N(7, 0.01)[0.001, \infty]$
τ_F Female early environment correction	-2.8729	-2.9399	-2.8074	$N(0, 0.001)$
τ_M Male early environment correction	-2.4479	-2.5157	-2.3832	$N(0, 0.001)$
τ_M Mass precision	0.0002	0.0002	0.0002	$G(0.01, 0.01)$
cv_L Length coefficient of variation	0.0984	0.0969	0.0999	$G(0.01, 0.01)$

698

699

700

Table 5: Harvest model for angler-caught walleye in Leech Lake, MN, USA. p_0 parameters are intercepts and p_1 parameters are length effects for each bin-regulation set combination. All priors are normally distributed and specified as $N(\text{mean}, \text{precision})$.

Regulation set	Bin	Parameter	Mean	2.5% CI	97.5% CI	Prior
1 over 20"	Small liberal	p_0	-4.1360	-4.3116	-3.9634	$N(0, 0.0001)$
1 over 20"	Large restricted	p_0	-3.0771	-3.2248	-2.9289	$N(0, 0.0001)$
18-26" protected slot	Small liberal	p_0	-7.7703	-7.9047	-7.6356	$N(0, 0.0001)$
18-26" protected slot	Illegal	p_0	-0.3881	-0.4450	-0.3312	$N(0, 0.0001)$
18-26" protected slot	Large restricted	p_0	-1.2142	-1.4105	-1.0156	$N(0, 0.0001)$
20-26" protected slot	Small liberal	p_0	-4.2958	-4.4261	-4.1647	$N(0, 0.0001)$
20-26" protected slot	Illegal	p_0	-2.7650	-2.8775	-2.6547	$N(0, 0.0001)$
20-26" protected slot	Large restricted	p_0	-1.2058	-1.4860	-0.9292	$N(0, 0.0001)$
1 over 20"	Small liberal	p_1	0.1160	0.1114	0.1206	$N(0, 0.0001)$
1 over 20"	Large restricted	p_1	0.0235	0.0066	0.0404	$N(0, 0.0001)$
18-26" protected slot	Small liberal	p_1	0.2232	0.2195	0.2269	$N(0, 0.0001)$
18-26" protected slot	Illegal	p_1	-0.2384	-0.2466	-0.2303	$N(0, 0.0001)$
18-26" protected slot	Large restricted	p_1	-0.1116	-0.1697	-0.0577	$N(0, 0.0001)$
20-26" protected slot	Small liberal	p_1	0.1212	0.1177	0.1247	$N(0, 0.0001)$
20-26" protected slot	Illegal	p_1	-0.0492	-0.0657	-0.0327	$N(0, 0.0001)$

20-26" protected slot	Large restricted	p_1	-0.1115	-0.1942	-0.0356	$N(0, 0.0001)$
701						
702						

Table 6: Retention probability averaged across each sex and life-stage combination of walleye caught at Leech Lake, MN, USA.

Regulation set	Sex	Stage	Mean	2.5% CI	97.5% CI
1 over 20"	Female	Overall	0.20	0.19	0.21
1 over 20"	Female	Juvenile	0.43	0.42	0.44
1 over 20"	Female	Adult	0.14	0.13	0.15
1 over 20"	Male	Overall	0.30	0.29	0.30
1 over 20"	Male	Juvenile	0.31	0.30	0.32
1 over 20"	Male	Adult	0.30	0.29	0.30
18-26" protected slot	Female	Overall	0.18	0.17	0.19
18-26" protected slot	Female	Juvenile	0.42	0.41	0.42
18-26" protected slot	Female	Adult	0.11	0.10	0.13
18-26" protected slot	Male	Overall	0.24	0.23	0.24
18-26" protected slot	Male	Juvenile	0.24	0.24	0.25
18-26" protected slot	Male	Adult	0.24	0.23	0.24
20-26" protected slot	Female	Overall	0.23	0.21	0.24
20-26" protected slot	Female	Juvenile	0.43	0.43	0.44
20-26" protected slot	Female	Adult	0.18	0.16	0.19
20-26" protected slot	Male	Overall	0.30	0.29	0.30
20-26" protected slot	Male	Juvenile	0.31	0.30	0.31
20-26" protected slot	Male	Adult	0.30	0.29	0.30

704 Figure 1: Predicted probability of maturity as a function of age differed for male and female
705 walleye in Leech Lake, MN, USA. The majority of males matured between ages 2 and 3 whereas
706 the majority of females matured between ages 3 and 4. Mean model estimates are represented by
707 solid lines and 95% credible intervals are represented by dashed lines. Labels in boxes represent
708 average percent of cohort mature at each age estimated from the raw data.

709 Figure 2: Predicted biphasic growth and maturation of male and female walleye in Leech Lake,
710 MN, USA, varied by sex. Males grew slightly faster as juveniles, matured earlier and at smaller
711 sizes, and ultimately reached smaller adult sizes than females. Solid lines represent mean
712 predicted length based on the growth model, dashed lines indicate 95% credible intervals, and
713 points represent raw data. Straight lines represent predicted juvenile growth and curved lines
714 indicate adult growth. Maturation is indicated by the diamond-shaped points.

715 Figure 3: Retention probability increased as a function of fish length in small liberal size bins
716 under all three harvest regulations in Leech Lake, MN, USA. Harvest of fish in illegal and large
717 restricted size bins was overall low and relatively unselective with regard to fish length. Solid
718 black lines indicate prediction means, dashed gray lines indicate 95% credible intervals, and
719 breakpoints indicate changes in regulation size bins.

720 Figure 4: Retention probability for male and female walleye in Leech Lake, MN, USA at
721 different life-stages varied as a function of size and angler behavior under different harvest
722 regulations per maturation, growth, and harvest models. Juvenile female walleye were more
723 likely to be harvested given capture than adult female walleye under all harvest regulations, but
724 especially under the 18-26" protected slot and to a lesser extent the 20-26" protected slot. Males
725 were exposed to higher retention probability for much more of their reproductive lives than were
726 females, and had a higher average retention probability than females.

727

728

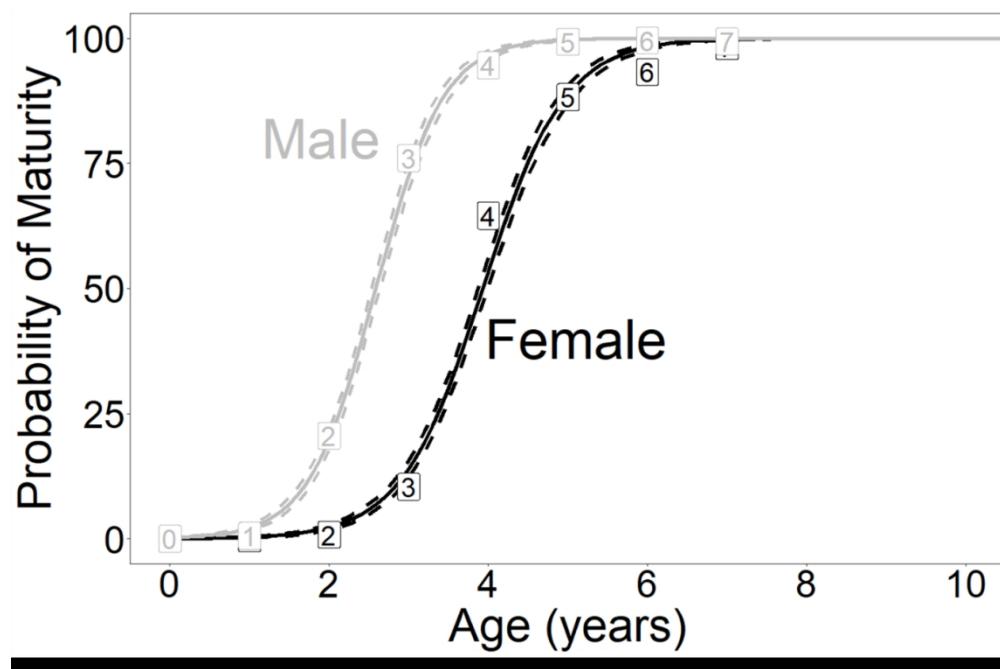


Figure 1: Predicted probability of maturity as a function of age differed for male and female walleye in Leech Lake, MN, USA. The majority of males matured between ages 2 and 3 whereas the majority of females matured between ages 3 and 4. Mean model estimates are represented by solid lines and 95% credible intervals are represented by dashed lines. Labels in boxes represent average percent of cohort mature at each age estimated from the raw data.

940x623mm (38 x 38 DPI)

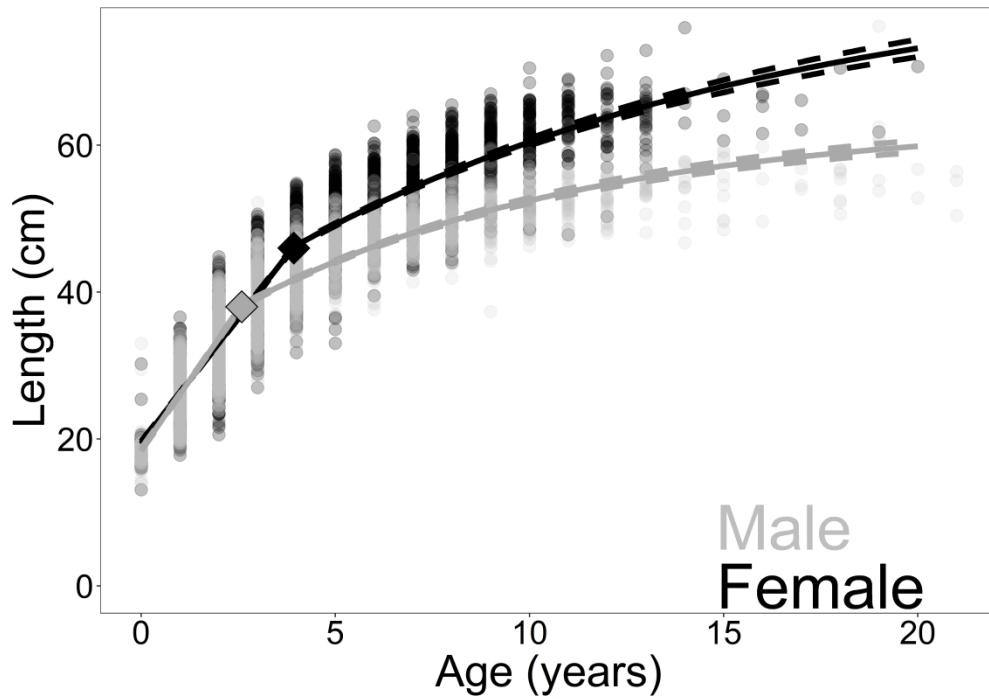


Figure 2: Predicted biphasic growth and maturation of male and female walleye in Leech Lake, MN, USA, varied by sex. Males grew slightly faster as juveniles, matured earlier and at smaller sizes, and ultimately reached smaller adult sizes than females. Solid lines represent mean predicted length based on the growth model, dashed lines indicate 95% credible intervals, and points represent raw data. Straight lines represent predicted juvenile growth and curved lines indicate adult growth. Maturation is indicated by the diamond-shaped points.

653x459mm (236 x 236 DPI)

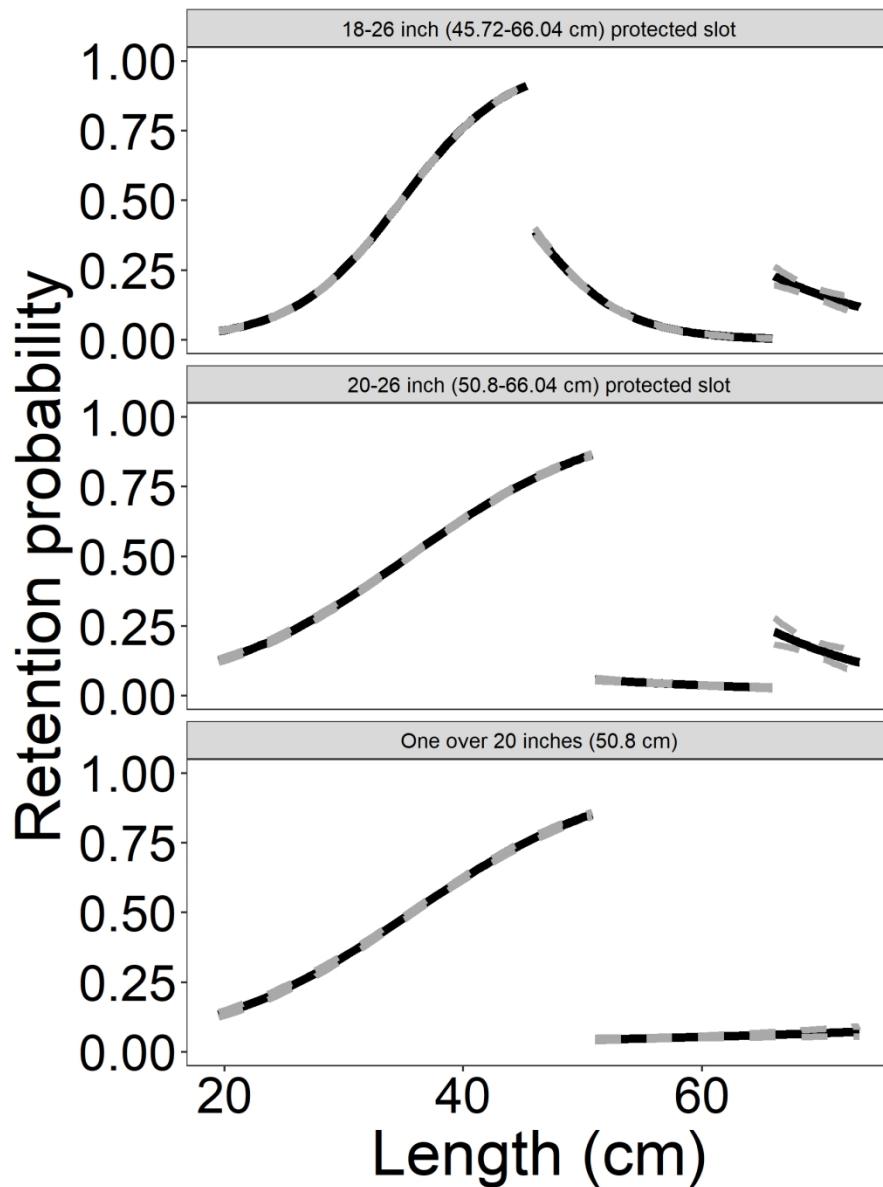


Figure 3: Retention probability increased as a function of fish length in small liberal size bins under all three harvest regulations in Leech Lake, MN, USA. Harvest of fish in illegal and large restricted size bins was overall low and relatively unselective with regard to fish length. Solid black lines indicate prediction means, dashed gray lines indicate 95% credible intervals, and breakpoints indicate changes in regulation size bins.

387x516mm (118 x 118 DPI)

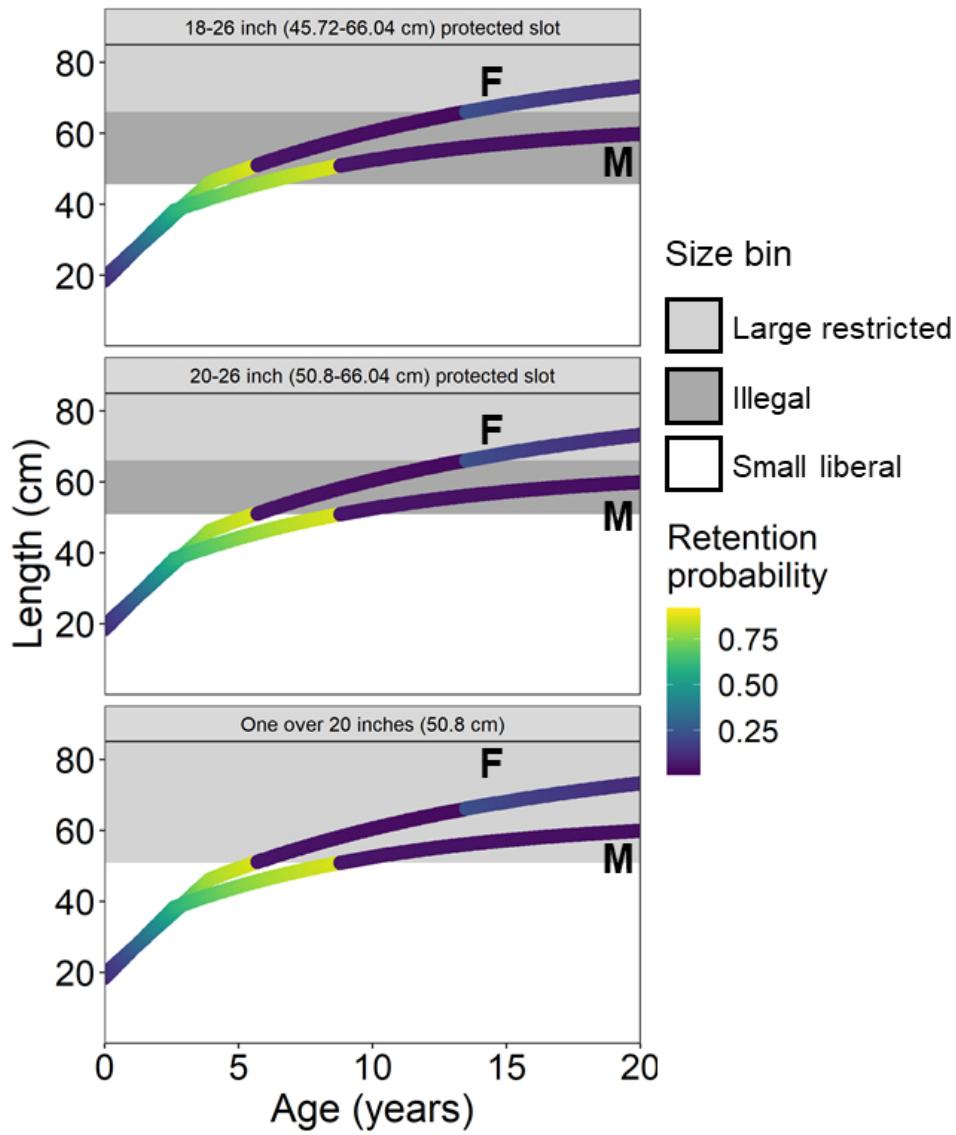


Figure 4: Retention probability for male and female walleye in Leech Lake, MN, USA at different life-stages varied as a function of size and angler behavior under different harvest regulations per maturation, growth, and harvest models. Juvenile female walleye were more likely to be harvested given capture than adult female walleye under all harvest regulations, but especially under the 18-26" protected slot and to a lesser extent the 20-26" protected slot. Males were exposed to higher retention probability for much more of their reproductive lives than were females, and had a higher average retention probability than females.

449x513mm (38 x 38 DPI)