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Lyndsie S. Wszola

University of Nebraska-Lincoln, lyndsie.wszola@huskers.unl.edu

Zachary S. Feiner

University of Wisconsin-Madison

Christopher J. Chizinski

University of Nebraska-Lincoln, cchizinski2@unl.edu

Jamilynn B. Poletto

University of Nebraska - Lincoln, jpoletto2@unl.edu

John P. DeLong

University of Nebraska-Lincoln, jpdelong@unl.edu

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

Lyndsie S. Wszola,¹ Zachary S. Feiner,^{2,3}
Christopher J. Chizinski,⁴ Jamilynn B. Poletto,⁴
and John P. DeLong¹

1 School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE, USA

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

3 Center for Limnology, University of Wisconsin–Madison, Madison, WI, USA

4 School of Natural Resources, University of Nebraska–Lincoln, Lincoln, NE, USA

Corresponding author — Lyndsie Wszola; email Lyndsie.Wszola@huskers.unl.edu

ORCID

Lyndsie S. Wszola <https://orcid.org/0000-0002-2660-2048>

Zachary S. Feiner <https://orcid.org/0000-0001-7880-0778>

Christopher J. Chizinski <https://orcid.org/0000-0001-9294-2588>

Abstract

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

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Résumé

La réglementation relative aux pêches sportives en eau douce constitue un outil d'importance capitale pour l'atteinte des objectifs sociaux et écologiques des pêches. Les interactions des comportements des pêcheurs et de la biologie des poissons peuvent toutefois influencer l'efficacité de la réglementation de manière imprévue. Nous combinons des modèles de croissance des poissons et de comportement des pêcheurs afin d'examiner l'effet de l'interaction du comportement des pêcheurs et du cycle biologique des poissons sur la probabilité de récolte de poissons au vu des prises selon l'âge, de l'étape du cycle de vie et du sexe de dorés jaunes (*Sander vitreus*). Comparativement aux femelles, les mâles croissent plus vite quand ils sont juvéniles, arrivent à maturité plus tôt et atteignent des tailles maximums plus petites. Les dorés mâles sont donc plus vulnérables à la récolte pour une plus grande partie de leur vie reproductive que les femelles parce qu'ils passent plus de temps à des tailles qui les rendent plus susceptibles d'être récoltés par les pêcheurs. Nous suggérons que le fait de restreindre la récolte aux grands individus pour des espèces qui présentent un dimorphisme sexuel pourrait favoriser la survie des grandes femelles en âge de reproduction. Nous démontrons en outre que le jumelage de modèles de croissance des poissons et de comportement des pêcheurs peut fournir de l'information utile sur l'effet de la récolte sur les poissons aux cycles biologiques complexes au fil de leur vie.



1. Introduction

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

Effective regulations describe biologically meaningful traits of harvest-legal and harvest-illegal individuals to a regulation-adherent user base (Ainsworth et al. 2012; Johnston et al. 2018; Ahrens et al. 2020). The primary tools available to fisheries managers for managing the effects of harvest on population age, sex, and life stage structure are

combined bag and length limits. Bag limits specify how many fish may be harvested per day, and length limits specify what lengths those fish may be. Length, however, has a complex relationship with fish physiology and population ecology (Arlinghaus et al. 2010; Gwinn et al. 2015). Fish growth is influenced by diverse factors, including population density, maternal effects, predation, and environmental variation (Shaw et al. 2018; Thorson 2020). Many fish consequently exhibit indeterminate growth and plasticity in age or size at maturity (Charnov et al. 2001). The resulting fish length is often directly related to fecundity (Barneche et al. 2018), making it an important determinant of a fish's value to the fishery. Thus, the consequences of removing a fish at a given length may be quite different across systems depending on a population's underlying life history and interactions with its environment.

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

Variation in anglers' responses to regulations may affect the distribution of mortality within fish populations in subtle ways. Stewardship ethics and enlightened self-interest may drive anglers to self-impose minimum and maximum length limits on their harvest in addition to official length regulations (Chizinski et al. 2014; Kaemingk et al. 2020). Anglers motivated by eating their catch may preferentially harvest larger fish (Hunt et al. 2002; Feiner et al. 2021; Roop et al. 2021). Conversely, anglers may voluntarily release very large fish because they are wary of bioaccumulated toxins or perceive releasing large individuals to be a form of resource stewardship (Fayram 2003; Reitz and Travnichek 2006). Furthermore, length and bag limits may interact to shape angler

perceptions and behavior. When a bag limit is reduced, anglers may respond by changing fishing locations or harvest decisions, redistributing mortality risk across landscapes and within populations (Beard et al. 2003; Woodward and Griffin 2003; Fayram and Schmalz 2006; Feiner et al. 2021).

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

2. Methods

2.1. Study system

We used data from an intensively studied walleye (*Sander vitreus*) fishery to evaluate the hypothesis that angler harvest selectivity interacts with regulations and fish life history to shape the distribution of retention probability across ages, life stages, and sexes of a population. Walleye are widely studied and harvested in recreational, subsistence, and commercial fisheries across their native range in Canada, the United States, and Tribal waters (Bozek et al. 2011). Previous investigations of walleye angler behavior have demonstrated that retention probability increases as a function of fish length up to a point, after which it asymptotes or even declines (Kaemingk et al. 2020). The extent to which this voluntary release of large fish is reflected across different regulation types has not been intensively examined, nor has the impact of within-regulation angler behavior on patterns of fish mortality.

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

We modeled walleye life history and angler harvest decisions using data from the walleye fishery in Leech Lake, MN, USA. Leech Lake is located within the Chippewa National Forest and much of it is within the Leech Lake Indian Reservation. Leech Lake is accordingly managed by treaty agreement between the Minnesota Department of Natural Resources and the Leech Lake Band of Ojibwe. It comprises approximately 41662 hectares with a maximum depth of 46 m. The lake supports a diverse fish community, including warm-water species like bluegill (*Lepomis macrochirus*) and largemouth bass, as well as large cool-water predators, including walleye, muskellunge (*Esox masquinongy*), and northern pike (*Esox lucius*).

2.2. Walleye sampling

We extracted walleye length, age, sex, and life stage (juvenile or adult) data from the annual Leech Lake walleye fall gillnet survey including study years 1990–2019. Walleye were sampled via experimental gill net array annually in the first 2 weeks of September using 77 m long gill nets with five different mesh sizes: 1.91, 2.54, 3.18, 3.81, and 5.08 cm in panels with a stretch length of 15.25 m. Surveyors conducted 36 roughly 24 h net sets most years. Walleye were measured to total length, weighed, aged using otoliths, and evaluated for sex and sexual maturity via internal examination. More comprehensive descriptions of the Leech Lake system and annual walleye survey may be found in the Leech Lake 2016–2020 Fisheries Management Plan (Ward 2015, their supplementary material).

2.3. Creel sampling

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

The Leech Lake creel data include three regulation periods between the years 2008 and 2020, creating the opportunity to observe how anglers make harvest decisions within varying regulation structures. Regulation periods 1 and 2 were protected slot limits, and regulation period 3 allowed harvest of any sized walleye but restricted the number of large fish that could be harvested:

1. 2005–2013: Fish less than 18 in. (45.72 cm) may be kept. All fish from 18 to 26 in. (45.72–66.04 cm) must be immediately released. One fish over 26 in. (66.04 cm) allowed in possession. Possession limit four.
2. 2014–2018: Fish less than 20 in. (50.8 cm) may be kept. All fish from 20 to 26 in. (50.8–66.04 cm) must be immediately released. One fish over 26 in. (66.04 cm) allowed in possession. Possession limit four.
3. 2019–present: Fish less than 20 in. (50.8 cm) may be kept. Only one fish over 20 in. (50.8 cm) allowed in possession. Possession limit four.

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

2.4. Modeling walleye growth and life history

We modeled walleye life history using a sexually dimorphic extension of the biphasic growth model (Lester et al. 2004, 2014). The biphasic model corrects the tendency of other models to ignore differences in energy allocation between adults and juveniles by relating growth across the fish’s life cycle to observable life history traits. The model predicts fish length L as a function of fish age t , sex s , linear juvenile growth rate h , unitless gonadosomatic index g (gonad mass expressed as a fraction of somatic mass), age at 50% probability of maturing $T50$, and τ , a temporal offset reflecting the effect of early environmental conditions on juvenile growth. Juvenile length $L_{js}(t)$ is modeled as a linear function of age because juveniles dedicate all energy exceeding maintenance to somatic growth:

$$L_{js}(t) = h_s(t - \tau_s) \quad (1)$$

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

$$L_{As}(t) = L_{\infty} \{1 - \exp[-k_s(t - t_{0s})]\} \quad (2)$$

where

$$L_{\infty} = \frac{3h_s}{g_s} \quad (3)$$

$$k_s = \ln \left(1 + \frac{g_s}{3} \right) \quad (4)$$

and

$$t_{0s} = T50_s + \frac{\ln [1 - g_s(T50_s - \tau_s)/3]}{\ln (1 + g_s/3)} \quad (5)$$

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

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

$$A \sim B(\theta_s) \tag{6}$$

$$\theta_s = \frac{1}{1 + \exp[-(\theta_{0s} + \theta_{1s}t)]} \tag{7}$$

We extracted sex-specific estimates of $T50$, the age at which 50% of a cohort was predicted to be mature (i.e., we set eq. 7 = 0.5 and solved for t) and used them in place of individual age at maturation to model sex- and stage-specific biphasic length and mass growth using a hierarchical Bayesian approach (per Wilson et al. 2018). The model describes fish length (L) of each gillnet-sampled fish as a random variable drawn from a normal distribution with mean μ_L and coefficient of variation CV_L :

$$L \sim N(\mu_L, CV_L) \tag{8}$$

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

$$\mu_L = \begin{cases} t < T50_s, L_j(t) \\ t \geq T50_s, L_A(t) \end{cases} \tag{9}$$

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

$$M = a_s L^{b_s} \tag{10}$$

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

$$M \sim N(\mu_M, \text{prec}_M) \quad (11)$$

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

2.5. Modeling harvest

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

$$H \sim B(p_r) \quad (12)$$

$$p_r(L) = \frac{1}{1 + \exp[-(p_{0,r} + p_{1,r}L)]} \quad (13)$$

We evaluated the effect of fish length on retention probability by calculating the difference between the length bin minimum and the fish's length. For example, under regulation set 1 (18–26 in. \approx 46–66 cm protected slot), a fish with length equal to 50 cm would be in the illegal bin with bin length equal to 4.28 cm. Expressing fish length as the difference between total length and the length bin minimum rather than raw total length allowed us to predict retention probability within each regulation–bin combination using the bin length minimum as the intercept, rather than 0, facilitating easier comparison among regulation size bins. Further information on the bin length calculations is available in the supplementary material, and all priors for the harvest model are described in Table 4.

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

3. Results

We used 8668 walleye samples from the Leech Lake gillnet database including 4717 females and 3945 males (Table 1). The gillnet sample included 3851 adult fish, 4766 juvenile fish, and 6 fish unidentified to sex or life stage. The mean length of gillnet-sampled fish was 39 cm (SD=11 cm), and the mean age of gillnet-sampled fish was 4 years (SD = 3 years). Mean mass of gillnet-sampled fish was 658 g (SD = 556 g). Males were on average younger than females and had smaller average lengths and masses than females as both juveniles and adults (Table 1). We extracted 212 990 walleye harvest and release records from the creel database. Overall, 38% of captured fish were retained (Table 2). Fish captured in the small liberal size bins were most likely to be retained (55%–57% harvested). Fish in the large restricted size bins were retained at comparatively low rates (18% in the protected slot regulations and 5% in the “1 over 20 in.” regulation). Fish in the illegal size bins also were harvested at low rates (5%–10%).

Males matured at younger ages than females per the sexually dimorphic maturation model (Table 3; Fig. 1). Mean age at 50% maturity was 2.59 years for males (2.5% CI = 2.54 years, 97.5% CI = 2.64 years) and 3.93 years for females (2.5% CI = 3.87 years, 97.5% CI = 3.99 years). The life history differences between males and females also were apparent in the growth model (Table 4; Fig. 2). Males grew faster as juveniles than females, at a rate of $7.57 \text{ cm}\cdot\text{year}^{-1}$ (2.5% CI = $7.45 \text{ cm}\cdot\text{year}^{-1}$, 97.5% CI = $7.70 \text{ cm}\cdot\text{year}^{-1}$) compared to females' $6.79 \text{ cm}\cdot\text{year}^{-1}$ (2.5%

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

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

Table 2. Numbers, mean lengths, percent harvested, and lengths of harvested and released walleye from creel surveys at Leech Lake, MN, USA.

Years effective	Regulation	Bin	N	Length (cm)		Harvested		Released length (cm)	
				Mean	SD	Mean length (cm)	%	Mean	SD
2005–2013	18–26 in. protected slot	Small liberal	71,040	36	6	39	4	33	7
		Illegal	47,579	55	5	51	5	56	5
		Large restricted	1,800	69	3	69	4	69	3
2014–2018	20–26 in. protected slot	Small liberal	40,120	37	7	40	4	35	8
		Illegal	19,771	57	4	56	4	57	4
		Large restricted	884	69	3	69	4	69	3
2019–2020	1 over 20 in.	Small liberal	20,993	37	7	40	4	35	8
		Large restricted	10,803	57	5	58	6	57	5

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 in.” regulation, the small liberal size bin contains lengths below 20 in., and the large restricted size bin contains lengths greater than or equal to 20 in. ≈ 51 cm.

Table 3. Maturation model parameter means, priors, and 95% credible intervals of walleye from Leech Lake, MN, USA.

<i>Parameter</i>	<i>Mean</i>	<i>2.5% CI</i>	<i>97.5% CI</i>	<i>Prior</i>
θ_{0F} (female intercept)	-7.65	-8.14	-7.20	N(0, 0.0001)
θ_{0M} (male intercept)	-6.18	-6.60	-5.77	N(0, 0.0001)
θ_{1F} (female effect of age)	1.95	1.83	2.07	N(0, 0.0001)
θ_{1M} (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

All priors are normally distributed and specified as N(mean, precision).

Table 4. Sexually dimorphic biphasic growth model parameter means, priors, and 95% credible intervals for walleye from Leech Lake, MN, USA.

<i>Parameter</i>	<i>Mean</i>	<i>2.5% CI</i>	<i>97.5% CI</i>	<i>Prior</i>
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)[0001, ∞]
b_M (male mass exponent)	3.1678	3.1458	3.1904	N(3, 0.01)[0001, ∞]
g_F (female gonadosomatic index)	0.2422	0.2330	0.2516	U(0.001, 3/($T50_F \cdot \tau_F$))
g_M (male gonadosomatic index)	0.3584	0.3469	0.3697	U(0.001, 3/($T50_M \cdot \tau_M$))
h_F (female linear growth rate)	6.7885	6.6977	6.8797	N(7, 0.01)[0.001, ∞]
h_M (male linear growth rate)	7.5744	7.4453	7.7007	N(7, 0.01)[0.001, ∞]
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)
$prec_M$ (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)

Priors specified with brackets are bounded within the brackets. All normally distributed priors are specified as N(mean, precision), uniform priors are specified as U(minimum, maximum), and gamma-distributed priors are specified as G(shape, scale).

CI = 6.70 cm·year⁻¹, 97.5% CI = 6.88 cm·year⁻¹). The model also estimated a higher gonadal-somatic index 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 = 0.25). When biphasic model parameters were translated into von Bertalanffy growth model parameters, males expressed larger *k* growth coefficients and smaller asymptotic lengths. Male *k* was 0.11 (2.5% CI = 0.11, 97.5% CI = 0.12), whereas female *k* was 0.08 (2.5% CI = 0.07, 97.5% CI = 0.08). Though they grew faster as juveniles, males approached smaller asymptotic lengths (63.39 cm, 2.5% CI = 62.23 cm, 97.5% CI = 64.62 cm) than females (84.08 cm, 2.5% CI = 81.76 cm, 97.5% CI = 86.51 cm).

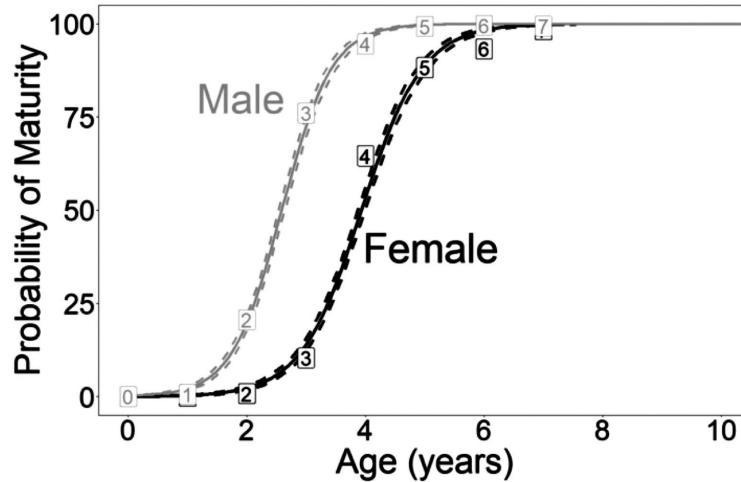


Fig. 1. Predicted probability of maturity as a function of age differed for male and female walleye in Leech Lake, MN, USA. The majority of males matured between ages 2 and 3, whereas the majority of females matured between ages 3 and 4. Mean model estimates are represented by solid lines, and 95% credible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

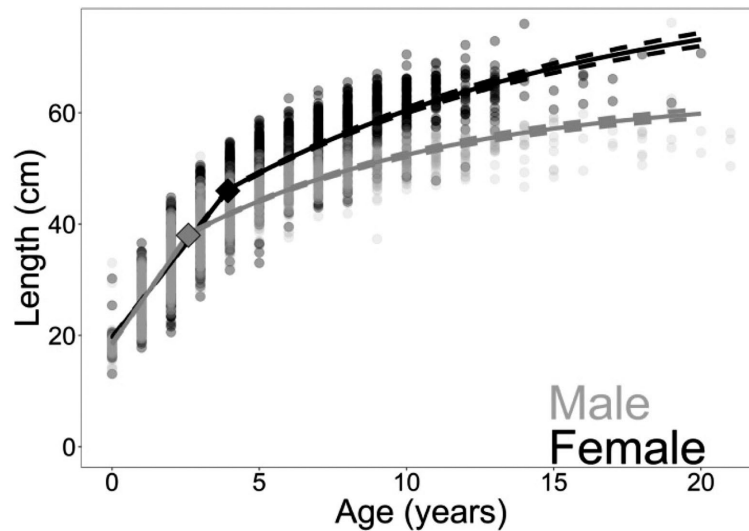


Fig. 2. Predicted biphasic growth and maturation of male and female walleye in Leech Lake, MN, USA, varied by sex. Males grew slightly faster as juveniles, matured earlier and at smaller sizes, and ultimately reached smaller adult sizes than females. Solid lines represent mean predicted length based 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.

In all regulation regimes, retention probability in the small liberal size bin was relatively high (55%–57%) and increased as a function of fish length (Tables 5–6; Fig. 3). Retention probability in the large restricted bins was relatively low across regulations, but especially in the

Table 5. Harvest model for angler-caught walleye in Leech Lake, MN, USA.

Regulation set	Bin	Parameter	Mean	2.5% CI	97.5% CI	Prior
1 over 20 in.	Small liberal	p_0	-4.1360	-4.3116	-3.9634	N(0, 0.0001)
	Large restricted	p_0	-3.0771	-3.2248	-2.9289	N(0, 0.0001)
18–26 in. protected slot	Small liberal	p_0	-7.7703	-7.9047	-7.6356	N(0, 0.0001)
	Illegal	p_0	-0.3881	-0.4450	-0.3312	N(0, 0.0001)
20–26 in. protected slot	Small liberal	p_0	-4.2958	-4.4261	-4.1647	N(0, 0.0001)
	Illegal	p_0	-2.7650	-2.8775	-2.6547	N(0, 0.0001)
1 over 20 in.	Small liberal	p_1	0.1160	0.1114	0.1206	N(0, 0.0001)
	Large restricted	p_1	0.0235	0.0066	0.0404	N(0, 0.0001)
18–26 in. protected slot	Small liberal	p_1	0.2232	0.2195	0.2269	N(0, 0.0001)
	Illegal	p_1	-0.2384	-0.2466	-0.2303	N(0, 0.0001)
20–26 in. protected slot	Small liberal	p_1	0.1212	0.1177	0.1247	N(0, 0.0001)
	Illegal	p_1	-0.0492	-0.0657	-0.0327	N(0, 0.0001)
	Large restricted	p_1	-0.1115	-0.1942	-0.0356	N(0, 0.0001)

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(mean, precision).

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 in.	Female	Overall	0.20	0.19	0.21
		Juvenile	0.43	0.42	0.44
		Adult	0.14	0.13	0.15
	Male	Overall	0.30	0.29	0.30
		Juvenile	0.31	0.30	0.32
		Adult	0.30	0.29	0.30
18–26 in. protected slot	Female	Overall	0.18	0.17	0.19
		Juvenile	0.42	0.41	0.42
		Adult	0.11	0.10	0.13
	Male	Overall	0.24	0.23	0.24
		Juvenile	0.24	0.24	0.25
		Adult	0.24	0.23	0.24
20–26 in. protected slot	Female	Overall	0.23	0.21	0.24
		Juvenile	0.43	0.43	0.44
		Adult	0.18	0.16	0.19
	Male	Overall	0.30	0.29	0.30
		Juvenile	0.31	0.30	0.31
		Adult	0.30	0.29	0.30

“1 over 20 in.” regulation. The interaction among walleye life history, regulations, and angler behavior shaped fishes’ retention probability at different sexes, ages, and life stages (Fig. 4). Overall, males were more likely to be retained than females under all three regulations because they grew slightly faster to harvestable size, but their smaller size at age as adults ensured they stayed within the small liberal size bins for most of their lives. For example, a 6-year-old female walleye would be on average 52 cm and harvested in 5% (2.5% CI = 4%, 97.5% CI = 5%) of

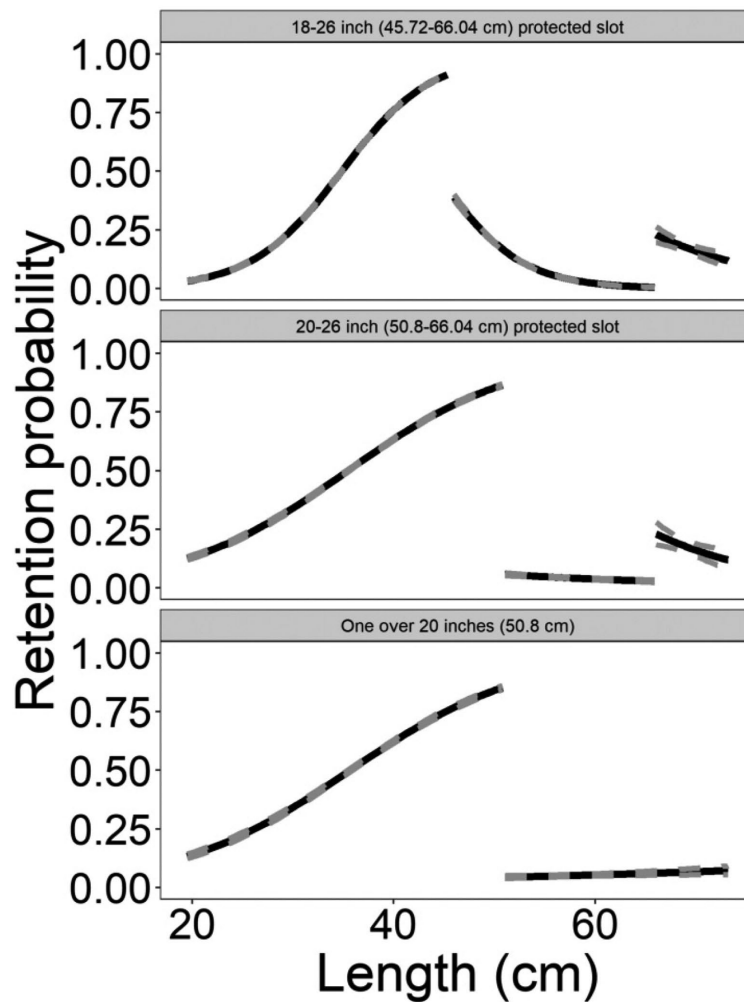


Fig. 3. Retention probability increased as a function of fish length in small liberal size bins under all three harvest regulations in Leech Lake, MN, USA. Harvest of fish in illegal and large restricted size bins was overall low and relatively unselective with regard to fish length. Solid black lines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

capture events under the “1 over 20 in.” regulation, whereas a 6-year-old male walleye would be on average only 46 cm but have a 48% (2.5% CI = 42%, 97.5% CI = 54%) retention probability. Assuming that walleye survived to the system maximum of 20 years, males and females also experienced different stage-specific and average retention probabilities.

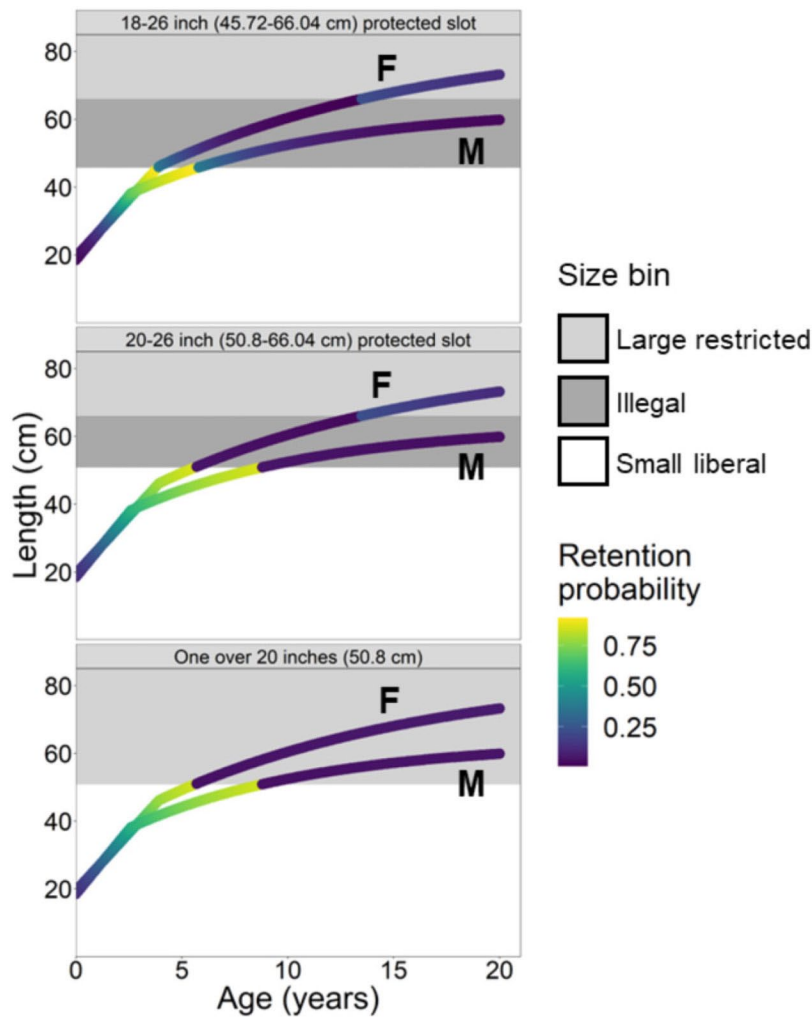


Fig. 4. Retention probability for male and female walleye in Leech Lake, MN, USA, at different life stages varied as a function of size and angler behavior under different harvest regulations per maturation, growth, and harvest models. Juvenile female walleye were more likely to be harvested given capture than adult female walleye under all harvest regulations, but especially under the 18–26 in. protected slot and to a lesser extent the 20–26 in. 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.

Under all three regulations, female retention probability was lower for adults than for juveniles, but juvenile male retention probability was similar to that of adult males (Table 6). Males were additionally more likely to be harvested given capture over the full span of their life cycle than females were (Fig. 4).

4. Discussion

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

We found that retention probability in the large restricted size bins of all three regulations was always relatively low compared to that of the small liberal size bins. Additionally, the “1 over 20 in.” regulation produced much lower large restricted retention probabilities than did the slot limits. There are several plausible explanations for the frequent release of large walleye. Anglers could be voluntarily imposing minimum and maximum length limits on their catch, as has been previously observed for anglers targeting walleye (Chizinski et al. 2014; Kaemingk et al. 2020). Such a pattern would add to previous evidence that anglers perceive releasing very small or very large fish to be an element of good resource stewardship (Uphoff and Schoenebeck 2012; Cooke et al. 2013). It is further possible that the angler release of large restricted fish resulted from anglers catching a large fish early in their trip and releasing all subsequent very large catches as they were legally required to do while seeking to fill their remaining bag limit of small liberal fish.

Conversely, anglers may have been releasing large fish because they were waiting on a trophy-sized individual in the large restricted size bins and did not want to “waste” their large restricted allocation.

The observation that the “1 over 20 in.” regulation resulted in much lower retention probabilities in the large restricted size bin than did the slot regulations likely resulted from the regulations interacting with the size structure of the walleye population. Large restricted fish composed a much larger percentage of the total catch in the “1 over 20 in.” regulation (34%) than in either slot regulation (1.5% in both slot regulations). This likely occurred because the large restricted size bin in the “1 over 20 in.” regulation contained a larger range of lengths and included more small and intermediate lengths. Smaller lengths would have corresponded to younger, and thus more abundant, fish. However, anglers could only retain one large restricted fish under all three regulations. It is therefore logical that anglers allowed to harvest only one large fish would retain a much smaller percentage of the more-frequently caught “1 over 20 in.” large fish than the less-frequently caught slot regulation large fish. A similar process was likely at play in the small liberal size bins of the two slot regulations. Anglers fishing under the 18–26 in. (≈ 46 – 66 cm) protected slot limit were more likely to harvest 17–18 in. (43–46 cm) fish than were anglers in the 20–26 in. slot (≈ 51 – 66 cm) limit despite being allowed to harvest up to four fish in both regulations. This pattern is indicative of an angler population that still wanted to fill their quota of food-sized fish, and thus adjusted their behavior to harvest more 18 in. fish when they were the largest available in the size bin. Similar shifts in angler behavior have been previously noted when regulations tighten the number or size range of fish available for legal harvest (Feiner et al. 2021). Put simply, anglers redistributed the same total amount of fish retention over the size bins stipulated by regulations.

We found that retention probability increased as a function of fish length in small liberal size bins under all three regulations, whereas the relationship between fish length and retention probability in the large restricted size bins varied among regulations. Though retention probability declined slightly as a function of fish length in the large restricted size bin of the protected slot regulations, it increased slightly as a function of fish length in the large restricted size bin of the “1 over 20 in.” regulation. One potential explanation for this apparent shift in behavior

is that anglers interpreted the new regulation as a sign that the population was doing well. If this was the case, they might perceive harvest of large fish to be more in keeping with stewardship ethics than it would have been during the protected slot periods. It is also possible that being exposed to a more continuous distribution of legally harvestable fish sizes resulted in a behavior where anglers simply sought to harvest the largest legal individuals in both size bins. Ultimately, the differences in retention probability and its relationship to size across size bins and regulations suggest that when the size allocation structure of a regulation changes without changing the bag limit, anglers will respond by shifting their harvest behavior relative to fish size such that they still meet their harvest objectives. Such a redistribution of harvest suggests that changing regulation size bins without changing bag limits is more likely to redistribute harvest mortality across age, sex, and life stage groups than to holistically increase or decrease it.

Angler behavior within regulations interacted with walleye sexual dimorphism to shape the distribution of retention probability across ages, life stages, and sexes. Males grew to smaller sizes and were slower to exit the small liberal size bins where retention probability was greatest, exposing them to increased retention probability for much of their lives. This result is commensurate with previous findings that male walleyes are more likely to be harvested than females due to variation in size and behavior between sexes (Spirk 2012; Myers et al. 2014; Koupal et al. 2015; Bade et al. 2019). In addition to anticipated differences in retention probability among males and females, we also found evidence that retention probability is distributed asymmetrically among ages and life stages for both sexes. Females were subject to their highest retention probability right around the size and age of maturity because retention probability increased as a function of fish length in the small liberal size bins. This period of increased retention probability extended further into adulthood under the 20–26 in. (≈ 51 –66 cm) protected slot and the “1 over 20 in.” regulations than under the 18–26 in. (≈ 46 –66 cm) protected slot regulation. Females over age 5 were much more likely to be released than harvested under all three harvest regulations, but especially under the 18–26 in. (≈ 46 –66 cm) protected slot regulation. Females therefore experienced a sharp decline in their retention probability after they matured, whereas male retention probability was similar for adults and juveniles. This outcome is likely good news from a

management perspective. Recruitment in broadcast-spawning fish like walleye is often driven by the number of large egg-producing females in the population. Walleye recruitment in particular may be improved by decreasing the mortality rate of large females in good body condition (Hixon et al. 2014; Shaw et al. 2018; Feiner et al. 2019). Concentrating harvest on males and juvenile females may therefore create satisfying harvest experiences for anglers who simultaneously act as good stewards of the fishery.

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

The combination of size-dependent fecundity, high juvenile mortality, and low adult mortality often induces biomass compensation or overcompensation responses (Allen et al. 1998). When a smaller number of large adult fish experience high survival and lower competition, they convert prey directly into new juveniles, often much more efficiently than would a larger number of smaller adults (Ohlberger et al. 2011; Lester et al. 2014). A harvest and natural mortality structure that reduces mortality as females reach large size and reproductive age may therefore be conducive to creating high reproductive output and recruitment to fishable size. In applied terms, this means that size-selective walleye anglers who harvest small fish and release very large fish may protect very large females and limit their competition for resources. Beyond

walleye fisheries, our findings demonstrate that the effects of sexual dimorphism and other life history complexity on regulation efficacy are likely to be wide-ranging and worthy of study.

The varying responses of anglers to regulations demonstrate that more in-depth examinations of angler decisions in the context of varying regulations will likely prove scientifically interesting and practically important. In particular, as social norms surrounding recreational fishing and fish harvest change (e.g., Solomon et al. 2020), understanding the social mechanisms motivating angler harvest decisions will be essential to anticipating the biological impacts of recreational fishing. Unfortunately, the Leech Lake data did not include such a longitudinal survey of angler demographics or opinions, but it is promising that many current creel programs (Lynch et al. 2021) are collecting such social data. As with any project using data collected over many years, investigators seeking to replicate our approach should proceed with caution. The Leech Lake monitoring program is remarkably consistent and well-resourced due to the lake's great social and ecological importance. Additionally, the access point intercept design used to conduct the Leech Lake creel program has been shown to result in minimal bias of observed caught and released fish size structure (Malvestuto et al. 1978; Robson and Jones 1989; Newman et al. 1997; Ditton and Hunt 2001; Kozfkay and Dillon 2011; Chizinski et al. 2014; Shaw et al. 2019; Gundelund et al. 2021; Johnston et al. 2021; Trudeau et al. 2021). However, it is always possible for recall bias to be introduced when interviewers must rely on angler recall of released fish sizes, and anglers may sometimes exaggerate the size of the "one that got away." 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 drove the distribution of retention across ages, life stages, and sexes demonstrates that human social behavior interacts with underlying patterns of ecology and evolution to shape the consequences of harvest. Freshwater fisheries are facing an era of rapid social and environmental change. Integrating the long freshwater recreational fisheries tradition of exceptional social science with emerging models of fish ecology and evolution will empower researchers, managers, and anglers to face a dynamic future as collaborators working for the good of the fisheries we all value.

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