

EFFICACY OF THE GULL ISLAND SHOAL LAKE TROUT REFUGE IN LAKE
SUPERIOR

by

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ABSTRACT

Historically, Lake Superior supported one of the largest and most diverse lake trout fisheries in the Laurentian Great Lakes. The Apostle Islands region is unique in Lake Superior, with a diversity of shoals that each supported unique spawning stocks of lake trout. Lake trout stocks collapsed throughout Lake Superior because of excessive fishery exploitation and sea lamprey predation, so stocking, sea lamprey control, and fishery regulations were enacted to support stock restoration. A refuge was established around Gull Island Shoal to enable recovery of the lake trout stock that spawned on this historically important spawning shoal in the Apostle Islands region. In the early 2000s, evidence suggested that stocks in the Apostle Islands Region were rehabilitated and near carrying capacity. My objective was to determine if future sustainability of lake trout stocks will depend on the Gull Island Shoal refuge. I constructed an age-structured simulation model to assess the effect of excluding and including the refuge, as a harvest management tool, on sustainability. The model was used to estimate median abundance, probability of collapse, and time to extinction. Median abundance was estimated for age 4, age 4-and-older, and age 8-and-older lake trout, and probability of collapse was estimated for age 4-and-older and age 8-and-older lake trout. Harvest was simulated as a range of commercial fishing mortality rates, while holding recreational mortality constant, a range of recreational mortality rates, while holding commercial mortality constant, and a range of equal commercial and recreational mortality rates. Natural mortality was modeled as a fixed-base rate and a randomly varying sea lamprey mortality rate. Recruit abundance was modeled as a density-dependent function of adult lake trout abundance. Random process error was incorporated into sea lamprey mortality and recruitment sub-models to simulate model uncertainty. Parameter uncertainty was incorporated into the recruitment sub-model. Combinations of

fishing mortality rates were varied under different movement rates to assess effectiveness of the refuge on lake trout sustainability. In general, median abundance of age 4, age 4-and-older, and age 8-and-older collapsed at lower instantaneous fishing mortality rates when the refuge was abandoned. With the refuge in place, the fishing mortality rate that resulted in collapse depended on the rate of movement into and out of the refuge. When movement was low, too many fish stayed in the refuge, and conversely, when movement was high, too many fish became vulnerable to fishing, so the refuge was ineffective at both low and high rates of movement. With the refuge in place and movement into and out of the refuge, extinction did not occur at any level of simulated fishing mortality. In contrast, when the refuge was removed, extinction occurred for all combinations of commercial and recreational fishing mortality. In conclusion, the lake trout population in Eastern Wisconsin waters of Lake Superior was sustained by the refuge under even impossibly high fishing mortality rates, whereas removal of the refuge increased the risk of collapse at much lower fishing mortality rates. Without the refuge, exploitation rates cannot remain at current levels because no fish outside or inside the refuge would be protected from exploitation to sustain a fishable population. Therefore, retaining the refuge is the optimal solution to long-term sustainability of the lake trout population in eastern Wisconsin waters of Lake Superior.

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INTRODUCTION

Increasing pressure on the world's natural resources increases the need for sustainable resource management. However, the lag between management action and observed effects, combined with systems that are too large for experimental manipulation with limited budgets makes managing natural resources challenging. To overcome these obstacles, managers often rely on models to better understand the resource and to predict the impact of management actions prior to implementation (Buckland et al. 2007).

Modeling population dynamics dates back to the 17th century when scientists began theorizing about human population growth. John Graunt was the first to hypothesize about exponential population growth and limits by the environment on this growth, which has since become known as carrying capacity (Ricker 1975). Further advancements in the 18th century by Rev. T. R. Malthus showed that the population growth rate declined as abundance increased, which is now referred to as density dependence (Getz 1996). The 19th century led to more advances in the study of population dynamics, as statisticians Adolphe-Lambert-Jacques Quetelet and Pierre-Francois Verhulst developed the logistic equation to more accurately describe population growth (Getz 1996). Alfred James Lotka and Vito Volterra expanded the logistic equation to include multiple species in the early 20th century, which became known as Lotka-Volterra competition and predation models (Vano et al 2006).

Advancements in technology and a solid foundation of theoretical models gave rise to modern models used by fishery researchers. Baranov's catch equation, developed in 1910, allowed researchers to examine the effect of changing the rate of exploitation on the total mortality rate and assumes that natural mortality and fishing mortality compete with each other (Ricker 1975). The surplus production model, derived from the logistic equation by

Graham in 1935 as a stock assessment tool, treats a population as one pool of biomass, with all individuals having the same growth and mortality rates, thereby limiting its use in fisheries because most fish populations are structured by individuals that do not have the same growth and mortality rates. In addition, Graham's surplus production model does not account for uncertainty and population dynamics, so can lead to collapse of fish populations (Ricker 1975). Von Bertalanffy developed a continuous growth model in 1938 using length-at-age (most common) and weight-at-age to depict growth of fish species and allow for variability in environmental factors such as temperature and food availability (Haddon 2001). Ricker's stock-recruitment model, developed in 1954, builds on previous recruitment models by allowing for other factors that affect recruitment. In real populations, recruitment is not as simple as being a function of adults, so environmental variables also need to be taken into account (Ricker 1975). The yield per recruit model developed by Beverton-Holt in 1957 treats yield as a trade-off between harvest mortality and age at entry, but assumes constant mortality and growth and fixed recruitment that is not reflective of natural populations. Pope expanded on this in 1972 with his cohort analysis model that accounts for dynamics among years and ages and also incorporates abundance, not just catch rates. The disadvantage to Pope's model is that it relies on many estimates that are not available in smaller systems, so it is more widely used on larger systems that maintain high-intensity, multi-species fisheries (Ricker 1975). Further expanding on this, Fournier and Archibald (1982) developed the statistical catch-at-age model that accounts for incomplete cohorts, so agencies with gaps in their data can use sporadic assessment catches to model populations (Haddon 2001). These models do not usually stand alone and are often combined into complex models that would not be possible without the aid of computers. Complex models, that consider multiple

variables, more accurately reflect natural systems and give managers the ability to make predictions that aid in managing natural resources.

The use of modeling in fisheries management is becoming more widespread as managers work with poorly understood and complex populations and often must rely on models to gain insight into these populations and comprehend their complexities (Allen and Hightower 2010). Computer simulation models can aid managers in testing their assumptions for managing environmental systems where manipulating the system in question is not feasible (Ford 1999). While no model can fully describe biological reality, models are used to improve understanding and aid in making management decisions (Rose and Cowan 2003).

The yellow perch *Perca flavescens* population within Green Bay, Lake Michigan, supported a commercial and recreational fishery from the late 1800s through its collapse in 1965. The Wisconsin Department of Natural Resources, WDNR, conducted numerous studies during 1965–1980 to determine the status of the population and to develop management strategies to restore the population's ability to support commercial and recreational fisheries (Johnson 1995). In 1983, an adjustable quota was set for the commercial fishery, and the WDNR used modeling to simulate effects of different methods for setting harvest quotas. The model accounted for yellow perch population dynamics, variation in year class strength, density dependent growth, and dynamics of effort, harvest, and value of commercial and recreational fisheries. The model indicated that the Green Bay yellow perch fishery could be improved with quota management and provided the WDNR with a foundation to begin setting quotas. The fishery continues to be regulated by harvest quotas and has improved (Johnson 1995).

Efforts to revive Pacific salmon *Oncorhynchus* stocks throughout the Pacific Northwest have been highly controversial involving politicians, scientists, government agencies and the public. Researchers rely on models to quantify risks facing salmon stocks to determine the most effective management strategies (Oosterhout and Mundy 2001). Within the Snake River, a tributary of the Columbia River, all salmon stocks have been listed as threatened or endangered under the federal Endangered Species Act. Wild chinook salmon *Oncorhynchus tshawytscha* in the Snake River have declined in numbers of spawners since the 1980s and in most brood years from 1980 to the early 1990s failed to replace themselves on spawning grounds (Oosterhout and Mundy 2001). Salmon depend on cooler ocean temperatures and adequate rainfall to maintain sustainable populations. With rising ocean temperatures and the area experiencing more periods of drought, adult survival was low and out-migrating smolt survival was threatened by low flows. The population was modeled in 1998 to determine the future trajectory of the population, and biologists discovered that the population was predicted to go extinct by 2033 under current conditions (Oosterhout and Mundy 2001). Reversing the decline in Snake River salmon stocks would be difficult in such a short amount of time, but in situations where the time to extinction is further in the future, opportunities to save the species from extinction may exist.

Simulating the status of valuable fish populations in the future can be beneficial to managers by illustrating how different management strategies affect a population. Within the Great Lakes, several fish species have collapsed and are currently being managed for sustainability. Many of these populations are being managed using data collected decades ago and the populations have since improved, thereby leading the public to question the necessity of such management for these species. The status of lake trout in the Great Lakes

is an example of controversy between managers and stakeholders where modeling could provide insight into future population status to enable more informed decisions.

The history of the collapse and recovery of lake trout in Lake Superior has been well documented (Hansen et al. 1995). When first exploited, lake trout populations were thought to be inexhaustible. Europeans had begun commercial and recreational fisheries by the early 1800s in Lake Superior and moved across the lake as fisheries stocks were depleted (Lawrie and Rahrer 1972; Goodier 1989). Annual harvest was between 1 and 3 million kg from 1879 to 1950, and advancements in technology, especially increased efficiency of gill nets, allowed for sustained yield despite decreasing abundance (Hile et al. 1951; Pycha and King 1975). Because lake trout are a long-lived, slow-growing and late-maturing species, this level of exploitation was not sustainable (Russ and Alcala 1996).

Invasion by the sea lamprey, *Petromyzon marinus*, in the 1940s added pressure to an already struggling population and by 1962 lake trout stocks collapsed in Lake Superior (Hansen et al. 1995). To restore lake trout populations, the Lake Superior Lake Trout Technical Committee developed plans to increase recruitment by stocking hatchery-origin fish and reduce mortality by implementing fishing regulations and sea lamprey control (Lawrie and Rahrer 1973; Hansen et al. 1995; Linton et al. 2007). Lake trout were regularly stocked beginning in 1963, but abundance of lake trout continued to decline through the 1980s (Hansen et al. 1994; Linton et al. 2007). Low survival of stocked lake trout was attributed to commercial fishing effort and predation by wild lake trout (Hansen 1996). Stocked lake trout were contributing more to recruitment than wild lake trout in an early lake-wide stock-assessment (Lawrie and Rahrer 1973; Hansen et al. 1995), but wild lake trout were the main source of recruitment at Gull Island Shoal, an important spawning reef in

Wisconsin waters of Lake Superior (Schram et al. 1995). During 1980–2003, wild lake trout abundance exceeded stocked lake trout abundance, thereby indicating that wild lake trout predominated (Corradin et al. 2008).

Rehabilitation of lake trout in Lake Superior did not solely depend on stocking programs, fishery regulation, and sea lamprey control. While stocking, fishery regulation, and sea lamprey control were underway, managers implemented two harvest free zones, Devils Island refuge and Gull Island Shoal refuge, within the Apostle Islands area of Lake Superior. Gull Island Shoal refuge was established in 1976 following a period of overfishing that led to collapse of lake trout stocks from 1970 to 1975 (Swanson and Swedberg 1980; Schram et al. 1995; Nieland et al. 2008). Devil’s Island refuge was established in 1981 to establish a spawning stock. Harvest free zones are designed to facilitate recuperation of exploited stocks by preserving genetic diversity, maintaining age structure and population size, and providing recruitment outside the refuge (Carr and Reed 1993; Man et al. 1995; Russ and Alcala 1996; Halpern 2003). Retaining older, larger individuals and recruiting younger, smaller individuals increases population size, protects spawning biomass, increases genetic diversity, reduces overfishing, and enhances age structure (Carr and Reed 1993; Man et al. 1995; Lauck et al. 1998; Agardy 2000). Implementation of refuges in Lake Superior should increase lake trout size, biomass, density, and diversity.

Establishment of harvest free zones, stocking programs, sea lamprey control, and other management practices contributed to recovery of Lake Superior lake trout stocks. By the mid-1990s, lake trout populations in the Apostle Islands region were building toward carrying capacity, so the lake trout population could sustain harvest in the near future (Corradin et al. 2008). Evidence of a fully rehabilitated stock has led some to question the

need for lake trout refuges. The state-tribal fishing agreement that regulates many aspects of the commercial fishery in the Apostle Islands region is set to expire in 2015. Discussions about the efficacy and necessity of the Gull Island Shoal refuge are expected.

Increasing pressure on the Lake Superior lake trout fishery increases the need for sustainable management. However, the lag between management action and observed effects, combined with a system that is too large for experimental manipulation with limited budgets, makes managing lake trout populations challenging. To overcome these obstacles, managers may be able to use models to determine future importance of the Gull Island Shoal refuge on sustainability of the lake trout population in the region (Buckland et al. 2007).

My objective was to determine if lake trout population sustainability in the Apostle Islands region depends on the Gull Island Shoal refuge. To achieve this objective, I constructed an age-structured stochastic simulation model to assess the effect of excluding and including the refuge on sustainability of the lake trout stock in western Lake Superior. I evaluated effects of the refuge on abundance at age 4 to address recruitment, age 4-and-older to address the population vulnerable to fishing, and age 8-and-older to address the spawning population by simulating median abundance, probability of collapse, and time to extinction. Natural mortality was modeled as a fixed rate and a simple random sea lamprey mortality rate. Recruit abundance was modeled as a density-dependent function of adult lake trout abundance with parameter uncertainty and process error. Random process error was incorporated into the sea lamprey mortality sub-model to simulate model uncertainty. The model was used to simulate long-term effects of a range of commercial and recreational harvest allocations. Gear selectivity differs between the commercial gill net and sport

angling fisheries. Fishing mortality rates were varied for a range of movement rates to evaluate the effect of the refuge on lake trout sustainability.

METHODS

Study Area

Lake Superior is a unique ecosystem that contains 10% of the world's surface freshwater, more than half of the water in the Laurentian Great Lakes, and the largest surface area of any freshwater lake in the world (82,414 km²) (Hansen 1995). Lake Superior has a low mean temperature ($\leq 6^{\circ}\text{C}$), deep water (406 m max and 148 m mean), low dissolved solids ($\sim 60\text{ mg/L}$), low average annual fish yield (0.8 kg/ha) and low primary productivity (1.6-5.6 mgC/m³/hr/mo) that result in a highly oligotrophic state (Hansen 1995). Due to its oligotrophic state, Lake Superior has less capacity for supporting aquatic life, so the fishery produces only 10% of what Lake Michigan, a comparatively nutrient rich lake, produces annually. Lake Superior supports 88 species of fish, 19 of which are non-native (Habermann and Stykel 2012). Lake trout are the apex predator (Kapuscinski et al. 2005).

Lake Superior is partitioned into management zones for regulating lake trout fisheries (Figure 1). Wisconsin waters are divided into two lake trout management zones: the western portion (WI-1) and the Apostle Islands (WI-2). The focus of this study is WI-2, which contains the Gull Island Shoal refuge and more sport and commercial fishing and surveying effort than WI-1. WI-2 contains 22 Apostle Islands and encompasses 4,473 km². Water depth is shallow, generally less than 65 m, except for a 140 m trench along the eastern boundary of the islands. The Apostle Islands contain two refuges for protecting lake trout, the Gull Island Shoal refuge that encompasses 336 km² and the Devil's Island Shoal refuge that encompasses 283 km², where commercial and recreational fishing are prohibited (Figure 2, Hansen 1995, Linton et al. 2007).

The Gull Island Shoal refuge contains the shoal, Gull and Michigan islands, and a nursery area encompassing 70,000 ha near the eastern edge of the Apostle Islands. Spawning habitat depth ranges 1–20 m and is surrounded by water deeper than 70 m, and covers an area nearly 3,100 ha. Nursery habitat depth ranges 10–40 m and is surrounded by water deeper than 70 m. Nursery habitat consists mainly of sand substrate with some isolated rock ridges (Bronte et al. 1995; Schram et al. 1995). Age-0 lake trout move to the Michigan Island nursery area from the spawning habitat at Gull Island Shoal (Bronte et al. 1995).

Model Structure

An age-structured population model was built for the lake trout population in Wisconsin waters of Lake Superior to simulate future population status (Nieland 2006). The simulation model was modified to assess sustainability of the lake trout population with and without the refuge (Figure 3). The simulation model was parameterized using statistical catch-at-age (SCAA) model estimates for wild lake trout populations outside the refuge in eastern Wisconsin waters of Lake Superior during 1980–2012. The SCAA model was used to estimate recreational and commercial fishery harvest, abundance-at-age, age-specific mortality, year-specific mortality, gear selectivity, catchability, and assessment catch per unit effort (CPUE) for age-4-and-older lake trout during 1980–2001 (Linton et al. 2007). The Wisconsin Department of Natural Resources (WDNR) subsequently updated the SCAA model through 2012. Median abundance, probability of collapse, and time to extinction were used to evaluate sustainability of the lake trout population subjected to a range of fishing mortality rates. The model was used to simulate probability distributions of population metrics over a range of size-selective total annual mortality rates that mimicked presence and

absence of the lake trout refuge as a control on fishing mortality. The model included two stocks, one that was subjected to fishing and one that was protected from fishing.

Initial abundance N_{ij} at age j for year $i=0$ for the simulation model was derived from age-specific wild lake trout abundance estimates from the SCAA model for 2012. The SCAA model estimates abundance for non-refuge waters only, so a refuge sub-model was created using area-weighted CPUE data. First, I determined the non-refuge area of WI2 and the area of the Gull Island Shoal refuge. Next, I multiplied CPUE estimates from refuge and non-refuge waters by the surface area covering refuge and non-refuge waters to produce an area-weighted CPUE. Next, I divided area-weighted CPUE estimates for the refuge by area-weighted CPUE estimates for non-refuge waters and then multiplied the ratio by the SCAA model estimate of non-refuge abundance for age 7+ lake trout in each year to estimate the refuge abundance of age 7+ lake trout. Last, I used age-frequency of the abundance estimate of age 7+ lake trout to estimate abundance of lake trout from age 0 to age 30. Age-specific abundance estimates for 2012 were used to predict abundance at age in the next year:

$$N_{i+1,j+1} = N_{ij}e^{-Z_{ij}};$$

where $N_{i+1,j+1}$ is the number of lake trout surviving in each age class j and year i to the next age class $j+1$ and year $i+1$, N_{ij} is the number of lake trout in age class j in year i , and Z_{ij} is the total instantaneous mortality rate for each age class j in year i (Quinn and Deriso 1999; Haddon 2001; Figure 3). The total instantaneous mortality rate Z_{ij} for each age class j and year i was the sum of total instantaneous natural mortality rate M ($M = 0.181843$) previously estimated as a constant over all ages and years in the SCAA model, instantaneous sea lamprey mortality rate M_{Lij} for age class j in year i , and total instantaneous fishing mortality rate F_{ij} for age class j in year i :

$$Z_{ij} = M + M_{Lij} + F_{ij}.$$

Instantaneous sea lamprey mortality M_{Lij} of age class j in year i was modeled as a simple random variable based on the mean and standard deviation of fully-selected sea lamprey mortality estimated from the SCAA model during 1980–2012, estimated from wounding rates:

$$M_{Lij} = s_j b_0 + \varepsilon$$

where s_j is the relative selectivity of sea lamprey mortality for each age class j derived from the average of the ratios of sea lamprey mortality rate on each age class to the fully selected sea lamprey mortality rate on age 15-and-older lake trout from the SCAA model during 1980–2012. Instantaneous sea lamprey mortality on age-15-and-older lake trout was used as the fully-selected sea lamprey mortality rate because sea lamprey selectivity increases with lake trout size to a maximum at age-15+ (Swink 1991, 2003).

The total instantaneous fishing mortality rate F_{ij} of age j lake trout in year i was separated into components for commercial F_{Cij} and recreational F_{Rij} fisheries:

$$F_{ij} = F_{Cij} + F_{Rij}.$$

For the commercial gill-net fishery, instantaneous fishing mortality F_{Cij} of age class j in year i was the product of the fully-selected instantaneous fishing mortality rate F_{Ci} in year i and the relative selectivity s_{Cj} of age class j :

$$F_{Cij} = s_{Cj} F_{Ci};$$

where s_{Ci} is the relative selectivity of large-mesh gill nets for age class j was described as a gamma function. For the recreational angling fishery, total instantaneous fishing mortality rate F_{Rij} and angling selectivity s_{Rj} were estimated similarly. Selectivity curves were

estimated within the SCAA model (J. Myers, Wisconsin Department of Natural Resources, unpublished; Figure 4).

The number of age-0 lake trout $N_{i+1,j=0}$ that recruited to the population in each year $i + 1$ was predicted from the number of adult lake trout $N_{i,j=8+}$ that spawned in the previous year i using a Ricker stock-recruitment model (Ricker 1975; Nieland et al. 2008):

$$N_{i+1,j=0} = \alpha(N_{i,j=8+})(e^{-\beta N_{i,j=8+}})e^{\varepsilon} ;$$

where α is the recruits per adult at low adult density, $N_{i,j=8+}$ is the abundance of age-8-and-older lake trout in year i , β is the instantaneous decline in the recruitment rate as parental abundance increases, and ε is the multiplicative process error. To account for parameter uncertainty, a different set of model parameters α and β were selected for each simulation from a joint posterior probability distribution of MCMC estimates, for which α was log-normally distributed with mean 2.09 and variance 0.18 (Nieland et al. 2008). Age-8 and older lake trout were used to index spawning stock density because 50% of female lake trout reach sexual maturity at age 8 (Peck and Sitar, 2000). A recruitment scalar was used for refuge and non-refuge sub-models to mimic abundance during 1980–2012. The refuge scalar was the ratio of refuge area to non-refuge area in WI2, whereas the non-refuge scalar was a constant that resulted in simulated abundance in years 51–200 that mimicked abundance during 1980–2012.

Fish can move between refuge and non-refuge waters, so I estimated the rate of movement into and out of the refuge from mark-recapture data. Fish are marked during fall spawning surveys on Gull Island Shoal and recaptures were recorded during surveys in non-refuge waters. I only accounted for fish that were marked inside the refuge and recaptured outside the refuge in WI-2 waters. First, I expanded the number of recaptured tags to the

total number of tags present outside the refuge that originated from within the refuge in the previous autumn by dividing the number of recovered tags by the total catch and then multiplying by the non-refuge abundance estimate for each year. Next, to estimate the movement rate across refuge boundaries, I divided this estimate by refuge abundance to obtain the percentage of fish that originated in the refuge but were captured outside the refuge. I repeated this for each year of the SCAA model (Figure 5). To account for uncertainty of the estimated movement rate, I simulated the population under no movement, lower 2.5-percentile movement, median movement, upper 97.5-percentile movement, maximum movement, and two times maximum movement (Table 1). To account for movement of fish from non-refuge to refuge waters, I assumed that fish moved into the refuge from non-refuge waters at the same rate for all age classes.

Simulations

A range of fishing mortality rates was tested for each fishery, to encompass the maximum sustainable total instantaneous fishing mortality rate. First, a constant fully-selected commercial fishing mortality, $F_C = 0.4$, was tested over a range of total fully-selected fishing mortality rates, $F = 0-1.8$, by varying fully-selected recreational fishing mortality F_R . Next, a constant fully-selected recreational fishing mortality, $F_R = 0.1$, was tested over a range of total fully-selected fishing mortality rates, $F = 0-1.8$, by varying fully-selected commercial fishing mortality. Last, equal levels of fully-selected commercial and recreational fishing mortality, F_C and F_R , were tested over a range of total fully-selected fishing mortality, $F = 0-1.8$. For each simulation, the total annual mortality A was calculated from the total instantaneous mortality rate Z :

$$A = 1 - e^{-Z_{ij}}.$$

Each combination of mortality and movement was simulated 1,000 times for 200 years (Nielsen et al. 2008). Simulations recorded the fishable population of lake trout, so refuge fish that moved into non-refuge waters and were thereby susceptible to fishing mortality were recorded as part of the non-refuge population. When the refuge was removed, all fish that were part of the refuge population were subjected to fishing so were added to the non-refuge population.

Median abundance, probability of collapse, and time to extinction were used to evaluate sustainability of total instantaneous fishing mortality. Median abundance was calculated as the median abundance of age 4, age 4-and-older, and age 8-and-older lake trout from year 51 to 200 for each simulation. A population was considered to go extinct in the first year when age-4-and-older abundance equaled zero. The probability of collapse was the proportion of 1,000 simulations when abundance fell below 10% of the 1980–2012 abundance for age 4-and-older and 8-and-older lake trout. The instantaneous fishing mortality that resulted in collapse was used to assess sustainability of the population for each scenario. A 95% confidence interval was calculated for the probability of collapse using the exact upper and lower 95% confidence limits for a binomial proportion (Zar 1999). The time to extinction was the median number of years until age-4-and-older lake trout abundance declined to zero. Simulations that did not result in an extinction event were assigned an extinction time of 200 years because the lake trout population was assumed to go extinct after the 200 years simulated in the model. A 95% confidence interval was calculated for the time to extinction as the 2.5-percentile and the 97.5-percentile of the time to extinction for the 1,000 simulations.

RESULTS

Age-4 lake trout were better protected against stock collapse by the refuge, regardless of the movement rate or fishing mortality, than when the refuge was removed. Median abundance of age-4 lake trout declined steadily as total instantaneous fishing mortality (F) increased, but was lowest when recreational and commercial fishing mortality were equal, next lowest when commercial fishing mortality was fixed, and highest when recreational fishing mortality was fixed (Figure 6). Without the refuge, abundance of age-4 lake trout was much higher initially than with the refuge (because all fish were vulnerable to fishing mortality), but declined more rapidly as F increased than when the refuge was retained, regardless of the fishing mortality or movement rate (Figure 6). Abundance of age-4 lake trout collapsed at much lower F when the refuge was abandoned than when the refuge was retained, regardless of the movement or fishing mortality rate, except when movement was zero (Figure 6). With the refuge, fixed recreational fishing mortality required a higher F to induce collapse than other combinations of fishing mortality (Table 2). With the refuge, as movement increased from 0 to 22%, abundance at $F = 0$ declined and the F that induced collapse peaked between movement rates of 10% and 15% (Figures 7, 8). The F that induced collapse with the refuge ranged between 0.62 and 1.73, depending on the movement rate, whereas the F that induced collapse without the refuge was 0.71 (Figure 7; Table 2).

Age 4-and-older lake trout were better protected against stock collapse by the refuge, regardless of the movement rate or fishing mortality, than when the refuge was removed. Median abundance of age 4-and-older lake trout declined steadily as F increased, but was lowest when recreational and commercial fishing mortality were equal, next lowest when commercial fishing mortality was fixed, and highest when recreational fishing mortality was

fixed (Figure 9). Without the refuge, abundance of age 4-and-older lake trout was much higher initially than with the refuge, because all fish were vulnerable to fishing mortality, but declined more rapidly as F increased than when the refuge was retained, regardless of the fishing mortality or movement rate (Figure 9). Abundance of age 4-and-older lake trout collapsed at much lower F when the refuge was abandoned than when the refuge was retained, regardless of the movement or fishing mortality rate, except when movement was zero (Figure 9). With the refuge, fixed recreational fishing mortality required a higher F to induce collapse than other combinations of fishing mortality (Table 2). With the refuge, as movement increased from 0 to 22%, abundance at $F = 0$ declined and the F that induced collapse peaked between movement rates of 10% and 15% (Figures 7, 8). The F that induced collapse with the refuge ranged between 0.62 and 1.63, depending on the movement rate, whereas the F that induced collapse without the refuge was 0.72 (Figure 7; Table 2).

Age 8-and-older lake trout were better protected against stock collapse by the refuge, regardless of the movement rate or fishing mortality, than when the refuge was abandoned. Median abundance of age 8-and-older lake trout declined steadily as F increased, but was lowest when recreational and commercial fishing mortality were equal, next lowest when commercial fishing mortality was fixed, and highest when recreational fishing mortality was fixed (Figure 10). Without the refuge, abundance of age 8-and-older lake trout was much higher initially than with the refuge (because all fish were vulnerable to fishing mortality), but declined more rapidly as F increased than when the refuge was retained, regardless of the fishing mortality or movement rate (Figure 10). Abundance of age 8-and-older lake trout collapsed at much lower F when the refuge was abandoned than when the refuge was retained, regardless of the movement or fishing mortality rate, except when movement was

zero (Figure 10). With the refuge, fixed recreational fishing mortality required a higher F to induce collapse than other combinations of fishing mortality (Table 2). With the refuge, as movement increased from 0 to 22%, abundance at $F = 0$ declined and the F that induced collapse peaked between movement rates of 12% and 17% (Figures 7, 8). The F that induced collapse with the refuge ranged between 0.62 and 1.22, depending on the movement rate, whereas the F that induced collapse without the refuge was 0.70 (Figure 7; Table 2). Age 8-and-older lake trout collapsed at lower F than either age 4 or age 4-and-older (Figure 7; Table 2).

Age 4-and-older and 8-and-older lake trout were better protected from stock collapse by the refuge, regardless of the movement rate or fishing mortality, than when the refuge was abandoned. The probability of collapse increased from 0 to 1 at higher F with the refuge than without the refuge, except when movement was zero (Figure 11). With the refuge, the probability of collapse increased from 0 to 1 at lower F for age 8-and-older lake trout than age 4-and-older lake trout, except when movement was zero, but when the refuge was abandoned, both age 8-and-older and age 4-and-older collapsed at similar F (Figure 11). With the refuge, the F that induced collapse peaked between movement rates of 10% and 15% for both age classes (Figure 11). Age 4-and-older lake trout were better protected from collapse with a fixed recreational fishing mortality when movement was intermediate (Figure 11). Without the refuge, the probability of collapse increased from 0 to 1 for both 4-and older and 8-and older lake trout at lower F and at a faster rate (Figure 11).

The refuge, when movement was above zero, kept the lake trout population from extinction within 200 years, whereas removal of the refuge resulted in extinction within 200 years (Figure 12). With the refuge, but without movement, time to extinction began to

decline below 200 years under equal levels of commercial and recreational fishing mortality when $F = 1.02$, under a constant recreational mortality when $F = 0.9$, and under a constant commercial fishing mortality when $F = 1.0$ (Figure 12). Without the refuge, time to extinction declined from 200 to 80 years as F increased from 0.78 to 1.8 with equal levels of commercial and recreational fishing mortality; from 200 to 147 years as F increased from 0.78 to 1.0 with constant commercial fishing mortality, and from 200 to 177 years as F increased from 0.86 to 1.0 with constant recreational fishing mortality (Figure 12).

DISCUSSION

The refuge was most effective at protecting age-4 lake trout that moved at intermediate rates (10–15%), like other studies that showed effectiveness of a refuge is partially attributable to movement out of the refuge, where rates too high or too low are not adequate to protect the population (Gerber et al. 2003, West et al. 2009; Lindholm et al. 1998). Further, larger areas are needed to benefit fish populations as movement increases, which may suggest that the Gull Island Shoal refuge may not be large enough to support higher movement rates tested (Gerber et al. 2003). With the refuge, age-4 lake trout collapsed when movement was zero because, as other studies have shown, providing recruitment to non-refuge waters is fundamental to success of a refuge, so without movement across refuge boundaries, the refuge is not supplementing the non-refuge population (Man et al. 1995; Lauck et al. 1998; Agardy 2000).

Age 4-and-older lake trout also remained sustainable with the refuge at increasingly higher F and were best protected at intermediate movement rates (10–15%). Refuge removal induced collapse of age 4-and-older lake trout at $F = 0.72$ under all combinations of fishing mortality, which is higher than the Lake Pend Oreille lake trout population that collapsed as F increased from 0.4 to 0.5 for gillnetting and as F increased from 0.6 to 0.7 for angling, possibly because fish were added to the population following refuge removal in my study (Hansen 2007; Hansen et al. 2010). In a previous modeling study of the same population, age 4-and-older lake trout collapsed when $F = 0.41$ – 1.40 , dependent on the mortality source, whereas my results showed that mortality source did not greatly affect collapse, likely because selectivity curves for commercial and recreational fisheries were much more similar in my model than in the earlier model used by Nieland et al. (2008).

Age 8-and-older lake trout were sustainable with the refuge, but fixed recreational fishing mortality induced collapse at higher F than other combinations of fishing mortality, which suggests that age 8-and-older lake trout were less susceptible to varying levels of commercial fishing mortality than varying levels of recreational fishing mortality, unlike other lake trout modeling studies in Wisconsin waters of Lake Superior (Nielsen et al. 2008) and Lake Pend Oreille (Hansen et al. 2010). In a previous study of the same population, 8-and-older lake trout declined more when recreational fishing mortality was held constant and commercial mortality was varied (Nielsen et al. 2008). Similarly, lake trout in Lake Pend Oreille were suppressed more effectively by gillnetting than angling (Hansen et al. 2010). With the refuge, I found that age 8-and-older lake trout collapsed at lower fishing mortality rates, for all movement rates, than age-4 or age 4-and-older, which suggests that age 8-and-older lake trout are more susceptible to fishing mortality than younger age classes, like a previous study that showed age 8-and-older lake trout declined at lower fishing mortality rates than age 4-and older lake trout, although the refuge was not included in the earlier study (Nielsen et al. 2008). Without the refuge, I found that all age groups (age-4, age-4-and-older, and age-8-and-older) collapsed at similar fishing mortality rates, unlike the earlier study (Nielsen et al. 2008), likely because selectivity curves in my model were more similar than selectivity curves in the model used by Nielsen et al. (2008).

Presence of the refuge protected age 4-and-older and 8-and-older lake trout from collapse at higher F than refuge removal, but collapse was induced for age 8-and-older lake trout at lower F , which suggests spawning-age fish are more susceptible to fishing mortality than younger fish, like an earlier study that showed age 8-and-older lake trout declined at lower F than younger lake trout (Nielsen et al. 2008). I found that the refuge was best at

protecting fish that moved at intermediate rates (10–15%), like other studies that showed high movement rates are suboptimal, because as movement increases, the ability of a refuge to protect stocks from collapse generally decreases, but when movement is low, yield per recruit is low because fish rarely move out of the refuge to be captured (DeMartini 1993; Gerber et al. 2003; West et al. 2009). Removal of a refuge results in a population that is unable to sustain high levels of fishing mortality, thereby making the population more vulnerable to collapse, as in a study of several species of large predatory coral reef fish, where density was monitored following application and removal of no-take marine reserves, and all species declined significantly when reserve protection was removed (Russ and Alcala 2003).

I found that the refuge protected the lake trout population from extinction within 200 years under all simulated fishing mortality rates, except when no movement occurred, like an earlier simulation of the effects of a reserve on the Mediterranean hake *Merluccius merluccius* that demonstrated a marine reserve provided resilience because extinction was predicted at a much higher rate when a reserve was in place (Apostolaki et al. 2002). Spillover increases fishery yields to allow a refuge to buffer against extinction from fishing mortality, so when I simulated no movement the lake trout population responded similarly to abandonment of the refuge (Gerber et al. 2003, Russ and Alcala 1996, McClanahan and Mangi 2000). I found that time to extinction declined below 200 years when the refuge was removed at $F = 0.78$ – 0.86 , which was higher than a previous study where time to extinction for lake trout in WI2 fell below 200 at $F = 0.38$ for commercial fishing mortality and $F = 0.49$ for recreational fishing mortality, although the earlier model did not account for a refuge (Nielsen 2006). I found that removal of the refuge caused extinction at lower fishing

mortality rates than retention of the refuge, like in other studies where extinction risk from fishing was high, a refuge provides recruits to overfished areas that promotes a sustainable level of catch (Gerber et al. 2003; Man et al. 1995).

MANAGEMENT IMPLICATIONS

My findings will aid fishery management in Wisconsin waters of Lake Superior in two ways. First, I found that retention of the refuge would likely prevent stock collapse over an extraordinarily large range of fishing mortality, regardless of the mix of commercial and recreational fisheries, which would thereby afford fishery managers with a tool for sustaining the lake trout stock regardless of their choice of fishery allocation. In contrast, if the refuge is abandoned, fishery managers will need to reduce the fishing mortality rate below current levels, through harvest quotas or allowable fishing effort, to sustain the population. The Gull Island Shoal would protect the lake trout population from collapse, regardless of such fishery management actions, as has been found for other fisheries (Quinn et al. 1993; Wallace 1998; Neubert 2003; Russ and Alcala 2003). Second, I found that the refuge afforded optimal protection at movement rates that were near the upper limit of the distribution of rates estimated from mark-recapture, which assures fishery managers that the Gull Island Shoal refuge is appropriately sized for the plausible range of movement rates between refuge and non-refuge portions of the management zone (WI2). Importantly, as the density of lake trout within the refuge increases toward carrying capacity of the area, the movement rate of fish would likely increase from refuge to non-refuge waters, thereby subjecting more fish to fishery exploitation. The Gull Island Refuge is sized appropriately for such higher movement rates.

REFERENCES

- Agardy, T. 2000. Information needs for marine protected areas: scientific and societal. *Bulletin of Marine Science* 66:875–888.
- Alcala, A. C., G. R. Russ, A. P. Maypa, and H. P. Calumpong. 2005. A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. *Canadian Journal of Fisheries and Aquatic Science* 62:98–108.
- Allen, M. S., and J. E. Hightower. 2010. Fish population dynamics: mortality, growth and recruitment. Pages 43–79 *in* Hubert, W.A. and M.C. Quist, editors. *Inland fisheries management in North America*, third edition. American Fisheries Society, Bethesda, Maryland.
- Apostolaki, P., E. J. Milner-Gulland, M. K. McAllister, and G. P. Kirkwood. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. *Canadian Journal of Fisheries and Aquatic Science* 59:405–415.
- Bronte, C. R., S. T. Schram, J. H. Selgeby, and B. L. Swanson. 1995. Density-independent survival of wild lake trout in the Apostle Islands area of Lake Superior. *Journal of Great Lakes Research* 21 (Supplement 1):246–252.
- Buckland, S.T., K. B. Newman, C. Fernandez, L. Thomas, and J. Harwood. 2007. Embedding population dynamics models in inference. *Statistical Science* 22:44–58.
- Carr, M. H., and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Science* 50:2019–2027.

- Corradin, L.M., M. J. Hansen, D. R. Schreiner, and M. Seider. 2008. Recruitment dynamics of lake trout in western Lake Superior during 1980–1995. *North American Journal of Fisheries Management* 28:663–677.
- DeMartini, E. E. 1993. Modeling the potential for fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* 91:414–427.
- Ford, A. 1999. *Modeling the Environment: An Introduction to System Dynamics Modeling of Environmental Systems*. Island Press, Washington, DC.
- Fournier, D., and C.P. Archibald. 1982. A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1195–1207.
- Gerber, L.R., L.W. Botsford, A. Hastings, H.P. Possingham, S.D. Gaines, S.R. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecological Applications* 13:47–64.
- Getz, W. M. 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology* 77:2014–2026.
- Goodier, J. L. 1989. Fishermen and their trade on Canadian Lake Superior: one hundred years. *Inland Seas* 45:284–306.
- Habermann, R., S. Moen, and E. Stykel. 2012. *Superior Facts*. Minnesota Sea Grant, Publication S25, Duluth, MN.
- Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Chapman and Hall, London.
- Hall, C. A. S., and J. W. Day, Jr. 1977. Systems and models: terms and basic principles. Pages 5–36 in C. A. S. Hall and J. W. Day, Jr., editors. *Ecosystem modeling in*

- theory and practice: an introduction with case histories. John Wiley & Sons, New York.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13(Supplement 1):S117–S137.
- Hansen, M. J. 2007. Predator-prey dynamics in Lake Pend Oreille. Idaho Department of Fish and Game Report 07–53, Boise, Idaho.
- Hansen, M. J., D. Schill, and J. Fredericks. 2010. Salmonid predator-prey dynamics in Lake Pend Oreille, Idaho, USA. *Hydrobiologia* 650: 85–100.
- Hansen, M. J., J. W. Peck, R. G. Schorfhaar, J. H. Selgeby, D. R. Schreiner, S. T. Schram, B. L. Swanson, W. R. MacCallum, M. K. Burnham-Curtis, G. L. Curtis, J. W. Heinrich, and R. J. Young. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. *Journal of Great Lakes Research* 21(Supplement 1):152–175.
- Hansen, M. J., M. P. Ebener, R. G. Schorfhaar, S. T. Schram, D. R. Schreiner, and J. H. Selgeby. 1994. Declining survival of lake trout stocked during 1963–1986 in U.S. Waters of Lake Superior. *North American Journal of Fisheries Management* 14:395–402.
- Hansen, M. J., M. P. Ebener, R. G. Schorfhaar, S. T. Schram, D. R. Schreiner, J. H. Selgeby, and W.W. Taylor. 1996. Causes of declining survival of lake trout stocked in U.S. Waters of Lake Superior in 1963–1986. *Transactions of the American Fisheries Society* 125:831–843.

- Healey, M. C. 1978. The dynamics of exploited lake trout populations and implications for management. *Journal of Wildlife Management* 42:307–328.
- Hile, R., P. H. Eschmeyer, and G. F. Lunger. 1951. Status of the lake trout fishery in Lake Superior. *Transactions of the American Fisheries Society* 80:278–312.
- Johnson, B. L. 1995. Applying computer simulation models as learning tools in fishery management. *North American Journal of Fisheries Management* 15:736–747.
- Kapuscinski, K. L., M. J. Hansen, and S. T. Schram. 2005. Movement of lake trout in U.S. waters of Lake Superior, 1973–2001. *North American Journal of Fisheries Management* 25:696–708.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8(Supplement 1):S72–S78.
- Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. *Journal of the Fisheries Research Board of Canada* 29:765–776.
- Lawrie, A. H., and J. F. Rahrer. 1973. Lake Superior: a case history of the lake and its fisheries. Great Lakes Fishery Commission, Technical Report 19, Ann Arbor, Michigan.
- Lindholm, J., M. Ruth, L. Kaufman, and P. Auster. 1998. A modeling approach to the design of marine refugia for fishery management. Pages 138–150 in N. W. P. Munro and J. H. M. Willison, editors. *Linking protected areas with working landscapes*. Science and Management of Protected Areas Association, Wolfville, Nova Scotia, Canada.

- Linton, B. C. 2002. Population dynamics of a recovering lake trout population in Wisconsin waters of Lake Superior, 1980–2001. Master's thesis. University of Wisconsin – Stevens Point.
- Linton, B. C., M. J. Hansen, S. T. Schram, and S. P. Sitar. 2007. Dynamics of a recovering lake trout population in Eastern Wisconsin Waters of Lake Superior, 1980–2001. *North American Journal of Fisheries Management* 27:940–954.
- Man, A., R. Law, and N. V. C. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biological Conservation* 71:197–204.
- McClanahan, T. R., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* 10:1792–1805.
- Neubert, M. G. 2003. Marine reserves and optimal harvesting. *Ecology Letters* 6:843–849.
- Nieland, J. L. 2006. Modeling the sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior. Master's thesis. University of Wisconsin – Stevens Point.
- Nieland, J. L., M. J. Hansen, M. J. Seider, and J. J. Deroba. 2008. Modeling the sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior. *Fisheries Research* 94:304–314.
- Oosterhout, G. R., and P. R. Mundy. 2001. The doomsday clock 2001: an update on the status and projected time to extinction for Snake River wild spring/summer Chinook stocks. Trout Unlimited, Portland, Oregon, USA.
- Peck, J. W., and S. P. Sitar. 2000. Lake trout assessment and management in Michigan waters of Lake Superior, 1993–97. Michigan Department of Natural Resources, Fisheries Research Report 2053, Lansing.

- Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fishery Commission, Technical Report 28, Ann Arbor, Michigan.
- Quinn II, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- Quinn, J. F., S. R. Wing, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* 33:537–550.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of the Fisheries Research Board of Canada, Ottawa, Ontario.
- Rose, K. A., and J. H. Cowan Jr. 2003. Data, models and decision in US marine fisheries management: lessons for ecologists. *Annual Review of Ecology, Evolution and Systematics* 34:127–151.
- Russ, G. R., and A. C. Alcala. 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6:947–961.
- Russ, G. R., and A. C. Alcala. 2003. Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. *Ecological Applications* 13:1553–1565.
- Schram, S. T., J. H. Selgeby, C. R. Bronte, and B. L. Swanson. 1995. Population recovery and natural recruitment of lake trout at Gull Island Shoal, Lake Superior, 1964–1992. *Journal of Great Lakes Research* 21(Supplement 1):225–232.

- Swanson, B. L., and D. V. Swedberg. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. Canadian Journal of Fisheries and Aquatic Sciences 37:2074–2080.
- Swink, W. D. 1991. Host-size selection by parasitic sea lampreys. Transactions of the American Fisheries Society 120:637–643.
- Swink, W. D. 2003. Host selection and lethality of attacks by sea lampreys (*Petromyzon marinus*) in laboratory studies. Journal of Great Lakes Research 29 (Supplement 1):307–319.
- Vano, J. A., J. C. Wildenberg, M. B. Anderson, J. K. Noel, and J. C. Sprott. 2006. Chaos in low-dimensional Lotka-Volterra models of competition. Nonlinearity 19:2391–2404.
- Wallace, S. S. 1998. Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. Conservation Biology 13:882–887.
- West, C. D., C. Dytham, D. Righton, and J.W. Pitchford. 2009. Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. ICES Journal of Marine Science 66:1919–1930.
- Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Table 1. Movement scenarios and commercial and recreational fishing mortality rates simulated for the lake trout population in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).

Movement Scenarios			Fishing Mortality Rates	
Scenario	Movement Rate	Scenario Description	Commercial	Recreational
1	0	No Movement	0.4	0.05
2	0.02119	Median Movement	0.4	0.1
3	0.09577	Upper Confidence Movement	0.4	0.2
4	0.11044	Max Movement	0.4	0.4
5	0.22088	2x Max Movement	0.4	0.6
6	0	No Refuge	0.4	1.0
			0.4	1.4
			0.2	0.1
			0.3	0.1
			0.4	0.1
			0.5	0.1
			0.6	0.1
			0.8	0.1
			1.1	0.1
			1.4	0.1
			1.7	0.1
			0.1	0.1
			0.2	0.2
			0.3	0.3
			0.4	0.4
			0.5	0.5
			0.7	0.7
			0.9	0.9

* Each scenario was simulated for each combination of fishing mortality rates.

Table 2. Instantaneous fishing mortality rates, F , that induced collapse of age-4, age 4-and-older, and 8-and-older lake trout at varying movement rates and combinations of commercial and recreational fishing mortality in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).

Movement Rate	Fishing Pressure	F		
		Age 4	Age 4+	Age 8+
0	Constant Commercial	0.647	0.648	0.623
	Constant Recreational	0.662	0.663	0.643
	Equal Commercial and Recreational	0.619	0.624	0.597
0.02119	Constant Commercial	1.261	1.261	0.946
	Constant Recreational	1.448	1.453	1.073
	Equal Commercial and Recreational	1.286	1.291	0.957
0.09577	Constant Commercial	1.734	1.642	1.2
	Constant Recreational	1.987	1.912	1.365
	Equal Commercial and Recreational	1.725	1.63	1.221
0.11044	Constant Commercial	1.634	1.549	1.181
	Constant Recreational	1.892	1.816	1.342
	Equal Commercial and Recreational	1.592	1.511	1.195
0.22088	Constant Commercial	1.28	1.248	1.077
	Constant Recreational	1.435	1.4	1.185
	Equal Commercial and Recreational	1.303	1.273	1.108
No Refuge	Constant Commercial	0.725	0.729	0.718
	Constant Recreational	0.739	0.744	0.715
	Equal Commercial and Recreational	0.71	0.716	0.7

*Initial collapse defined by abundance that reaches <10% 1980-2012 values

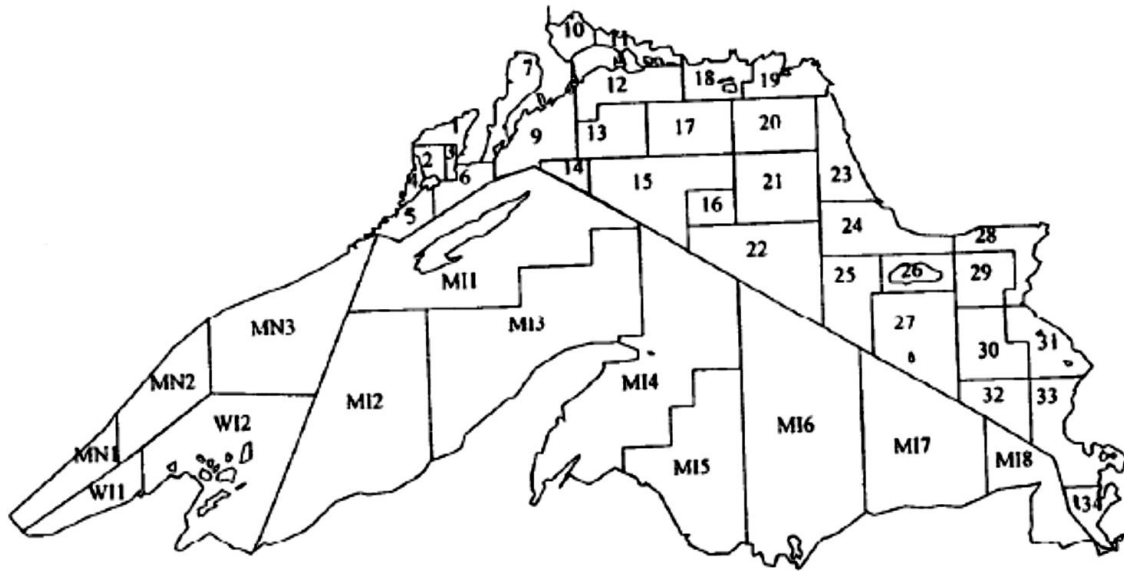


Figure 1. Lake trout management areas in Lake Superior. United States management areas are denoted by state: Michigan – MI, Minnesota – MN, and Wisconsin – WI. Canadian management areas are marked using only numbers.

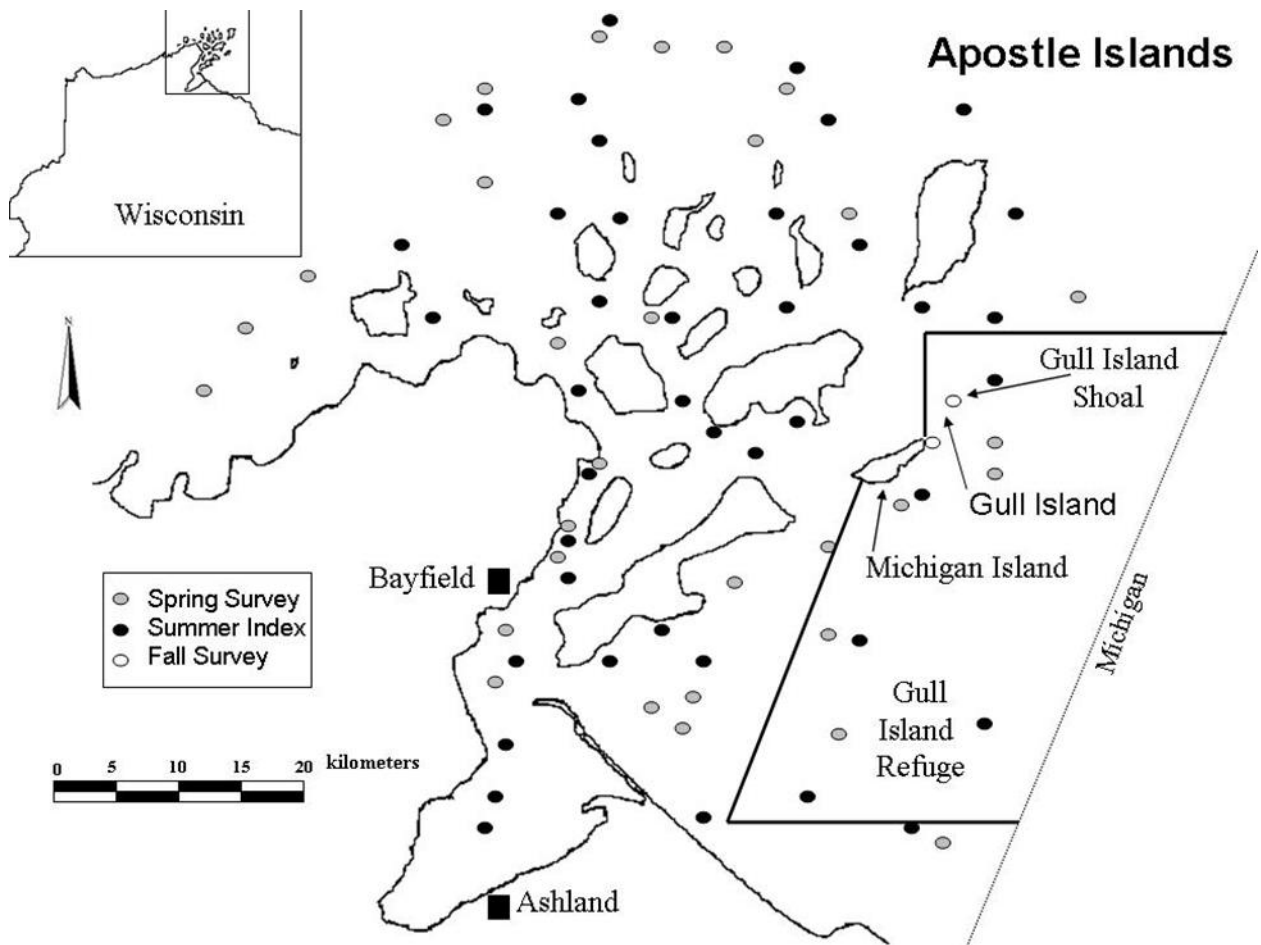


Figure 2. Location of Gull Island Shoal refuge in the Apostle Islands region of Wisconsin waters of Lake Superior.

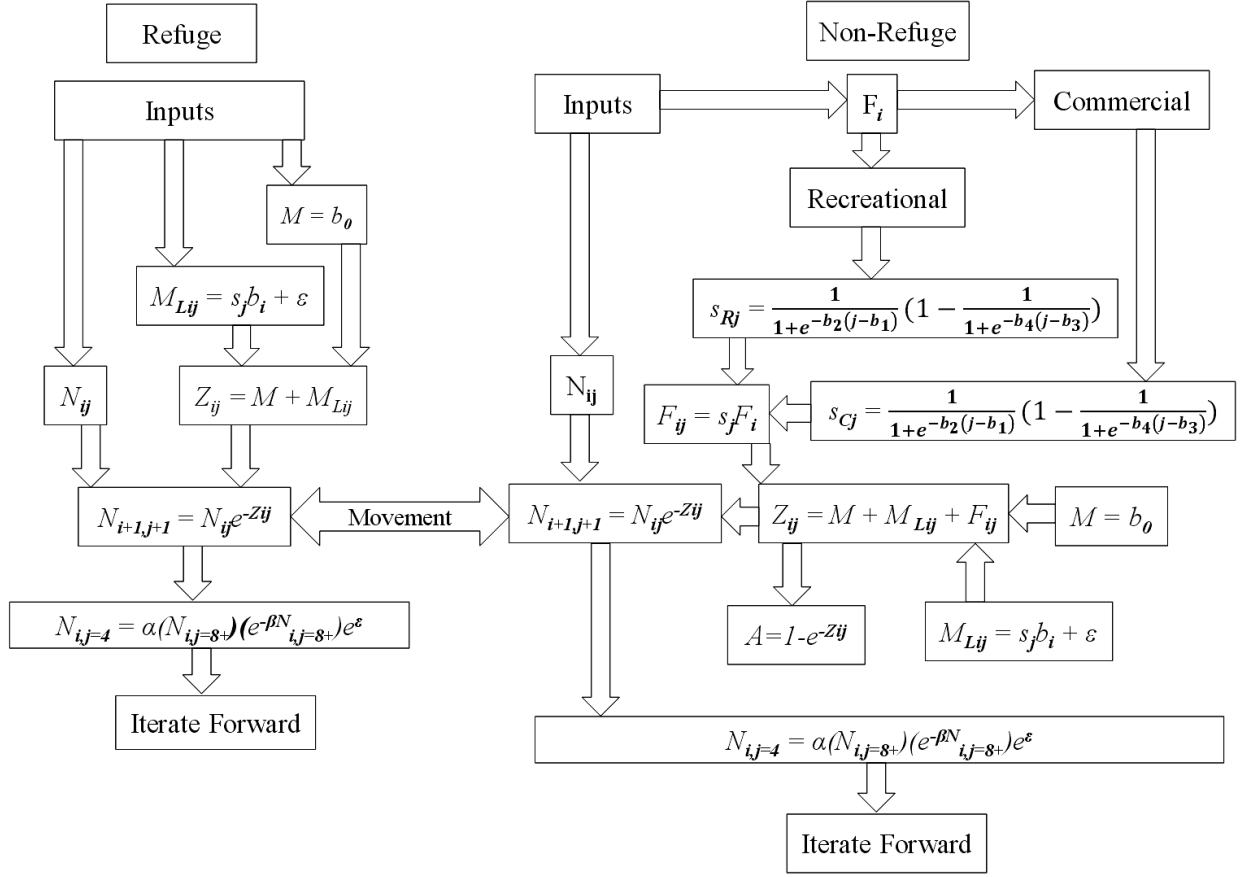


Figure 3. Schematic diagram of a model used for simulating future lake trout abundance in eastern Wisconsin waters of Lake Superior, where i = year, j = age, F_i = total instantaneous fishing mortality rate in year i , and N_{ij} = initial abundance in year i for age j .



Figure 4. Age-specific selectivity of commercial gill-net fisheries (solid line) and recreational angling fisheries (dashed line) for lake trout in eastern Wisconsin waters of Lake Superior during 1980–2012 (Wisconsin State/Tribal Technical Committee 2012).

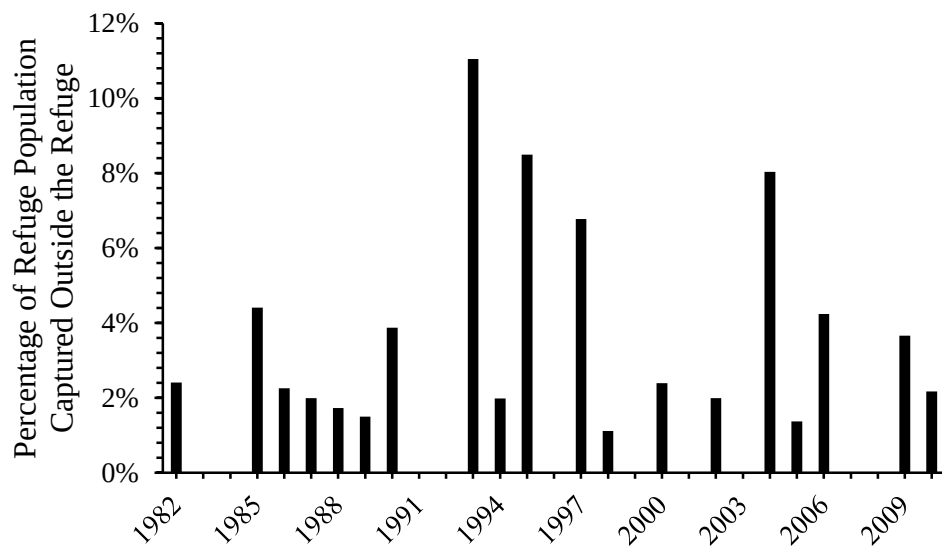


Figure 5. Movement rate (%) of lake trout from refuge to non-refuge portions of eastern Wisconsin waters of Lake Superior during 1982–2010.

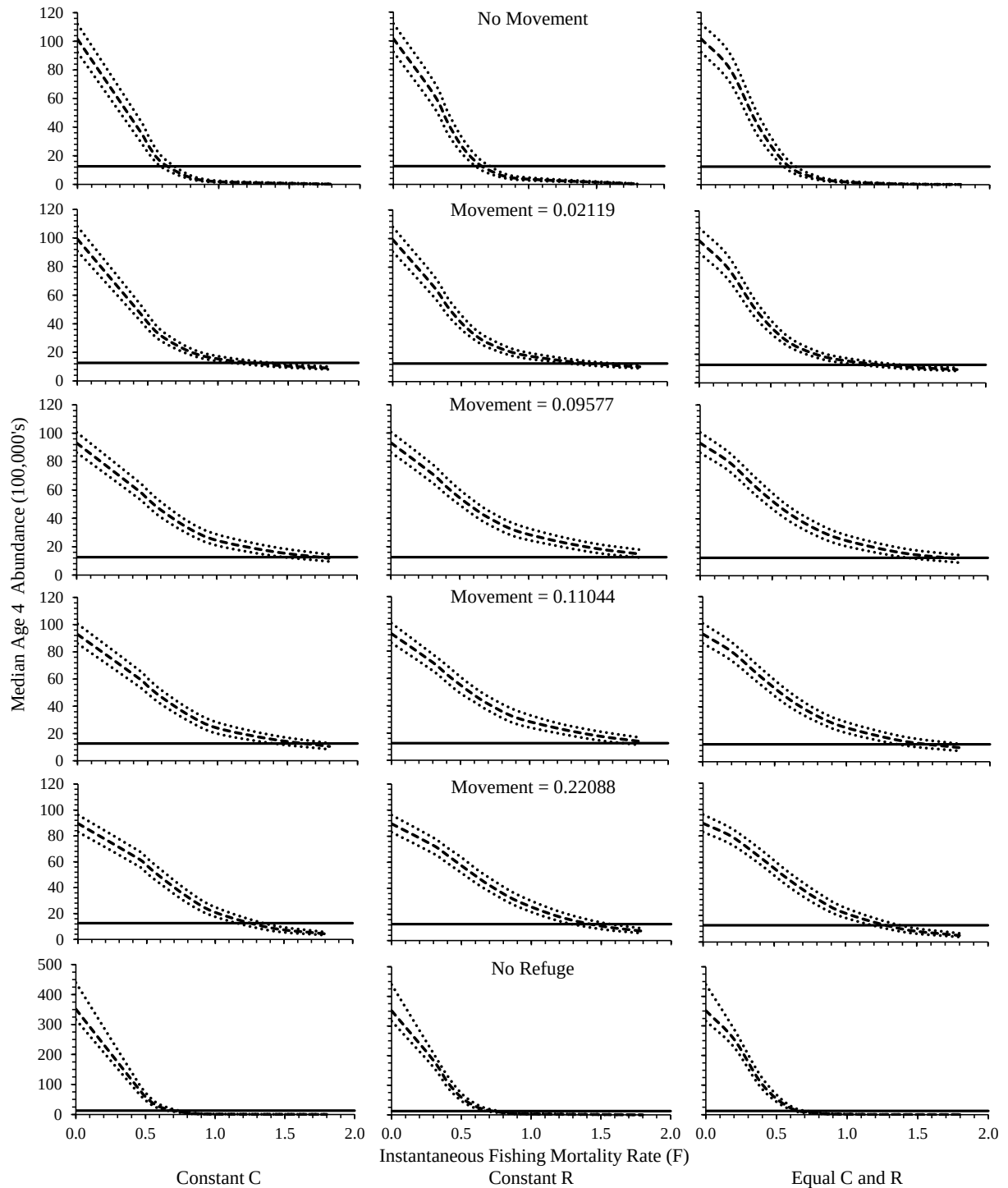


Figure 6. Median simulated abundance of age-4 lake trout ($\pm 95\%$ confidence interval) versus instantaneous fishing mortality rate, F , under varying movement rates and combinations of commercial and recreational fishing mortality in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years). The horizontal line depicts 10% of the estimated lake trout abundance during 1980–2012, as a reference for collapse.

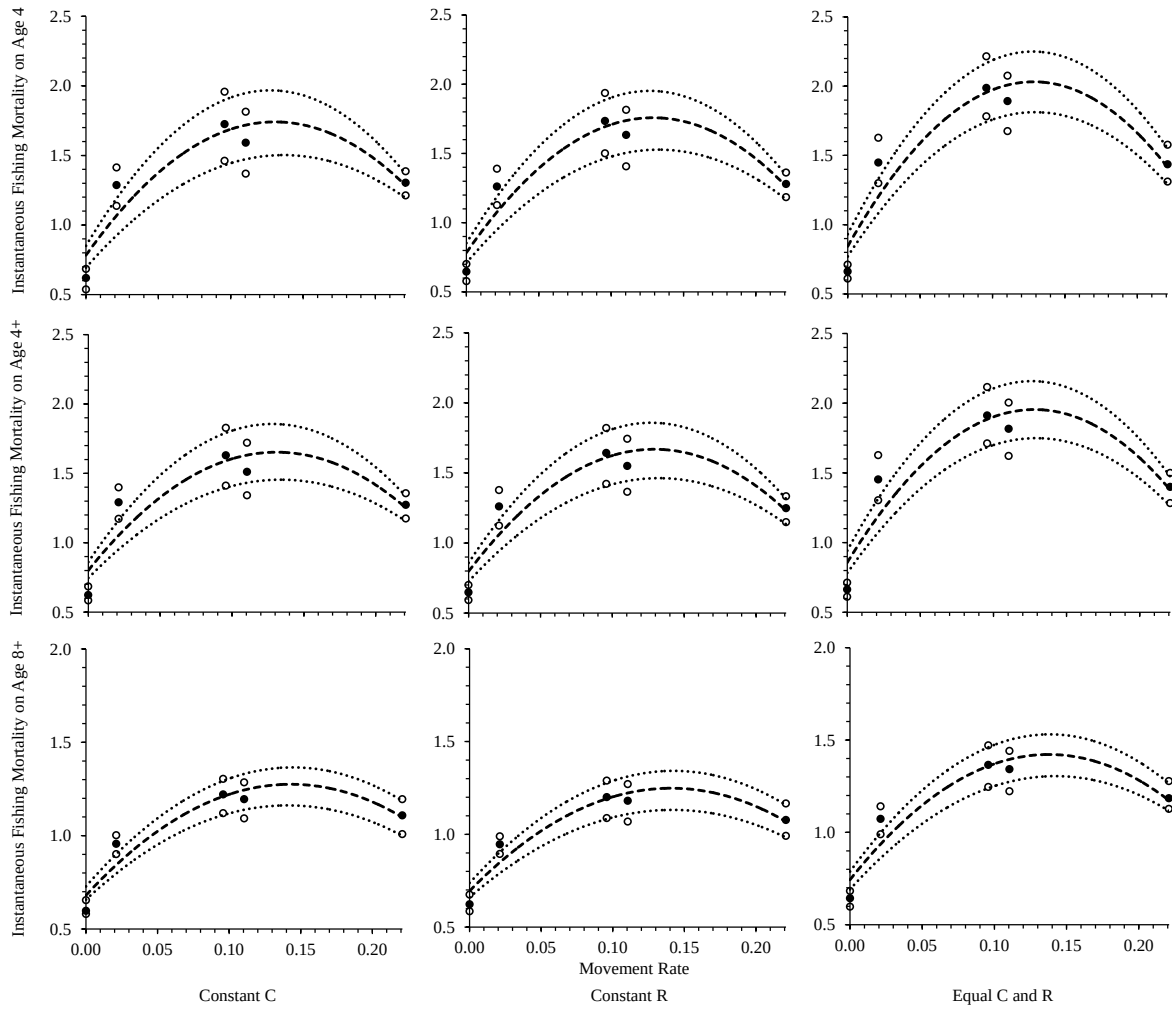


Figure 7. Instantaneous fishing mortality, F , at collapse, $<10\%$ of 1980–2012 abundance ($\pm 95\%$ confidence limits), versus movement rate under varying combinations of fishing mortality for age-4, age 4-and-older, and age 8-and-older lake trout in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).

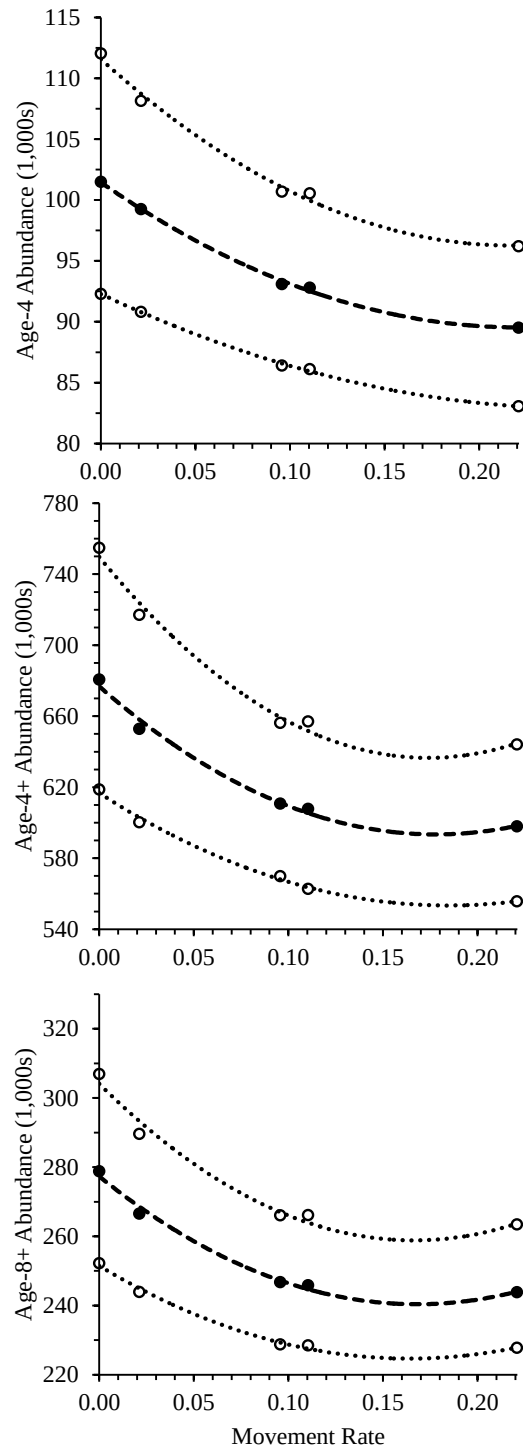


Figure 8. Abundance at $F=0$ versus movement rate for age 4, 4-and-older and 8-and-older lake trout in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).

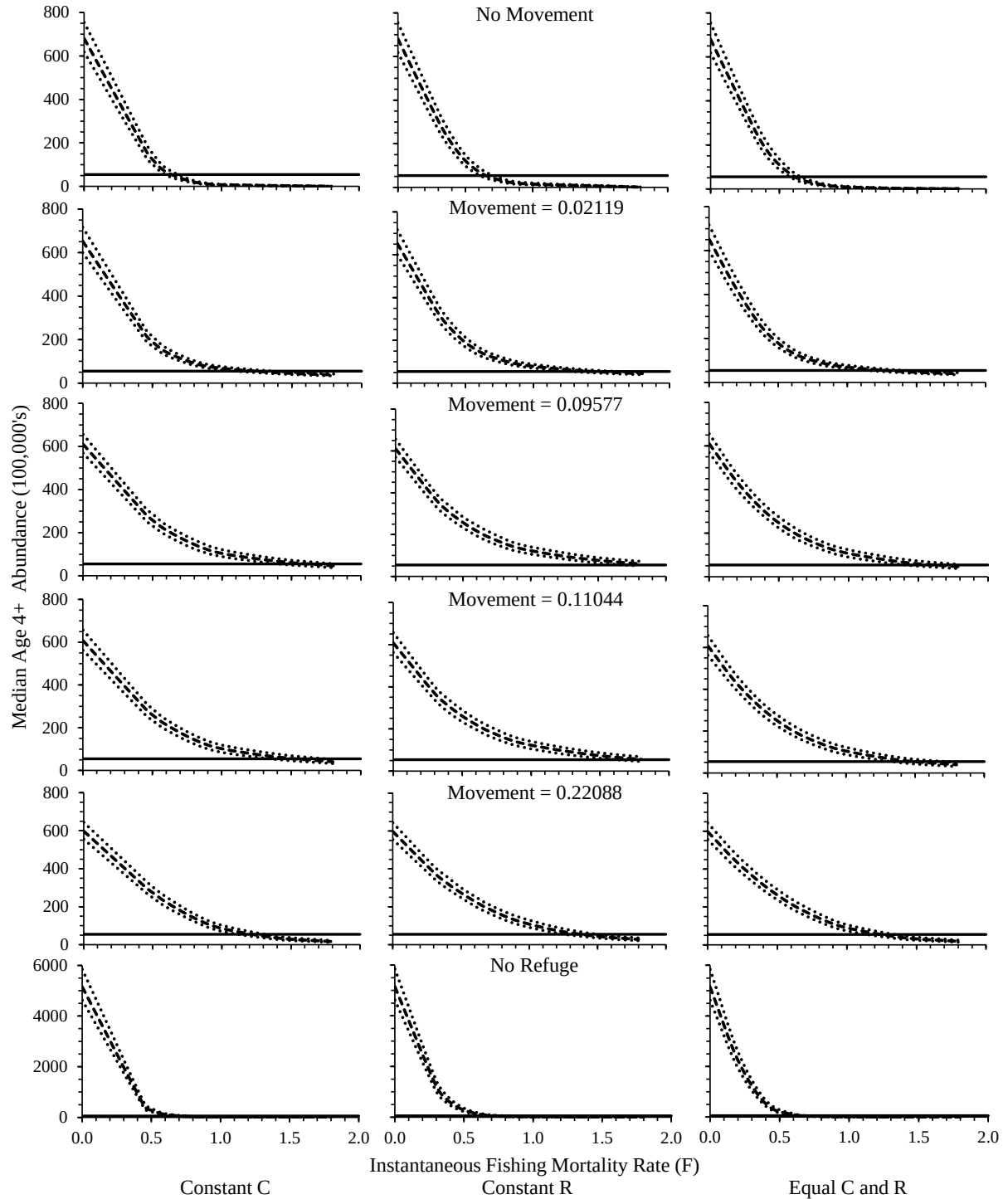


Figure 9. Median simulated abundance of age 4-and-older lake trout ($\pm 95\%$ confidence interval) versus instantaneous fishing mortality rate, F , under varying movement rates and combinations of commercial and recreational fishing mortality in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years). The horizontal line depicts 10% of the estimated lake trout abundance during 1980-2012, as a reference for collapse.

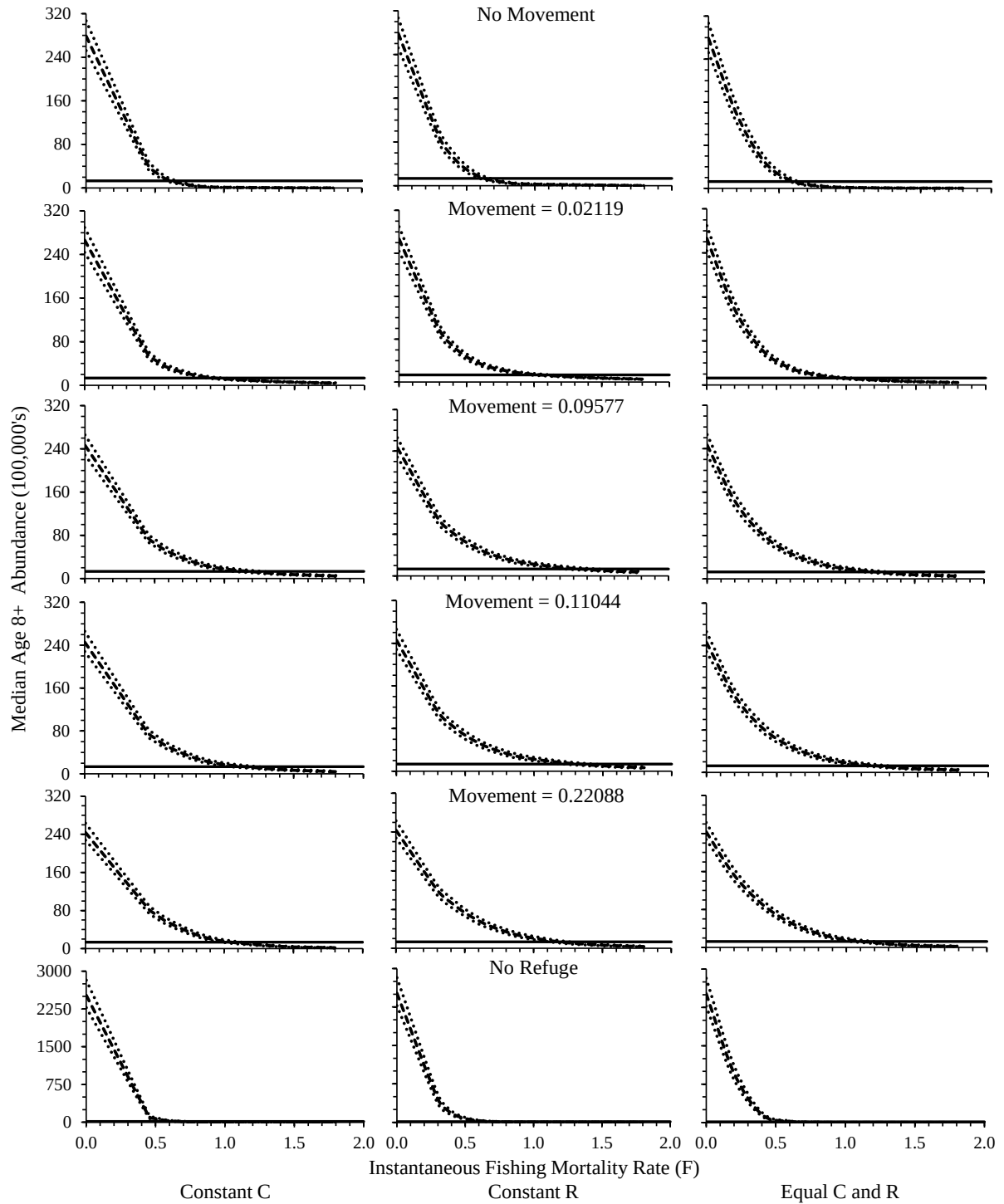


Figure 10. Median simulated abundance of age 8-and-older lake trout ($\pm 95\%$ confidence interval) versus instantaneous fishing mortality rate, F , under varying movement rates and combinations of commercial and recreational fishing mortality in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years). The horizontal line depicts 10% of the estimated lake trout abundance during 1980-2012, as a reference for collapse.

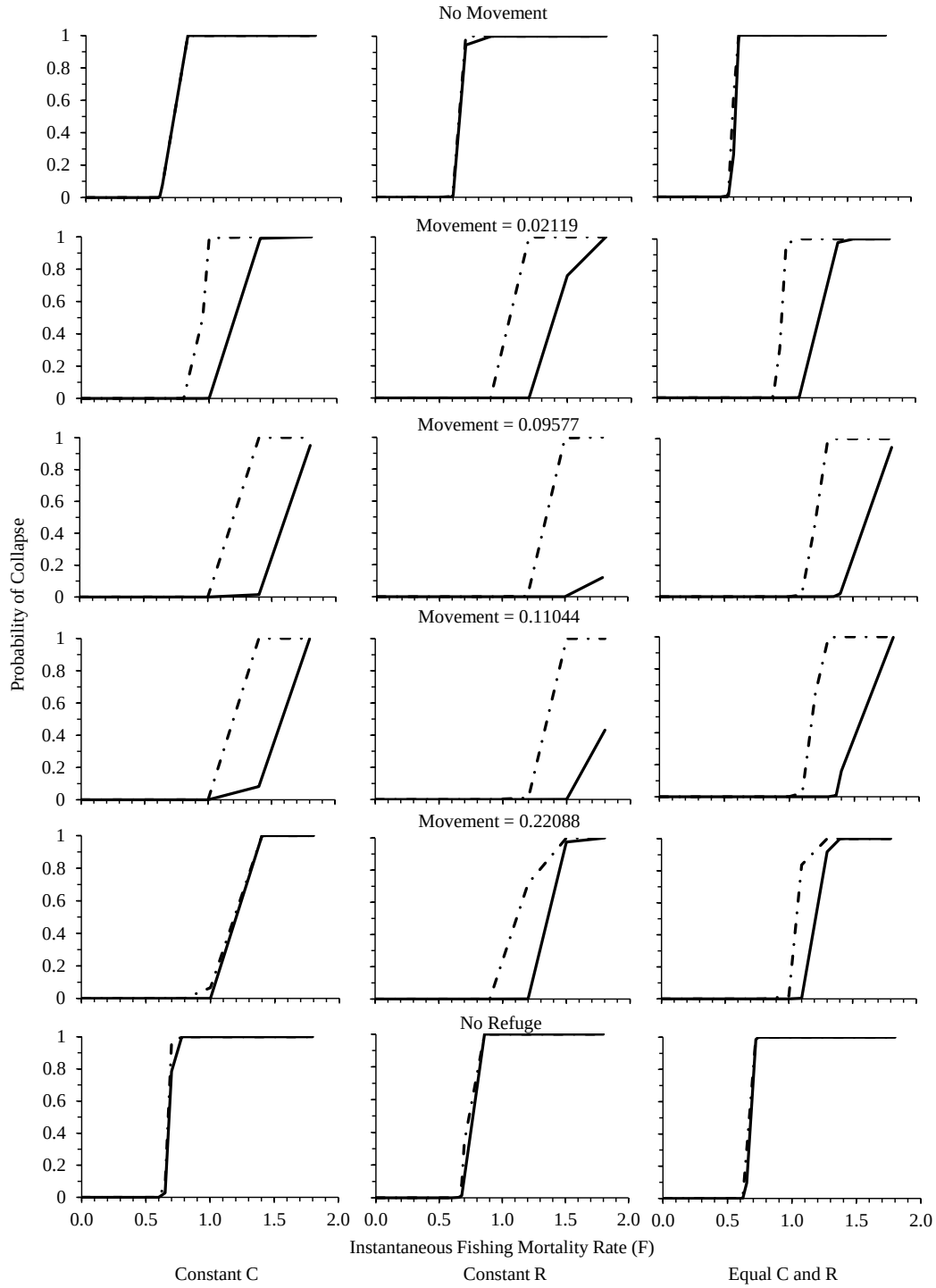


Figure 11. Probability of collapse versus the instantaneous fishing mortality rate, F , of age 4-and-older (solid line) and age 8-and-older (dashed line) lake trout under varying movement rates and combinations of fishing mortality for the lake trout population in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).

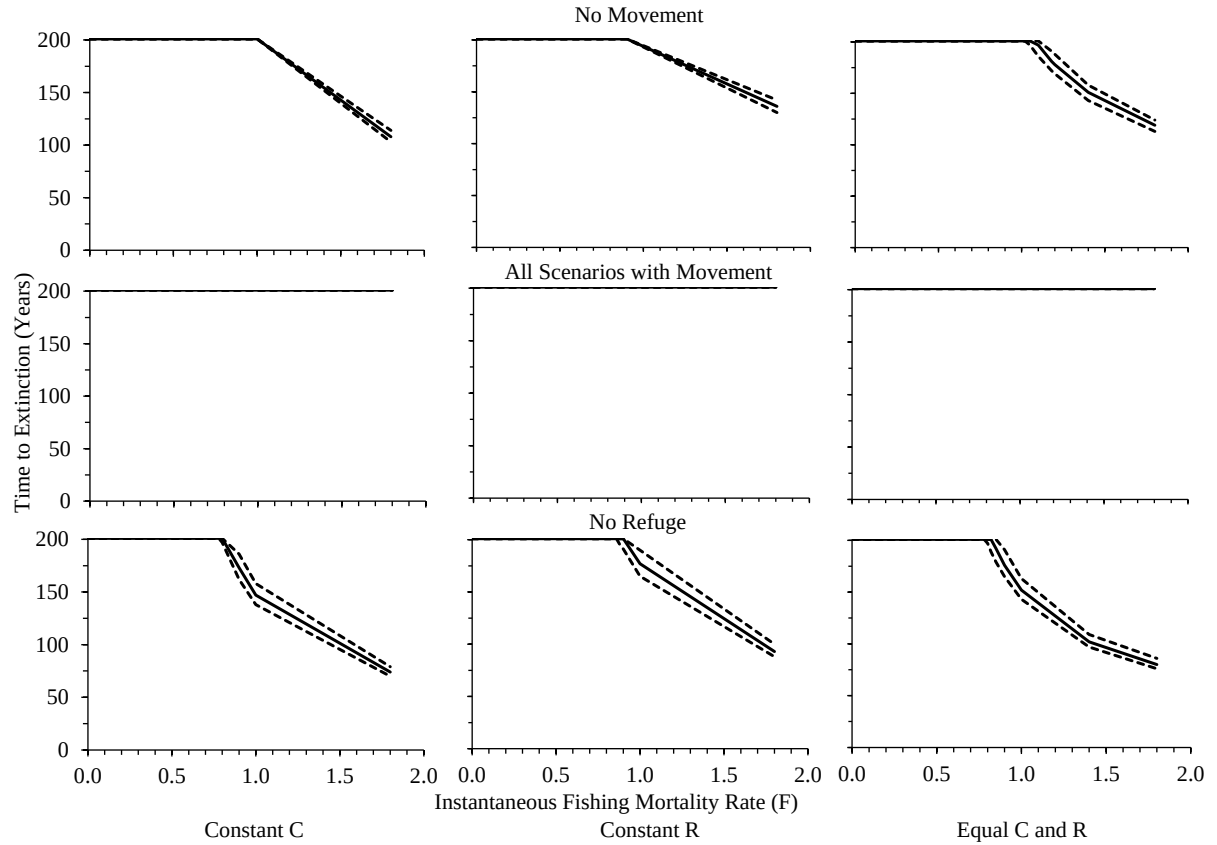


Figure 12. Time to extinction ($\pm 95\%$ confidence interval) versus instantaneous fishing mortality rate, F , under varying movement rates and combinations of fishing mortality for the lake trout population in eastern Wisconsin waters of Lake Superior (iterations = 1,000; time = 200 years).