## Managing recreational Lake Trout *Salvelinus namaycush* fisheries for the future: developing harvest regulations for an unexploited population and investigating the effect of climate on spawning phenology

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A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science in Renewable Resources © Melissa Anne Lenker 2015

#### Abstract

The abundance and size structure of North America's recreational fisheries have declined and continue to be threatened by overfishing, aquatic invasive species, and environmental degradation. High quality recreational fisheries are thus rare and economically valuable resources. Some fish species are more sensitive to exploitation than other species, and require careful management to maintain the abundance and size structure associated high quality recreational fisheries. The coldwater fish Lake Trout Salvelinus namaycush is one such popular, economically valuable species which must be managed in accordance to its slow growth and late maturity. With a few exceptions, southern Lake Trout fisheries are heavily exploited, and previously unexploited northern populations are facing increased fishing pressure due to the increased popularity of northern tourism and unprecedented access to remote lakes. This coldwater fish species is additionally threatened by climate change: warming temperatures are predicted to extirpate Lake Trout from low elevations and the southern extent of their range. In Chapter I, we develop an age-structured model to assess the effects of six common management strategies (catch and release, trophy, minimum and maximum size limits, slot limits) on Lake Trout abundance, catch per unit effort, and harvest over a range of angler effort on Follensby Pond, an unexploited 393 hectare lake in the Adirondacks region of New York State. The results of Chapter I help assess the risks of different management options and match regulations to management goals. In Chapter II, we use five decades of historical Lake Trout spawning records and climate data from a 1,993 hectare lake in upstate New York to determine the effect of Lake Trout's plastic response to temperature on egg quality and the timing of the spawning period. The results presented in Chapter II add to the growing body of literature exploring Lake Trout spawning phenology and the sub-lethal effects of climate change on thermally sensitive coldwater fish species. Management agencies can use the results of Chapters I and II to assess how previously unfished populations should be managed to maximize social and economic benefits, and whether current Lake Trout exploitation rates are sustainable given the unknown impact of climate change on Lake Trout reproductive capacity.

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#### Résumé

L'abondance et l'étendue de la pêche récréative en Amérique du Nord ont décliné et continuent à être menacées par la surpêche, les espèces aquatiques invasives et la dégradation environnementale. Les pêches récréatives de haute qualité sont donc rares et constituent des ressources économiques précieuses. Certaines espèces de poissons sont plus sensibles à l'exploitation que d'autres espèces et nécessitent une gestion prudente pour maintenir l'abondance et l'étendue des pêches récréatives de haute qualité. Poisson d'eau froide, le touladi Salvelinus namaycush, est une de ces espèces populaires et économiquement précieuse qui doit être gérée en tenant compte de sa croissance lente et de sa maturité tardive. À quelques exceptions près, la pêche du touladi est fortement exploitée dans le Sud, et les populations inexploitées du Nord sont confrontées à une pression de pêche qui a augmenté en raison de la popularité croissante du tourisme dans le Nord et d'un accès sans précédent à des lacs éloignés. Cette espèce de poisson d'eau froide est en outre menacée par le changement climatique: le réchauffement des températures pourraient faire disparaitre le touladi dans les basses latitudes et à la limite sud de son aire de répartition. Dans le chapitre I, nous avons développé un modèle structuré par âge pour évaluer les effets de six stratégies de gestion communes (pêche avec remise à l'eau, trophée, tailles limites minimale et maximale, limites de catégories) sur l'abondance du touladi, la capture par unité d'effort et la récolte en fonction de l'effort du pêcheur, sur un lac inexploité de 393 hectares dans la région des Adirondacks de l'État de New York. Les résultats du chapitre I aident à évaluer les risques liés à différentes options de gestion et correspondent aux régulations des objectifs de gestion. Dans le chapitre II, nous avons utilisé cinq décennies d'enregistrements historiques de ponte chez le touladi et les données climatiques d'un lac de 1993 hectares dans le nord de l'État de New York, pour déterminer l'effet de la réponse plastique du touladi à la température sur la qualité des œufs et la période de ponte. Les résultats présentés dans le chapitre II s'ajoutent à la masse croissante de publications qui explorent la phénologie du touladi et les effets sub-létaux du changement climatique sur les espèces de poissons d'eau froide sensibles à la chaleur. Les organismes de gestion peuvent utiliser les résultats du chapitre I et II pour évaluer comment des populations auparavant non exploitées devraient être gérées afin de maximiser les avantages sociaux et économiques, et pour déterminer si les taux actuels d'exploitation des touladis sont durables compte tenu de l'impact inconnu du changement climatique sur la capacité de reproduction de cette espèce.

#### **Contribution of authors**

This thesis consists of two chapters intended for publication. Chapter I investigates the effect of six common management strategies on an unfished population of Lake Trout in upstate New York, and is currently in review at the North American Journal of Fisheries Management. The science behind Chapter I was developed for and funded by The Nature Conservancy, Adirondack Chapter, in part of a research grant to Christopher Solomon, Brian Weidel, and Olaf Jensen. The candidate's supervisor Christopher Solomon provided support in project planning, data analysis, and interpretation. Brian Weidel led the hydroacoustic surveys, and provided advice and assistance with preparing and interpreting otoliths. Olaf Jensen provided advice and assistance with the population model. The degree candidate was responsible for data collection, data analysis, and manuscript preparation. All coauthors provided substantial feedback and advice during the writing and analytical process.

Chapter II examines the relationship between Lake Trout spawning phenology and climate in upstate New York. The original research idea was developed by the degree candidate and her supervisor Christopher Solomon. The degree candidate was responsible for data collection from the New York State Department of Environmental Conservation, data analysis, and manuscript preparation. Christopher Solomon provided feedback and advice on data analysis and the writing process.

#### Acknowledgements

First and foremost, I would like to thank my supervisor Christopher Solomon (McGill University) for providing me with the unexpected opportunity to attend graduate school and live abroad in Quebec, Canada. I would also like to thank Clifford Kraft (Cornell University) for sending me off on that initial northward push and providing continued advice throughout my two year adventure. I want to thank and acknowledge Brian Weidel (United States Geological Survey) and Olaf Jensen (Rutgers University) for hosting me in New York and New Jersey respectively, and helping get the Follensby manuscript off the ground and running.

I am incredibly grateful to the members of The Nature Conservancy, Adirondack Chapter, for funding the Follensby Pond project and providing me with the opportunity of a lifetime. I particularly want to thank Dirk Bryant, Mary Thill, Mike Carr, Michelle Brown, and Tom Lake of the Nature Conservancy for their continued support, and the time and advice given by Rich Preall and Jon Fieroh (New York State Department of Environmental Conservation), and Daniel Josephson and Clifford Kraft (Cornell University) on the Follensby project.

I also want to thank my fellow lab mates, Jacob Ziegler, Nicola Craig, Raphaëlle Thomas, Pierre-Olivier Benoit, and Katrine Turgeon, for their friendship and support. Thank you for listening to me complain about the cold, for teaching me how to prepare otoliths, and for fighting bed bugs. A very special thank you goes to Jake, Nikki, Raph, and Shannon Boyle for braving the cold, and sometimes the snow, to catch Lake Trout with me in the Adirondacks, and Curt Karboski and Matt Paufve for their help with the hydroacoustic surveys. I also want to thank McGill's non-academic staff, particularly Ann Gossage and Ian Ritchie, who helped me navigate McGill and answered my countless questions. I also want to thank and acknowledge McGill's Department of Natural Resource Sciences for proving a differential fee waiver and a graduate excellence award to help support me for the duration of my degree.

Lastly, I want to thank my family, especially my parents Karen and Jay, my sister Jenny, and my partner Tory Farney, for keeping me (relatively) sane through the rough Canadian winters.

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#### **General introduction**

*Declining recreational fisheries.*—Recreational fishing, or fishing for pleasure or sport, encompasses a large sector the North American economy. In 2011, 33.1 million recreational fishermen spent an estimated \$41.8 billion on fishing related expenses in the United States (USFWS 2012). High quality recreational fisheries are characterized by high abundance, high species richness, and favorable size structure (e.g. trophy fish), and attract more fishermen than their overfished counterparts. Despite the economic advantage afforded by high quality recreational fisheries, these assets are becoming increasingly scarce due to overfishing and habitat degradation (Post et al. 2002).

In contrast to the well-publicized decline of commercial fisheries, the decline of North America's recreational fisheries has remained relatively unrecognized by the public, and only recently recognized by fishery scientists and managers (Post et al. 2002). The restoration of degraded populations typically requires significantly restricting fishing pressure or temporarily closing the fishery. However, this type of resource restriction can be unpopular, particularly if fishery decline is unrecognized, such as in the shifting baseline syndrome, where shifting baselines refers to the comparison of fishery abundance and size structure against a degraded, previously exploited state instead of the fishery's original, unfished state (Pauly 1995). Opening previously unfished lakes to public exploitation presents unique opportunities for fishery managers to create new guidelines that allow angler effort but maintain angling quality near the lake's unfished state, effectively eliminating the shifting baseline and setting new standards for regional fishery quality.

Some fish species are more sensitive to exploitation than other species, and require careful management to maintain abundance and size structure. Lake Trout *Salvelinus namaycush* are one such popular, economically valuable species which must be managed in accordance to its slow growth and late maturity (Page and Burr 1997). However, not all management regimes are sufficient to maintain fishery quality when faced with high angling pressure, as evidenced by Lake Trout's decline in abundance across its range (Post et al. 2002).

This thesis focuses on sustainable Lake Trout management in New York State's Adirondack Park: Chapter I develops a recreational fishery model for an unexploited Lake Trout population and Chapter II investigates the effect of climate on the timing of Lake Trout's spawning period.

*Lake Trout biology.*—Lake Trout, also known as Touladi, Lake Char, and Mackinaw, are a type of freshwater char indigenous to Canada, Alaska, and portions of the northeastern United States (Page and Burr 1997). Lake Trout are also found invasively in several areas of the U.S., most notably, Yellowstone National Park where they have severely impacted indigenous Cutthroat Trout *Oncorhynchus clarkii* populations (Ruzycki et al. 2003). Mature male and female Lake Trout are very difficult to distinguish by physical examination outside of the spawning period. Unlike many other salmonid species, most adult male Lake Trout lack a distinguishing kype or hooked lower jaw. Lake Trout coloration varies between populations and ranges from olive, to silver, to dark brown (Royce 1951; Scott and Crossman 1973).

Lake Trout are a coldwater fish species and require deep, cold, oxygen rich lakes (>3 mg/L) for survival (Lee and Bergersen 1996). Lake Trout will forage for prey fish above the thermocline in dimictic lakes, but typically remain in the hypolimnion during summer lake stratification. With streamlined bodies and sharp teeth, Lake Trout are designed for predation; they primarily eat Whitefish, Smelt, Alewife, and Ciscoes (Dryer et al. 1965; Madenjian et al. 1998; Pycha and King 1975), but also prey upon insects, small mammals, crustaceans, freshwater sponges, and a variety of other fish species, including smaller Lake Trout (Scott and Crossman 1973). If prey fish are unavailable, adult Lake Trout will eat zooplankton like their juvenile counterparts. Planktivorous populations of Lake Trout grow more slowly than piscivorous populations (Konkle and Sprules 1986; Madenjian et al. 1998; Martin 1966; Martin 1952). Lake Trout biology is highly population specific and varies by latitude and specific lake characteristics (McDermid et al. 2010). Lake Trout tend not to migrate, even when movement between water bodies is physically possible (McCracken et al. 2013); this lack of movement can lead to genetic diversification between populations. Many large lakes have developed distinct Lake Trout morphotypes, such as the deep and shallow morphotypes of Lake Mistassini, Quebec (Zimmerman et al. 2007), and the siscowet ("fat") and lean morphotypes of the Laurentian Great Lakes (Moore and Bronte 2001).

Lake Trout are slow-growing, long-lived, and late to mature (Page and Burr 1997), making this species highly sensitive to exploitation. Allocation away from growth and towards reproduction has been shown to cause biphasic growth in Lake Trout, or linear growth before sexual maturity and decelerated growth past the age of reproduction (Quince et al. 2008a; Quince

et al. 2008b). Many exploited populations are stocked with hatchery-raised Lake Trout to bolster population abundance and angler catch per unit effort (CPUE; Post et al. 2002).

Lake Trout spawn from September to November when the days become shorter and the water temperature drops between 8 to 13 °C (Muir et al. 2012). Although uncommon, there have been accounts of stream (Loftus 1958), spring (Bronte 1993), and early winter spawning (Martin 1957). While most Lake Trout populations along the southern portion of this species' range spawn yearly, many northern populations spawn every other year, such as in Great Slave Lake in the Northwest Territories of Canada (Kennedy 1954). The timing of spawning is relatively constant within populations (Royce 1951), but shifts yearly through phenotypic plasticity due to annual variation of environmental variables. Phenotypic plasticity is the ability to change certain physical or developmental characteristics in response to environmental cues (Robinson and Parsons 2002); in the case of salmonids, the timing of the spawning period is controlled by photoperiod and water temperature (Breton et al. 1977; Hazard and Eddy 1951; Henderson 1963; Hokanson et al. 1973). Spawning date also shifts between different bodies of water, different morphotypes (Royce 1951), and latitudinally (Sly and Evans 1996).

Lake Trout characteristically spawn on coarse, windswept rubble (1" to 3' in diameter; Deroche 1969) off of rocky shoals along the lake shore (Eschmeyer 1955). Males arrive on the spawning beds approximately three days before females (Royce 1951; Sly and Widmer 1984), and smaller, younger Lake Trout are thought to spawn before older, larger Lake Trout (Martin 1957; Martin and Olver 1980). Unlike many other salmonids, males do not build nests or redds, but clean the rock beds prior to the spawn. Spawning starts at dusk and lasts several hours (Martin 1957; Royce 1951). One to several males flank a female and quiver until the female has released all of her eggs. The eggs fall into crevices between the rocks and remain there until they hatch in the late winter or early spring (Martin 1957). Spawning duration typically lasts two to three weeks. The length of the spawning period is longer in large lakes and shorter in smaller lakes (Royce 1951).

Egg volume or weight is influenced by the size of spawning females, where larger females produce more eggs and larger eggs than smaller females (Beacham and Murray 1985; Gjerde 1986; Ojanguren et al. 1996). Larger eggs contain more yolk (fat) than smaller counterparts (Moodie et al. 1989; Wallace and Aasjord 1984), and hatch larger fish; increased larval size remains throughout the first few months of life (Springate and Bromage 1985;

Wallace and Aasjord 1984). In Brook Trout *Salvelinus fontinalis* (Hutchings 1991), Arctic Char *Salvelinus alpinus* (Wallace and Aasjord 1984), and other salmonids, alevins hatched from larger eggs survive longer without food than alevins hatched from smaller eggs. This early life advantage of possessing a larger yolk sac may be more advantageous in a wild setting where resources are uncertain or scarce (Blaxter and Hempel 1963). Egg size may have no effect on fry survival in hatchery or laboratory settings where food is available (Blanc 2002). Some authors argue that the advantage of size is uncertain because larger eggs take longer to hatch (Miller et al. 1988; Wootton 1994), and larger larval fish might be more visible to potential predators (Kjesbu et al. 1996). However, larger larval fish are also more likely to escape predators due to their enhanced swimming ability (Miller et al. 1988). After these first few months of life, the advantage of egg size is seemingly lost as growth becomes similar for all fish regardless of egg size (Blanc 2002). Parental diet, genetics, temperature, water chemistry have also been shown to influence egg quality (Bromage et al. 1992; Brooks et al. 1997).

*Lake Trout and climate change.*— Physiological processes in fish, such as growth, metabolism, and spawning, are governed by environmental temperature. Environmental temperatures can therefore alter the distribution of aquatic species by defining northern and southern range limits (Carpenter et al. 1992; Chu et al. 2005; Ficke et al. 2007). Warming temperatures are particularly detrimental to coldwater resident fish species, like Lake Trout *Salvelinus namaycush*, that are constrained to thermal refugia and unlikely to escape increasing lake temperatures through northward migration (McCracken et al. 2013).

Climate change has been attributed to increasing concentrations of atmospheric greenhouse gases, like methane (CH<sub>4</sub>) and carbon dioxide (CO<sub>2</sub>), which absorb thermal radiation and radiate it back towards earth (IPCC 2014). Warming atmospheric air temperatures have been predicted to significantly alter the quantity and chemical composition of freshwater, inland lakes. Lake temperatures are expected to rise, causing longer periods of stratification in dimictic lakes and shorter periods of winter ice cover. Longer periods of lake stratification will result in deeper thermoclines and lower concentrations of hypolimnetic dissolved oxygen (Carpenter et al. 1992; Taner et al. 2011).

Warmwater species like Smallmouth Bass *Micropterus dolomieu* are expected to expand their range and move northward; some models predict Arctic lakes may be vulnerable to

Smallmouth Bass invasion by 2100 (Sharma et al. 2007). In contrast, the southern distribution of coldwater fish species' range is expected to shrink; this contraction will be partially offset by northern range expansion. Lake Trout habitat in the Canadian province of Ontario is projected to contract 30% by the year 2100 (Minns et al. 2008). Twenty-five to seventy-five percent of Wisconsin's Cisco populations, a coldwater species and primary prey fish of Lake Trout, are also predicted to be eradicated by 2100, depending on the amount of warming (Sharma et al. 2011).

As the climate warms, some Lake Trout populations may be able to offset some of the detrimental effects of climate change through genetic change or phenotypic plasticity; for example, southern populations may consistently spawn later in time to achieve optimal water temperatures for egg development. Climate change may also affect Lake Trout's egg quality, reproductive capacity, and the efficiency of government egg take programs for hatchery rearing. Lake Trout's ability to moderate the effects of climate change through phenotypic plasticity will only work to a limit; if Lake Trout cannot escape to an oxygen rich hypolimnion (DO > 3 mg/L) during summer months, they will perish regardless of the timing of the spawning period.

*Lake Trout management.*—Lake Trout are highly prized as a recreational sportfish in the Canadian province of Ontario, where 20-25% of the world's Lake Trout lakes are located (OMNR 2006). Lake Trout are also an important recreational sportfish in upstate New York, including the Finger Lakes, and the Laurentian Great Lakes. New York State anglers spent an estimated 954,511 (± 100,865) days fishing for Lake Trout in 2007 (Connelly and Brown 2009). Lake Trout were commercially fished in the Laurentian Great Lakes until the 1940's and 1950's until stocks were extirpated by overharvest, lampreys, and environmental degradation (Coble et al. 1990; Eshenroder 1987; Krueger et al. 1995).

While a few privately owned lakes still foster unexploited Lake Trout populations in the continental United States, most lightly or unexploited Lake Trout populations are located in northern Canada and Alaska; however, these populations are increasingly at risk from the increased popularity of northern tourism and access provided by off-road vehicles and forestry roads (Gunn and Sein 2000; Selinger et al. 2006). Several studies have established broad Lake Trout management frameworks for regional application (Lester et al. 2003; Shuter et al. 1998). These regional, generalized models allow for lake-specific harvest regulations without the burden of resource-intensive field sampling and population modeling (Lester et al. 2003; Shuter

et al. 1998). However, these generalized models, which are largely modeled upon fished populations, may not be effective in preserving the economically and culturally valuable features of previously unfished populations when first subjected to public exploitation. The need for additional Lake Trout management, especially programs tailored to unexploited populations, is rising with the increasingly susceptibility of northern Lake Trout populations to human influence.

Fishery managers use several management strategies to limit effort and harvest. Common management strategies include minimum and maximum size limits, slot limits, creel limits, and seasonal effort restrictions. Slot limits involve setting minimum and maximum size restrictions that create a slot within which fish can or cannot be harvested (e.g. harvest of fish 457-533 mm or harvest of fish < 457 and > 533 mm). Creel limits restrict the number of fish that can be harvested in one day per angler (e.g. maximum three fish per day per angler). Seasonal effort restrictions restrict harvest by prohibiting angling for certain seasons, like excluding ice fishing. These effort restrictions are most often applied separately for each species; for example, one lake might have no harvest or effort restrictions on Smallmouth Bass, but a three Lake Trout creel limit on fish > 533 mm. The goal of these management regulations is often to maintain a high quality, sustainable fishery. Sustainable fisheries are defined in this context as populations in which abundance has reached a stable equilibrium and does not decline over time in response to fishing pressure; this equilibrium occurs after the dissipation of initial transient dynamics associated with the onset of fishing in a previously unfished system. Fisheries with unsustainable levels of angling effort are often maintained by stocking or introducing hatchery raised fish into the population to bolster angler CPUE.

*Thesis contents.*— Chapter I builds an age-structured population model to investigate the effect of a diverse suite of management strategies on Follensby Pond, an unexploited Lake Trout lake in upstate New York. Management agencies can use these results to match fishery regulations to management goals and assess the risks of different management strategies for unexploited Lake Trout populations and fish species with similar life-history traits. Chapter I further serves as a practical case-study of how to combine field and literature data to rapidly assess population dynamics and develop a management plan. Chapter II uses historical Lake Trout spawning records from Raquette Lake, NY to investigate the impact of climate on Lake Trout spawning

phenology and egg quality to explore the sub-lethal impacts of climate change on Lake Trout and other thermally sensitive resident fish species. See Appendix I for the geographical relation between Follensby Pond and Raquette Lake.

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# Chapter I: Developing recreational harvest regulations for an unexploited Lake Trout population

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#### 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 size limits, slot limits) on an unexploited population of Lake Trout Salvelinus namaycush in Follensby Pond, a 393 hectare lake located in New York State's Adirondack Park. We combined field and literature data, hydroacoustic surveys, 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<sup>-1</sup>). Lake Trout density (43.3 ha<sup>-1</sup> for fish  $\geq$  age-1 and 3.2 ha<sup>-1</sup> for fish  $\geq$  age-13, the estimated age at maturity) was similar to densities observed in other unexploited systems, but growth rate was relatively slow (von Bertalanffy K=0.034;  $\sigma$ =0.011). Maximum harvest occurred at levels of effort < 1,000 angler-days y<sup>-1</sup> in all scenarios considered. Regulations that permitted harvest of large post-maturation 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 assess the risks of different management options for unexploited Lake Trout populations and fish species with similar life-history traits.

#### Introduction

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 to local economies (Connelly and Brown 2009a; Ditton et al. 2002) and promoting nonmarket goods like the wellbeing derived from angling (Rudd et al. 2002). Other benefits include the social aspects of promoting ecological responsibility and furthering environmental education (Kearney 2002). 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 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 similar 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 1997). 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 increasing popularity of northern tourism and access provided by forestry roads (Gunn and Sein 2000; Selinger et al. 2006). 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, catch per unit effort, 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 where 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 is Follensby Pond (44.177° N, 74.372° W), an oligotrophic lake in Harrietstown, Franklin County, NY, located inside of New York State's Adirondack Park (Table 1). The unexploited 392.9 hectare lake reaches a maximum depth of 33 meters. It has three shallow bays which lack hypolimnetic habitat during the stratified season (when thermocline depth is 8-10 meters) and may provide a refuge from Lake Trout predation for prey fishes. It 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 small mesh gillnets (1.5–2.5"; spring and limited fall sets), Oneida trap nets (fall sets), and angling (limited spring and fall) from May 2013 to November 2014. For all Lake Trout captured, we measured total length to the nearest millimeter and mass to the nearest 10 grams, and inserted a Passive Integrated Transponder (PIT) tag (Oregon RFID FDX-B 12 x 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 angling or gillnetting. Sagittal otoliths were removed and fish age was interpreted from transverse sections (n=26) following the protocol in Jenke (2002). Stomach contents from 25 fish were identified as benthic or pelagic invertebrates and fish species.

*Estimating abundance.*—We estimated Lake Trout abundance using mark-recapture experiments and hydroacoustic surveys. We used the continuous Schnabel method to estimate population size through mark-recapture techniques, 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 ( $\check{N}$ ):

#### $[1] \check{N} = \Sigma(M \cdot N) / [\Sigma R + 1]$

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 an annual natural mortality rate of 5.3% (estimated adult mortality), 86.6% 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 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).

In addition to mark-recapture, we estimated population abundance using hydroacoustic surveys on the nights of September 9-10, 2013 and August 24-26, 2014, following a modified version of the methodology outlined in Parker-Stetter et al. (2009). The hydroacoustic survey path was a zig-zag pattern of transects throughout the lake. We excluded transects from the 2013 and 2014 data sets when the transect did not include cold water habitat suitable for Lake Trout (transect depth < 10 m). We estimated Lake Trout suitable habitat to be 120-130 hectares of the 393 total hectares. Data were collected using a Biosonics DtX 123 kHz, 7.8° beam width transducer. The units were calibrated in the spring and the performance checked against a standard calibration sphere. The transducer was towed at a depth of ~1.0 m and data were stored directly on the hard drive of a laptop computer. Acoustics data were analyzed with Sonardata

Echoview v.4.30 software. On the echograms for each transect, the surface (0.5 m) and the bottom (~0.2 m from the actual bottom) were removed to isolate the open water area for fish density analysis. Fish density (#/m<sup>2</sup>) was calculated using the area backscattering coefficient and average in-situ target strength. Target strengths of -60 dB and larger were considered to be fish targets based on target strength distributions of Alewife *Alosa pseudoharengus* in cages (Brooking and Rudstam 2009). We checked target strength distributions to remove echoes which were too small to be fish, along with surface, bottom, and other noise. We set a threshold target strength of -32 dB (~460 mm; Middel 2005, cited by Parker-Stetter et al. 2009), above which we considered all fish to be Lake Trout and estimated the abundance thereof.

*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 the catch 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 ( $h_a$ ).

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

Post-release mortality ( $P_{t,a}$ ) was calculated by applying a post-release mortality rate (p) to Lake Trout that are caught and released.

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

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 post-release mortality  $(P_{t,a})$ .

$$[2c] N_{t+1,a+1} = s_a \cdot N_{t,a} - C_{t,a} - P_{t,a} \qquad a > 1$$

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:

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

where  $N_{t,l}$  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  $\varphi$  $(B_0/R_0)$  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  $\geq 13$  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 (Eqn. 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 our calculated value of natural mortality. We used a species-specific estimate of 0.86 for the steepness parameter (z) from Myers et al. (1999) and 13 years as the age at maturity from which to calculate spawning stock biomass in kilograms. 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 transformed gillnet catch from length to age in order to estimate Follensby Pond's initial age structure. We assume no length selectivity bias in gillnet gear and equal probability of capture once Lake Trout are large enough to be caught in the gillnets

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

[3] 
$$L_a = L_{\infty} \cdot (1 - e^{-K(a-a0)})$$

where  $L_a$  is the total length at age a,  $L_{\infty}$  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, Otter Research Ltd., Sidney, British Columbia), using data from other North American Lake Trout populations (Giroux 2003; Hansen et al. 2012; He and Stewart 2001; Keller et al. 1990; Lavigne et al. 2010; Payne et al. 1990; Trippel and Beamish 1989; Appendix 1) to construct Gaussian prior distributions for the growth rate coefficient (K;  $\mu$ =0.171;  $\sigma$ =0.059; n=70) and x-intercept ( $a_0$ ;  $\mu$ =-0.864;  $\sigma$ =1.515; n=17). We did not include a prior distribution for the asymptotic average maximum body size ( $L_{\infty}$ ) because  $L_{\infty}$  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:

 $[4] W_a = \alpha \cdot L_a^{\beta}$ 

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

We estimated the adult instantaneous natural mortality rate  $(m_a)$  of Follensby Lake Trout from our estimate of the von Bertalanffy growth coefficient *K*, using an empirical relationship that describes the tendency for slow-growing fish to be longer-lived (Jensen 1996; Pauly 1980). [5]  $m_a = 1.6 \cdot K$ 

We used the slope of log-transformed catch at age gillnet data (i.e., a catch curve) to calculate the juvenile instantaneous natural mortality rate (ages 7-11). Age classes too small to be fully recruited to the gillnets ( $\leq 6$  years) were also assigned the juvenile natural mortality rate (Table 2).

We used 220 hours of Follensby 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

### $[6] q = C / (E \cdot N)$

where *C* is the catch per angler-day (assuming 4 hour per angler-d<sup>-1</sup>), *E* is the effort (1 anglerday), and *N* is the estimated population size of Lake Trout vulnerable to angling (those  $\geq$  350 mm length). The observed catchability estimate (9.07  $\cdot$  10<sup>-4</sup> angler-d<sup>-1</sup>) compared favorably to an independently derived catchability estimate (8.13  $\cdot$  10<sup>-4</sup> angler-d<sup>-1</sup>) 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 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 varies between 1.0 and 5.5 angler-days ha<sup>-1</sup> y<sup>-1</sup>, suggesting that, based on its area, Follensby might receive between 930 and 1,525 angler-days y<sup>-1</sup> of effort at equilibrium (Table 3).

The six potential harvest regulations that we considered were standard New York State harvest regulations (harvest >457 mm or >21"), catch and release (no harvest), trophy (harvest >762 mm or >30"), maximum length limit (harvest <457 mm or <18"), slot limit protecting spawning stock (harvest <609 mm and >763 mm, or <24" and >30"), and a slot limit exploiting stock 533-610 mm (harvest 21-24"). In all of these scenarios, we assume that 5% of hooked illegal-sized fish are retained in violation of the law, and post-release 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, NY from 2009 to 2011 (Pinheiro 2013; Zollweg 2010; Zollweg 2011).

#### Results

*Size structure.*—The size structure of the Lake Trout population in Follensby Pond appeared bimodal based on the gillnet catch data, with peaks around 275 mm and 675 mm total length (Fig. 1A). The peak at 275 mm presumably occurred at least in part because of incomplete recruitment of smaller fish to our gillnet sampling method, so the true abundance of smaller fish was probably higher than estimated. 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 diet data and estimated age at maturity for this population (see below). The peak at 675 mm was also reflected in the angling catch (Fig. 1B) as well as in the gillnets. Most fish caught by angling (82%) were between 550 and 750 mm total length. Relatively few fish were smaller than 550 mm (11%) or larger than 750 mm (7%).

The estimated size structure from the hydroacoustic survey followed a slightly different pattern, peaking around 400 mm and declining rapidly thereafter (Fig.1C). No targets corresponding to fish > 650 mm in total length were detected during the hydroacoustic survey. Both the hydroacoustic and gillnet data indicated higher relative frequencies of smaller, juvenile Lake Trout (<500 mm) than adult Lake Trout.

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;  $\mu$ =0.034;  $\sigma$ =0.011), asymptotic length ( $L_{\infty}$ ;  $\mu$ =1398.8;  $\sigma$ =309.1), and the x-intercept ( $a_0$ ;  $\mu$ =-0.021;  $\sigma$  =0.644) were used in subsequent analyses (Table 2; Fig. 2). The allometric relationship between weight and length was log(weight) = -13.23 (SE 0.15) + 3.24 (SE 0.02)  $\cdot$  log(length);  $\sigma^2$ =0.028; n=275;  $R^2$ =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 522 mm total length, which corresponds to 13 years old given our fitted age-length relationship.

The instantaneous rate of natural mortality for adult fish ( $\geq$ 13 years) was estimated from the fitted von Bertalanffy *K* parameter as 0.054 (± 0.017 sd; Jensen 1996; Pauly 1980). For juvenile fish (< 13 years), the instantaneous rate of natural mortality was estimated from the catch curve as 0.289 (± 0.054 sd).

*Diet.*—Stomach contents from 25 dissected Lake Trout ranging from 212 to 813 mm indicated an ontogenetic diet shift from benthic invertebrates to fish when Lake Trout are between 300 and 450 mm in total length. Although just 44% of the diets examined contained fish remains, 91% of these remains were found in Lake Trout > 300 mm. Invertebrate remains were not found in Lake Trout > 450 mm. Vertebrates in Lake Trout stomach contents were identified as Lake Trout (n=2), Lake Cisco (n=6), Yellow Perch *Perca flavescens* (n=1), *Micropterus* spp (n=2), and unidentified fish (n=3).

*Abundance.*—The estimated abundance of Lake Trout > 460 mm (estimated age 12), based on mark-recapture data and the continuous Schnabel model, was 1,266 individuals, with a 95%

confidence interval extending from 841 to 2,556. This estimate is based on totals over the four sampling periods of 193 captured, 135 marked, and 13 recaptured fish. Although the rate of PIT tag loss is generally low in salmonids (Dare 2003; Hockersmith et al. 2003; Ombredane et al. 1998), we caught three fish that had no PIT tag yet seemed to have tagging scars; one of these three fish had an adipose clip. If all three of these fish had indeed been tagged, then our estimated tag loss rate is 12.5% and our abundance estimate would be 1,108 individuals (95% CI: 751-2,108).

The mark-recapture abundance estimate agreed well with our hydroacoustic estimate from 24-26 August 2014, but not with our hydroacoustic estimate from 9-10 September 2013. In both years we detected few targets larger than the -32 dB (~ 460 mm) size threshold at which we felt confident identifying targets as Lake Trout. In 2014 we detected 21 such targets, for an average density of 3.74 ha<sup>-1</sup> and total abundance of 1,470 fish >460 mm. In 2013, we detected 14 such targets, for an average density of 0.48 ha<sup>-1</sup> and total abundance of 190 fish >460 mm.

We used our abundance estimates and other data to estimate an initial age structure to use in our simulation analyses (Fig. 3). We assumed that our mark-recapture estimate is our best available abundance estimate; that the 2014 hydroacoustic estimate supports the mark-recapture estimate; and that the 2013 hydroacoustic estimate is erroneously low due to small sample size. Assuming that abundance of Lake Trout  $\geq$  460 mm is 1,266 individuals and that Lake Trout completely recruit to gillnets at size 280 mm, we use the relative proportion of each size class in the gillnets to calculate abundance from 280-800+ mm (ages 7-25). We calculate abundance for ages < 7 by extrapolating backwards from the age 7 abundance using the estimated juvenile natural mortality rate. Given these assumptions, we estimated that the population currently includes 17,031 fish  $\geq$  age-1; 1,966 fish vulnerable to angling (>350 mm); 1,265 sexually mature fish; and 116 trophy-sized (>762 mm) fish. These abundances correspond to densities of 43.3 ha<sup>-1</sup> for fish  $\geq$  age-1 and 3.2 ha<sup>-1</sup> for fish  $\geq$  age-13, the estimated age at maturity.

*Management scenarios.*—Transient non-equilibrium dynamics of abundance and age structure typically persisted for <80 years in our simulations. We focus on reporting equilibrium conditions at the end of 1000-year simulation runs.

Modeled equilibrium fish abundance and angler CPUE were negatively related to effort in all of the harvest regulation scenarios (Fig.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 (Fig. 4A-C). Given the assumptions of our model, effort levels between 875 and 2,025 angler-days y<sup>-1</sup> were sufficient to drive the abundance of Lake Trout vulnerable to angling to zero in all but the catch and release scenario, which required 2,600 angler-days y<sup>-1</sup>. Even in the catch and release scenario, post-release mortality and illegal harvest lead 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  $y^{-1}$  (Fig. 4C-E). Harvest of individuals was fairly constant across broad ranges of effort for the standard 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 (Fig. 4D). Similar patterns held for harvest in biomass units (Fig. 4E), although 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 (Fig. 4D, E). Maximum sustainable harvests did not exceed 140 individuals  $y^{-1}$  or 105 kg  $y^{-1}$  for any of the regulations.

Estimated sustainable effort levels are much lower if catchability varies inversely with abundance (Fig. 5). The results described above (Fig. 4) assume that catchability remains constant at  $8.13 \cdot 10^{-4}$  angler-d<sup>-1</sup> regardless of Lake Trout abundance. If Lake Trout catchability does in fact vary inversely with abundance as described by Shuter et al. (1998), then levels of effort between 225 and 700 angler-d y<sup>-1</sup> are sufficient to drive abundance 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 (Fig. 5).

There are substantial uncertainties in our analysis, which affect the predicted equilibrium status of the stock at a given level of effort (Fig. 6). To illustrate these uncertainties, we considered "best-case" and "worst-case" versions of the standard harvest regulation strategy, in which we set uncertain initial conditions and parameters to extreme but plausible values. The best-case version used lower harvest (0.2), lower post-release mortality (0.10), no poaching, age 12 at maturity, constant catchability, a higher SRR steepness parameter estimate ( $z_{80}$  for

salmonids; 0.89; Myers et al. 1999), and higher initial abundance (high 95% CI =2,556 Lake Trout > 460 mm). The worst-case version used higher harvest (0.8), higher post-release mortality (0.20), higher poaching (0.10), age 15 at maturity, either constant or variable catchability, a lower SRR steepness parameter estimate ( $z_{20}$  for salmonids; 0.80 Myers et al. 1999), and lower initial abundance (low 95% CI =841 Lake Trout > 460 mm). In the nominal standard harvest regulation strategy, predicted equilibrium abundance was zero when effort was  $\geq$  1,775 angler-d y<sup>-1</sup> (Fig. 4, Fig. 6). In the worst-case and best-case versions of this harvest regulation scenario, the effort required to drive predicted abundance to zero ranged from 75 to 1,650 angler-d y<sup>-1</sup> (Fig. 6).

We also investigated how long it would take an overfished Lake Trout population to return to pre-exploitation abundance in the absence of fishing by allowing the simulated equilibrium age structure at 800 annual angler-days effort in the NYS standard fishery strategy to run in time without fishing pressure. It took approximately 30 years to restore the population to pre-exploitation abundance (Fig. 7).

#### 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, post-maturation fish (i.e. NYS standard harvest >457 mm and trophy >762 mm) result in low harvest but high angler CPUE. In contrast, regulations that permit harvest of small, often immature Lake Trout (i.e. maximum <457 mm, and protected slot <609 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, the regulations that produce high harvest also result in rapidly diminishing harvest (and population) size when effort is greater than the level which yields optimal harvest. Management using these regulations should be coupled with strict control and monitoring of effort, or perhaps avoided altogether, to avoid fishery collapse.

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 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 size structure similar to catch and release. Fishery managers may favor regulations that offer compromise because they satisfy multiple constituencies or management goals.

Fishery managers may also need to consider the economic impacts of management regulations. For instance, a high quality fishery is likely to be maintained with fewer angler days per year than a lower quality fishery. However, if anglers in both scenarios value their fishing experiences equally, it may not be economically advantageous to maintain the higher quality fishery. Highly specialized anglers are more likely to value a trophy fishing experience than less specialized anglers, who are more likely to fish for family-oriented recreation and escape (Chipman and Helfrich 1988). An undeveloped, high quality fishing area like Follensby is likely to attract both types of anglers: specialized fisherman and generalized anglers who value the lake more for its wilderness and scenery than its abundance of trophy fish.

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 (Post et al. 2002; Purchase et al. 2005; Shuter et al. 1998). 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, Follensby's density is typical for an unexploited lake (Burr 1997; Mills et al. 2002) but its somatic growth, as measured by the Gallucci and Quinn (1979)  $\omega$  parameter ( $K \cdot L_{\infty}$ ), is particularly slow compared to Lake Trout populations in British Columbia (Giroux 2003), Quebec (Hansen et al. 2012), Ontario (Payne et al. 1990; Trippel and Beamish 1989), and the Laurentian Great Lakes (He and Stewart 2001; Keller et al. 1990). Follensby's slow growth 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 (SA) and total dissolved solids (TDS) to estimate a variety of parameters including growth rates and yield. Given Follensby Pond's parameters (SA=393 ha; TDS=18.09), the Shuter

model estimates a significantly smaller, faster growing Lake Trout population than what we observed in Follensby Pond (Table 4). 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 (Enberg et al. 2012; Law 2000). Our model does not consider the ways in which fishing might influence the productivity of the population via density-dependent growth or selective pressure changes in growth rate and earlier maturation. We expect these effects, if they occur, to increase the productivity of the population; in this sense our model is conservative. 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.

We were unable to capture the temporal stochasticity associated with variables like recruitment and abundance during the two year study period. This variation may affect our results by making the model more or less sensitive to fishing pressure, which ultimately alters suggested angling pressure. We advise that future research focus on refining estimated abundance, natural mortality, growth, and the 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.

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 population response to fishing, which would be a significant management concern.

Given that fishery quality can be substantially degraded by levels of effort 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 lake-wide effort but not higher angling quality or CPUE. Restricting effort by limited-entry is therefore more likely to result in high angling quality than stocking on heavily exploited lakes (Cox et al. 2002). 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 the St. John River in New Brunswick, Canada for Atlantic Salmon *Salmo salar* (Cox et al. 2002) and in Central Europe by private fishing rights holders (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 (Fig. 7).

We studied the Follensby Pond population for approximately two 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 (Lester et al. 2003; Shuter et al. 1998). According to the Shuter et al. (1998) regional Lake Trout model, Follensby Pond's population should support a harvest of 310.4 kg per year. In comparison, the Follensby model produced maximum annual sustainable yield at 157.8 kg, assuming harvest of all legal sized ( $\leq$  560 mm or 22") 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 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.

#### Acknowledgements

We would like to thank Jacob Ziegler, Nicola Craig, Raphaëlle Thomas, Curt Karboski, Matt Paufve, and Shannon Boyle for their support in the field. We would also like to thank the Adirondack Chapter of The Nature Conservancy for funding our study and Dirk Bryant, Mary Thill, Michael Carr, Michelle Brown, Rich Preall, Jon Fieroh, Daniel Josephson, and Clifford Kraft for their support and advice. And lastly, we would like to thank and acknowledge Tom Lake for always keeping one eye on the lake, and the other on us. Mention of specific products does not constitute endorsement by the U.S. Government.

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### Tables

**Table 1.** Physical and chemical characteristics of Follensby Pond. We collected a pooled mixed sample from 0, 2, and 4 meters in May 2014 before thermocline formation.

Test	Value
Total nitrogen	0.327 mg/L
Total phosphorus	4.8 µg/L
Dissolved organic carbon	$3.75\pm0.05~mg/L$
Total dissolved solids	$18.1\pm0.3~mg/L$
Conductivity	$27.85\pm0.44~\mu S/cm$

Parameter	Value	Unit	Method and (or) source			
Growth						
von Bertalanffy growth rate ( <i>K</i> )	0.034 (sd 0.011)	year <sup>-1</sup>	Fit to length and age data			
von Bertalanffy asymptotic length $(L_{\infty})$	1398.8 (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 ( $\alpha$ )	-13.23 (sd 0.15)	g·mm <sup>-1</sup>	Fit to length and weight data			
Length-weight exponent $(\beta)$	3.24 (sd 0.02)	-	Fit to length and weight data			
Recruitment						
Beverton-Holt unfished recruitment $(R_0)$	2.164	kg	Calculated from estimated <i>m</i> and assumption of equilibrium age			
	2202 55		structure and abundance			
Beverton-Holt unfished spawning biomass	3282.75	kg	Adult unfished biomass based on			
	0.07		mark-recapture abundance estimate			
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						
Adult instantaneous. rate of natural mortality $(m_a)$	0.054 (sd 0.017)	_	Jensen (1996) method			
Juvenile instantaneous rate of natural mortality $(m_i)$	0.289 (sd 0.054)	-	Gillnet catch curve			
Post-release mortality	0.15	_	Loftus et al. 1988; Muoneke and			
-			Childress 1994			
Age structure						
Abundance (≥age-12)	1,266 (CI 841-	indv.	Mark-recapture analysis			
	2,556)					
Plus group	25	years	von Bertalanffy age corresponding			
			to largest Lake Trout caught			

## Table 2. Model parameter summary

**Table 3.** Angling effort data from Adirondack lakes with Lake Trout fisheries. *County* is the county in which the lake is located and *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-d y<sup>-1</sup> and angler-d ha<sup>-1</sup> y<sup>-1</sup> (*Effort* – *LT*; mean and 95% CI). 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-d y<sup>-1</sup>; 95% CI 930-1,525).

Lalva	Country	Area (ha)	0/ I T	Effort - LT	Effort – LT	
Lake	County	Area (na)	70 L I	$(dy^{-1})$	$(d y^{-1} ha^{-1})$	
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)	

**Table 4.** Follensby 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 vs. 157.8 kg) highlights the difference between population-specific models and generalized, regional models.

Davamator	Unit	Shuter et al. (1998)	Follensby model	
	Unit	estimate	estimate	
von Bertalanffy asymptotic length $(L_{\infty})$	mm	568	1399	
Product of $L_{\infty}$ and $K(\omega)$	mm·year <sup>-1</sup>	89.4	47.6	
von Bertalanffy growth rate ( <i>K</i> )	year <sup>-1</sup>	0.16	0.034	
Asymptotic weight $(W_{\infty})$	kg	2.2	28.4	
Length at 50% maturity $(L_{m50})$	mm	402	500	
Instantaneous natural mortality (m)	-	0.20	0.054	
Yield (kg per lake per year)	kg·year <sup>-1</sup>	310.4	157.8	
Length at 50% vulnerability ( $L_c$ )	mm	320	425	

## Figures

**Figure 1.** Relative frequency of Lake Trout by size class in catches from (A) gillnets (n=197) (B) angling (n=118), and (C) hydroacoustic surveys (2014: -32 dB cutoff).





**Figure 2.** von Bertalanffy (Eqn. 3) fit to length-at-age data for 26 Lake Trout. Parameter estimates are in Table 2.

**Figure 3.** Age structure of Lake Trout in Follensby Pond, estimated from data and used as the initial condition in simulation models.



**Figure 4.** Simulated equilibrium of (A) spawning biomass, (B) abundance of fish vulnerable to angling (>350 mm), (C) angler catch per unit effort, (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; no harvest is allowed in the catch and release ("Release") scenario. All parameters except those describing the harvest scenarios were held at the base values given in Table 2.



**Figure 5.** Differences in simulated equilibrium conditions if catchability is constant ("Constant q") or varies inversely with abundance ("Variable q"). Panels show (A) spawning biomass, (B) abundance of fish vulnerable to angling (>350 mm), (C) angler catch per unit effort, (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.



**Figure 6.** Simulated equilibrium abundance fish vulnerable to angling (> 350 mm) across a range of angler effort in nominal, best-case, and worst-case versions of the standard harvest regulation scenario. The nominal scenario uses parameter values from Table 2 and is also plotted in Figure 4B. In the best-case we used a lower harvest rate (0.2), lower post-release mortality (0.10), no poaching, age 12 at maturity, constant catchability, a higher SRR steepness parameter estimate (z80 for salmonids; 0.89; Myers et al. 1999), and set initial abundance to the high end of its estimated 95% confidence interval (=2,556 Lake Trout > 460 mm). In the worst-case we used a higher harvest rate (0.8), higher post-release mortality (0.20), higher poaching (0.10), age 15 at maturity, either constant or variable catchability, a lower SRR steepness parameter estimate (z20 for salmonids; 0.80 Myers et al. 1999), and set the initial abundance to the low end of its estimated 95% confidence interval (=841 Lake Trout > 460 mm).



**Figure 7.** Abundance of angling vulnerable Lake Trout (>350 mm) in the absence of fishing for the simulated equilibrium age structure at 800 annual angler days of effort in the New York State standard harvest scenario. The restoration of Follensby Pond's depleted fishery to pre-exploitation levels requires approximately 30 years in the absence of fishing.



#### **Connecting statement**

Chapter I developed management recommendations for a previously unfished Lake Trout population. Previously unexploited Lake Trout fisheries are rare resources; many Lake Trout populations are heavily fished and maintained by the stocking of hatchery-reared Lake Trout (Post et al. 2002). Lake Trout stocking programs often involve taking gametes from wild populations during the spawning season, typically from the same wild population year after year. In Chapter II, we used one such time series from a lake in the Adirondack region of New York to investigate a possible change in the timing of the Lake Trout spawning period in response to climate change.

New York Lake Trout typically spawn from September to November (Royce 1951) when the days become shorter and the water temperature drops between 8 to 13°C (Muir et al. 2012). The timing of salmonid spawning is controlled by photoperiod and water temperature (Breton et al. 1997; Hazard and Eddy 1951; Henderson 1963; Hokanson et al. 1973). Lake temperatures are expected to rise in conjunction with climate change (IPCC 2014), causing longer periods of stratification in dimictic lakes, lower concentrations of hypolimnetic dissolved oxygen, and shorter periods of winter ice cover (Carpenter et al. 1992; Taner et al. 2011). Warming lake temperatures will not only increase physiological stress in thermally sensitive Lake Trout, but also alter Lake Trout spawning phenology. Analysis of Lake Trout spawning phenology and egg quality in respect to climate increases our understanding of natural Lake Trout reproduction and highlights climate change's sub-lethal effect on naturally reproducing coldwater fish populations.

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# Chapter II: Climate affects Lake Trout spawning phenology and egg weight in an Adirondack lake

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#### Abstract

Climate change is expected to increase lake temperatures, lower thermocline depth, and decrease hypolimnetic dissolved oxygen content in dimictic lakes. Climate change will be particularly detrimental to coldwater resident freshwater fish species, like Lake Trout Salvelinus namaycush, that are largely constrained to thermal refugia and unlikely to escape sub-optimal environments. Lake Trout characteristically spawn once a year from September to November on rocky, windswept shoals; the timing of the Lake Trout spawning period is triggered by photoperiod and water temperature. We use five decades of New York State Department of Environmental Conservation Lake Trout spawning records from a 1,993 hectare lake in upstate New York to determine the effect of Lake Trout's plastic response to temperature on egg quality and the timing of the spawning period. We found inconclusive evidence to suggest that the timing of Lake Trout spawning has changed from 1961 to 2014. Although our data suggests that Lake Trout are spawning 1.2 days (95% CI 0.4-1.9) earlier per decade, we found no associated change in the middle or end of the spawning period. No observed change in the timing of the spawning period is consistent with no significant observed change in September and October mean atmospheric air temperature and surface water temperature for the duration of our study. We also observed no evidence that the timing of the fall spawning period affects egg weight. However, late summer temperatures seem to affect mean egg weight, where warmer August temperatures produce heavier eggs than colder August temperatures. An increase in egg weight associated with warmer August temperatures is consistent with our findings that both average egg weight and monthly mean August air temperatures have increased over the study period. Our research adds to the growing body of literature exploring Lake Trout spawning phenology and the sublethal effects climate change on thermally sensitive coldwater fish species.

#### Introduction

Climate change is predicted to significantly alter the thermal structure, chemical composition, and quantity of earth's freshwater resources (IPCC 2014). Warming temperatures are forecasted to reduce winter ice cover and increase the stratification period in dimictic lakes. Longer periods of stratification are predicted to lower thermocline depth and hypolimnetic dissolved oxygen content (Carpenter et al. 1992; Taner et al. 2011). The effects of climate change will be particularly detrimental to coldwater resident freshwater fish species, like Lake Trout *Salvelinus namaycush* and other salmonids, that are largely constrained to thermal refugia (Isaak et al. 2015) and unable or unlikely to escape sub-optimal environments through northward migration (McCracken et al. 2013).

Thermally sensitive fish species may be able to mitigate some of the detrimental effects of a warming climate through phenotypic plasticity, the ability to change certain physical or developmental characteristics in response to environmental cues (Robinson and Parsons 2002). The connection between temperature and phenology has been well-established in many species; for example, the timing of insect development (Bentz et al. 1991; Hill and Hodkinson 1995) and emergence (Dewar and Watt 1992; Doi 2008), bud break (Hänninen 1995; Moncur et al. 1989), and bird migration (Cotton 2003; Marra et al. 2005) are temperature and light dependent. The plastic response of light and temperature on salmonid spawning phenology is well-known from controlled laboratory experiments on Brook Trout *Salvelinus fontinalis* (Hazard and Eddy 1951; Henderson 1963; Hokanson et al. 1973), and Rainbow Trout *Oncorhynchus mykiss* (Breton et al. 1977).

Lake Trout characteristically spawn once a year from September to November on rocky, windswept shoals (Deroche 1969; Eschmeyer 1955) when the days become shorter and the water temperature drops between 8 to 13 °C (Muir et al. 2012). The timing of the spawning period varies by latitude (Sly and Evans 1996), genetically distinct sub-populations (morphotypes), different bodies of water, and yearly with annual variation of environmental variables (Royce 1951). Males arrive on the spawning beds approximately three days before females (Royce 1951; Sly and Widmer 1984), and younger Lake Trout spawn before older Lake Trout (Martin 1957; Martin and Olver 1980). Spawning typically lasts two to three weeks; the length of the spawning period is longer in large lakes and shorter in smaller lakes (Royce 1951).

Egg quality in salmonids and other fish species varies with female age, genetics, and diet, and water temperature and chemistry (Bromage et al. 1992; Brooks et al. 1997). Older females produce more eggs and larger eggs than younger females (Beacham and Murray 1985; Gjerde 1986; Ojanguren et al. 1996). Larger eggs contain more yolk (Moodie et al. 1989; Wallace and Aasjord 1984), and hatch larger larvae (Springate and Bromage 1985; Wallace and Aasjord 1984). Alevins with large yolk sacs survive longer without food (Hutchings 1991; Wallace and Aasjord 1984), which may aid survival in natural settings with uncertain resources. However, larger larvae may face increased predation because they are more visible to predators (Kjesbu et al. 1996) and take longer to hatch (Miller et al. 1988; Wootton 1994); increased predation may be partially offset by larger larvae's enhanced swimming ability (Miller et al. 1988).

The New York State Department of Environmental Conservation (NYSDEC) captures spawning Lake Trout each fall to gather eggs and milt for government stocking programs. To maximize resources during the egg take, government biologists aim to capture Lake Trout during the peak of spawning activity, where peak spawn is loosely defined by high numbers of Lake Trout on the spawning beds, an approximate 1:1 ratio of males to females, and high quality eggs (NYSDEC unpublished data). For all Lake Trout captured, the NYSDEC also records sex and gonad condition (ripe, hard, or spent).

Despite extensive laboratory research, few studies have used field data to investigate the impact of climate on the timing of spawning for resident salmonids (for exceptions see Blanchfield and Ridgway 1997; Royce 1951; Sly and Widmer 1984; Warren et al. 2012). We use five decades of historical NYSDEC Lake Trout spawning records from Raquette Lake, a 1,993 hectare lake in upstate New York, to determine the effect of Lake Trout's plastic response to temperature on egg quality and the timing of the spawning period. We assume photoperiod is constant and focus on the effect of monthly mean air temperature on spawning phenology and egg quality.

To our knowledge, NYSDEC egg collection data has been used at least twice to analyze Lake Trout spawning habits. Royce (1951) used NYSDEC egg collection data from the 1930's and early 1940's to confirm that the day of maximum egg take was advanced by lower late summer temperatures and delayed by warmer temperatures; Raquette Lake is one of the many study lakes included in this analysis. Similarly, Sly and Widmer (1984) used NYSDEC Seneca Lake data from 1960 to 1981 to conclude that the years with higher late summer to early fall heat

budgets had later median spawn dates, and that long term seasonal lake heating is most likely responsible for the timing of female ripening and development. Our research adds to the growing body of literature exploring Lake Trout spawning phenology (Royce 1951; Sly and Widmer 1984) and the sub-lethal effects climate change on thermally sensitive coldwater fish species (Sharma et al. 2011; Shuter et al. 2012; Warren et al. 2012).

#### Methods

*Study Site.*—Raquette Lake is a 1,993 hectare waterbody located in New York's Adirondack State Park. The popular angling lake reaches a maximum depth 27.4 m and supports both hatchery-reared and wild Lake Trout. Stocked hatchery Lake Trout are reared from Raquette Lake eggs and milt; we assume no change in spawning behavior between wild and hatchery Lake Trout of the same genetic "Adirondack strain" background (Sly and Evans 1996).

*Data collection.*—Lake Trout data were collected by the NYSDEC from 1961 to 2014 at Raquette Lake, Hamilton County, NY (Table 1). Lake Trout for size structure analysis were caught in mid-June to early July (1989, 1993, 1998, 2004, and 2014) by six paneled multifilament nylon gillnets (94 by 1.5 m, or 300' by 5'), where each gillnet contained two panels of 38 mm (1.5"), 51 mm (2.0"), and 64 m (2.5") stretch mesh.

Lake Trout for spawning analyses were captured in Oneida-style trap nets (1.8 by 1.8 m, or 6' by 6' car) set on the spawning beds in early October to early November. Sex and female gonad condition (ripe, hard, or spent) were recorded for each Lake Trout caught. "Ripe" females have ovulated and can be stripped of eggs, "hard" females cannot be stripped, and "spent" females have already spawned and deposited eggs. Ripe females were stripped of eggs, and egg weight was measured as the number of eggs per ounce. The number of eggs per ounce for each year was calculated as the weighted average of daily mean egg weight and the number of egg ounces taken each day. Egg weight was not available for all years in the study period; for years in which egg weight was available, it is included in the analysis regardless of whether spawning date estimates were included or excluded.

Although Lake Trout eggs were taken nearly every year during the study period, we exclude spawning date estimates from years with fewer than five days of sampling to reduce uncertainty. In some cases, years with more than five days of sampling, but with uninformative

data and poor logistic regression model fit (below: *Statistical analysis*), were also excluded from the spawning date estimate (Table 1). The number of sampling days in the resulting 43 years of data ranges from 5 to 22 ( $\mu$ =11.2;  $\sigma$ =4; Fig. 1). The NYSDEC generally attempts to sample during Lake Trout peak spawn activity to increase the egg take relative to days sampled. As a result, the data contains a relatively high proportion of beginning and mid-spawn data compared to end of spawn data.

Historical climate data were accessed online from the U.S. National Climatic Data Center's Global Historical Climatology Network (Menne et al. 2012). We used air temperature data from the Indian Lake weather station (GHCND-USC00304102) because it was the closet weather station to Raquette Lake (~30 km) with complete data for the time period investigated.

*Statistical analysis.*—To determine the progression and dynamics of the spawning period, we fit yearly Lake Trout spawning data to a logistic regression with the binomial response variable of spawned (spent females) or not spawned (ripe and hard females) and logit link (Fig. 2). We calculated the beginning, middle, and end of the spawning period as the day of the year where an estimated 5%, 50%, and 95% of females had respectively spawned.

We used late summer to early fall (July to October) monthly mean air temperature to determine the effect of climatic variation on spawning phenology because other studies have indicated that this time period critically influences the fall spawning phenology of Lake Trout (Goetz et al. 2011; Royce 1951; Sly and Widmer 1984) and Brook Trout (Warren et al. 2012). We used monthly mean air temperature instead of water temperature in the analysis because water temperature data was unavailable outside of the sampled spawning period. Monthly mean air temperature also corresponds well to fluctuations in epilimnetic water temperature (Livingstone and Lotter 1998), and provides a simplistic and easily accessible proxy for water temperature. Air temperature additionally allows for more direct interpretation of results in the context of climate change models, which typically use air temperature as a primary response variable.

We used linear regressions to determine the effects of time and climatic variables on spawning phenology and egg quality, where egg quality was determined by egg weight (n=28; 1961 to 2014) defined as the number of eggs per ounce. The residuals of the regressions of spawn date and egg weight by year were significantly lag-1 autocorrelated; these regressions

were fit by the generalized least squares function in the R package "nlme" (Pinheiro et al. 2013). The other linear regressions were fit by the linear model function in the R package "stats" (R Core Team 2013). All models were weighted by the variance of the response variables spawning date and egg weight, where applicable, to account for uncertainty in the response variable. Linear regressions were further used to determine whether mean monthly air temperature and October water temperature had changed over time. We use surface water temperature taken at the spawning site from Julian day 290 (n=46; 1961 to 2014) in the water temperature analysis to maintain consistency with seasonal temporal fluctuations. Julian day 290 was chosen because more data was available for Julian day 290 than any other day in the dataset. For all regressions, p-vales are shown in text and detailed statistics are supplied in Table 2.

#### Results

Spawning phenology.—The average start date of the spawning period was Julian day 288 (Oct 15;  $\sigma$ =5.2), the average midpoint was Julian day 296 (Oct 23;  $\sigma$ =4.7), and the average end date was Julian day 304 (Oct 31;  $\sigma$ =6.8). The spawning period at Raquette Lake lasted an average of 16 days ( $\sigma$ =7.8). The number of days sampled was positively correlated (r=0.68) with the estimated midpoint of the spawning period. The correlation between days sampled and estimated spawn date likely stems from NYSDEC sampling methodology and does not affect presented results: the NYSDEC begins sampling at Raquette Lake at roughly the same time every year (Julian day 286;  $\sigma$ =2.1), but if Lake Trout are spawning later than usual due to climatic variables or other factors, the NYSDEC samples for a longer period to meet egg and milt collection requirements for hatchery stocking programs.

We found no change in the timing of the estimated midpoint (p=0.06) and end (p=0.307) of spawning period from 1961 to 2014 (Fig. 3). In contrast, the beginning date of the spawning period shifted 1.2 days (95% CI 0.4-1.9) earlier each decade, and cumulatively displaced the beginning of the spawn by 6.1 days (95% CI 2.1-10.2) over the course of the 53 year study period (p=0.004). However, given the constraints of our data, the calculated spawn begin date and midpoint are likely to contain less error than the estimated end of the spawning period. We use the spawn midpoint in further analyses to determine the influence of climate on the timing of the spawning period.

The midpoint date of Lake Trout spawning was significantly affected by mean monthly air temperature in September (p=0.008) and October (p=0.003; Fig. 4). Mean monthly temperatures from July and August were not significantly related to the spawn midpoint date. The regressions indicate that a cold fall advances the spawning period while a warm fall delays the spawning period. More specifically, a 1°C increase in September and October mean monthly temperatures delay the spawning period by 0.9 days (95% CI 0.3-1.7) and 1.2 days (95% CI 0.4-2) respectively. When spawn midpoint was regressed on both September and October mean monthly temperatures together, September temperatures were no longer significant indicating that October temperatures (p=0.028) are more influential than September temperatures (p=0.201).

Surface water temperature from the spawning period, for this purpose defined as days from which spent Lake Trout were caught, ranged from 7.8°C to 15.6°C ( $\mu$ =11.4°C;  $\sigma$ =1.5°C). Spawning period surface water temperature (p=0.571), and September (p=0.073) and October (p=0.239) mean monthly temperature did not significantly change from 1961 to 2014. Mean monthly temperature in July (p=0.042) and August (p=0.007) increased 1.1 °C (95% CI 0.04-2.1) and 1.5°C (95% CI 0.4-2.5) respectively over the 53 year study period.

*Egg quality.*—We found little evidence to suggest that the timing of the spawning period, as determined by estimated starting date (r=0.002) and midpoint (r=-0.227), was related to egg weight. However, our results suggest that egg weight has increased over time (p=0.015), as indicated as an average decline of 24.8 eggs per ounce (95% CI 5.3-44.3) over the 53 year study period. We also found that warmer August temperatures produced larger, heavier eggs than colder August temperatures (p=0.027). A 1°C increase in August mean monthly air temperature was associated with 7.1 eggs (95% CI 0.9-13.3) less per ounce (Fig. 5). Other monthly air temperature variables did not significantly affect egg weight.

#### Discussion

We found inconclusive evidence to suggest that the timing of Lake Trout spawning in Raquette Lake has changed from 1961 to 2014. Although the estimated begin date of the spawning period has shifted earlier in time, we deem the estimated midpoint to be a more accurate representation of the timing of the spawning period due to the constraints of our data, and neither the estimated spawn midpoint or end date have significantly changed. However, the regression on midpoint spawn date and year was nearly significant (p=0.06), and the negatively sloped trend line indicated a possible shift earlier in time (Fig. 3).

We expect Lake Trout to respond to warming fall temperatures by shifting the spawning period later in time towards colder, more optimal spawning conditions. A change towards earlier spawning is thus inconsistent with how we expect Lake Trout to respond to climate change. However, earlier spawning may indicate that the size structure of Lake Trout in Raquette Lake has shifted towards smaller individuals rather than larger individuals because smaller Lake Trout spawn before larger Lake Trout (Martin 1957; Martin and Olver 1980). Figure 6, which shows selected gillnet catch frequencies from 1989 to 2012, supports this hypothesis by indicating a shift in size structure towards smaller fish, at least during the last twenty years of the study period. That being said, no change in the observed timing of the spawning period is consistent with no significant change in September and October mean atmospheric air temperature and surface water temperature for the duration of our study. A clearer pattern of how the timing of Lake Trout spawning has changed over time, if at all, may emerge with additional data collection and analysis.

We also observed no evidence that the timing of the fall spawning period affects egg weight. However, late summer temperatures seem to affect mean egg weight, where warmer August temperatures produce heavier eggs than colder August temperatures. An increase in egg weight associated with warmer August temperatures is consistent with our findings that both average egg weight and monthly mean August air temperatures have increased over the study period. According to our estimates, a 1.5°C increase in mean monthly August temperature from 1961 to 2014 would be associated with a decline of ~10.6 eggs per ounce (95% CI 1.3-20), which is within the confidence intervals of the estimated decline in egg weight during the same time period (24.8 eggs per oz.; 95% CI 5.3-44.3). The control of August temperatures on Lake Trout egg weight is consistent with previous findings that gonadosomatic index begins increasing in August for the siscowet and lean Lake Trout of southern Lake Superior (Goetz et al. 2011). Female ovarian development in salmonids, including Lake Trout, is likely controlled by factors, like temperature and diet, months before the actual spawn (Bromage et al. 1992; Brooks et al. 1997). Our analysis corroborates the results of Royce (1951), Sly and Widmer (1984), and others in which cold early fall temperatures advanced the Lake Trout spawning period and warm temperatures delayed the spawning period. A similar pattern has been observed for a closely related species in the same region, where Warren et al. (2012) concluded that warmer summer temperatures delayed spawning and redd construction in Adirondack Brook Trout.

Average annual mean temperatures in the northeastern United States are predicted to increase 1.9 °C (low emissions) to 6.3°C (high emissions) by 2085 (Kunkel et al. 2013). As the climate warms, Lake Trout and species with similar life history traits may be able to offset some of the detrimental effects of climate change on their reproductive capacity through phenotypic plasticity. For example, southern populations of Lake Trout, like those found in New York, may consistently spawn later in time to achieve optimal water temperatures for egg development. In the short term, mild warming may actually lead to larger eggs and improve the survival rates of larval fish in natural reproductive settings due to larger larvaes' increased ability to survive without food (Hutchings 1991; Wallace and Aasjord 1984) and escape predation (Miller et al. 1988). However, Lake Trout's ability to moderate the effect of warming lake temperatures on spawning phenology through phenotypic plasticity will only work to a limit: in the long term, climate change induced warming is likely to diminish Lake Trout's reproductive capacity by hindering growth (King et al. 1999), increasing physiological stress, and extirpating Lake Trout from low elevations and the southern extent of their range (De Stasio et al. 1996; Minns et al. 2008).

Increasingly warm spring temperatures in dimictic lakes are projected to advance thermocline formation, increase water temperature, and reduce summer concentrations of hypolimnetic dissolved oxygen (Carpenter et al. 1992; Taner et al. 2011). The increased physiological stress of sub-optimal temperatures and low dissolved oxygen content can cause delayed hatching, larval growth abnormalities, egg mortality (Carlson and Siefert 1974; Garside 1959), and adult mortality (Lee and Bergersen 1996; Menne et al. 2012). King et al. (1999) found that Lake Trout grow more slowly in years with earlier onset to stratification, which may be caused by decreased access to littoral prey, and exacerbated by increased metabolic rates caused by warmer water temperatures (Gibson and Fry 1954; McDonald et al. 1996; Snucins and Gunn 1995). If warming lake temperatures prohibit Lake Trout from escaping to an oxygen rich hypolimnion during summer months, populations will perish regardless of their ability to shift

the timing of the spawning period in accord to yearly climate (Lee and Bergersen 1996; Minns et al. 2008). For example, Lake Trout habitat in the Canadian province of Ontario, where twenty to twenty-five percent of the world's Lake Trout lakes are located (OMNR 2006), is projected to contract 30% by the year 2100 (Minns et al. 2008).

Both Royce (1951) and Sly and Widmer (1984) noted the potential of wind to influence the timing of the spawning period, and during our NYSDEC egg take record collection, several employees remarked that the Lake Trout seemed more likely to reach peak spawn after a strong wind storm. Sly and Widmer (1984) found no strong connections between wind stress and the female Lake Trout phenology, but noted that male stimulation during the spawning period was highly correlated to wind stress, likely due to wind and internal wave induced fluctuation of lake temperature regimes. Although we did not investigate the effect of wind on Lake Trout spawning phenology, we recommend further research to investigate wind's role in influencing spawn dynamics. For instance, early fall temperatures and photoperiod may shift the timing of the Lake Trout spawning period to a suitable thermal and temporal regime, but high wind speed and lake mixing could induce more Lake Trout to spawn on a given night within that temperature and light determined period.

#### Acknowledgements

We would like to thank the New York State Department of Environmental Conservation staff who contributed to the Lake Trout spawning dataset at Raquette Lake throughout the decades. We would also like to particularly thank Rich Preall, James Pinheiro, Brett D'Arco, Neil McCarthy, and Thomas Kielbasinski of the NYSDEC for assistance accessing the spawning data, Tory Farney for advising on the climate analysis, and Jordan Read for offering guidance on the physical limnology aspects of our research. MAL's work on this project was supported by an award from The Nature Conservancy, Adirondack Chapter to CTS, Olaf Jensen, and Brian Weidel.

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#### Tables

**Table 1.** Spawning data summary, where sampling "start" and "end" columns refer to the Julian day on which the first and last trap nets were pulled in each year, "Egg weight" is the yearly weighted average number of eggs per ounce, and "n ripe", "n hard", and "n spent" refer to the number of females captured each year in respect to gonad condition. The last three columns are the logistic regression derived Julian dates of the beginning (5% spawned), midpoint (50%), and end (95%) of the spawning period.

Voor	Sampling start <i>DOY</i>	Sampling end <i>DOY</i>	Eggs weight: <i>no. per oz.</i>	n ring	<i>n</i> hard	n	Spawn bogin	Spawn midnoint	Spawn
I cal				fem	fem	fem	DOY	DOY	DOY
1961	285	303	241.2 (SE 10.6)	111	266	107	298	301	305
1962	284	303	235.2 (SE 3.5)	215	616	144	296	301	305
1963 <sup>a</sup>	287	299	_	-	_	_	_	-	_
1964	290	297	265.9 (SE 7.1)	191	95	176	290	293	296
1965	290	298	248.1 (SE 5.4)	171	106	93	292	295	298
1966	285	294	264.9 (3.7)	300	192	268	284	290	297
1967	284	297	263.7 (SE 1.7)	185	708	106	291	297	302
1968	284	298	246 (SE 6.1)	141	210	140	281	295	310
1969	288	303	237.6 (SE 2.5)	114	223	59	294	299	304
1970	287	302	241.3 (SE 4.3)	52	116	16	294	305	315
1971	288	309	_	109	156	28	303	311	319
1972	293	299	256.1 (SE 6.6)	32	16	64	282	295	307
1973 <sup>a</sup>	289	295	-	66	_	_	_	_	_
1974 <sup>a,b</sup>	285	287	-	97	_	_	_	_	_
1975	284	295	-	132	321	22	292	297	302
1976	287	293	235.7 (SE 2.5)	146	195	71	287	294	301
1977 <sup>a</sup>	-	_	-	-	_	_	_	_	_
1978	284	293	276.3 (SE 3.5)	133	204	24	289	298	307
1979	284	296	229.1 (SE 3.7)	158	204	73	288	294	300
1980	289	294	267.2 (SE 7.2)	246	64	203	288	292	297
1981	283	290	275.9 (SE 3.6)	159	32	122	281	286	291
1982	286	300	242 (SE 3.4)	158	222	70	292	299	306
1983	286	297	229.6 (SE 2.5)	169	137	88	287	297	306
1984 <sup>d</sup>	287	293	237.7 (SE 6)	161	165	68	-	-	-
1985	285	295	257.6 (SE 3.9)	281	401	121	289	295	302
1986 <sup>a</sup>	284	290	260.2 (SE 7.5)	-	-	-	-	-	-
1987 <sup>b</sup>	283	286	280.5 (SE 5.4)	232	188	186	-	-	-
1988 <sup>a,b</sup>	287	290	246.6 (SE 6.7)	-	-	-	-	-	-
1989 <sup>a</sup>	-	-	_	-	-	-	-	-	-
1990	286	290	245.6 (SE 6.3)	207	110	34	288	290	293
1991	286	295	232.7 (SE 2.8)	227	474	40	292	297	302
1992	287	301	265.3 (SE 2.3)	187	294	122	290	300	311

1993	286	291	234.3 (SE 3.1)	280	126	109	285	292	299
1994	285	290	241 (SE 5.4)	259	158	81	286	290	294
1995	284	296	-	181	326	77	289	298	307
1996	286	294	-	214	160	59	288	296	304
1997	287	296	-	237	124	85	283	299	315
1998	286	295	-	164	81	164	282	292	301
1999	285	295	-	186	115	93	281	296	311
2000	285	291	-	218	239	186	286	290	295
2001	285	295	-	269	522	74	289	303	316
2002	285	296	-	205	754	196	292	295	299
2003	284	296	-	162	530	532	285	291	298
2004	286	298	-	207	603	252	291	298	304
2005	285	297	-	146	391	281	286	295	303
2006	285	291	-	160	411	190	281	292	303
2007	285	301	-	109	373	101	295	301	307
2008	289	297	259.5 (SE 8.5)	146	300	60	293	298	303
2009	287	292	233.8 (SE 2.9)	94	8	89	282	289	295
2010 <sup>c</sup>	_	-	-	-	-	-	-	-	-
2011 <sup>d</sup>	285	294	246.5 (SE 6)	177	364	101	-	-	-
2012	290	296	217.8 (SE 3.7)	180	133	161	277	296	315
2013	289	298	231 (SE 2.9)	175	425	105	289	301	313
2014	288	297	-	104	155	27	288	302	315

<sup>a</sup> Missing data

<sup>b</sup> Less than five days of sampling

<sup>c</sup> No egg collection this year

<sup>d</sup> Uninformative data and poor logistic regression fit
Table 2. Statistics for linear regressions on year, midpoint spawn date, and egg weight. "Slope" is the line gradient; "Intercept" is the point at which the line crosses the y-axis; "p" is the level of marginal significance within the regression, where we consider p < 0.05 significant; "df" is the residual degrees of freedom; "SE" is the residual standard error; " $\phi$ " is the mean square contingency coefficient; "F" is the F-statistic; and "R<sup>2</sup>" is the coefficient of determination.

	Slope	Intercept	р	df	SE	φ	F	R <sup>2</sup>
Regression: year (independent variable)								
Spawn 5% DOY	-0.116 (SE 0.038)	518.8 (SE 75.1)	0.004	41	13.55	0.052	-	-
Spawn 50% DOY	-0.075 (SE 0.039)	442.1 (SE 76.5)	0.06	41	12.62	0.2	-	-
Spawn 95% DOY	-0.055 (SE 0.053)	406.5 (SE 104.6)	0.307	41	15.13	0.473	-	-
Eggs: no. per oz.	-0.468 (SE 0.18)	1174.6 (SE 357.6)	0.015	30	1.49	-0.013	-	-
Jul mean air temp	0.198 (SE 0.095)	-219.1 (SE 189.4)	0.042	48	10.64	-	4.354	0.083
Aug mean air temp	0. 277 (SE 0.099)	-383.4 (SE 196.7)	0.007	48	11.04	_	7.841	0.14
Sep mean air temp	0.232 (SE 0.126)	-333.3 (SE 251.1)	0.073	49	14.12	_	3.362	0.064
Oct mean air temp	0.225 (SE 0.189)	-383.5 (SE 375.7)	0.239	49	21.13	_	1.422	0.028
Oct water temp (DOY 290)	0.062 (SE 0.109)	-3.2 (SE 216.4)	0.571	42	11.51	_	0.326	0.008
Regression: midpoint spawn date (dependent variable)								
Jul mean air temp	-0.084 (SE 0.055)	308.8 (SE 9.5)	0.132	40	12.75	-	2.367	0.056
Aug mean air temp	-0.014 (SE 0.043)	296.7 (SE 7.2)	0.741	40	13.19	-	0.111	0.003
Sep mean air temp	0.097 (SE 0.034)	281.6 (SE 4.6)	0.008	41	11.96	-	7.914	0.162
Oct mean air temp	0.124 (SE 0.039)	286.6 (SE 2.5)	0.003	41	11.71	-	10.01	0.196
Sep and Oct mean air temp	0.065 (SE 0.036) 0.095 (SE 0.041)	279.9 (SE 4.4)	0.074 0.028	40	11.39	-	6.973	0.259
Regression: egg weight (no. per oz.; dependent variable)								
Jul mean air temp	-0.026 (SE 0.273)	250.7 (SE 47.9)	0.926	29	1.67	_	0.009	< 0.001
Aug mean air temp	-0.708 (SE 0.305)	364.8 (SE 51.1)	0.027	30	1.51	-	5.395	0.15
Sep mean air temp	-0.233 (SE 0.317)	274.7 (SE 39)	0.469	30	1.63	-	0.538	0.018
Oct mean air temp	-0.256 (SE 0.173)	261.5 (SE 10.8)	0.149	30	1.59	_	2.198	0.068

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## Figures

**Figure 1.** The period during which spawning Lake Trout were sampled each year (indicated by extent of vertical bars) and the spawning period midpoint estimated by logistic regression (points). The sampling period ranged from 5 to 22 days ( $\mu$ =11.2;  $\sigma$ =4).



**Figure 2.** Yearly Lake Trout spawning data fit to a logistic regression with the binomial response variable of spawned (spent females) or not spawned (ripe and hard females) and logit link, where (A) illustrates a year with highly informative data (2003) and (B) illustrates a year with uninformative data (2014). The dashed lines represent the 95% confidence interval for the regression relationship. The beginning, middle, and end of the spawning period (hollow triangles) correspond to the day of the year (DOY) where an estimated 5%, 50%, and 95% of females have respectively spawned.



**Figure 3.** Weighted regressions of year and the logistic regression estimated spawning period (A) begin date (p=0.004) (B) midpoint (p=0.06) and (C) end date (p=0.307). Spawn begin date = 518.8 (SE 75.1) – 0.116 (SE 0.038) · year Spawn midpoint date = 442.1 (SE 76.5) – 0.075 (SE 0.039) · year Spawn end date = 406.5 (SE 104.6) – 0.055 (SE 0.053) · year



**Figure 4.** The timing of Lake Trout spawning, as determined by the estimated midpoint of the spawning period, is significantly affected by mean monthly air temperature in September (p=0.008) and October (*shown*; p=0.003). A 1°C increase in September and October mean monthly temperatures delays the spawning period by 0.9 days (95% CI 0.3-1.7) and 1.2 days (95% CI 0.4-2) respectively. Otherwise stated, a cold fall advances the spawning period while a warm fall delays the spawning period.

Spawn midpoint = 286.6 (SE 2.5) + 0.124 (SE 0.039) · mean monthly Oct temp  $(^{1}/_{10} °C)$ 



**Figure 5.** Our results suggest that egg weight has increased over time (p=0.015), as indicated as an average decline of 24.8 eggs per ounce (95% CI 5.3-44.3) over the 53 year study period. Warmer August temperatures also seem to produce larger, heavier eggs than colder August temperatures (p=0.027). A 1°C increase in August mean monthly air temperature is associated with 7.1 eggs (95% CI 0.9-13.3) less per ounce.

(A) No. per oz. = 1174.6 (SE 357.6) – 0.468 (SE 0.18) · year

(B) No. per oz. = 364.8 (SE 51.1) – 0.708 (SE 0.305) · mean monthly Aug temp  $\binom{l}{10}$ °C)



**Figure 6.** Raquette Lake gillnet catch frequencies by length (mm) for 1989, 1993, 1998, 2004, and 2012, where "n" refers to sample size. Catch frequencies from 1989 to 2012 indicate that population size structure may have shifted towards smaller, younger individuals during the course of the study period.



## **General conclusion**

Unexploited Lake Trout *Salvelinus namaycush* lakes are rare, culturally and economically valuable resources. Due to Lake Trout's high sensitivity to harvest (Post et al. 2002), many Lake Trout populations require careful management and monitoring to maintain high abundance and favorable size structure when confronted with angling pressure and harvest. As the results of Chapter I illustrate, even modest levels of effort can have a large effect on Lake Trout abundance. The future of recreational fishery management for slow growing species like Lake Trout, and rare resources like the previously unfished Follensby Pond, may lie in effort restrictions that maintain high angling quality while allowing some harvest and fishing pressure. Although there is no intrinsically right or wrong way to manage a fishery, different management strategies achieve different management results. Management agencies can the results presented in Chapter I to match regulations to management goals and assess the risks of different management options for unexploited Lake Trout populations and other slow growing, recreationally fished species.

In addition to angling pressure, thermally sensitive resident freshwater species like Lake Trout are also threatened by warming lake temperatures brought about by climate change. The historical spawning records used in Chapter II corroborate other studies (Royce 1951; Sly and Widmer 1984) in which warm fall air temperatures delayed the Lake Trout spawning period and cool fall air temperatures advanced the spawning period. We predict that climate change will induce Lake Trout to spawn increasingly later to achieve optimal water temperature. Although moderate warming of late fall temperatures seemed to increase average egg weight, which may aid larval survival in a natural setting, we do not know if this relationship will hold with additional warming. Understanding how climate affects Lake Trout spawning phenology not only explores the sub-lethal impacts of climate change on Lake Trout and other thermally sensitive resident fish species, but allows management agencies to assess whether current Lake Trout exploitation rates are sustainable given predicted changes in reproductive capacity.

Low dissolved oxygen content (<3 mg/L; Lee and Bergersen 1996) and warm water temperatures (>23.5°C; Gibson and Fry 1954) are predicted to extirpate Lake Trout from low elevations and the southern extent of their range. In contrast to predicted southern extirpations, rising Arctic temperatures may increase northern Lake Trout habitat and range (Minns et al. 2008). However, rising temperatures may also bring warmwater invasive species like

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Smallmouth Bass *Micropterus dolomieu* into northern Lake Trout habitat (Sharma et al. 2009), which negatively affect Lake Trout by competing for littoral prey (Vander Zanden et al. 1999). Under the assumption that warming temperatures will eventually extirpate southern Lake Trout populations, the spawning phenology of surviving northern populations may be the most affected by warming atmospheric temperatures. Coincidentally, it is also these northern Lake Trout populations that are most in need of management regulations tailored towards previously unexploited fisheries due to the increased threat of fishing pressure brought about by the increased popularity of northern tourism and unprecedented accessibility to remote lakes (Gunn and Sein 2000; Kaufman et al. 2009; Selinger et al. 2006).

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## Appendix

**Appendix 1.** Map of (A) Follensby Pond, (B) Raquette Lake, and (C) the Indian Lake weather station (GHCND-USC00304102; Menne et al. 2012). Follensby Pond contains the unexploited Lake Trout population upon which the population model for Chapter I is built. Chapter II uses Lake Trout spawning data from Raquette Lake and historical climate records from the Indian Lake weather station to assess the effect of climate on Lake Trout spawning phenology. Follensby Pond and Raquette Lake are located in New York State's Adirondack Park.



**Appendix 2.** Literature review of growth and reproductive parameters. We used the means and standard deviations of von Bertalanffy literature values (growth rate coefficient *K*; x-intercept  $a_0$ ) to construct Gaussian prior distributions for the growth rate coefficient (*K*;  $\mu$ =0.171;  $\sigma$ =0.059; n=70) and x-intercept ( $a_0$ ;  $\mu$ =-0.864;  $\sigma$ =1.515; n=17) for the Bayesian Follensby Pond growth model.

<b>K</b>	$a_{\theta}$	n	Province	Lake	Reference		
years	years	40	or state	D: 1	Circore 2002		
0.085	-	40	BC	Pinkul Taltanin	Giroux 2003		
0.089	-	43	BC		Giroux 2003		
0.119	_	31	BC	Augier	Giroux 2003		
0.132	-	42	BC	Chapman	Giroux 2003		
0.119	-0.78	74	QC	Lake Mistassini	Hansen et al. 2012		
0.244	-	-	ON	Lake Ontario	He and Stewart 2001		
0.251	_	-	ON	Lake Ontario	He and Stewart 2001		
0.16	0.04	-	MI	Southern Lake Michigan	Keller et al. 1990		
0.19	0.04	-	MI	Central Lake Michigan	Keller et al. 1990		
0.19	0.05	-	MI	Northern Lake Michigan	Keller et al. 1990		
0.0367	-3.89	44	QC	Amichinatwayach	Lavigne et al. 2010		
0.0357	-2.24	40	QC	Tilly	Lavigne et al. 2010		
0.0833	-5.21	110	QC	Chibougamau	Lavigne et al. 2010		
0.137	-	1009	ON	Squeers	Payne et al. 1990		
0.124	_	132	ON	Boshkung	Payne et al. 1990		
0.092	_	6015	ON	Opeongo	Payne et al. 1990		
0.112	_	602	ON	Joseph	Payne et al. 1990		
0.121	-	174	ON	Pickeral	Payne et al. 1990		
0.137	_	51	ON	Little Gull	Payne et al. 1990		
0.11	_	282	ON	Smoke	Payne et al. 1990		
0.123	_	51	ON	Lake of Bays	Payne et al. 1990		
0.16	_	75	ON	Burnt Island	Payne et al. 1990		
0.164	_	447	ON	Gull	Payne et al. 1990		
0.115	_	35	ON	Eagle	Payne et al. 1990		
0.157	_	2993	ON	Happy Isle	Payne et al. 1990		
0.163	_	312	ON	Kennisis	Payne et al. 1990		
0.116	_	569	ON	Lavieielle	Pavne et al. 1990		
0.154	_	108	ON	Loch Erne	Pavne et al. 1990		
0.151	_	410	ON	Nelson	Payne et al. 1990		
0.162	_	175	ON	Greenwater	Payne et al. 1990		
0.182	_	111	ON	Goulais	Payne et al. 1990		
0.203	_	80	ON	Redstone	Payne et al. 1990		
0.168	_	225	ON	Rig Salmon	Payne et al. $1990$		
0.168	-	225	ON	Big Salmon	Payne et al. 1990		

0.164	_	45	ON	Robinson	Payne et al. 1990
0.168	-	605	ON	Semiwhite	Payne et al. 1990
0.127	_	79	ON	Gong	Payne et al. 1990
0.258	_	153	ON	Wollaston	Payne et al. 1990
0.242	_	264	ON	Greenwhich	Payne et al. 1990
0.166	_	2142	ON	Flack	Payne et al. 1990
0.25	_	708	ON	Bone	Payne et al. 1990
0.193	_	94	ON	Miskwabi	Payne et al. 1990
0.137	_	344	ON	Temagami	Payne et al. 1990
0.137	_	199	ON	Lake of the Woods	Payne et al. 1990
0.241	_	264	ON	Big Clear	Payne et al. 1990
0.198	_	272	ON	Devil	Payne et al. 1990
0.237	_	571	ON	Louisa	Payne et al. 1990
0.181	_	285	ON	Charleston	Payne et al. 1990
0.167	_	1255	ON	Chiblow	Payne et al. 1990
0.246	_	155	ON	Kawagama	Payne et al. 1990
0.229	_	92	ON	Islets	Payne et al. 1990
0.207	_	86	ON	Little Joe	Payne et al. 1990
0.188	_	133	ON	Muskoka	Payne et al. 1990
0.291	_	299	ON	Adelaide	Payne et al. 1990
0.21	_	85	ON	South Otterskin	Payne et al. 1990
0.2	_	111	ON	Rosseau	Payne et al. 1990
0.174	_	278	ON	Wakekobi	Payne et al. 1990
0.235	_	251	ON	Ranger	Payne et al. 1990
0.355	_	240	ON	Dickey	Payne et al. 1990
0.233	_	270	ON	Big Rideau	Payne et al. 1990
0.303	_	204	ON	Christman	Payne et al. 1990
0.141	-0.65	283	ON	Greenwich	Trippel and Beamish 1989
0.128	-0.14	48	ON	Robinson	Trippel and Beamish 1989
0.13	-0.40	87	ON	Burnt Island	Trippel and Beamish 1989
0.109	-0.89	189	ON	Greenwater	Trippel and Beamish 1989
0.143	0.04	45	ON	Pickerel	Trippel and Beamish 1989
0.157	-0.04	100	ON	Islets	Trippel and Beamish 1989
0.155	-0.09	118	ON	Loch Erne	Trippel and Beamish 1989
0.206	-0.12	67	ON	Little Gull	Trippel and Beamish 1989
0.205	-0.20	97	ON	Little Joe	Trippel and Beamish 1989
0.229	-0.21	91	ON	South Otterskin	Trippel and Beamish 1989