North American Journal of Fisheries Management 31:826-831, 2011 © American Pisheries Society 2011 ISSN: 0278-5947 print / 1548-8675 online DOI: 10.1080/02755947.2011.623759

ARTICLE

Mortality of Walleyes Angled from the Deep Waters of Rainy Lake, Minnesota

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Abstract

Existing models of hooking mortality for walleyes Sander vitreus in large polymictic lakes are inadequate for estimating the number of catch-and-release mortalities in deeper, stratified lakes where fish are predominantly caught from depths greater than 10 m. To improve the understanding of how water depth affects catch-and-release mortality, logistic regression was used to investigate how depth of capture, fish length, and epilimnetic water temperature affect hooking mortality rates. In 2006 and 2007, 319 walleyes were caught by anglers at 5.8–17.1-m depths during a total of 10 angling events (July-September) on Rainy Lake, Minnesota. Fish were released into holding cages that allowed them the opportunity to reestablish themselves at their depths of capture; survival was recorded after 5 d (2 d for one cage). After accounting for the effects of experimental handling time (i.e., the time between hook removal and fish placement in the holding cage), capture depth had the largest effect on mortality; increases in either factor were associated with higher mortality rates. A mixed-effects model showed that pseudoreplication (i.e., correlations in survival rates among fish held in the same cage) did not detrimentally affect model parameter estimates or significance tests. In contrast to previous studies of hooking mortality in Minnesota, neither water temperature nor fish length best explained the mortality rates. By providing improvements over previous models, the logistic hooking mortality model developed in this study will allow managers to more effectively estimate hooking mortality rates in Rainy Lake and other deep lakes.

To manage a fishery for walleyes *Sander vitreus* in the face of ever-increasing pressures on aquatic resources, managers have incorporated many different approaches to determine the amount of harvest a particular fishery can sustain (Radomski 2003). Consequently, to meet safe harvest objectives, length-based regulations that mandate the release of particular-sized fish have become common management tools. For a length-based regulation to be effective, anglers must comply with the regulation (Gigliotti and Taylor 1990) and the released fish must survive at a sufficient level to prevent excessive total fishing mortality. Although angler compliance with regulations can be improved by increased education and enforcement, survival of released fish is dependent on lake conditions and angling methods. Ultimately, managers must determine the total kill (angler harvest plus hooking mortality) of a species to assess overall

mortality; therefore, some means to estimate hooking mortality for released fish is needed.

Effects of catch and release and the coinciding mortality rates have been examined in numerous studies of walleye populations across the country. Tournament mortality of walleyes has been rigorously investigated (Goeman 1991; Fielder and Johnson 1994; Hoffman et al. 1996; Graeb et al. 2005; Suski et al. 2005; Killen et al. 2006). Walleye mortality rates from nontournament angling have generally been much lower than the rates observed for tournament events. Estimated nontournament rates for hooking mortality of walleyes have ranged from 0.8% to 16% (Fletcher 1987; Payer et al. 1989; Schaefer 1989; Bruesewitz et al. 1993; Reeves and Bruesewitz 2007).

Reeves and Bruesewitz (2007) developed a model (hereafter, "Mille Lacs model") that provides the most thorough evaluation

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of nontournament walleye hooking mortality in Minnesota. In their study, fish length and water temperature explained significant variability in the rate of hooking mortality in Mille Lacs—a large, mesotrophic, polymictic lake with a maximum depth of approximately 12.8 m and an average depth of 7.8 m.

Rainy Lake supports a popular walleye fishery located along the international border between Minnesota and Ontario. Rainy Lake is closely monitored through annual net and creel surveys and is managed for long-term sustainable yields (OMNR 2004). Fisheries managers set safe harvest levels, referred to as "harvest targets," to promote long-term viability of the fishery resources; in 1994, managers implemented a regulation requiring the immediate release of all walleyes between 430 and 710 mm total length (TL; further regulations reduced the daily limit to 4 walleyes). Accurate estimates of the total walleye kill (including hooking mortality) are required to determine whether harvest targets are being met. Historically, estimated rates of hooking mortality for Rainy Lake followed those suggested by Payer et al. (1989): 6% for walleyes larger than 300 mm TL; and 10% for walleyes smaller than 300 mm TL. Beginning in 2006, hooking mortality rates were estimated by use of the Mille Lacs model; however, the authors of that model (Reeves and Bruesewitz 2007) cautioned against applying the model to walleyes caught at water depths greater than 10 m because in their study, no fish were caught in such deep water. Fish caught from deeper depths may experience additional stressors related to temperature and pressure changes (Feathers and Knable 1983; Schramm et al. 2010). In Rainy Lake, anglers commonly target walleyes from depths greater than 10 m during the late summer (mid-July-September), when epilimnetic water temperatures are usually above 18°C. Thus, application of the Mille Lacs model to deeper lakes such as Rainy Lake may result in biased estimates of walleye hooking mortality.

To improve estimates of hooking mortality for calculating total walleye kill in Rainy Lake, we examined the effects of depth on walleye hooking mortality and evaluated the validity of the Mille Lacs model for use with a deepwater fishery like that in Rainy Lake. A further goal (if depth had a significant effect on mortality and if the Mille Lacs model was insufficient) was to develop a model to estimate hooking mortality of walleyes during the open-water season on Rainy Lake. More generally, results from this study will improve the understanding of how capture depth affects the survival of walleyes that are released by anglers in deep, dimictic lakes.

METHODS

Study area.—Rainy Lake is located in northern Minnesota along the Minnesota—Ontario border. Once a natural reservoir, Rainy Lake was impounded, which caused an expansion of the surface area to 89,424 ha. Approximately 25% (21,927 ha) of the surface area of Rainy Lake is located in Minnesota; 14,175 ha in Minnesota are located within the boundaries of Voyageurs National Park. Rainy Lake is mesotrophic and has soft, infertile waters typical of lakes on the Canadian Shield. The mean depth

of Rainy Lake is 9.75 m and the maximum depth is 49 m. Thirty-five percent of the lake is less than 5 m deep.

Data collection.—Two holding cages were built to hold walleyes for 120 h, allowing for examination of immediate and delayed mortality. The cages were 2×2 m and either 10 or 17 m deep; they were composed of 6-mm nylon mesh material that was supported by 38-mm-diameter polyvinyl chloride pipe frames, which provided rigidity and flotation. A 38-mm steel grid was tied to the bottom of each cage to provide weight and to ensure that the cage remained on the bottom where it was set. The cages were set in areas where the total depth matched the cage depth (i.e., 10 or 17 m).

During July-September 2006 and 2007, organized groups of experienced anglers and agency personnel fished using methods that maintained bottom contact (i.e., weighted jigs or snell lines) for a total of 10 event-days. Anglers were instructed to target walleyes in depths greater than 10 m and to handle fish as they normally would. If anglers caught a walleye in less than 10 m of water, it was still included in the study and the angler was instructed to focus on depths greater than 10 m. Upon catching a walleye, an angler would hail a chase boat that would transport the walleye to a holding cage; while waiting for the chase boat, anglers placed the fish into a tub filled with freshwater. Anglers were asked about the capture depth and the amount of time the fish spent in the temporary holding bin (usually a plastic tote or cooler). In addition to gathering information from the anglers, personnel in the chase boat recorded the fish's TL (mm), the total experimental handling time (time the fish spent in the boat from hook removal until placement in the holding cage; not to be confused with angler handling time), whether the gas bladder was expanded, and whether the fish floated or swam away when released into the cage. The fins of each fish were hole-punched with a unique sequence for identification. Dissolved oxygen and temperature were recorded at 1-m intervals within 1 week of when fish were placed in the cage. All fish were caught in the epilimnion; consequently, the temperature recorded for a given fish was the mean temperature of the epilimnion. With the exception of the first event (after which fish were held for 48 h), the fish were retained for approximately 120 h to conform to other regional studies of hooking mortality (Reeves and Bruesewitz 2007; Schramm et al. 2010). After 120 h, the cages were lifted, fish were identified, and survival was determined.

Statistical analyses.—We first assessed the ability of the Mille Lacs model to predict the number of mortalities observed in Rainy Lake. The logistic mortality model presented by Reeves and Bruesewitz (2007) was used to predict the probability of mortality for each individual fish as

$$\log_e \left[p_i / (1 - p_i) \right] = -4.48 + 0.312(WT) - 0.0215(TL) + 0.0000226(TL)^2, \tag{1}$$

where p_i for i = 1, ..., n is the probability of mortality for the *i*th fish caught in Rainy Lake, WT is mean water temperature (°C) of the epilimnion, and TL is fish TL in millimeters. The

expected number of mortalities was $E(M) = \sum_{i=1}^{n} p_i$, and its variance was $Var(M) = \sum_{i=1}^{n} p_i (1 - p_i)$. We used a normal approximation (Berry and Lindgren 1996) to calculate a 95% confidence interval for the predicted number of mortalities in this study ($E[M] \pm 1.96\sqrt{Var[M]}$). The observed number of mortalities was compared with the confidence interval for mortalities derived from the Mille Lacs model.

Next, we examined a multivariate logistic model (Kutner et al. 2005) that contained the explanatory variables used in the Mille Lacs model plus capture depth and experimental handling time,

$$\log_{e}[p_{i}/(1-p_{i})] = \beta_{0} + \beta_{1}(WT) + \beta_{2}(TL) + \beta_{3}(TL)^{2} + \beta_{4}(CD) + \beta_{5}(HT),$$
 (2)

where β_0, \ldots, β_5 are regression parameters, CD is capture depth, and HT is experimental handling time. We did not include angler handling time in the model because we viewed it as an intrinsic part of catch-and-release angling, whereas experimental handling time is a potential confounding factor resulting from the study process. We removed factors in a backwardselimination stepwise procedure (Kutner et al. 2005) and used the Bayesian information criterion (BIC) to find the most parsimonious submodel (of the model in equation 2; i.e., model 2) that adequately described the data (Schwarz 1978). Because the Mille Lacs model may contain the correct factors affecting mortality but incorrect parameter estimates for Rainy Lake, we also compared BIC scores between the submodels of model 2 and the Mille Lacs model (model 1) fitted to Rainy Lake data. The model with the lowest overall BIC score (best-performing model) was evaluated with a Hosmer-Lemeshow goodness-offit test (Kutner et al. 2005) and was visually assessed with plots of predicted probabilities of mortality and their 95% confidence intervals.

Our mortality models used explanatory factors measured on individual fish (e.g., TL or capture depth) and thus used individual fish as the experimental unit (Pollock and Pine 2007); however, the mortality rates for individuals in the same holding cage could be correlated because of a number of factors, such as differences in holding time, exact cage location, or fish density. This would result in pseudoreplication of observations (Hurlbert 1984), possibly leading to bias in variance estimates and statistical tests. To diagnose whether cage effects on mortality affected our analyses, we fitted a mixed-effects version of the best submodel by using cage as a random effect (Kutner et al. 2005). The mixed-effects model allowed us to account for intracage correlation in mortality rates while still evaluating the effects of individual-level covariates. The mixed-effects model was evaluated based on whether it significantly improved fit to the data or changed the estimated effects of the explanatory variables. All statistical analyses were performed in R version 2.12.0 (R Development Core Team 2010); logistic models were fitted by using the glm and lmer functions of the R package lme4 (Bates and Maechler 2010).

RESULTS

Three-hundred-nineteen walleyes were caught by anglers and transported to the holding cages. Six fish were missing from the cages upon retrieval; no discernible pattern of condition was noted for the missing fish. Incomplete information was recorded for four fish, and these fish were therefore excluded from analyses. In 2006, a fungal outbreak occurred in a single cage; during the outbreak, many fish were covered with fungus, including both survivors and mortalities. Because our goal was to develop a mortality model for angler-released walleyes, all fish from that cage were excluded from the analyses because the fungal outbreak was deemed a potential mortality factor that was unrelated to hooking and thus was unlikely to affect fish released by anglers. The analyses included a total of 285 walleyes (TL range = 155-665 mm; mean TL = 370 mm; SE = 103). Capture depth ranged from 6.71 to 17.1 m (mean = 11.8 m; SE = 1.8). Water temperature ranged from 17.2°C to 22.9°C (mean = 20.1°C; SE = 1.9). Experimental handling time ranged from 40 to 621 s (mean = 189 s; SE = 98.5). Of the 285 walleyes included in analyses, 88 (31%) died as a presumed result of hooking mortality.

The Mille Lacs model, which is based on ambient water temperature and fish length, greatly underestimated the number of mortalities from the Rainy Lake fishing events; the model predicted 21 mortalities (95% confidence interval = 12.5-29.5), which is far lower than the 88 observed mortalities. However, the confidence interval did not account for the uncertainty in the Mille Lacs model parameter estimates, which caused each individual p_i estimate to have some associated uncertainty. Since the overall confidence interval greatly underestimated the observed number of mortalities, we examined whether the "worst-case" scenario for each p_i would increase the estimated number of mortalities to a level that was more congruent with the observed number. Even when each p_i estimate was at the largest value within its 95% confidence interval, the resulting confidence interval (23.0-43.5) for total mortalities still greatly underestimated the number of mortalities observed in Rainy Lake.

The model that incorporated capture depth and experimental handling time was the most parsimonious descriptor of hooking mortality rate (submodel 2d; Table 1); hooking mortality rates increased as capture depth and experimental handling time increased (Figure 1). The Hosmer-Lemeshow goodness-of-fit test indicated acceptable model fit (P=0.24, df = 8; i.e., failure to reject the null hypothesis indicates adequate fit). Cage effects did not appear to confound parameter estimates. The mixed-effects version of submodel 2d (submodel 2d.r; Table 1) neither reduced the BIC score nor produced parameter estimates that were different from those of submodel 2d (Table 2), thus indicating that there were no appreciable differences in the inherent mortality rates among the cages in the study. The

TABLE 1. Comparison of Bayesian information criterion (BIC) values among logistic models of walleye hooking mortality fitted to data from Rainy Lake, Minnesota (Δ BIC = difference in BIC; WT = water temperature; TL = fish total length; TL2 = fish total length squared; CD = capture depth; HT = experimental handling time; RC = random cage effect).

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Model	Model terms	df	BIC	ΔΒΙϹ
1	WT, TL, TL2	4	372.6	22.1
2	WT, CD, TL, TL2, HT	6	365.3	14.8
2b	WT, CD, TL, HT	5	360.2	9.7
2c	WT, CD, HT	4	354.5	4.0
2d	CD, HT	3	350.5	0.0
2e	CD	2	354.0	3.5
2f	HT	2	359.6	9.1
2d.r	CD, HT, RC	3	350.8	0.3

estimated effects of capture depth and experimental handling time were consistent among all models; parameter estimates for all models were within a 95% confidence interval of the parameter estimates from submodel 2d (Table 2). Models that contained mean epilimnetic water temperature and fish TL (i.e., similar to model 1, the Mille Lacs model) typically had higher BIC scores. Submodel 2c (Table 1), which contained water temperature in addition to capture depth and handling time, had a BIC difference (Δ BIC; difference in BIC between a given model and the model with the lowest BIC value—in this case, submodel 2d) of 4.0, indicating only a moderate level of evidence for submodel 2d over submodel 2c. There was also only moderate evidence for submodel 2d over submodel 2e (Δ BIC = 3.5; Table 1), which

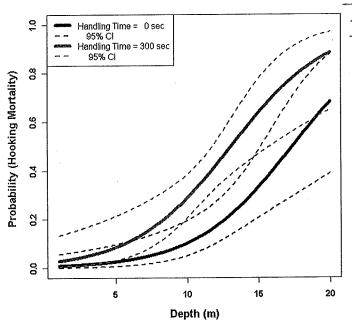


FIGURE 1. Predicted hooking mortality rates ($\pm 95\%$ confidence interval [CI]) for walleyes caught in Rainy Lake, Minnesota, as a function of capture depth and experimental handling time based on submodel 2d (described in Table 1).

TABLE 2. Parameter estimates and results of significance tests for fixed-effect (submodel 2d; Table 1) and mixed-effects (submodel 2d.r) logistic models of walleye hooking mortality in Rainy Lake (CD = capture depth; HT = experimental handling time).

Model	Coefficient	Estimate	SE	Z	P
2d	Intercept	-5.10	1.09	-4.67	< 0.0001
	CD (m)	0.29	0.08	3.67	0.0002
	HT (s)	0.0042	0.0014	2.96	0.003
2d.r	Intercept	-5.40	1.27	-4.26	< 0.0001
	CD (m)	0.30	0.09	3.20	0.001
	HT (s)	0.0046	0.0015	3.02	0.003
	Among-cage variance	0.21	0.37	0.57	0.57

included capture depth as the only explanatory variable. The Mille Lacs model fitted to the Rainy Lake data had a \triangle BIC of 22.1 (Table 1), suggesting very strong evidence (Raftery 1995) against that model in comparison with submodel 2d.

DISCUSSION

Depth of capture appears to be an important factor in determining the mortality of walleyes angled from Rainy Lake during July, August, and September. The relationship is curvilinear: the rate of mortality increases as capture depth increases. Fish that were captured in 9.1 m of water had an approximately 8% chance of dying after being released, whereas a fish that was caught from 12.2 m of water had greater than an 18% chance of dying. The probability of death increased sharply with increasing capture depth; a fish that was caught in 15.2 m of water had a 35% chance of dying. These mortality rates were greater than those observed in other nontournament hooking mortality studies conducted in northern Minnesota, particularly the Mille Lacs study, which found hooking mortality rates to be generally less than 5% (Reeves and Bruesewitz 2007).

The maximum depth in Reeves and Bruesewitz' (2007) Mille Lacs study was approximately 10 m, and they observed a positive yet nonsignificant relationship between capture depth and the rate of walleye mortality. Including their depth effect estimates into the Mille Lacs model would probably decrease the model's bias by increasing mortality estimates for the Rainy Lake study, during which fish were caught from water as deep as 17.1 m. However, this would be an extrapolation of the Mille Lacs model beyond its observed data range. In addition, given the observed large increase in mortality at capture depths of 6.1–15.2 m, the Mille Lacs model would probably still have some negative bias.

Research examining the effects of depths over 10 m for walleyes is limited, especially for walleyes caught during summer months. Bruesewitz et al. (1993) found low mortality rates (<10%) during winter months characterized by very cold water temperatures. In contrast, Meerbeek and Hoxmeier (2011) found

hooking mortality rates of 26.4% for saugers *S. canadensis* angled from the Mississippi River during winter months. Although both of these studies addressed water depth, neither addressed open-water angling during normal summer temperatures.

Angling at great depths has the potential to have critical physiological impacts on released fish, especially physoclistous species. Feathers and Knable (1983) found that bloating and external hemorrhaging occurred in largemouth bass *Micropterus salmoides* that were caught from depths of 18–27 m. Impacts, albeit less significant, also occurred at shallower depths. The study by Feathers and Knable (1983) demonstrated that increasing depth negatively affected the survival rate of fish. Although no walleyes in our study were caught from depths of 18–27 m, capture depth was strongly related to mortality rate.

The final logistic model from this study (submodel 2d; Table 2) was used to estimate mortality rates for released walleyes in Rainy Lake during the summer months. Experimental handling time was significant in the model but was set to zero in application because it was not part of normal catch-and-release fishing, although our study does suggest that an extended time before release (e.g., to take photographs) could increase walleye mortality rates. Information on the number of fish released and depth of capture was obtained from a sample of anglers during creel clerk interviews and was used to estimate the total number of walleyes that were caught and released in Rainy Lake during summer in each of 52 depth strata ranging from 1.2 to 16.75 m in 0.3048-m increments. For each stratum, submodel 2d was used to predict the log odds of mortality (i.e., $\log_e[p_k/\{1-p_k\}]$ for $k=1,\ldots,52$) and its SE. The log odds of mortality was back-transformed for an estimate of the average probability of mortality given depth for each stratum. The probability was multiplied by the estimated number of fish released in the given stratum; mortalities were then summed across strata to obtain an overall estimate. A 95% confidence interval for the total number of mortalities was calculated via simulation and included two sources of uncertainty: (1) prediction error in the mortality model and (2) binomial variation in the actual number of mortalities within a stratum for a given probability of mortality. For each run of 1,000 simulations, this entailed using the model-predicted log odds of mortality and associated SE to generate mortality rates for each stratum, which were then used in binomial models to simulate the number of mortalities in each stratum. As described above, the strata were summed to calculate the total number of mortalities; the 2.5th and 97.5th percentiles of the 1,000 simulated totals were used as confidence intervals.

The only realistic way to observe a large number of walleyes for hooking mortality involved moving the angled fish to cages and holding them for observation; this potentially added bias to our analysis of hooking mortality if the cages differentially affected mortality rates. Unfortunately, it was not possible to have "control" fish in the cages as there was no practical means of transferring fish into the cages from such depths without applying some additional stressor that would further confound the analyses. The mixed-effects model analysis produced no

evidence of among-cage variation in mortality rates, so the lack of control fish probably did not bias our estimates of the relative effects of different capture depths on mortality (Pollock and Pine 2007).

Management Implications

Managers should be cognizant of potential biases in our mortality model due to study design constraints. Because our fish were held in cages, we strictly estimated holding mortality for angled fish instead of the actual mortality of fish released back into the lake. If the cages induced stress in the fish, this could have increased the mortality rates, and thus the model estimates of hooking mortality could be biased high. Conversely, if the holding cages protected released fish that would have otherwise been more vulnerable to predation, the model estimates of mortality could be biased low. Despite these potential biases, we believe that the model developed in this study is a useful tool that can be used by managers to estimate the number of hooking mortalities as required to fully account for all forms of fishing mortality; however, follow-up studies in Rainy Lake and elsewhere would certainly improve our understanding of walleye hooking mortality and would increase the accuracy and precision of mortality estimates for fish caught in deep water.

Although it is apparent that each lake is unique in terms of sport fisheries, morphometry, and chemical parameters, the depth of capture can be an important factor when determining the hooking mortality rate of walleyes. A model that uses water temperature and fish length may best estimate mortality for fish caught at shallow depths, whereas the inclusion of capture depth as an explanatory factor may considerably improve mortality estimates when the water is deeper than 10 m.

The model developed in this study should have wide applicability to Canadian Shield lakes, but we caution against its use for warmwater and shallow-water lakes. Use of this model in Minnesota will be directed at systems with a significant deepwater fishery, stratification, and mean epilimnion water temperatures below 25°C. If water chemistry parameters and angling depths are similar to those evaluated in this study, the application of this model is warranted.

ACKNOWLEDGMENTS

We would especially like to thank Tim Goeman, Kevin Peterson, Keith Reeves, Doug Schultz, and Jack Wingate for providing guidance during the design and initiation of this research. We thank Steve Windels and Voyageurs National Park for the use of the cage-retrieving vessel. We are grateful to all those who assisted with the fishing efforts. Keith Reeves, Melissa Drake, Charles Anderson, Tom Heinrich, Don Pereira, and three anonymous reviewers provided reviews that improved this manuscript.

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