Articles

Effects of Gill-Net Trauma, Barotrauma, and Deep Release on Postrelease Mortality of Lake Trout

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Abstract

Unaccounted postrelease mortality violates assumptions of many fisheries studies, thereby biasing parameter estimates and reducing efficiency. We evaluated effects of gill-net trauma, barotrauma, and deep-release treatment on postrelease mortality of lake trout *Salvelinus namaycush*. Lake trout were captured at depths up to 65 m with gill nets in Priest Lake, Idaho, and held in a large enclosure for 10–12 d. Postrelease mortality was the same for surface-release–and deep-release–treated fish (41%). Mixed-effects logistic regression models were used to evaluate effects of intrinsic and environmental factors on the probability of mortality. Presence of gill-net trauma and degree of barotrauma were associated with increased probability of postrelease mortality. Smaller fish were also more likely to suffer postrelease mortality. On average, deep-release treatment did not reduce postrelease mortality, but effectiveness of treatment increased with fish length. Of the environmental factors evaluated, only elapsed time between lifting the first and last anchors of a gill-net gang (i.e., lift time) was significantly related to postrelease mortality. Longer lift times, which may allow ascending lake trout to acclimate to depressurization, were associated with lower postrelease mortality rates. Our study suggests that postrelease mortality may be higher than previously assumed for lake trout because mortality continues after 48 h. In future studies, postrelease mortality could be reduced by increasing gill-net lift times and increasing mesh size used to increase length of fish captured.

Keywords: barotrauma; gill-net trauma; postrelease mortality; lake trout

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Introduction

Postrelease mortality can be problematic for fisheries applications that require the release of live fish, such as tagging studies used to estimate population size, components of mortality, individual growth, and movement (Chopin and Arimoto 1995; Fabrizio et al. 1999; Pine et al. 2003; Pollock and Pine 2007). For example, abundance is overestimated in mark–recapture studies where postrelease mortality occurs (Arnason and Mills 1987; Welsford and Ziegler 2013). Without additional validation, detection of postrelease mortality can be difficult (Cone et al. 1988; Scanlon and Taras 2005). If postrelease mortality can be estimated, parameters of interest can be corrected (Welsford and Ziegler 2013). Postrelease mortality also reduces the efficiency of tagging studies by decreasing the number of tagged fish available for recapture, thereby decreasing precision (Hightower and Pollock 2013; Welsford and Ziegler 2013). Therefore, a better understanding of postrelease mortality is useful for developing correction factors that mitigate bias and for designing sampling protocols that increase efficiency of tagging studies by reducing mortality.

Estimates of postrelease mortality vary widely and seem to be influenced by methods and circumstances of fish capture and release. Average mortality in a meta-analysis of 274 catch-and-release survival studies was 18%, but ranged 0–95% (Bartholomew and Bohnsack 2005). In a Columbia River commercial gill-net fishery, the immediate mortality rate of Chinook salmon *Oncorhynchus tshawytscha* was close to 1% (Vander Haegen et al. 2004). Conversely, in a review of fish escaping from fishing gears, the mortality rate for Pacific salmon *Onchorynchus* spp. escaping from gill nets varied from 80 to 100%, primarily due to scale loss and stress of capture (Chopin and Arimoto 1995). Estimates likely vary because of differences in species-specific susceptibility to traumas, gear-specific injuries, and variation in environmental conditions. Therefore, postrelease mortality should be estimated rather than gleaned from the literature to avoid introducing unknown sources of bias (Hightower and Pollock 2013).

In addition to estimating postrelease mortality rates, knowledge of the relative importance of injuries and stressors is important for reducing postrelease mortality. Many factors have been correlated with postrelease mortality, including fish size, fish handling, capture depth, temperature, and recovery devices (Farrell et al. 2001; Bartholomew and Bohnsack 2005). Knowledge of factors that influence postrelease mortality can be used to design studies that minimize postrelease mortality (e.g., Bromaghin et al. 2007). Because drivers of mortality vary, postrelease mortality of individual species should be evaluated for specific sampling gears and handling practices.

Estimating postrelease mortality for profundal lentic species such as the lake trout *Salvelinus namaycush* is challenging because of two potential sources of mortality: gill-net trauma and barotrauma (Dextrase and Ball 1991; Johnson et al. 2004). Unfortunately, these sources of mortality are generally unavoidable when performing routine sampling for monitoring, population dynamics assessment, or diet studies of lake trout. Gill-net trauma is a well-known source of immediate and postrelease mortality that has been evaluated in a variety of systems (Johnson et al. 2004; Vander Haegen et al. 2004; Smith and Scharf 2011). Asphyxiation, trauma, scale loss, skin abrasion, and disruption of the mucous layer contribute to mortality of gill-net–captured fish (Chopin and Arimoto 1995; Farrell et al. 2001; Vander Haegen et al. 2004). Barotrauma is also a potential source of immediate and postrelease mortality. Adult lake trout occupy depths up to 80 m (Martin and Olver 1980), so they can experience as much as an eight-fold reduction in pressure when brought to the surface. Rapid depressurization can lead to an expanded gas bladder, exophthalmia, everted stomach, hemorrhage, and emboli formation (Schreer et al. 2009; Wilde 2009; Brown et al. 2014). Deep-release devices (e.g., recompression cages, weighted hooks) aim to mitigate mortality by releasing fish at depth, thereby reversing the effects of barotrauma (Butcher et al. 2012; Pribyl et al. 2012; Drumhiller et al. 2014). Although studies suggest that deep-release devices are effective for physoclistous marine fishes (Gitschlag and Renaud 1994; Hannah et al. 2008; Jarvis and Lowe 2008), less is known about barotrauma in freshwater systems (Schreer et al. 2009).

The goal of this study was to evaluate postrelease mortality of lake trout captured in a typical research setting. Although it is also desirable to determine and isolate the contribution of handling stress to postrelease mortality, that factor was outside the scope of this study. Our objective was to determine whether postrelease mortality of lake trout gill netted at depths up to 65 m was affected by gill-net trauma, barotrauma, and treatment with a deep-release cage. We used a large enclosure to 1) estimate the postrelease mortality rate, 2) quantify the probability of mortality for varying levels of gill-net trauma and barotrauma, 3) evaluate the effectiveness of a deep-release device, and 4) identify environmental covariates that contribute to postrelease mortality for gill-netted lake trout in northern Idaho. We hypothesized that postrelease mortality would increase with degree of gill-net trauma and barotrauma, whereas deep release would reduce postrelease mortality.

Methods

To replicate common sampling conditions, lake trout were sampled in Priest Lake, Idaho, a large (9,461-ha), deep lake (mean depth, 28 m; maximum depth, 112 m). Sampling was conducted May 13–23, 2014, by using sinking monofilament gill nets (1.8 m deep $\times$ 30.5 m long). Gill nets consisted of one of eight mesh sizes (50.8, 63.5, 76.2, 88.9, 101.6, 114.3, 127.0, and 139.7-mm stretch mesh). Twelve nets were randomly combined to form a 1,463-m-long gang, in which each mesh size was represented at least once, and four mesh sizes were represented twice (63.5, 88.9, 114.3, and 139.7-mm stretch mesh). Gangs were set in a serpentine pattern along an isobath, no deeper than 65 m, and soaked for 1 h. Gangs were lifted slowly (mean $\pm$ SD, 0.37 $\pm$ 0.04 m/s) with a hydraulic lifter.

Captured lake trout were measured (millimeters; total length [TL]) and tagged in the dorsal musculature with a uniquely numbered T-bar tag (Floy Tag, Seattle, WA). Each lake trout was assessed for gill-net trauma and barotrauma by using three-level condition ratings (mild, moderate, or severe). For gill-net trauma, fish with no apparent injuries were assigned a mild rating; fish with minor bruising, scale loss, or damaged fins were assigned a moderate rating; and fish with extensive bruising, extensive scale loss, torn fins, torn maxillaries, or bleeding gills were assigned a severe rating. Bruising or scale loss that covered approximately 20% or more of the dorsal surface was considered extensive. For barotrauma, fish that were upright, without any distension of the

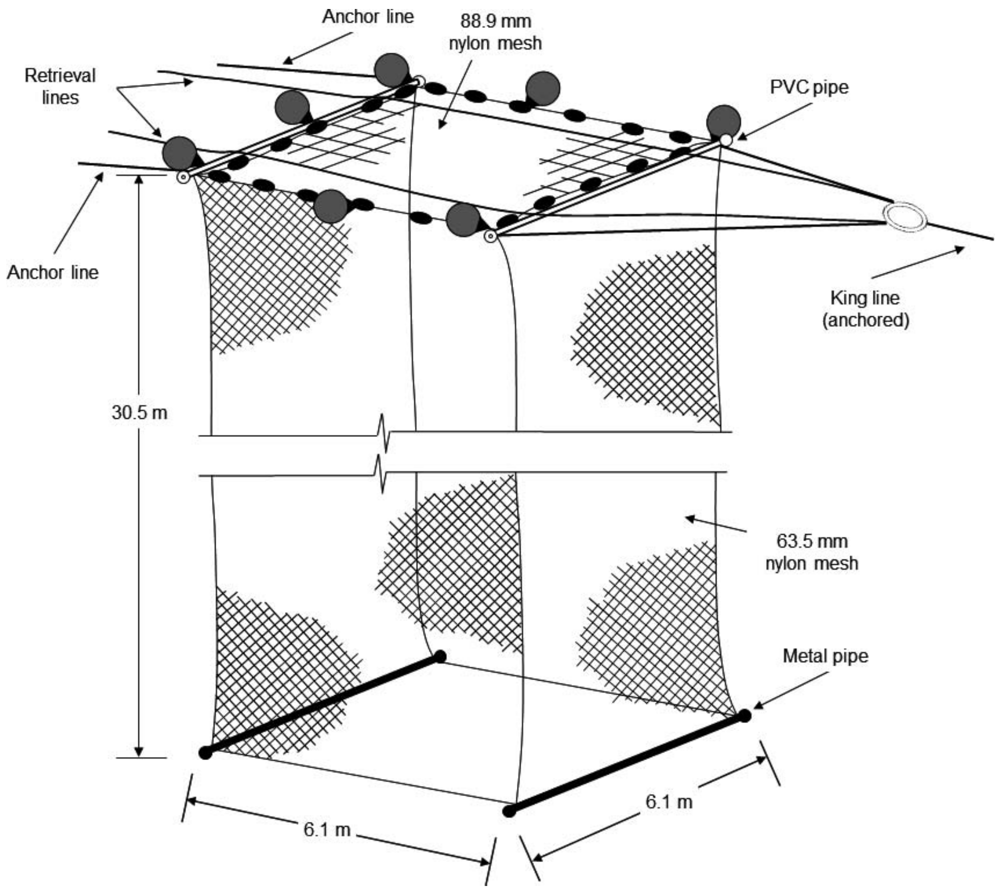

Figure 1. Diagram of a large enclosure (not to scale) used to study postrelease survival of gill-net–captured lake trout *Salvelinus namaycush* in Priest Lake, Idaho, in 2014. The enclosure was secured with five trap-net anchors (not shown). Fish were released into the enclosure through a 1.5-m opening in the lid of the enclosure. Treated fish were placed into a deep-release cage that was positioned through the opening in the lid of the enclosure. Fish in the enclosure were retrieved by sliding the enclosure over the boat until all the fish were near the pipe at the bottom. A zipper (not shown) was then opened to retrieve the fish.

abdomen, and swimming normally were assigned a mild rating; fish that were visibly bloated or had difficulty swimming were assigned a moderate rating; and fish with rigid bodies, inability to swim, or bleeding in the eyes (hemorrhage) were assigned a severe rating.

All fish were held in covered tanks (568 L) with fresh, continuously circulating lake water until the entire gang was lifted and fish were transported to a large enclosure. Soak time, lift time, run time, maximum depth, and tank temperature after the gang was lifted were recorded for each gang. Soak time was the elapsed time between setting and lifting the first anchor. Lift time was the elapsed time between lifting the first and last anchors. Run time was the elapsed travel time from the capture site to the enclosure.

To estimate postrelease mortality, lake trout were held in a large, multifilament nylon net enclosure (6.1 $\times$ 6.1 $\times$ 30.5 m; Figure 1) for 10 d (trial 1) or 11–12 d (trial 2). The enclosure was covered on all sides and resembled the pot of commercial trap nets commonly used in the Great Lakes, differing only in overall height. This design was selected because lake trout held in trap-net pots rarely experience mortality, despite being held at high densities for prolonged periods (Johnson et al. 2004; Hansen et al. 2008). For example, in an evaluation of postrelease mortality of lake trout captured in large trap nets in Lake Huron, mortality was estimated to be only 1.6% (n = 186; Johnson et al. 2004). Thus, we expected mortality due to confinement to be negligible relative to the precision of our estimates. The enclosure was positioned in a protected bay and encompassed the entire water column (30.5 m).

Live lake trout were systematically assigned to either a deep-release treatment group or surface-release treatment group. The first fish removed from a gang was randomly assigned to either the deep-release group or the surface-release group, and every other fish thereafter was assigned to the same treatment group. Fish that were assigned to the deep-release group were released into the enclosure at depth (29 m) by using a weighted deep-release cage (0.6 $\times$ 0.6 $\times$ 1.0 m; Figure 2). The cage was held at depth for 10 min to allow fish to swim out of the open bottom. After 10 min, the cage was lifted. If fish remained inside the cage, it was

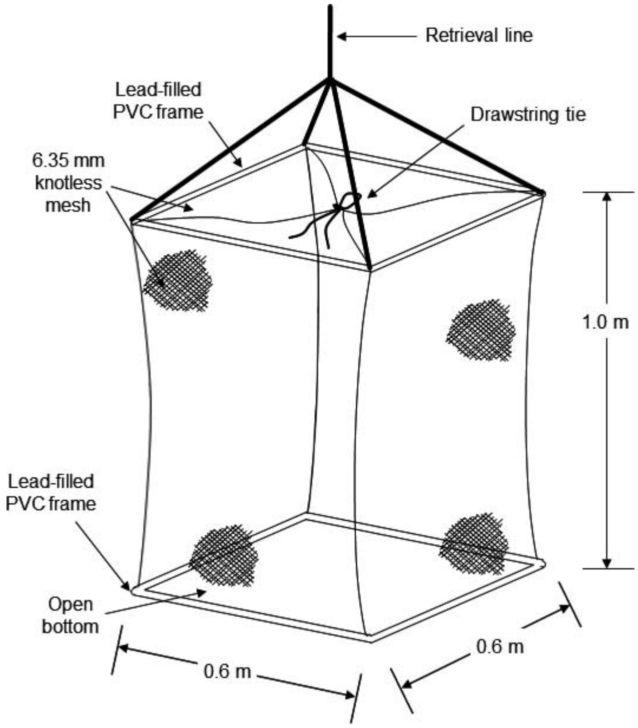

Figure 2. Diagram of a deep-release cage (not to scale) used to return lake trout *Salvelinus namaycush* to 29 m to alleviate barotrauma after gill netting in Priest Lake, Idaho, in 2014. Fish were inserted into the deep-release cage at the surface through the drawstring opening at the top of the cage. At any point, fish could exit the deep-release cage through the open bottom.

lowered to 29 m for 10 more minutes. Fish assigned to the surface-release group were released at the surface of the enclosure. Dead fish were removed from the surface of the enclosure daily. At the end of each trial, the enclosure was emptied and dead fish were counted. Binomial probabilities and 95% confidence intervals were used to describe postrelease mortality rates. Live fish were released into the lake.

The probability of postrelease mortality was modeled using mixed-effects logistic regression models (Bolker et al. 2009). A random intercept was specified for each gang because fish captured together in space and time were not independent (Nelson 2014). Based on previous field observations, we constructed 26 plausible, a priori candidate models by using combinations of deep-release treatment, gill-net trauma condition, barotrauma condition, fish length, and interactions between length and the other three covariates. Deep-release treatment was hypothesized to decrease postrelease mortality relative to surface release. Gill-net trauma and barotrauma condition were treated as categorical covariates relative to mild ratings, and postrelease mortality was hypothesized to increase with degree of trauma. Finally, fish length was included because large and small fish may be more sensitive to different stressors (Loftus et al. 1988; Davis 2002).

Akaike's Information Criterion, corrected for small sample sizes (AIC_c), was used to evaluate candidate models (Burnham and Anderson 2002). Akaike weights (w_i) represent the relative likelihood of each model, among all models considered, and were used to assess the relative plausibility of each candidate model. Candidate models with $\Delta AIC_c < 2$ were considered to have a substantial level of support (Burnham and Anderson 2002; Richards 2005). Fixed and random effects were estimated using the most parsimonious model (highest w_i). Effects of water temperature, lift time, soak time, run time, and maximum depth on postrelease mortality were evaluated in a linear model by using the random intercept for each gang as the response variable (Wagner et al. 2006). All analyses were conducted in R (Bates et al. 2014; R Core Team 2014).

Results

A temperature profile collected on May 14, 2014, at 1300 hours at the site of the net pen indicated that surface temperature was 14°C and bottom temperature was 6°C, with a weak thermocline at approximately 18 m. One-hundred-ninety lake trout were captured in four gang sets during the first trial, and 153 lake trout were captured in five gang sets during the second trial (Table 1; Table S1, *Supplemental Material*). Total length of the 348 lake trout captured during both trials of the survival study varied from 234 to 971 mm. Gill-net trauma condition (Wilcoxon rank-sum test: $W = 1.6 \times 10^4$, $P = 0.06$), barotrauma condition (Wilcoxon rank-sum test: $W = 1.6 \times 10^4$, $P = 0.06$), and total length ($t = -0.45$, $df = 326$, $P = 0.66$) did not differ significantly between trials. Across both trials, the most common gill-net trauma condition was moderate (54%), followed by mild (26%) and severe (18%), and the most common barotrauma condition was moderate (41%), followed by severe (35%) and mild (23%; Figure 3). The overall immediate mortality rate was 26% (95% CI: 21–31%). Immediate mortality rate increased with the severity of gill-net trauma; the incidence of severe gill-net trauma was 138% higher for immediate mortalities. Similarly, immediate mortality increased with severity of barotrauma, and the incidence of severe barotrauma was 216% higher for immediate mortalities. Immediate mortalities (mean TL, 412 mm) were also significantly smaller than fish that survived (mean TL, 477 mm; $t = 5.43$, $df = 177$, $P < 0.001$).

Of the 348 fish captured, 89 died immediately and were not placed in the enclosure. Of the remaining 259 lake trout, 127 were treated using the deep-release cage and 132 were released at the surface. Twelve deep-release and 29 surface-release fish were missing at the end of the study. Three of the largest individuals were sacrificed, and their stomach contents were examined for signs of cannibalism. All stomachs examined were empty. To evaluate potential bias introduced by the disappearance of fish, we used post hoc logistic regression to identify factors associated with higher probabilities of escape. Covariates in the candidate model set included trial (1 or 2), TL, gill-net trauma condition rating, barotrauma condition rating, treatment (surface or deep release), treatment–length interaction, and barotrauma–length interaction. The top model

Table 1. Characteristics of nine gang sets used to capture lake trout *Salvelinus namaycush* from Priest Lake, Idaho, in 2014. Date and time that each gang was set are given, in addition to the minimum and maximum depths, soak time, lift time, run time, temperature of the holding tank after the gang was lifted, the number of fish captured (count), the immediate mortality rate, and the postrelease mortality rate.

			Depth (m)							Mortality rate	
Gang	Date	Time (h)	Min.	Max	Soak (h)	Lift (h)	Run (h)	Temperature (°C)	Count	Immediate	Post-release
1	May 13, 2014	0534	36.3	46.6	1.03	1.08	0.32	8	59	0.14	0.58
2	May 13, 2014	0859	16.8	43.6	0.93	1.35	0.57	10	80	0.16	0.33
3	May 13, 2014	1231	25.0	63.7	1.22	1.10	0.67	11	24	0.38	0.45
4	May 13, 2014	1456	27.7	44.2	0.93	1.28	0.10	12	32	0.25	0.26
5	May 22, 2014	1025	28.3	48.8	1.17	1.08	1.17	15	14	0.57	0.50
6	May 22, 2014	1250	30.2	47.5	1.02	1.10	0.23	15	45	0.36	0.48
7	May 23, 2014	0845	28.7	43.9	1.08	1.00	0.30	14	8	0.00	0.38
8	May 23, 2015	1159	40.8	54.3	1.02	1.05	0.40	15	33	0.36	0.37
9	May 23, 2016	1450	37.8	44.5	0.92	1.00	0.42	16	53	0.28	0.39

included covariates for total length, barotrauma condition, and treatment. Smaller fish, fish with severe barotrauma, and surface-release fish were more likely to escape. The meshes used for the lid (88.9-mm stretch mesh) and sides (63.5-mm stretch mesh) of the enclosure were larger than the smallest gill-net mesh size used (50.8-mm stretch mesh). Thus, it is plausible that smaller fish and those at the surface (i.e., severe barotrauma, surface release) were more likely to escape because of the larger mesh size.

Once immediate mortalities and missing fish were excluded, 103 surface-release fish and 115 deep-release fish remained. Total length of the 218 lake trout varied from 268 to 971 mm and did not differ between treatment groups (t = −0.99, df = 214, P = 0.32; Figure 4). Neither gill-net trauma condition (Wilcoxon rank-sum test: $W = 6.0 \times 10^4$, P = 0.79; Figure 5) nor barotrauma condition (Wilcoxon rank-sum test: $W = 5.3 \times 10^4$, P = 0.12; Figure 6) differed between groups. The overall mortality rate for fish held in the enclosure

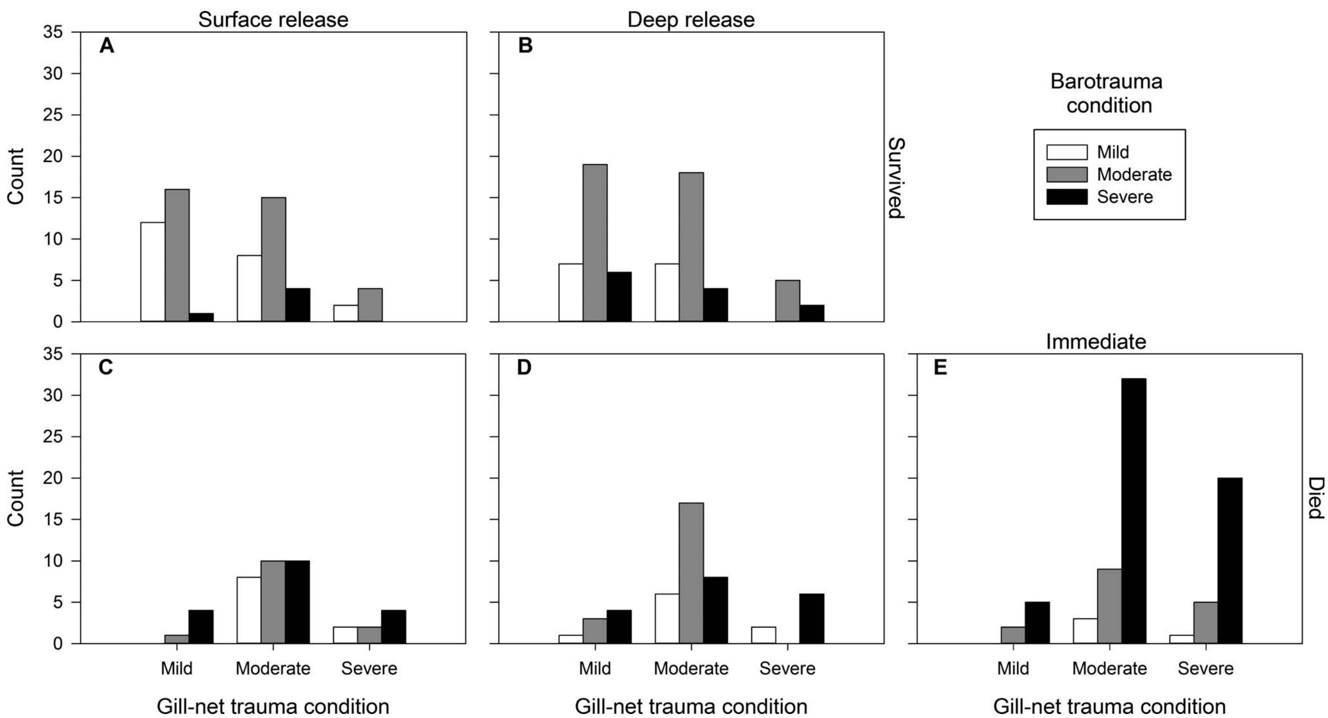

Figure 3. Distribution of gill-net and barotrauma condition scores, treatment, and fate of gill-net–captured lake trout *Salvelinus namaycush* in Priest Lake, Idaho, in 2014. In each panel, shaded bars represent the number of fish of each barotrauma condition score, which are grouped by the level of gill-net trauma experienced by each fish. Fish in each category are separated by treatment and fate: (**A**) surface-release fish that survived the postrelease period, (**B**) deep-release fish that survived the postrelease period, (**C**) surface-release fish that died during the postrelease period, (**D**) deep-release fish that died during the postrelease period, and (**E**) immediate mortalities (not released in the enclosure).

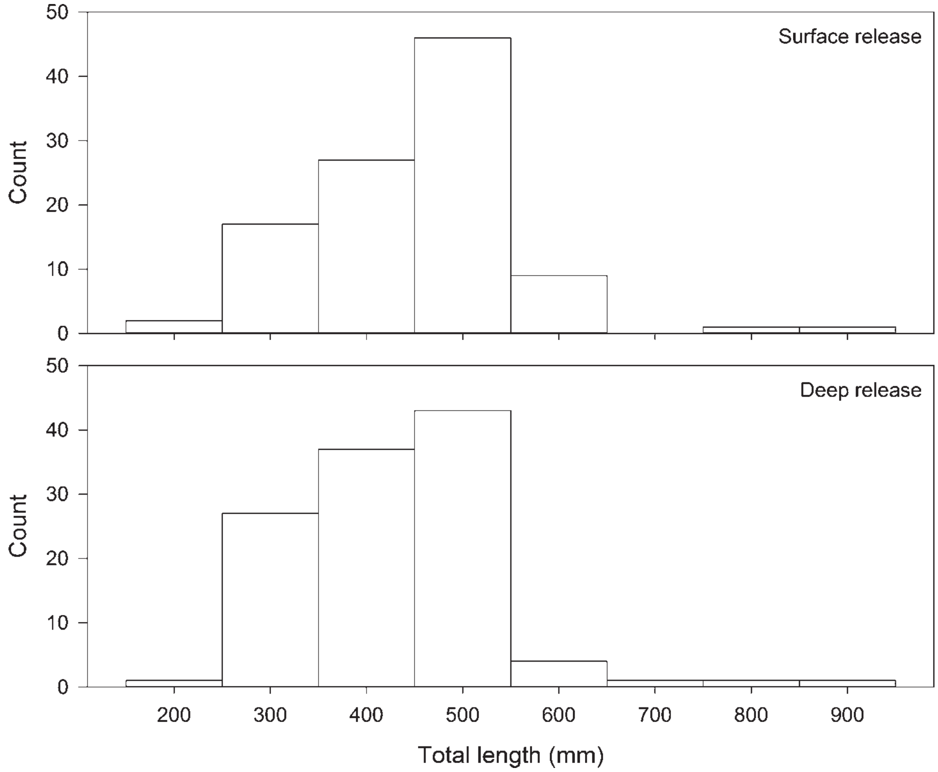

Figure 4. Distribution of total length for surface-release lake trout *Salvelinus namaycush* ($n = 103$; top) and deep-release lake trout ($n = 115$; bottom) that were accounted for after being held in a large enclosure in Priest Lake, Idaho, in 2014. Total length was not different between treatment groups ($t = -0.99$, $df = 214$, $P = 0.32$).

was 40% (34–47%). Although holding duration varied by up to 3 d, observed mortality rates also did not differ significantly between trials ($\chi^2 = 2.8 \times 10^{-3}$, $df = 1$, $P = 0.96$). Postrelease mortality was 40% (30–50%) for surface-release fish and 41% (32–50%) for deep-release fish. Postrelease mortality varied significantly between levels of gill-net trauma; mortality was 18% (9–26%) for mildly affected fish, 51% (42–61%) for moderately affected fish, and 55% (36–74%) for severely affected fish. Similar patterns were observed for levels of barotrauma; mortality was 35% (22–49%) for mildly affected fish, 30% (22–40%) for moderately affected fish, and 68% (54–80%) for severely affected fish.

The two logistic models with substantial support included covariates for gill-net trauma condition, barotrauma condition, and total length (Table 2). The most parsimonious model ($w_i = 0.50$) also included an effect of treatment and the interaction between length and treatment. The probability of postrelease mortality increased in the presence of gill-net trauma, but was not related to the degree of gill-net trauma (Table 3; Figure 7). That is, although fish with moderate and severe ratings had higher probabilities of mortality, fish with severe ratings did not have a higher probability of mortality than fish with moderate ratings. The probability of mortality was also higher with severe barotrauma, but not moderate barotrauma. Length was negatively related to probability of mortality, so smaller fish were more likely to suffer postrelease mortality. Unexpectedly, treatment with a deep-release cage was associated with increased postrelease mortality, although effectiveness of treatment increased with fish length.

Differences between gangs, including maximum depth (minimum–maximum, 43.6–63.7 m), holding tank temperature (8–16°C), number of fish (8–80), soak time (55–73 min), lift time (60–81 min), and run time (6.0–70.2 min), produced little variation ($s^2 = 0.047$) in the random effect for gang in the top model (Table 1). Lift time was the only significant covariate and was negatively related to postrelease mortality ($t = -2.9$, $df = 7$, $P = 0.02$).

Discussion

We found that 41% of lake trout captured with gill nets died within 10–12 d postrelease, which was higher than previously observed for lake trout (Loftus et al. 1988; Dextrase and Ball 1991; Gallinat et al. 1997). For example, only 28% of lake trout captured in commercial gill nets in Lake Superior, held in rearing tanks, died within 48 h (Gallinat et al. 1997). Although gill nets were soaked up to 5 nights, only fish considered likely to survive were included (Gallinat et al. 1997). In contrast, despite the shorter soak times used in our study, we evaluated survival for all live fish. If, instead, we had only evaluated survival for fish mildly affected by gill-net trauma and barotrauma (i.e., those most likely to survive), we would have observed 5% (0–25%) mortality rate. Similarly, only 10% of lake trout angled through ice in

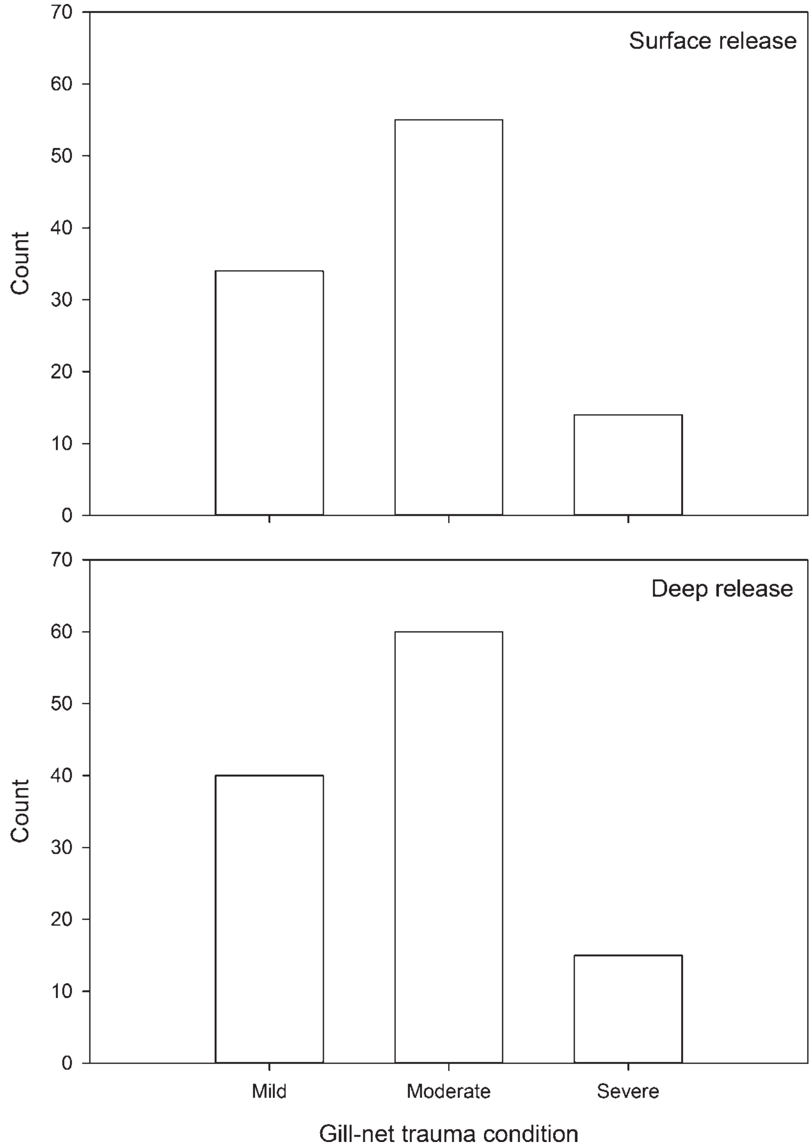

Figure 5. Distribution of gill-net trauma condition ratings for surface-release lake trout *Salvelinus namaycush* ($n = 103$; top) and deep-release lake trout ($n = 115$; bottom) that were accounted for after being held in a large enclosure in Priest Lake, Idaho, in 2014. Gill-net trauma condition did not differ between treatment groups (Wilcoxon rank-sum test: $W = 6.0 \times 10^4$, $P = 0.79$).

shallow water (maximum depth, 7 m) in Ontario, held in small (1.3 m diameter × 5.5 m deep) onshore holding tanks, died within 48 h (Dextrase and Ball 1991). Postrelease mortality may have been lower because barotrauma is minimal after capture from shallow depths, and trauma, duration of handling, and mortality rates tend to be lower for angled than gill-net–captured fish (Murphy et al. 1995; Mäkinen et al. 2000). In lakes Michigan, Huron, and Superior, only 15% of lake trout captured at depths up to 49 m, some with expanded gas bladders, and tethered for up to 48 h died (Loftus et al. 1988). Our estimate of postrelease mortality may be higher than these other studies because we evaluated effects of both gill-net trauma and barotrauma, which have not previously been studied concurrently for lake trout. We may have also have evaluated postrelease mortality for a wider range of fish conditions. Furthermore, we evaluated mortality over a longer period, and postrelease mortality may continue after 48 h. To disentangle the effects of holding time, future studies could evaluate the duration of postrelease mortality using survival analysis, which models time until death while explicitly considering temporal variation in survival (Pyke and Thompson 1986).

We found that the presence, but not the degree, of gill-net trauma was associated with higher postrelease mortality, perhaps because external indicators of physical damage do not sufficiently describe internal injuries (Mäkinen et al. 2000; Vander Haegen et al. 2004; Smith and Scharf 2011). For example, immediate and post-release mortalities of Atlantic salmon *Salmo salar* in subarctic Finland were attributed to unobserved internal hemorrhaging from gill netting (Mäkinen et al. 2000). Similarly, in a Columbia River commercial Chinook

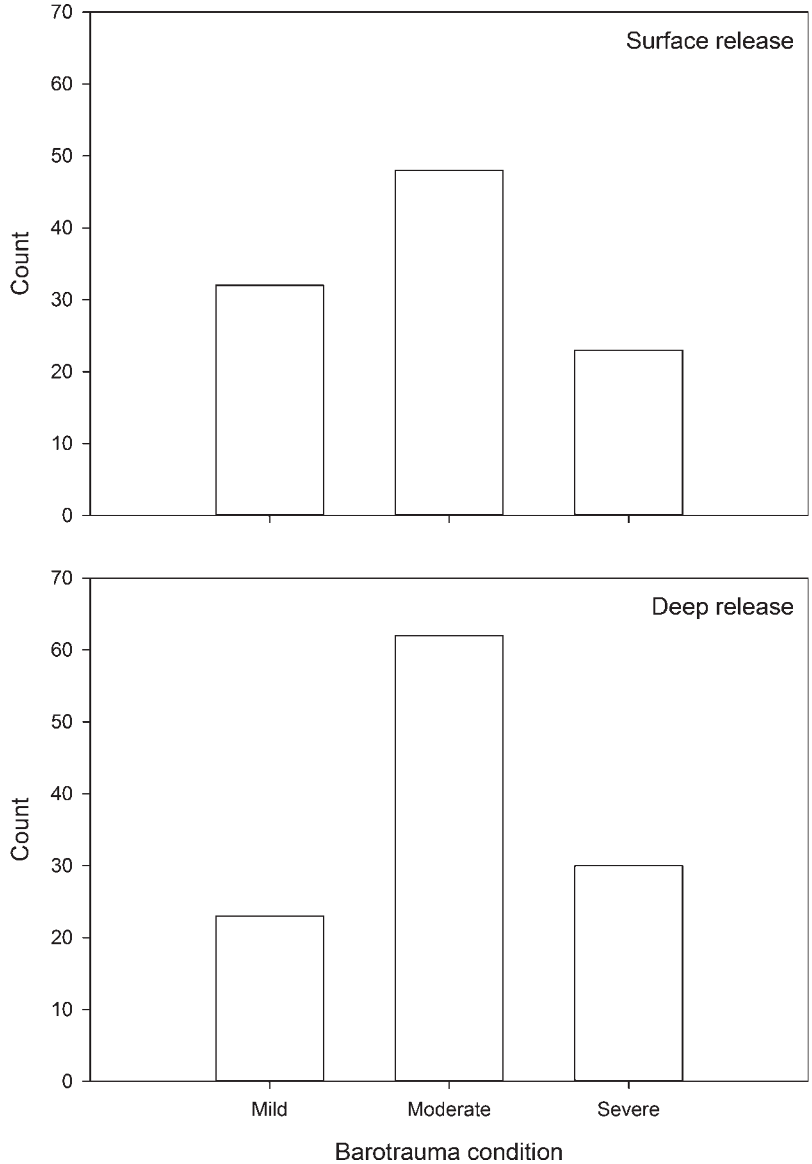

Figure 6. Distribution of barotrauma condition ratings for surface-release lake trout *Salvelinus namaycush* ($n = 103$; top) and deep-release lake trout ($n = 115$; bottom) that were accounted for after being held in a large enclosure in Priest Lake, Idaho, in 2014. Barotrauma did not differ between treatment groups (Wilcoxon rank-sum test: $W = 5.3 \times 10^4$, $P = 0.12$).

salmon fishery, lively condition did not ensure postrelease survival (Vander Haegen et al. 2004). However, both presence and degree of gill-net trauma were significantly related to postrelease mortality of southern flounder *Paralichthys lethostigma* discarded from commercial fisheries in North Carolina (Smith and Scharf 2011). Further work is needed to establish accurate metrics for gill-net trauma before the effect of gill-net-trauma severity on postrelease survival can be evaluated.

Our finding that postrelease mortality increased with severe barotrauma is similar to studies of barotrauma in lake trout and other salmonids (Lee and Bergersen 1996; Gallinat et al. 1997). Lake trout may be able to recover from moderate, but not severe, barotrauma because lake trout are physosotomes (i.e., able to release gas directly from the gas bladder through a pneumatic duct; Helfman et al. 2009). We observed fish releasing gas in such a manner, as has been observed previously in lake trout (Loftus et al. 1988). In a study of juvenile salmonids exposed to simulated hydroturbine passage, slow decompression did not cause mortality because fish expelled gas from their gas bladders (Brown et al. 2012). Ability to relieve pressure from the gas bladder may be inhibited by stress or by physical restrictions from stomach contents or gill nets. Furthermore, other deleterious effects of barotrauma such as tissue damage may persist after recompression, especially in severely affected fish (Morrissey et al. 2005).

Consistent with previous studies, the effect of treatment with a deep-release cage was highly variable (Wilde 2009; Brown et al. 2010; Sumpton et al. 2010). We found that postrelease mortality was not different for

Table 2. Set of candidate mixed-effects logistic regression models used to estimate the probability of postrelease mortality for gill-net–captured lake trout *Salvelinus namaycush* in Priest Lake, Idaho, in 2014. All models include a random effect for gang. The fixed effects are: Gill, a three-level factor indicating the severity of gill-net trauma; Baro, a three-level factor indicating the severity of barotrauma; TL, total length in mm; and Deep, an indicator variable for deep-release treatment. K is the number of parameters in each model, AIC_c is Akaike's Information Criterion corrected for small samples, ΔAIC_c is the difference in AIC_c between each model and the model with the lowest AIC_c value, and w_i is the model weight based on AIC_c.

Model name	K	AIC_c	ΔAIC_c	w_i
Gill + Baro + TL + Deep + Deep × TL	9	209.9	0.0	0.50
Gill + Baro + TL	7	211.8	1.9	0.20
Gill + Baro + TL + Baro × TL	9	212.0	2.1	0.17
Gill + Baro + Deep + TL + Baro × TL	10	214.1	4.2	0.06
Gill + Baro + TL + Gill × TL	9	214.4	4.5	0.05
Gill + Baro + TL + Deep + Gill × TL	10	216.4	6.5	0.02
Baro + Deep + TL + Deep × TL	7	225.4	15.5	0
Baro + TL + Baro × TL	7	225.8	15.9	0
Baro + TL	5	226.5	16.6	0
Baro + Deep + TL + Baro × TL	8	227.4	17.5	0
Baro + Deep + TL	6	227.7	17.8	0
Gill + Deep + TL + Deep × TL	7	246.2	36.3	0
Gill + TL	5	247.8	37.9	0
Gill + Deep + TL	6	249.9	40.0	0
Gill + Gill × TL + TL	7	250.3	40.4	0
Deep + Gill + TL + Gill × TL	8	252.4	42.5	0
Gill + Baro	6	257.2	47.3	0
Gill + Baro + Deep	7	259.3	49.4	0
Deep + TL + Deep × TL	5	264.5	54.6	0
TL	3	264.8	54.9	0
Deep + TL	4	266.7	56.8	0
Gill	4	275.7	65.8	0
Gill + Deep	5	277.8	67.9	0
Baro	4	278.6	68.7	0
Baro + Deep	5	280.7	70.8	0
Deep	3	299.6	89.7	0

deep-release and surface-release fish, but caution that our estimate for surface-release fish may have been negatively biased by the escape of small, poor-condition fish through the lid of the enclosure. Although overall effect of treatment was negative, fish size likely plays a complex role in susceptibility and mortality due to barotrauma. Length-related patterns in mortality are common in fishes, including lake trout. For example, gill-net–captured lake trout that were longer than 635 mm suffered the lowest mortality (Gallinat et al. 1997), and angled lake trout in the smallest size class (461–512 mm) suffered the highest mortality (Loftus et al. 1988). Small fish may be more susceptible than large fish to barotrauma mortality because they have smaller lethal emboli size, reduced ability to metabolize gas, and lower gill surface-to-body size ratio (Brown et al. 2009). Smaller

Table 3. Parameter estimates, SEs, and 95% confidence limits for the top mixed-effects logistic regression model used to estimate postrelease mortality for gill-net–captured lake trout *Salvelinus namaycush* in Priest Lake, Idaho, in 2014. A random effect for gang was included. Fixed effects included gill-net trauma, a three-level factor expressed as the odds ratio relative to mild condition; barotrauma, a three-level factor expressed as the odds ratio relative to mild condition; length, representing the odds ratio for a 100-mm increase in total length; treatment, an indicator variable for deep-release treatment; and the interaction between treatment and length.

			CL	
Fixed effects	Estimate	SE	Lower	Upper
Intercept	12.93	4.0	0.96	227.81
Gill-net trauma, moderate	5.79	1.6	2.50	14.43
Gill-net trauma, severe	6.80	1.9	2.07	24.29
Barotrauma, moderate	0.98	1.6	0.41	2.43
Barotrauma, severe	15.40	1.8	5.12	52.57
Length	0.36	1.3	0.20	0.62
Treatment	116.95	8.5	1.89	8,784.16
Treatment × length	0.34	1.6	0.14	0.82

fish may also be more susceptible to shock and stress from handling, which appear to increase their mortality rate disproportionate to larger fish (Davis 2002). Furthermore, large lake trout tend to be more buoyant than small lake trout (Zimmerman et al. 2006). Therefore, an expanded gas bladder may be a relatively greater source of trauma for large lake trout, as opposed to more fine-scale physiologic factors that affect small fish. Finally, deep-release treatment represents additional handling and stress, which may outweigh any benefits for small fish (< 500 mm). However, a deep-release cage could be beneficial for large fish (> 500 mm).

We found that longer lift times were associated with decreased postrelease mortality, a previously unidentified factor for lake trout. Longer lift times may allow ascending lake trout to acclimate to depressurization. Similarly, burbot *Lota lota* captured at depths of 1–35 m in cod traps in a southeastern British Columbia lake and anchored for 24 h in traps at one-half the capture pressure depth experienced less severe injuries and significantly lower mortality rates (Neufeld and Spence 2004). Furthermore, yellow perch *Perca flavescens* captured in fyke nets in 10 or 15 m of water in Lake Michigan suffered lower mortality when nets set at 10 m, but not at 15 m, were lifted with two 10–15-min pauses to allow for acclimation (Keniry et al. 1996). Therefore, lifting gill nets slowly could decrease mortality of lake trout by reducing barotrauma, although increasing lift time also increases time fish spend on board exposed to lower pressure, higher temperature, and potentially crowded tanks.

The effects of handling stress on postrelease mortality were outside the scope of this work because all fish experienced similar handling conditions (e.g., being held in tanks, netted during the same time of year). However, handling stress, in addition to gill-net trauma and barotrauma, contributes to postrelease mortality.

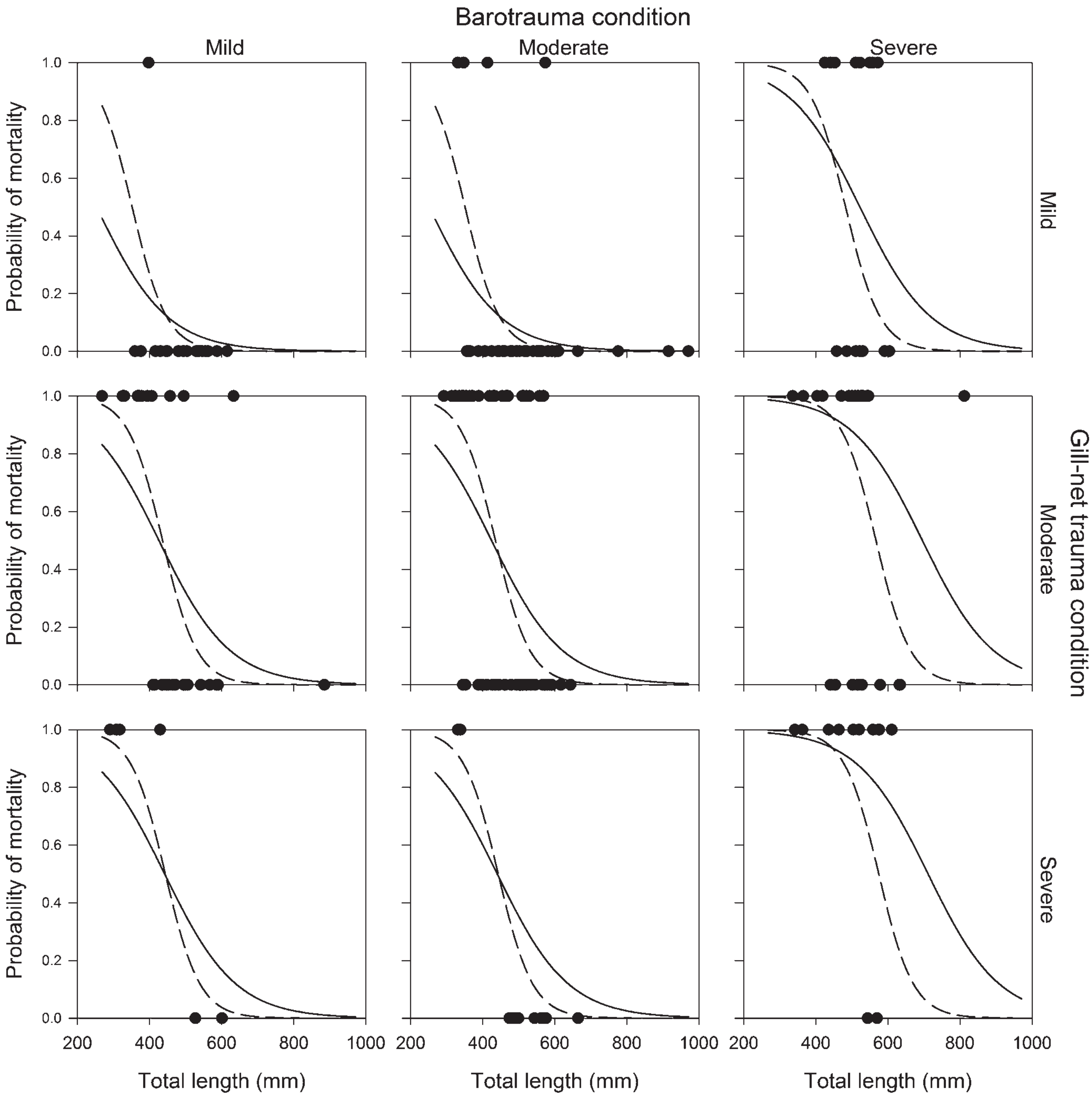

Figure 7. Probability of mortality for lake trout *Salvelinus namaycush* in Priest Lake, Idaho, in 2014 estimated using a mixed-effects logistic regression model, which included barotrauma condition, gill-net trauma condition, total length, treatment, and a treatment–length interaction. A random intercept was predicted for each gang, so results are displayed for only one gang with the smallest random intercept (1.7×10^{-4}). Severity of gill-net trauma condition increases from the top row to the bottom row. Severity of barotrauma increases from the left column to the right column. For each pair of condition scores, the probability of mortality at a given length is plotted for both surface-release (solid line) and deep-release (broken line) fish. Observed outcomes (1, mortality; 0, survival) are plotted for all fish (black dots).

Although we attempted to mimic sampling conditions common for lake trout in the western United States (e.g., Hansen et al. 2008; Dux et al. 2011), several steps could be taken to reduce overall mortality rates. Methods commonly used to reduce shock include icing, oxygenation, and salting of tank water, and possibly the addition of polymer-based water conditioners (Harnish et al. 2011) or an anesthetic, which alleviate shock by improving osmotic and metabolic regulation. For example, angled lake trout held in cold, well-oxygenated tanks experienced a greater than 50% reduction in mortality rate compared to lake trout that were tethered during an evaluation of hooking mortality in the Great Lakes (Loftus 1986). To evaluate the effects of stress due to gill netting and barotrauma experimentally, a future study could use hatchery-reared lake trout exposed to on-board handling procedures, but not gill netting.

Our estimate of postrelease mortality was high enough to violate assumptions of tagging studies. Estimates of postrelease mortality are useful not only as corrections to reduce bias of tagging studies but also to increase the efficiency of future studies. Despite careful fish handling practices, gill-net trauma may be unavoidable. Barotrauma can be avoided by limiting the depth of netting, but such practices are likely to drastically reduce catch rates of deep-water species. Our results indicate that future studies of lake trout captured with gill nets should alter netting practices (i.e., lift nets more slowly) to reduce postrelease mortality and thereby increase the efficiency and decrease the variance of such research. Because we found that large fish were less likely to die and that deep release was more effective for large fish, removing smaller mesh sizes to focus inferences on large lake trout may be another way to reduce effects of postrelease mortality. If sampling and release of small fish is necessary, researchers should be aware that mortality rates could be high, and estimates based on recaptures of small fish could be imprecise and potentially biased. Given the variability in estimates of postrelease mortality among species, locations, and gears, these types of survival studies are worthwhile investigations for any project where live fish must be released.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Data collected from individual lake trout *Salvelinus namaycush* during sampling with gill nets in Priest Lake, Idaho, in 2014. Each row represents an individual fish. Capture date, gang number, and trial number indicate the netting event in which each fish was caught (see Table 1 for gang covariates). Gill-net trauma is a three-level condition rating: mild, no apparent injuries; moderate, some bruising, scale loss, or bleeding; and severe, extensive bruising, scale loss or bleeding. Barotrauma in a three-level condition rating: mild, no apparent barotrauma; moderate, some bloating or difficulty swimming; and severe, rigid body, inability to swim, or ocular hemorrhage. If fish survived initial capture, they were systematically assigned to deep-release or surface-release groups and released into the enclosure. Fate (alive, dead, or missing) at the end of the holding period is also given.

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