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ARTICLE

Developing Recreational Harvest Regulations for an Unexploited Lake Trout Population

Melissa A. Lenker*
Department of Natural Resource Sciences, McGill University, 21,111 Lakeshore Road, Sainte-Anne-de-Bellevue, Quebec H9X 3V9, Canada

Brian C. Weidel
U.S. Geological Survey, Lake Ontario Biological Station, 17 Lake Street, Oswego, New York 13126, USA

Olaf P. Jensen
Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey 08901, USA

Christopher T. Solomon
Department of Natural Resource Sciences, McGill University, 21,111 Lakeshore Road, Sainte-Anne-de-Bellevue, Quebec H9X 3V9, Canada

Abstract
Developing fishing regulations for previously unexploited populations presents numerous challenges, many of which stem from a scarcity of baseline information about abundance, population productivity, and expected angling pressure. We used simulation models to test the effect of six management strategies (catch and release; trophy, minimum, and maximum length limits; and protected and exploited slot length limits) on an unexploited population of Lake Trout *Salvelinus namaycush* in Follensby Pond, a 393-ha lake located in New York State's Adirondack Park. We combined field and literature data and mark–recapture abundance estimates to parameterize an age-structured population model and used the model to assess the effects of each management strategy on abundance, catch per unit effort (CPUE), and harvest over a range of angler effort (0–2,000 angler-days/year). Lake Trout density (3.5 fish/ha for fish ≥ age 13, the estimated age at maturity) was similar to densities observed in other unexploited systems, but growth rate was relatively slow. Maximum harvest occurred at levels of effort ≤ 1,000 angler-days/year in all the scenarios considered. Regulations that permitted harvest of large postmaturation fish, such as New York's standard Lake Trout minimum size limit or a trophy size limit, resulted in low harvest and high angler CPUE. Regulations that permitted harvest of small and sometimes immature fish, such as a protected slot or maximum size limit, allowed high harvest but resulted in low angler CPUE and produced rapid declines in harvest with increases in effort beyond the effort consistent with maximum yield. Management agencies can use these results to match regulations to management goals and to assess the risks of different management options for unexploited Lake Trout populations and other fish species with similar life history traits.

Recreational fisheries provide numerous economic and social benefits, but overexploitation can lead to fish population collapse and loss of these benefits (Post et al. 2002). The economic benefits of recreational fisheries include generating revenue and employment in local economies (Ditton et al. 2002; Connelly and Brown 2009a) and promoting nonmarket goods, like the wellbeing derived from angling (Rudd et al. 2007). Other benefits include the social

*Corresponding author: melissa.lenker@mail.mcgill.ca
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aspects of promoting ecological responsibility and furthering environmental education (Kearney 2007). The economic benefits provided by high-quality fisheries can be substantial (Connelly and Brown 2009a), but they are diminished when populations are overfished and anglers seek better angling opportunities elsewhere (Johnson and Carpenter 1994). The restoration of depleted populations typically requires stocking, significantly restricting fishing pressure, or temporarily closing the fishery. Restoration in the form of resource restriction can be unpopular, particularly if the fishery decline is unrecognized, such as in the "shifting baseline" syndrome (Pauly 1995).

Unique challenges and opportunities arise when previously unexploited fisheries open to exploitation due to the acquisition of new public lands. The most significant challenge in opening an unexploited population to fishing is providing management that preserves the fishery's culturally and economically valuable features. This challenge is often exacerbated by a scarcity of baseline information about fish abundance, population productivity, and expected angling pressure. Despite the challenges, the benefit in opening previously unexploited lakes to angling is the opportunity to create exceptionally high-quality angling resources by providing management that maintains fish size structure and abundance as similar as possible to the unexploited state.

In this study, we explored potential management strategies for a previously unexploited population of Lake Trout *Salvelinus namaycush* in New York State's Adirondack Park. Lake Trout, a freshwater char indigenous to Canada, Alaska, and portions of the northeastern United States, are characterized by slow growth, long life, late maturity, and low reproductive potential (Page and Burr 1991). These characteristics make them particularly susceptible to overfishing, and many exploited populations have declined or are maintained by stocking (Post et al. 2002; Purchase et al. 2005). Even many northern populations that were previously unexploited or lightly fished are facing increasing fishing pressure due to the increasing popularity of northern tourism and the access provided by forestry roads (Gunn and Sein 2000; Kaufman et al. 2009). Our focal population in Follensby Pond has been under private land ownership and essentially unfished for at least 60 years, but managers are now considering opening it to public fishing.

We used field and literature data to parameterize an age-structured model for the Lake Trout population in Follensby Pond and used the model to test six potential fishery management strategies (catch and release; trophy, minimum, and maximum length limits; and protected and exploited slot length limits) across a range of angler effort. We describe how the management strategy and the level of effort affect Lake Trout abundance, CPUE, and harvest, thereby illustrating tradeoffs between potential alternative management goals. In addition to their obvious applicability to managing this particular population, our results will be of interest in other settings in which management decisions have to be made about previously unexploited populations of Lake Trout or other species with similar life histories.

METHODS

Study site.—Our study site was Follensby Pond (44.177°N, 74.372°W), an oligotrophic lake in Harrietstown, Franklin County, New York, located inside of New York State's Adirondack Park (Table 1). The unexploited 392.9-ha lake reaches a maximum depth of 33 m. It has three shallow bays that lack hypolimnetic habitat during the stratified season (when thermocline depth is 8–10 m) and may provide a refuge from Lake Trout predation for prey fishes. Follensby Pond sustains a wide variety of fish species, including Cisco *Coregonus artedi*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, sunfishes *Lepomis* spp., and others.

Data collection.—To assess population size and age structure, we sampled Lake Trout with six-paneled small-mesh gill nets (1.8 m [6 ft] high with two panels each of 38-mm [1.5-in], 50.8-mm [2.0-in], and 63.5-mm [2.5-in] stretch mesh; spring and limited fall sets), Oneida style trap nets (car 1.2 × 1.2 m, leader 21.9 m, wings 8.4 m; fall spawning season), and angling (limited spring and fall) from May 2013 to November 2014. Small-mesh (1.5–2.5-in mesh) gill nets fished for a short duration were used to minimize sampling mortality and allow for direct comparison to New York State Department of Environmental Conservation Adirondack Lake Trout surveys. Gill nets were set both parallel and perpendicular to shore in areas of high Lake Trout density to increase capture rate. Gill-net effort was focused on rocky ledges, the entrances to shallow bays, and deep, open water. The majority of gill nets were set for 90 min on the bottom of the lake in depths ranging from 1.6 to 30.9 m. Almost all fish sampled were caught by gill nets and angling; the primary spawning bed on Follensby Pond was too steep for the trap nets to be effective, and only one Lake Trout was caught by this method.

For all the Lake Trout captured, we measured total length to the nearest millimeter and mass to the nearest 10 g and inserted a passive integrated transponder (PIT) tag (Oregon RFID FDX-B; 12 mm × 2.15 mm at 134.2 kHz) with a syringe injector for mark–recapture analysis; 34% were double tagged with an adipose fin clip to assess PIT tag loss. We dissected Lake Trout that were accidentally killed during the course of

TABLE 1. Physical and chemical characteristics of Follensby Pond. We collected a pooled mixed sample from 0, 2, and 4 m in May 2014 before thermocline formation. Values are given as the mean or mean ± SD.

Test	Value
Total nitrogen	0.327 mg/L
Total phosphorus	4.8 μg/L
Dissolved organic carbon	3.75 ± 0.05 mg/L
Total dissolved solids	18.1 ± 0.3 mg/L
Conductivity	27.85 ± 0.44 μS/cm

angling or gillnetting. Lake Trout that did not recover from capture were euthanized and counted as accidental mortalities. Sagittal otoliths were removed and fish age was interpreted from transverse sections (n = 26) following the protocol in Jenke (2002).

Estimating abundance.—We estimated Lake Trout abundance with the continuous Schnabel mark–recapture method, using the spring 2013 and 2014 field seasons as sampling periods. The continuous Schnabel model uses the number of individuals captured (N), marked (M), and recaptured (R) in each sampling period to estimate population size ($\check{N}$) as follows:

$$\check{N} = \sum (M \cdot N) / \left[\sum R + 1 \right] \tag{1}$$

The sampling period of 1.5 years violates the continuous Schnabel's closed-population assumption; the resulting abundance estimate may be artificially inflated by the death of marked individuals. However, the effects of violating the closed-population assumption are likely minimal since the natural mortality rate of adult Lake Trout is low. For example, given the age-structured natural mortality rates estimated in Sitar et al. (1999), 84.6% of individuals tagged in the first sampling period would still be available for recapture during the last sampling period. Immigration and emigration of adult Lake Trout is likely negligible because Follensby Pond has a narrow, shallow entrance (2.1 m wide and 0.2–2.0 m deep) and genetic research has indicated little to no migration among Lake Trout, even in systems where movement between waterbodies is physically possible (McCracken et al. 2013).

Population model.—We built an age-structured population model to describe the dynamics of the Follensby Pond Lake Trout population, in which we keep track of the abundance and biomass (kg) of each age-group (a) in each year (t). The model uses equation (2a) to calculate angler catch ($C_{t,\ a}$) as a function of Lake Trout catchability (q_t), age-specific vulnerability to angling (v_a), angling effort (E_t), abundance ($N_{t,\ a}$), and the age-specific fraction of captured fish that are retained (h_a).

$$C_{t,a} = q_t \cdot v_a \cdot E_t \cdot N_{t,a} \cdot h_a \tag{2a}$$

Postrelease mortality ($P_{t,\ a}$) was calculated by applying a postrelease mortality rate (p) to Lake Trout that are caught and released:

$$P_{t,a} = q_t \cdot v_a \cdot E_t \cdot N_{t,a} \cdot (1 - h_a) \cdot p \tag{2b}$$

Population size at the next annual time step ($N_{t+1,\ a}$) was calculated as a function of the annual natural survival rate (s_a), last year's abundance ($N_{t,\ a}$), and fish that were removed from the population by harvest ($C_{t,\ a}$) or postrelease mortality ($P_{t,\ a}$):

$$N_{t+1,a+1} = s_a \cdot N_{t,a} - C_{t,a} - P_{t,a} \quad a > 1 \tag{2c}$$

Recruitment ($N_{t,\ 1}$; the number of age-1 fish added to the population from spawning in the previous year) was calculated as a function of adult spawning stock biomass using a Beverton–Holt stock–recruitment relationship (SRR). The Beverton–Holt model describes rapid increases in recruitment at low spawning stock sizes and relatively constant recruitment at larger spawning stock sizes. The Beverton–Holt SRR parameterization that we used is as follows:

$$N_{t,1} = (0.8 \cdot R_0 \cdot z \cdot B_t) / [0.2 \cdot \varphi \cdot (1-z) + (z-0.2) \cdot B_t] \quad a=1, \tag{2d}$$

where $N_{t,\ 1}$ is the recruitment of age-1 fish into the population at time t, R_0 is recruitment at the unfished spawning stock biomass, z is a steepness parameter that describes the proportion of R_0 produced by 20% of the unfished biomass (B_0), B_t is the spawning stock biomass at time t, and φ (B_0/R_0) is the spawning biomass produced per recruit at unfished equilibrium (Mace and Doonan 1988; Table 2). Spawning stock biomass (B_t) was calculated as the biomass for all Lake Trout ≥ 13 years in age, based on the mean length and weight for each age-class.

We used our estimates of abundance and size structure in combination with the allometric growth model (equation 4) to calculate unfished spawning stock biomass. Assuming that this unexploited population is at equilibrium, we calculated unfished recruitment as the biomass of age-1 fish required to replace individuals succumbing to natural mortality. To calculate spawning stock biomass (kg), we used a species-specific estimate of 0.86 for the steepness parameter (z) from Myers et al. (1999) and 100% maturity at 13 years of age. Age of maturity was determined by the length of the smallest Lake Trout caught during the spawning period.

We used 25 years of age as our plus group, the oldest modeled age of fish in the population, because the length of the largest fish caught during the field work (814 mm) roughly corresponded to an age of 25 years in our fitted von Bertalanffy growth model. A summary of all of the parameters with their estimated values appears in Table 2.

We used otoliths from 26 Lake Trout of known length to estimate growth rates using the von Bertalanffy growth model as follows:

$$L_a = L_\infty \cdot (1 - e^{-K(a-a_0)}), \tag{3}$$

where L_a is the total length at age a, L_∞ is the asymptotic average total length, K is a growth rate coefficient, and a_0 is the x-intercept or the hypothetical age at which a fish has zero length (Quinn and Deriso 1999). We fit this model via Markov Chain Monte Carlo sampling in AD Model Builder (ADMB software; Otter Research, Sidney, British Columbia), using data from other North American Lake Trout populations (Trippel and Beamish 1989; Keller et al. 1990; Payne et al. 1990; He and Stewart 2001; Giroux 2003; Lavigne et al. 2010; Hansen et al. 2012) to construct Gaussian prior distributions

TABLE 2. Summary of the model parameters.

Parameter	Value	Unit	Method and (or) source
Growth			
von Bertalanffy growth rate (K)	0.034 (SD, 0.011)	Year^{-1}	Fit to length and age data
von Bertalanffy asymptotic length (L_∞)	1,398.8 (SD, 309.1)	mm	Fit to length and age data
von Bertalanffy age intercept (a_0)	–0.021 (SD, 0.644)	Years	Fit to length and age data
Length–weight coefficient (α)	–13.23 (SD, 0.15)	g·mm^{-1}	Fit to length and weight data
Length–weight exponent (β)	3.24 (SD, 0.02)		Fit to length and weight data
Recruitment			
Beverton–Holt unfished recruitment (R_0)	0.83	kg	Calculated from natural mortality (Sitar et al. 1999) and assumption of equilibrium age structure and abundance
Beverton–Holt unfished spawning biomass (B_0)	3,023.3	kg	Adult unfished biomass based on mark–recapture abundance estimate and natural mortality (Sitar et al. 1999)
Beverton–Holt steepness (z)	0.86		Myers et al. (1999)
Average age at maturity	13	Years	Age corresponding to smallest size caught during spawn
Mortality			
Age-specific instant natural mortality (M_a)	0.108–0.797		Sitar et al. (1999)
Postrelease mortality rate (p)	0.15		Loftus et al. 1988; Muoneke and Childress 1994
Age structure			
Abundance (≥ age 12)	3,000 (CI = 2,036–5,708)	Individual	Mark–recapture analysis
Plus group	25	Years	von Bertalanffy age corresponding to largest Lake Trout caught

for the growth rate coefficient (K; μ = 0.171; σ = 0.059; n = 70) and x-intercept (a_0; μ= –0.864; σ = 1.515; n = 17). We did not include a prior distribution for the asymptotic average maximum body size (L_∞) because L_∞ literature values were strongly correlated with growth rate coefficient estimates (K; r = –0.556).

We convert from length to weight using an allometric growth model as follows:

$$W_a = \alpha \cdot L_\alpha^\beta, \tag{4}$$

where W_a is the weight at age a, L_a is again the length at age a, α is a scaling constant, and β is the allometric growth parameter (Quinn and Deriso 1999). We fit this model to the Follensby Pond data by least squares after a linearizing logarithmic transformation.

We applied the age-structured natural mortality relationship described in Sitar et al. (1999) to the Follensby Pond population. The Sitar et al. (1999) natural mortality estimates are parameterized with Lake Trout data taken from Lake Huron. The Sitar et al. (1999) relationship follows a type-III survivorship curve that asymptotes at age 5.

We used 220 h of Follensby Pond angling data from 25 anglers of mixed experience and skill level to calculate catchability (q), the proportion of the population removed by one unit of fishing effort, as follows:

$$q = C/(E \cdot N), \tag{5}$$

where C is the catch per angler-day (assuming 4 h/angler-day), E is the effort (1 angler-day), and N is the estimated population size of Lake Trout vulnerable to angling (those ≥ 350 mm length). The observed catchability estimate ($9.07 \cdot 10^{-4}$ angler-day^{-1}) compared favorably to an independently derived catchability estimate ($8.13 \cdot 10^{-4}$ angler-day^{-1}) calculated from estimated Lake Trout abundance in Follensby Pond and an empirical relationship described by Shuter et al. (1998) for Ontario lakes, in which catchability varies inversely with abundance. In the Shuter et al. (1998) relationship, catchability increases rapidly as population size nears zero, creating a

TABLE 3. Angling effort data from Adirondack lakes with Lake Trout fisheries. The county is the county in which the lake is located, and the area is the surface area of the lake. For each lake, we multiplied the total estimated angling effort for all species by the estimated proportion of the angling effort that is directed at Lake Trout (% LT) to estimate the effort directed at Lake Trout in angler-days/year and angler-days·year^{-1}·ha^{-1} (Effort–LT; mean with 95% CI in parentheses). Estimates of the proportion of effort directed at Lake Trout were available at the lake level for Lake George but at the county level for the other lakes. Data on total effort and proportional Lake Trout effort are from Connelly and Brown (2009a; 2009c), including unpublished data on Lake Placid. We used the grand mean and confidence bounds for Lake Trout effort from these five lakes to estimate plausible levels of effort for Follensby Pond (1,227 angler-days/year; 95% CI = 930–1,525) by multiplying the lake-average effort directed at Lake Trout per hectare (3.1 angler-days·year^{-1}·ha^{-1}; 95% CI = 2.4–3.9) by Follensby Pond's surface area (393 ha).

Lake	County	Area (ha)	% LT	Effort–LT (angler-days /year)	Effort–LT (angler-days ·year^{-1}·ha^{-1})
Indian Lake	Hamilton	1,766.5	0.135	3,628 (2,843–4,414)	2.1 (1.6–2.5)
Lake Placid	Essex	878.2	0.093	921 (715–1,127)	1.0 (0.8–1.3)
Raquette Lake	Hamilton	1,993.1	0.135	3,508 (2,149–4,867)	1.8 (1.1–2.4)
Schroon Lake	Hamilton	1,618.7	0.135	8,950 (6,253–11,647)	5.5 (3.9–7.2)
Lake George	Warren	11,395.9	0.206	59,536 (50,935–63,138)	5.2 (4.5–6.0)
Follensby Pond	Franklin	392.9	0.142	1,227 (930–1,525)	3.1 (2.4–3.9)

threshold of effort past which abundance and harvest decline rapidly with increasing harvest. We used the value that we derived from the Shuter et al. (1998) relationship in the fixed-catchability model scenarios that we present and allow catchability to vary with abundance according to Shuter et al. (1998) in our variable-catchability scenarios.

We simulated the implications of plausible levels of effort and catchability and six potential harvest regulations for the long-term population status and fishery quality of the Lake Trout fishery in Follensby Pond. We considered levels of effort consistent with observed effort directed at Lake Trout in other Adirondack lakes, ranging from 0 to 2,000 angler-days per year. Effort directed at Lake Trout on five other Adirondack lakes varied between 1.0 and 5.5 angler-days·year^{-1}·ha^{-1}, suggesting that, based on its area, Follensby Pond might receive between 930 and 1,525 angler-days/year of effort at equilibrium (Table 3).

The six potential harvest regulations that we considered were standard New York State harvest regulations (harvest > 533 mm or > 21 in), catch and release (no harvest), trophy (harvest > 762 mm or > 30 in), maximum length limit (harvest < 457 mm or < 18 in), slot limit protecting spawning stock (harvest < 610 and > 763 mm or < 24 and > 30 in), and a slot limit exploiting stock 533–610 mm (harvest 21–24 in). In all of these scenarios, we assume that 5% of hooked illegal-sized fish are retained in violation of the law and postrelease mortality kills 15% of all fish hooked (Loftus et al. 1988; Muoneke and Childress 1994). We also assume that anglers voluntarily release 62% of hooked legal fish, based on the yearly average reported creel rate ($\mu = 0.38$; $\sigma = 0.12$) for Lake Trout in Lake George, New York, from 2009 to 2011 (Zollweg 2010; Zollweg 2011; Pinheiro 2013).

Sensitivity analysis.—There are substantial uncertainties in our analysis which affect the predicted equilibrium status of the stock at a given level of effort. To illustrate these uncertainties, we analyzed the sensitivity of the model to key parameters based on the simulated equilibrium abundance of Lake Trout vulnerable to angling (> 350 mm) in the standard New York State harvest regulation scenario. The parameters that we varied were initial abundance, Beverton–Holt steepness, von Bertalanffy growth rate (K; includes variation in age at maturity), natural mortality, postrelease mortality, legal harvest, and illegal harvest. All parameter values except for SRR steepness were selected randomly from normal distributions. Variation in these parameters was allowed to propagate through the model; for instance, we recalculated the abundance of fish in each age-class based on the randomly selected value of initial abundance. Each simulation was run 1,000 times. Iterations that produced implausible (e.g., negative harvest) values were excluded from the analysis.

RESULTS

Size Structure

The size structure of the Lake Trout population in Follensby Pond appeared bimodal based on the gill-net catch data, with peaks around 275 mm and 675 mm total length (Figure 1A). The peak at 275 mm presumably occurred at least in part because of incomplete recruitment of smaller fish to our gill-net sampling method. The bimodal pattern could be explained by a period of accelerated growth between the age at which fish become large enough to eat energy dense Cisco and the age at which they mature; this explanation is consistent with our limited, unpublished diet data and estimated age at maturity for this population (see below). The peak at 675 mm was also reflected in the angling catch (Figure 1B). Most fish caught by angling (82%) were between 550 and 750 mm total

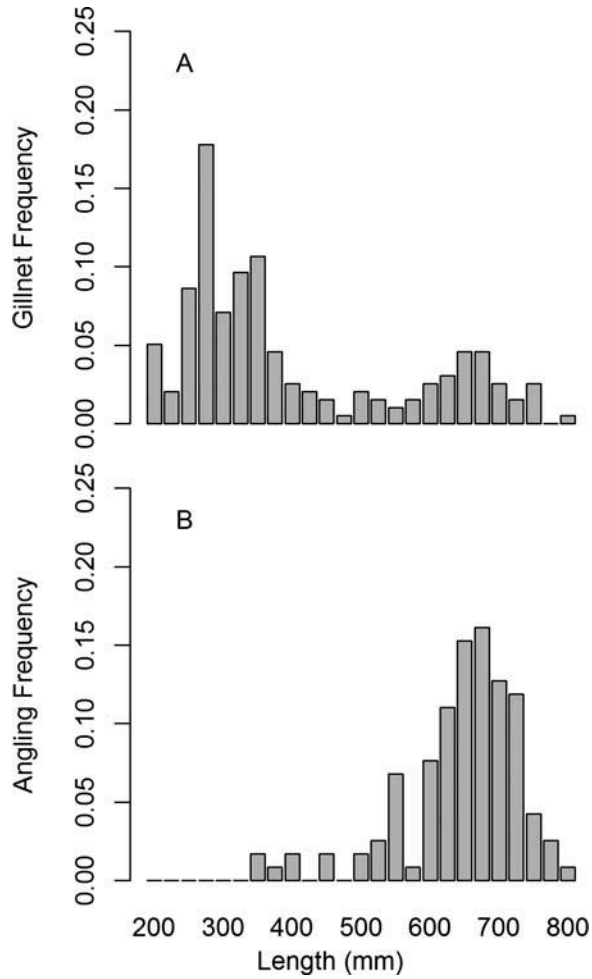

FIGURE 1. Relative frequency of Lake Trout by size-class in catches from **(A)** gill nets (n = 197) and **(B)** angling (n = 118).

length; relatively few were smaller than 550 mm (11%) or larger than 750 mm (7%).

Age, Growth, and Natural Mortality

We examined otoliths from 26 Lake Trout spanning nearly the full size range of captured fish, from 212 to 813 mm; the estimated ages of these fish ranged from 4 to 24 years. The fitted von Bertalanffy parameters for growth (K; μ = 0.034; σ = 0.011), asymptotic length (L_{∞}; μ = 1398.8; σ = 309.1), and the x-intercept (a_0; μ = –0.021; σ = 0.644) were used in subsequent analyses (Table 2; Figure 2). The allometric relationship between weight and length, including SE in the calculations, was as follows: log(weight) = (–13.23 ± 0.15) + (3.24 ± 0.02)·log(length), where σ^2 = 0.028, n = 275, and R^2 = 0.984.

We estimated the age at maturity for Lake Trout in Follensby Pond to be 13 years because the smallest of the 49 fish that we caught on or near the spawning grounds was a ripe female 522 mm in total length, which corresponds to 13 years old given our fitted age–length relationship.

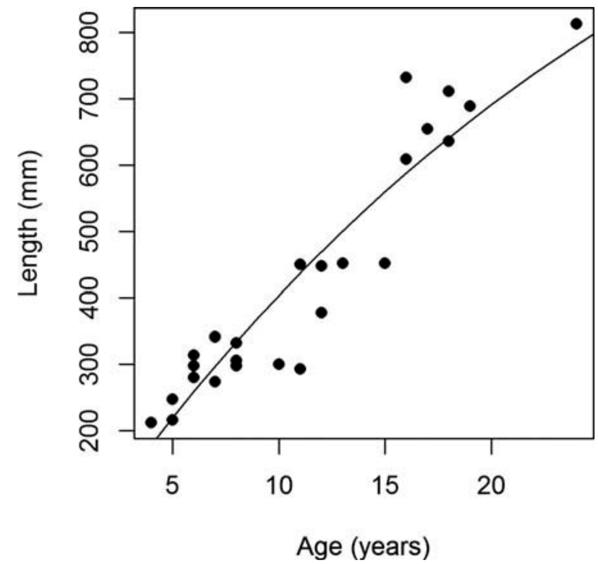

FIGURE 2. Graph of the von Bertalanffy growth model (equation 3) fit to the length-at-age data for 26 Lake Trout. The parameter estimates are given in Table 2.

Natural mortality was estimated from Sitar et al. (1999) for all age cohorts. Instantaneous natural mortality for age-1 Lake Trout was fixed at 0.8 and decayed exponentially to 0.1 by age 5; it remained constant thereafter.

Abundance

The estimated abundance of Lake Trout > 280 mm (estimated age 7), based on mark–recapture data and the continuous Schnabel model, was 3,000 individuals, with a 95% confidence interval of 2,036–5,708 fish. This estimate is based on totals over the four sampling periods of 315 captured, 215 marked, and 15 recaptured fish. Although the rate of PIT tag loss is generally low in salmonids (Ombredane et al. 1998; Dare 2003; Hockersmith et al. 2003), we caught three fish that had no PIT tag yet seemed to have tagging scars; one of these three fish had an adipose clip. We counted all three of these fish as recaptures and used this estimate for the remainder of the analysis. If all three of these fish had indeed been tagged, then our estimated tag loss rate is 20%. However, if the two fish with apparent tagging scars were not actually tagged, than our abundance estimate would be 3,430 individuals (95% CI = 2,279–6,923).

We used our abundance and natural mortality estimates to simulate an initial age structure to use in our analyses (Figure 3). We calculated abundance for Lake Trout < 280 mm (ages < 7) by extrapolating backwards from age-7 abundance using the estimated age-specific natural mortality rates. Given these assumptions, we estimated that the population currently includes 7,298 fish ≥ age 1,

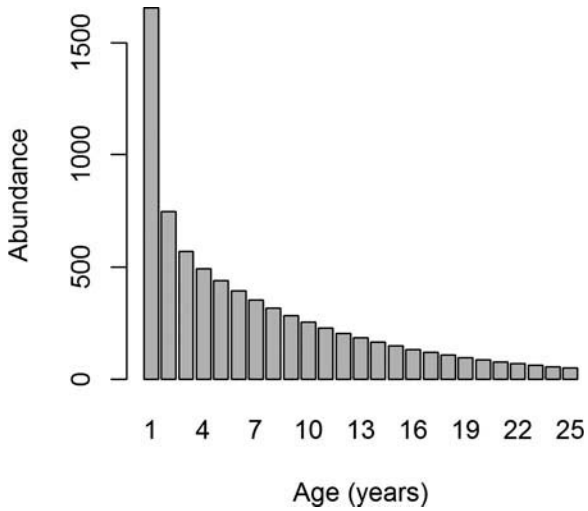

FIGURE 3. Age structure of angling-vulnerable Lake Trout (> 350 mm) simulated from estimated natural mortality (Sitar et al. 1999) and mark–recapture abundance and used as the initial condition in simulation models.

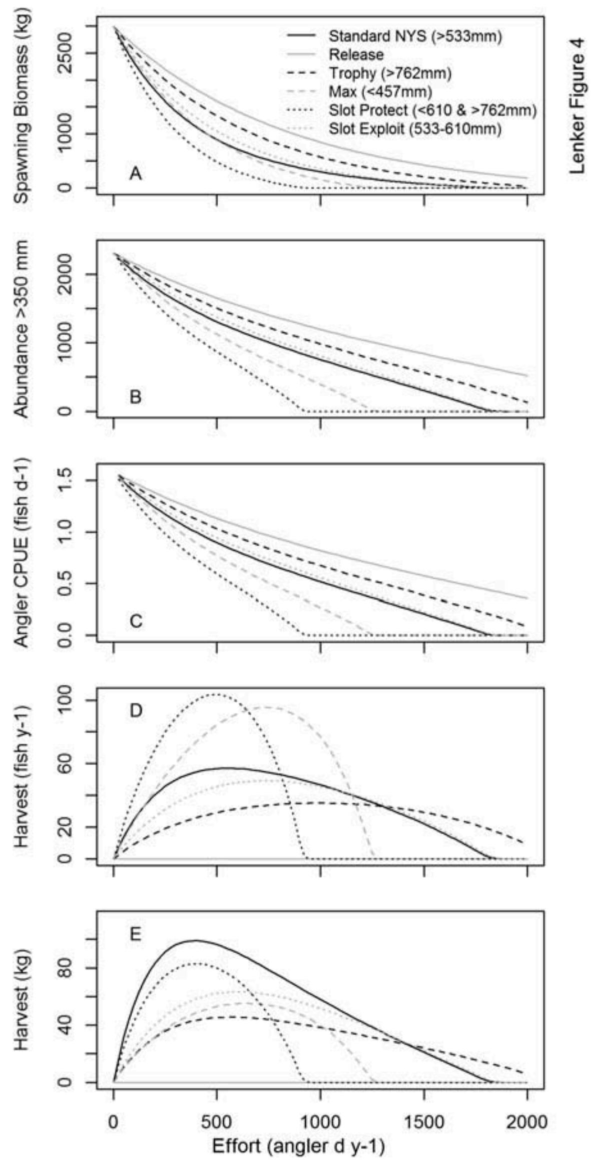

FIGURE 4. Simulated equilibrium of the **(A)** spawning biomass, **(B)** abundance of Lake Trout vulnerable to angling (> 350 mm), **(C)** angler CPUE, **(D)** harvest in individuals, and **(E)** harvest in kilograms across a range of angler effort for six different harvest regulation scenarios. The scenario names are given in panel A along with the sizes of fish that are allowed to be harvested in each scenario (NYS = New York State); no harvest is allowed in the catch-and-release scenario. All parameters except those describing the harvest scenarios were held at the base values given in Table 2.

2,330 fish vulnerable to angling (> 350 mm), 1,356 sexually mature fish, and 106 trophy-sized (> 762 mm) fish. These abundances correspond to densities of 18.6 fish/ha for fish ≥ age 1 and 3.5 fish/ha for fish ≥ age 13, the estimated age at maturity.

Management Scenarios

We focus on reporting equilibrium conditions at the end of 1,000-year simulation runs. Transient nonequilibrium dynamics of abundance and age structure typically persisted for < 100 years in our simulations.

Modeled equilibrium fish abundance and angler CPUE were negatively related to effort in all of the harvest regulation scenarios (Figure 4). The catch-and-release and trophy regulations, which minimize harvest, produced the highest fish abundances and angler CPUEs across the entire range of efforts (Figure 4A–C). Given the assumptions of our model, effort levels between 925 and 2,175 angler-days/year were sufficient to drive the abundance of angling-vulnerable Lake Trout to zero in all but the catch-and-release scenario, which required 2,800 angler-days/year. Even in the catch-and-release scenario, postrelease mortality and illegal harvest led to greatly reduced abundance at high but realistic levels of effort.

Maximum angler CPUE occurred at the lowest levels of effort, and maximum harvest occurred at levels of effort ≤ 1,000 angler-days/year (Figure 4C–E). The harvest of individuals was fairly constant across broad ranges of effort for the standard New York State, exploited slot, and trophy regulation strategies, which protected small fish and reduced the number of fish harvested. It was higher and more sharply peaked for the maximum size and protected slot regulation scenarios, which focused harvest on smaller individuals (Figure 4D). The management strategies that maximize the biomass harvested are not always those that maximize the number of individuals harvested. For instance, the standard regulations produced high harvest in biomass while the maximum length regulations produced high harvest in individuals

(Figure 4D, E). Maximum sustainable harvests did not exceed 104 individuals/year or 99 kg/year for any of the regulations.

Estimated sustainable effort levels are much lower if catchability varies inversely with abundance (Figure 5). The results described above (Figure 4) assume that catchability remains constant at $8.13 \cdot 10^{-4}$ angler-day^{-1} regardless of Lake Trout abundance. If Lake Trout catchability does in fact vary inversely with abundance as described by Shuter et al. (1998) and effort remains constant as abundance declines, then levels of effort between 175 and 550 angler-days/year are sufficient to drive the abundance of angling-vulnerable Lake Trout (> 350 mm) to zero in all of the regulation scenarios. Furthermore, when catchability varies in this manner, the relationships between effort and equilibrium abundance or catch have sharp thresholds so that small changes in fishing effort near the threshold can produce large changes in fishery status (Figure 5).

We investigated the uncertainties in our results by varying key parameters in a sensitivity analysis (Table 4; Figure 6). The results of Figure 6 indicate that the model is sensitive to changes in initial abundance, SRR steepness, postrelease mortality, and growth, which also incorporates the uncertainty present in the age-at-maturity estimate. In contrast, the model is much less sensitive to changes in natural mortality, legal harvest, and illegal harvest (poaching). Overall, the cumulative effect of the unknowns illustrated with varying catchability (Figure 5) and the sensitivity analysis (Figure 6) indicate that the Follensby Pond population could be significantly more vulnerable or resilient to harvest than our results currently indicate.

We also investigated how long it would take an overfished Lake Trout population to return to preexploitation abundance in the absence of fishing by allowing the simulated equilibrium age structure at 1,227 annual angler-days of effort in the standard New York State fishery strategy to run in time without fishing pressure. It took approximately 30 years to restore preexploitation abundance (Figure 7).

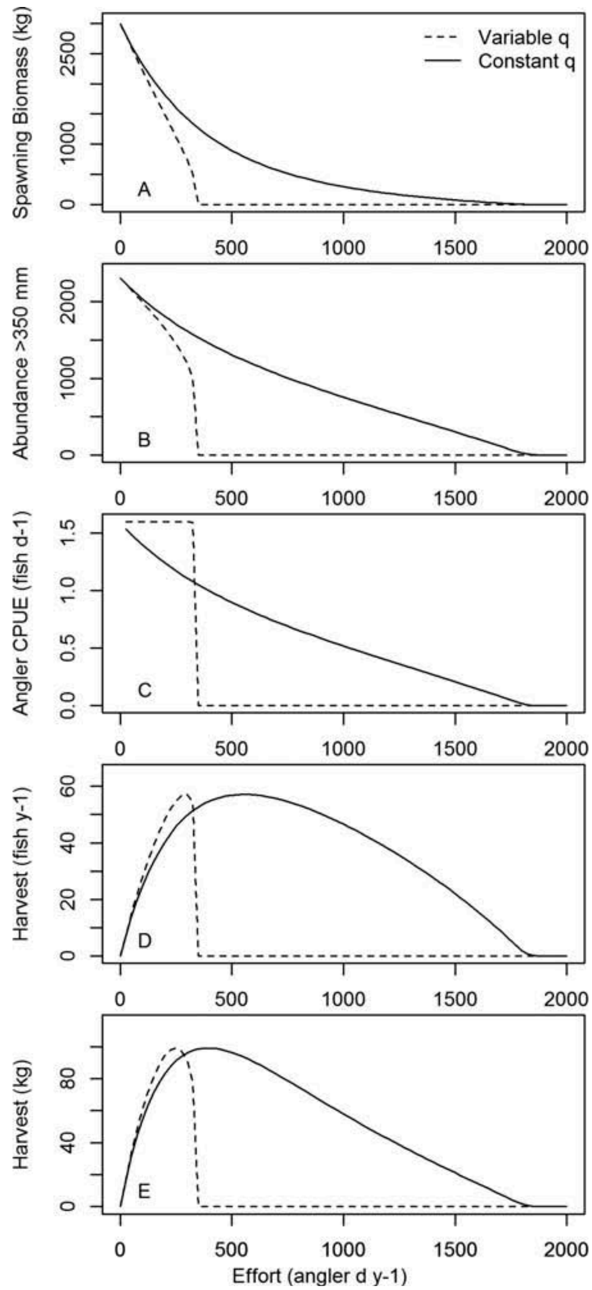

FIGURE 5. Differences in simulated equilibrium conditions if catchability is constant (Constant q) or varies inversely with abundance (Variable q). Panels show the **(A)** spawning biomass, **(B)** abundance of Lake Trout vulnerable to angling (> 350 mm), **(C)** angler CPUE, **(D)** harvest in individuals, and **(E)** harvest in kilograms across a range of angler effort for the standard harvest regulation scenario. In the variable catchability scenario, the catchability–abundance relationship follows Shuter et al. (1998); otherwise, parameter values are as described in Table 2.

DISCUSSION

Several contrasting management possibilities for populations like the Follensby Lake Trout population are emphasized by our harvest scenario analyses. Regulations that permit harvest of large, postmaturation fish (i.e., the exploited slot limit [533–610 mm] and the trophy length limit [> 762 mm]) result in low harvest but high angler CPUE. In contrast, regulations that permit harvest of small, often immature Lake Trout (i.e., the maximum length limit [< 457 mm] and the protected slot limit [< 610 mm and > 762 mm]) allow high harvest but result in smaller populations and thus low angler CPUE. Fisheries managers can use these results to match regulations to management goals and assess the risks of different management options. For instance, if the management goal is to minimize the impact of fishing while still providing angling opportunities, then we recommend catch-and-release regulations. If management goals also include limited Lake Trout harvest, then we recommend either trophy regulations or an exploited slot limit of postmaturation fish. Both the

TABLE 4. Distribution of parameters used in a model sensitivity analysis, where all parameters except for SRR steepness (*z*; see footnote) were varied based on a normal distribution with the stated mean and SD. Each simulation was run 1,000 times. Simulation runs that produced implausible (e.g., negative harvest) values were excluded from the analysis; *n* is the resulting number of simulations used for each parameter. The range describes the highest and lowest simulated parameter values used in each analysis. The variation in initial abundance and harvest was based off of the mark–recapture abundance estimate and Lake Trout legal harvest data from Lake George, respectively (Zollweg 2010; Zollweg 2011; Pinheiro 2013). We estimated SDs for growth (*K*) and natural mortality (minimum asymptotic rate) to produce a wide range of plausible values. Growth was varied from a truncated normal distribution to produce values ≥ 0.034. For postrelease mortality and illegal harvest, we estimated SD to be half of the parameter values used in the model. The results of the sensitivity analysis are shown in terms of angling-vulnerable (> 350 mm) Lake Trout abundance (Figure 6).

Panel (from Figure 6)	Parameter	Mean	SD	*n*	Range
A	Initial abundance (280–800 mm)	3,000	500	1,000	1,235–4,810
B	Beverton–Holt steepness (*z*)[a]	0.85	0.06	1,000	0.60–0.98
C	Growth	0.034	0.02	1,000	0.034–0.097
C	Age at maturity (years)	10.4	2.2	1,000	5–14
D	Natural mortality	0.108	0.025	1,000	0.036–0.198
E	Postrelease mortality	0.15	0.075	982	0.00–0.43
F	Harvest (legal)	0.38	0.12	997	0.01–0.82
G	Illegal harvest	0.05	0.025	983	0.00–0.13

[a]Values for the steepness parameter were drawn from a distribution based on the Lake Trout median and Salmonidae 20th and 80th percentiles reported by Myers et al. (1999). Specifically, we used a Beta (20, 4.5) distribution rescaled to be bounded between 0.2 and 1.0. This distribution has a mean of 0.85, a median of 0.86, and a SD of 0.06.

maximum size limit and protected slot limit produce a high harvest of individuals. However, these regulations also result in rapidly diminishing harvest (and population) size when effort is greater than the level that yields the optimal harvest; management using these regulations should be coupled with strict control and monitoring of effort, or perhaps avoided altogether, to avoid fishery collapse. If the management goal is high harvest, the standard New York State harvest regulations also result in high harvest but do not result in rapid population collapse past the point of maximum sustainable yield.

Catch-and-release regulations produce the highest catch rates and average size of fish caught, yet they may not be attractive to managers because some resource users place a high value on harvesting fish. This conflict may be particularly strong in regions like the Adirondacks, where significant differences exist in attitudes about fishery resource use (Connelly and Brown 2009b). Trophy regulations may be an attractive option in this setting because they allow some harvest but maintain catch rates and a size structure similar to catch and release. Fishery managers may favor regulations that offer compromise because they satisfy multiple constituencies or management goals.

Our results demonstrate both the challenge and the opportunity inherent in managing fisheries for Lake Trout and other large, slow-growing, late-maturing species. On one hand, these populations are extremely vulnerable to fishing pressure: limited effort can greatly reduce abundance and fishery quality (Shuter et al. 1998; Post et al. 2002; Purchase et al. 2005). On the other hand, well-informed and careful management has the opportunity to maintain high-quality fisheries for long-lived, slow-growing species, such as Taimen *Hucho taimen* in northern Mongolia (Jensen et al. 2009) or Bull Trout *Salvelinus confluentus* in Alberta, Canada (Post et al. 2003).

In comparison to other Lake Trout populations, the density in Follensby Pond is typical for an unexploited lake (Burr 1997; Mills et al. 2002), but the somatic growth, as measured by the Gallucci and Quinn (1979) ω parameter ($K \cdot L_\infty$), is particularly slow compared with Lake Trout populations in British Columbia (Giroux 2003), Quebec (Hansen et al. 2012), Ontario (Trippel and Beamish 1989; Payne et al. 1990), and the Laurentian Great Lakes (Keller et al. 1990; He and Stewart 2001). The slow growth in Follensby Pond is probably partly due to low nutrient concentrations and primary productivity (Table 1). We compared our population-specific results to the life-history-based model for Ontario Lake Trout developed by Shuter et al. (1998), which uses surface area and total dissolved solids to estimate a variety of parameters, including growth rates and yield. Given Follensby Pond's parameters (surface area = 393 ha, total dissolved solids = 18.09), the Shuter model estimates a significantly smaller, faster-growing Lake Trout population than what we observed in Follensby Pond (Table 5). These results suggest that nutrient availability may not be solely responsible for slow growth. Other contributing factors could include high density, which may slow growth via density-dependent effects (Johnston and Post 2009), competition with littoral piscivores for prey fishes (Vander Zanden et al. 1999), and long-term lack of fishing because fishing pressure can select for increased growth (Law 2000; Enberg et al. 2012).

Our model does not consider the ways in which fishing might influence the productivity of the population via

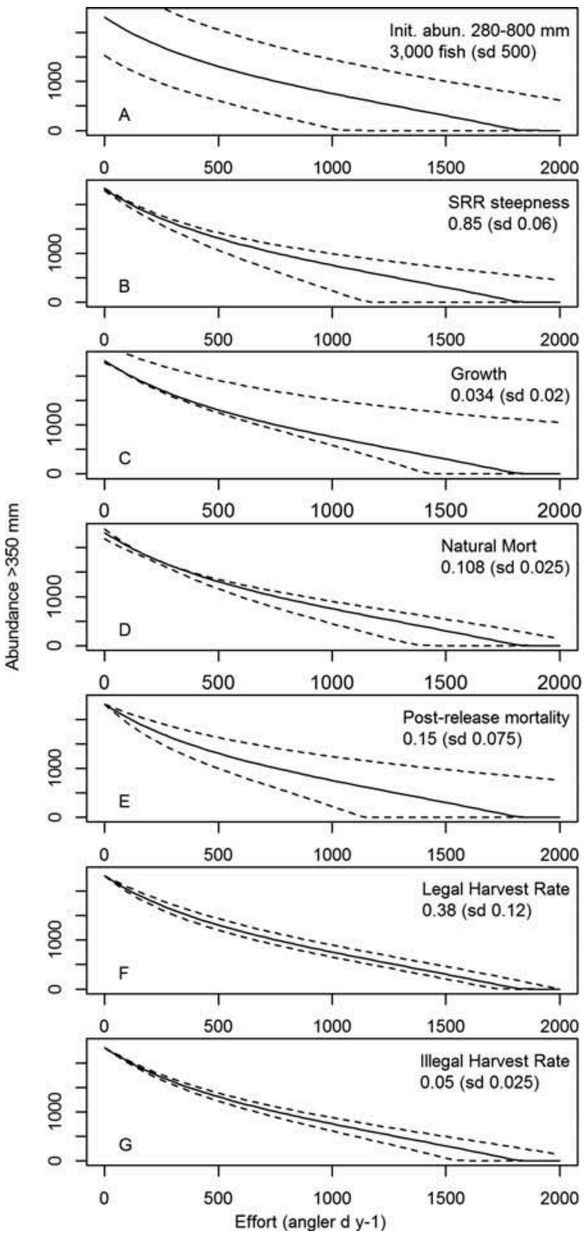

FIGURE 6. Sensitivity of the model to variation in key parameters. Each panel shows the simulated equilibrium abundance of Lake Trout vulnerable to angling (> 350 mm) across a range of angler effort under the standard New York State harvest regulations (> 533 mm; solid line) as one key parameter was varied. The varied parameter is indicated in the top right corner of each panel, along with the mean and SD of the distribution from which values of the parameter were chosen (normal distributions except for SRR steepness, for which we used a Beta distribution; see Table 4). The dashed lines show the the 2.5th and 97.5th percentiles of abundance across approximately 1,000 simulations (see “*n*” in Table 4); Init. abun. = initial abundance, Natural Mort = natural mortality.

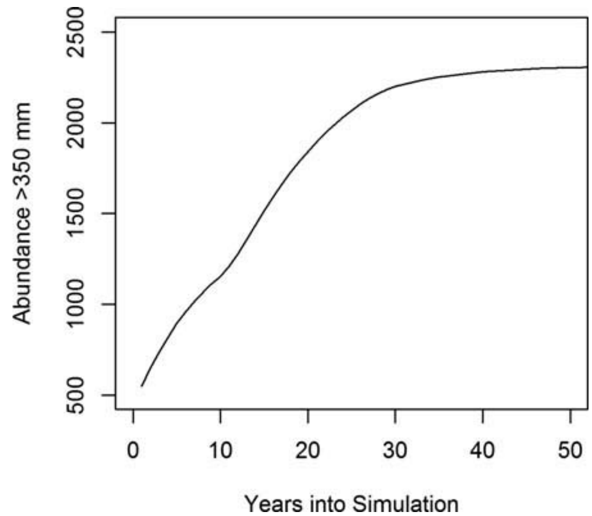

FIGURE 7. Abundance of angling-vulnerable Lake Trout (> 350 mm) in the absence of fishing for the simulated equilibrium age structure at 1,227 annual angler-days of effort in the New York State standard harvest scenario. The restoration of Follensby Pond’s depleted fishery to preexploitation levels required approximately 30 years in the absence of fishing.

TABLE 5. Follensby Pond model comparison to a life-history-based model for Ontario Lake Trout (Shuter et al. 1998), where Follensby Pond’s surface area is 393 ha and total dissolved solid content is 18.09 mg/L. The difference in yield estimates (310.4 versus 147.9 kg) highlights the difference between population-specific models and generalized, regional models.

Parameter	Unit	Shuter et al. (1998) estimate	Follensby model estimate
von Bertalanffy asymptotic length (L_∞)	mm	568	1,399
Product of L_∞ and K (ω)	mm/year	89.4	47.6
von Bertalanffy growth rate (K)	Year^{-1}	0.16	0.034
Asymptotic weight (W_∞)	kg	2.2	28.4
Length at 50% maturity (L_{m50})	mm	402	500
Maximum yield (kg per lake per year)	kg/year	310.4	147.9
Length at 50% vulnerability (L_c)	mm	320	425

density-dependent growth or selective pressure changes in growth rate and earlier maturation. We expect density-dependent effects, if they occur, to increase the productivity of the population; in this sense our model is conservative. For instance, increased growth and earlier maturation would lead to increased reproductive capacity and resiliency to fishing pressure (Johnston and Post 2009). Our model does not include density-dependent growth, but some density dependence is captured by the Beverton–Holt SRR, which allows for an increase in per capita recruitment at lower stock size. The point estimate of the stock–recruitment steepness parameter that we use in the model (z) is derived from a single population of Lake Trout (Myers et al. 1999), and SRR steepness is notoriously difficult to estimate (Lee et al. 2012). Other literature estimates for this parameter are considerably lower; for example, Nieland (2006; cited by Hansen et al. 2010) and Shuter et al. (1998) estimate recruitment corresponding to steepness parameters of 0.59 and 0.62, respectively. The Nieland (2006) and Shuter et al. (1998) estimates fall towards the tail of the parameter distribution considered in the sensitivity analysis; thus, some lower but plausible steepness values may be underrepresented in our sensitivity analysis. If SRR steepness is less than 0.86, spawning biomass will produce fewer recruits than currently predicted at low levels of abundance and the population will be less resilient to harvest.

Our model also does not consider how fishing effort may change in response to changes in fishing quality. In the absence of explicit controls on effort, we expect high initial effort due to high fishery quality and the novelty of a previously closed area; this high initial effort would eventually decline with diminishing catch rates and length at capture (Johnson and Carpenter 1994; Post et al. 2008). This decline in effort could be at least partially offset by increasing catchability if the Follensby Lake Trout population follows the inverse relationship established between abundance and catchability in Ontario Lake Trout lakes (Shuter et al. 1998). If this is the case, catchability will increase as abundance declines and surviving Lake Trout will be more susceptible to harvest per unit of fishing effort. Our results suggest that this pattern could result in sharp thresholds in the population response to fishing, which would be a significant management concern.

Monitoring changes in growth and maturation should be a priority for resource managers and would allow model-generated predictions and management recommendations to be refined. In particular, we advise that future research focus on refining estimated abundance, natural mortality, growth, and maturation schedule by capturing additional Lake Trout during the spawning period, continued tagging and recapture of fish for the mark–recapture analysis, and dissecting accidental mortalities for additional information on age, gender, and maturity.

We used a 5% poaching rate for all management scenarios, but work in Lake Michigan suggests that noncompliance varies with the restrictiveness of the regulation. Caroffino (2013) found that restrictive slot limits were associated with much higher noncompliance rates than minimum size limits, under which a greater percentage of catch was legal harvest. If the same trend in noncompliance rates applies to Follensby Pond, we would expect poaching to be higher under the relatively restricted regulations of catch and release, trophy length, maximum size limit, and exploited slot limit than under either the minimum size limit or the protected slot limit. Higher poaching rates would cause a greater decline in size structure and abundance than currently predicted at a given effort level.

Given that the fishery quality in Follensby Pond can be substantially degraded by levels of effort that are consistent with those observed on other nearby Adirondack lakes, controlling effort may be essential for preserving the unique and potentially valuable characteristics of this fishery. Controlling angling quality by stocking or other production-related techniques often results in higher lakewide effort but not higher angling quality or CPUE. Restricting effort by limited entry is therefore more likely to result in high angling quality than is stocking on heavily exploited lakes (Cox and Walters 2007). While there is widespread use of limited-entry systems for big game hunting, the same effort controls are rarely used for recreational fisheries in the northeastern United States. However, this type of effort limitation regulation is used to manage fishing in other regions, such as in the St. John River in New Brunswick for Atlantic Salmon *Salmo salar* (Cox and Walters 2007) and in Central Europe by holders of private fishing rights (Arlinghaus 2006). Limited-entry permits may be essential for maintaining a high-quality self-sustaining Lake Trout fishery at Follensby Pond and similarly situated areas. The cost of restoring an overfished Lake Trout fishery is high as fishery managers must prohibit or significantly reduce Lake Trout fishing pressure for several decades because of this species' long life and late sexual maturity (Figure 7).

We studied the Follensby Pond population for approximately 2 years to parameterize our model. In contrast, some management regimes are based on decades of data in well-studied systems, while less studied populations are often managed with more generalized, regional models. These generalized models allow management agencies to set lake-specific harvest regulations without resource-intensive sampling and population modeling (Shuter et al. 1998; Lester et al. 2003). According to the Shuter et al. (1998) regional Lake Trout model, Follensby Pond's population should support a harvest of 310.4 kg/year. In comparison, the Follensby model produced a maximum annual sustainable yield at 147.9 kg, assuming a harvest of all the legal-sized (≥ 508 mm or 20 in) fish caught. The Follensby-specific estimate corroborates Healey's (1978) results suggesting that Lake Trout exploitation should not exceed 0.5 kg/ha. The 50% difference in yield between the lake-specific and generalized model estimates is likely because the Shuter model seems to be parameterized on exploited populations with faster growth than the Follensby Pond population. Harvesting the generalized model's suggested yield in Follensby Pond would severely reduce abundance and CPUE. However, given the resource investment required to create a population-specific model, the benefits might only outweigh the costs when the goal is to maintain or restore a particularly high-quality or special-interest fishery. We recommend that future research focus on this cost-benefit analysis so regulatory agencies can make both biologically and economically informed decisions.

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REFERENCES

Arlinghaus, R. 2006. Overcoming human obstacles to conservation of recreational fishery resources, with emphasis on central Europe. Environmental Conservation 33:46–59.

Burr, J. M. 1997. Growth, density, and biomass of Lake Trout in arctic and subarctic Alaska. Pages 109–118 *in* J. B. Reynolds, editor. Fish ecology in Arctic North America. American Fisheries Society, Symposium 19, Bethesda, Maryland.

Caroffino, D. C. 2013. Angler compliance with Lake Trout length limit regulations in Great Lakes waters. North American Journal of Fisheries Management 33:1203–1209.

Connelly, N., and T. Brown. 2009a. New York statewide angler survey—2007; report 1: angler effort and expenditures. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Albany.

Connelly, N., and T. Brown. 2009b. New York statewide angler survey—2007; report 2: angler characteristics, preferences, satisfaction, and opinion on management topics. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Albany.

Connelly, N., and T. Brown. 2009c. New York statewide angler survey—2007; report 3: estimated angler effort and expenditures in New York State counties. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Albany.

Cox, S., and C. Walters. 2007. Maintaining quality in recreational fisheries: how success breeds failure in management of open-access sport fisheries. Pages 107–119 *in* T. J. Pitcher and C. E. Hollingworth, editors. Recreational fisheries: ecological, economic and social evaluation [online book]. Blackwell Scientific Publications, Oxford, UK.

Dare, M. R. 2003. Mortality and long-term retention of passive integrated transponder tags by spring Chinook Salmon. North American Journal of Fisheries Management 23:1015–1019.

Ditton, R. B., S. M. Holland, and D. K. Anderson. 2002. Recreational fishing as tourism. Fisheries 27(3):17–24.

Enberg, K., C. Jørgensen, E. S. Dunlop, Ø. Varpe, D. S. Boukal1, L. Baulier, S. Eliassen, and M. Heino. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecology 33:1–25.

Gallucci, V. F., and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society 108:14–25.

Giroux, P. 2003. Assessment of Lake Trout (*Salvelinus namaycush*) stocks and an evaluation of netting and analysis techniques in Chapman, Augier, Pinkut, Taltapin, and Doris lakes, BC. Ministry of Water, Land and Air Protection, Fish and Wildlife, Skeena Fisheries Report SK-143, Smithers, British Columbia.

Gunn, J. M., and R. Sein. 2000. Effects of forestry roads on reproductive habitat and exploitation of Lake Trout (*Salvelinus namaycush*) in three experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences 57(Supplement 2):97–104.

Hansen, M. J., N. A. Nate, C. C. Krueger, M. S. Zimmerman, H. G. Kruckman, and W. W. Taylor. 2012. Age, growth, survival, and maturity of Lake Trout morphotypes in Lake Mistassini, Quebec. Transactions of the American Fisheries Society 141:1492–1503.

Hansen, M. J., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA. Hydrobiologia 650:85–100.

He, J. X., and D. J. Stewart. 2001. Age and size at first reproduction of fishes: predictive models based only on growth trajectories. Ecology 82:784–791.

Healey, M. 1978. The dynamics of exploited Lake Trout populations and implications for management. Journal of Wildlife Management 42:307–328.

Hockersmith, E. E., W. D. Muir, S. G. Smith, and B. P. Sandford. 2003. Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling Chinook Salmon in the Snake and Columbia rivers. North American Journal of Fisheries Management 23:404–413.

Jenke, J. 2002. A guide to good otolith cutting. Department of Fisheries, Fisheries Research Report 141, North Beach, Western Australia, Australia.

Jensen, O. P., D. J. Gilroy, Z. Hogan, B. C. Allen, T. R. Hrabik, B. C. Weidel, S. Chandra, and M. J. Vander Zanden. 2009. Evaluating recreational fisheries for an endangered species: a case study of Taimen, *Hucho taimen*, in Mongolia. Canadian Journal of Fisheries and Aquatic Sciences 66:1707–1718.

Johnson, B. M., and S. R. Carpenter. 1994. Functional and numerical responses: a framework for fish-angler interactions? Ecological Applications 4:808–821.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19:449–467.

Kaufman, S. D., E. Snucins, J. M. Gunn, and W. Selinger. 2009. Impacts of road access on Lake Trout (*Salvelinus namaycush*) populations: regional scale effects of overexploitation and the introduction of Smallmouth Bass (*Micropterus dolomieu*). Canadian Journal of Fisheries and Aquatic Sciences 66:212–223.

Kearney, R. E. 2007. Recreational fishing: value is in the eye of the beholder. Pages 17–33 *in* T. J. Pitcher and C. E. Hollingworth, editors. Recreational fisheries: ecological, economic and social evaluation [online book]. Blackwell Scientific Publications, Oxford, UK.

Keller, M., K. D. Smith, and R. W. Rybicki. 1990. Review of salmon and trout management in Lake Michigan. Michigan Department of Natural Resources, Fisheries Division, Fisheries Special 14, Charlevoix.

Lavigne, M., M. Lucotte, and S. Paquet. 2010. Relationship between mercury concentration and growth rates for Walleyes, Northern Pike, and Lake Trout from Quebec lakes. North American Journal of Fisheries Management 30:1221–1237.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science Journal du Conseil 57:659–668.

Lee, H.-H., M. N. Maunder, K. R. Piner, and R. D. Methot. 2012. Can steepness of the stock–recruitment relationship be estimated in fishery stock assessment models? Fisheries Research 125–126:254–261.

Lester, N. P., T. R. Marshall, K. Armstrong, W. I. Dunlop, and B. Ritchie. 2003. A broad-scale approach to management of Ontario's recreational fisheries. North American Journal of Fisheries Management 23:1312–1328.

Loftus, A. J., W. W. Taylor, and M. Keller. 1988. An evaluation of Lake Trout (*Salvelinus namaycush*) hooking mortality in the upper Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 45:1473–1479.

Mace, P. M., and I. Doonan. 1988. A generalised bioeconomic simulation model for fish population dynamics. New Zealand Fisheries Assessment Research Document 88/4.

McCracken, G. R., R. Perry, D. Keefe, and D. E. Ruzzante. 2013. Hierarchical population structure and genetic diversity of Lake Trout (*Salvelinus namaycush*) in a dendritic system in northern Labrador. Freshwater Biology 58:1903–1917.

Mills, K. H., S. M. Chalanchuk, and D. J. Allan. 2002. Abundance, annual survival, and recruitment of unexploited and exploited Lake Charr, *Salvelinus namaycush*, populations at the Experimental Lakes Area, northwestern Ontario. Environmental Biology of Fishes 64:281–292.

Muoneke, M. I., and W. M. Childress. 1994. Hooking mortality: a review for recreational fisheries. Reviews in Fisheries Science 2:123–156.

Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.

Nieland, J. L. 2006. Modeling the sustainability of Lake Trout fisheries in eastern Wisconsin waters of Lake Superior. Master's thesis. University of Wisconsin–Stevens Point, Stevens Point.

Ombredane, D., J. Baglinière, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile Brown Trout (*Salmo trutta* L.) and their use for studying movement in a small river. Pages 99–106 *in* J.-P. Lagardère, M.-L. Anras, and G. Claireaux, editors. Advances in invertebrates and fish telemetry, volume 130. Springer, Dordrecht, The Netherlands.

Page, L. M., and B. M. Burr. 1991. A field guide to freshwater fishes: North America north of Mexico. Houghton Mifflin, Boston.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10:430.

Payne, N. R., R. M. Korver, D. S. MacLennan, S. J. Nepszy, B. J. Shuter, T. J. Stewart, and E. R. Thomas. 1990. The harvest potential and dynamics of Lake Trout populations in Ontario: Lake Trout synthesis, population dynamics working group. Ontario Ministry of Natural Resources, Toronto.

Pinheiro, J. 2013. Lake George coldwater angler diary cooperator summary for the 2011 fishing season. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Region 5 Fisheries Unit, Warrensburg.

Post, J., L. Persson, E. Parkinson, and T. van Kooten. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecological Applications 18:1038–1049.

Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to Bull Trout. North American Journal of Fisheries Management 23:22–34.

Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27(1):6–17.

Purchase, C., N. Collins, and B. Shuter. 2005. Sensitivity of maximum sustainable harvest rates to intra-specific life history variability of Lake Trout (*Salvelinus namaycush*) and Walleye (*Sander vitreus*). Fisheries Research 72:141–148.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, Oxford, UK.

Rudd, M. A., H. Folmer, and G. C. van Kooten. 2007. Economic evaluation of recreational fishery policies. Pages 34–52 *in* T. J. Pitcher and C. E. Hollingworth, editors. Recreational fisheries: ecological, economic and social evaluation [online book]. Blackwell Scientific Publications, Oxford, UK.

Shuter, B., M. Jones, R. Korver, and N. Lester. 1998. A general, life history based model for regional management of fish stocks: the inland Lake Trout (*Salvelinus namaycush*) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55:2161–2177.

Sitar, S. P., J. R. Bence, J. E. Johnson, M. P. Ebener, and W. W. Taylor. 1999. Lake Trout mortality and abundance in southern Lake Huron. North American Journal of Fisheries Management 19:881–900.

Trippel, E. A., and F. W. H. Beamish. 1989. Lake Trout (*Salvelinus namaycush*) growth potential predicted from Cisco (*Coregonus artedii*) population structure and conductivity. Canadian Journal of Fisheries and Aquatic Sciences 46:1531–1538.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467.

Zollweg, E. C. 2010. Lake George angler diary cooperator summary for the 2009 fishing season. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Region 5 Fisheries Unit, Ray Brook.

Zollweg, E. C. 2011. Lake George coldwater angler diary cooperator summary for the 2010 fishing season. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Region 5 Fisheries Unit, Ray Brook.