

**Effect of Movement on Lake-Wide Sustainability of Lake Trout Stocks in Lake Superior**

by

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## ABSTRACT

Historically, lake trout in Lake Superior supported a large fishery, but stocks collapsed in the lake in the 1950s primarily due to overexploitation and predation by the invasive sea lamprey. Stocking, sea lamprey control, and harvest control were implemented to facilitate stock recovery. Following recovery of lake trout stocks in Lake Superior, agencies developed statistical-catch-at-age (SCAA) models to set harvest quotas for limiting fishing mortality. Stock assessment models were developed for individual lake trout management units and movement among units is assumed negligible. Recent studies have shown that lake trout move among management units. Therefore, I developed a simulation metapopulation model which coupled previously estimated abundance, mortality, and recruitment from SCAA models and movement rates to evaluate future sustainability of lake trout stocks. I simulated two movement scenarios (with and without movement) under varying total instantaneous fishing mortality rates in Apostle Islands region of Lake Superior, to estimate the response of lake trout abundance. I found that movement of lake trout among stocks increased abundance and sustainability of lake trout within Wisconsin waters of Lake Superior. Median abundance of age-4, age-4-and-older, and age-8-and-older lake trout was higher with movement than without movement within eastern Wisconsin waters (WI-2). Abundance in WI-2 steeply declined as fishing mortality increased in the absence of movement, but not with movement, which suggests the WI-2 management zone is functioning as a sink for lake trout in Lake Superior. Other management units in Michigan and Minnesota (MN1-WI1, MI-2, and MI-7) also functioned as sinks for age-4, age-4-and-older, and age-8-and-older lake trout. Abundance in MI-5 was higher with movement than without movement for age-4-and-older and age-8-and-older fish, but not for age-4 fish, so this management unit functioned as a sink for the first two age groups of lake trout but was neither a

source nor a sink for age-4 lake trout. Similarly, MN-2 functioned as a sink only for age-8-and-older lake trout, whereas, for age-4 and age-4-and-older lake trout, abundance did not differ with or without movement. Median abundance of age-4, age-4-and-older, and age-8-and-older lake trout was higher without movement than with movement for MN-3, so this management unit functioned as a source for all age classes of lake trout. MI-3 and MI-6 functioned as sources for age-4 and age-4-and-older lake trout, but were not sources or sinks for age-8-and-older lake trout. Median abundance for age-4, age-4-and-older, and age-8-and-older lake trout was not different with or without movement for MN-2 and MI-4. In conclusion, with movement, the lake trout population in eastern Wisconsin was protected from extinction even at high levels of fishing mortality. Without movement, the lake trout population in eastern Wisconsin declined to extinction in less than 100 years. Metapopulation dynamics prevented lake trout stocks from declining in most areas, and functioned differently for younger and older lake trout in some areas. Therefore, accounting for movement in stock assessment models is recommended to better estimate dynamics of lake trout in Lake Superior.

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## INTRODUCTION

Understanding movement of animals is fundamental to managing animal populations (Lidicker and Caldwell 1982). Movement refers to any change in the location of individuals in a population along both spatial and temporal scales (Quinn and Deriso 1999, Turchin 1998). Animal movements are primarily associated with food availability and finding suitable habitat while avoiding mortality (McCormick et al. 1998). Movement plays a critical role in the life history, evolution, and genetic variability in a species (Lidicker and Caldwell 1982). Movement may influence population dynamics of a species through the addition and subtraction of individuals, which alters abundance and the population growth rate of stocks. The transfer of individuals, and thus genes, among stocks alters species interactions and increases genetic variation (Lidicker and Caldwell 1982, Turchin 1998).

Understanding movements of a species lends insight into spatial and temporal habits. Although the study of understanding population dynamics has historically been more focused on temporal dynamics in fisheries, understanding spatial structure can lead to important insight into understanding fish stocks (Kerr et al. 2010). Population abundance can be strongly influenced by movement patterns, so understanding movement may be crucial to accurately estimating abundance of a population, especially of commercially exploited species (Schmalz et al. 2002). Even when extinction is not a high concern, migration commonly affects population dynamics (Hanski 1999). Even low levels of movement can lead to significant gene flow and allow a population to be more resilient against ecosystem change (Wright et al. 2006; Rennie et al. 2008). Knowledge of spawning and nursery habitat of animals can be important in identifying critical habitat for a species, providing further insight into predicting movement patterns (Landsman et al. 2011).

Finding suitable habitat is a primary driver of animal movement. The source-sink concept of population dynamics argues that differences in habitat quality results in differences in birth and death rates among populations or subpopulations (Andreasen et al. 2012; Pulliam 1988). Sink populations are defined by areas in which reproduction within the population is too low to balance local mortality rates (Pulliam 1988). Sink populations may be maintained by immigration of animals from source populations, which are more productive than sink populations (Pulliam 1988). This is known as the “rescue effect” (Gotelli 1991). Source-sink dynamics can have important implications in exploited populations if unexploited source stocks are supplementing the sink stocks (Robinson et al. 2008). Metapopulation theory can also be relevant to fisheries management as understanding population dynamics on a wide scale can lead to understanding and predicting the dynamics of subdivided populations (McCullough 1996). Metapopulations can be broadly defined as referring to any population that has spatial structure and they commonly consist of subdivided populations connected through migration or movement among individuals (Hanski 1999). The metapopulation concept can thus be applied to populations that are arbitrarily divided into spatial units (Hanski 1999).

In the Laurentian Great Lakes, modeling population abundance for management has a long history, but incorporating movement into these models is a recent development. Walleye *Sander vitreus* are an economically and recreationally valuable species throughout North America and a top predator in Great Lakes cool-water food webs (Haas et al. 1988). In Lake Erie, the production of walleye is the largest of the Great Lakes. Lake Erie’s three distinct basins vary in depth, temperature, and productivity and thus influence spatial distribution and abundance of walleye (Schertzer 1999; Wang et al. 2007). Several genetically distinct stocks of walleye in Lake Erie varied in movement patterns based on basin (location and habitat), sex,

spawning stocks, and prey abundance (Wang et al. 2007). The findings of this study also suggested that migratory walleye from one stock were supporting commercial and recreational harvest of walleye in other stocks (Wang et al. 2007). Similarly, smallmouth bass *Micropterus dolomieu* move greater distances in larger ecosystems such as the Great Lakes, display site fidelity, and occupy different thermal regimes before spawning than after spawning (Kaemingk et al. 2011). In Lake Michigan, smallmouth bass movement is heavily influenced by location, spawning season, and sex of the fish (Kaemingk et al. 2011). Migration rates of smallmouth bass in northern Lake Michigan may be higher than once thought, thus indicating a possible need for these fish to be considered one management unit rather than several distinct units (Kaemingk et al. 2011). Lake whitefish *Coregonus clupeaformis* are an economically valuable species throughout the Great Lakes region, leading management to be focused on protecting individual spawning stocks (Ebener et al. 2008; Ebener et al. 2010). A mark-recapture study of four major whitefish stocks in Lake Michigan suggested that movement and distribution of lake whitefish differed significantly among those four stocks (Ebener et al 2010). These findings resulted in the conclusion that the current management boundaries for lake whitefish in Lake Michigan were too small (Ebener et al. 2010).

In the Great Lakes, lake trout *Salvelinus namaycush* are an ecologically and economically valuable species (Lawrie and Rahrer 1972). Lake trout are a native apex predator that historically dominated the coldwater fish community (Hansen et al. 1995). Lake trout evolved to fill multiple ecological niches by differentiating into multiple morphotypes and forming discrete spawning stocks throughout the Great Lakes region (Moore and Bronte 2001; Krueger and Ihssen 1995). Although many morphotypes once existed in the Great Lakes, only four remain due to high fishing pressure. These four are the lean lake trout, the siscowet lake trout, the

humper lake trout, and the redbfin (Muir et al. 2014). Both the siscowet and the humper are only found in the deeper waters of Lake Superior (Moore and Bronte 2001; Krueger and Ihssen 1995). Lean lake trout have the lowest body fat content of the three morphotypes, are slender with straight snouts, and typically inhabit depths of 70 meters or less. Siscowet, or “fat” lake trout, have the highest body fat content with blunt snouts and inhabit depths of 5–150 meters (Moore and Bronte 2001.) Humper lake trout have an intermediate body fat content, have deep bodies with blunt snouts, and typically inhabit isolated shoals 50 meters deep surrounded by water greater than 100 meters in depth (Krueger and Ihssen 1995; Taylor and Ferreri 2002).

Lean lake trout have been a highly targeted species since the 1700s. As Europeans began to settle the region in the early 1800s, lake trout became part of large commercial and recreational fisheries that began in Lake Ontario and Lake Erie and rapidly expanded to the upper Great Lakes as fisheries stocks were depleted (Lawrie and Rahrer 1972; Goodier 1989). Due to their great size, populations of the Great Lakes fishes were thought to be inexhaustible, so settlements spread and fisheries developed with little consideration of human impact (Hansen et al. 1995). Commercial fisheries rapidly expanded through the process of fishing up, whereby fishing effort is directed to previously unexploited grounds as other areas are depleted (Goodier 1989). Even as abundance declined due to fishing pressure, yield continued to increase due to increased effort and improved technology (Hile et al. 1951; Pycha and King 1975). Steam-powered fishing tugs allowed for further travel, as fisheries expanded from local, inshore fishing grounds to offshore grounds. Steam-powered gill net lifters, nylon gill nets, and motor boats increased efficiency of harvest (Pycha and King 1975).

Populations strained by exploitation were further threatened by sea lamprey *Petromyzon marinus* predation (Coble et al. 1990). The sea lamprey first entered Lake Ontario through the

Erie Canal, fully invaded by 1835, but only accessed the Great Lakes in the 1940s through the Welland Canal (Lawrie 1970). The sea lamprey was first found in Lake Erie in 1921, Lake Huron in 1937, Lake Michigan in 1936, and Lake Superior in 1946 (Pearce et al. 1980). Although lake trout stocks began to decline in Lake Superior before the onset of sea lamprey predation, a combination of overfishing, sea lamprey predation, and habitat degradation from settlements ultimately led to the collapse of stocks across the Great Lakes by 1950 (Sakagawa and Pycha 1971; Hansen et al. 1995). By the early 1960s, spawning activity had ceased at most traditional spawning grounds except for Gull Island Shoal in Lake Superior (Swanson and Swedberg 1980; Schram et al. 1995).

The collapse of lake trout stocks prompted fishery managers in the Great Lakes region to preserve and restore remaining stocks before they were completely eradicated. The Lake Superior Technical Committee, comprised of fishery researchers and managers from management agencies around the lake, was formed to develop rehabilitation goals and management strategies (Hansen 1996; Linton et al. 2007). Early rehabilitation efforts focused primarily on the use of stocking to increase recruitment, chemical treatment of rivers to control sea lamprey populations, and restrictions on fishery harvest (Hansen et al. 1995). In 1962, fisheries were completely closed to harvest to allow for rehabilitation. Stocks gradually began to recover, but when the fishery was re-opened harvest continued to rise in some areas until stocks once again began to decline (Linton et al. 2007). Stocking was ceased in most areas of Lake Superior as populations became self-sustainable. As management shifted towards limiting fishing mortality, harvest quotas were developed and fish refuges were formed in Lake Superior to protect spawning stocks and young fish (Linton et al. 2007).

The stock assessment models used to set harvest quotas evolved over time, and agencies began using statistical catch-at-age (SCAA) models to determine if total annual mortality rates were sustainable (Fournier and Archibald 1982). These SCAA models assumed that immigration and emigration rates among stocks were equal (or negligible) and thus could be ignored; this is a major assumption of all stock-based management which involves assigning spatial management units to set harvest quotas within those units (Molton et al. 2012). Lake Superior is divided into individual management units for stock assessment, each of which has been treated as a separate stock and were initially formed for the purpose of fishery catch reporting (Smith et al. 1961). Although these lake trout management units have been treated as discrete in the past, recent research has indicated the need to examine lake trout population dynamics on a larger spatial scale (Kapuscinski et al 2005). A study of movements of lake trout through the U.S. waters of Lake Huron showed that movement of lake trout was less localized than initially assumed, including a high proportion of fish that moved among statistical districts during the fishing season (Alderstein et al. 2007). Lake Superior lake trout are highly mobile while demonstrating strong homing instincts (Rahrer 1968). Lake Superior lake trout also did not move between management units at equal rates (Kapuscinski et al. 2005). Harvest quotas set based on an incorrect assumption of negligible movement may not be sustainable for these populations. In particular, lake trout populations that are low in productivity or functioning as sink stocks are at risk for overharvest (Molton et al. 2012).

My objective was to evaluate long-term sustainability of the lake trout population in Wisconsin waters of Lake Superior. To achieve my objective, I developed a multiple-population simulation model to determine the extent to which long-term sustainability of the population in Wisconsin waters was altered by movement among populations in other areas of the lake. I

simulated long-term abundance with and without movement, as a basis for understanding how movement altered long-term sustainability over a wide range of fishing mortality rates. My findings will provide Wisconsin fishery managers with guidance as to whether the current management approach is adequate for ensuring long-term protection of spawning populations of lake trout in Lake Superior while allowing sustainable harvest.

## **METHODS**

### ***Study Area***

Lake Superior has the largest surface area of all freshwater lakes (82,414 km<sup>2</sup>), the second largest volume of all freshwater lakes (11,920 km<sup>3</sup>) and contains 10% of the world's surface freshwater. Lake Superior is the deepest of the five Great Lakes (maximum depth 406m, mean depth 148m) and holds over half of the Great Lakes' water in total. Lake Superior is considered highly oligotrophic because of its great depth, low productivity, low mean temperature (6°C), low dissolved solids (60 mg/L), and low average annual fish yield (0.8kg/ha), (Matheson and Munawar 1978).

Lake Superior's waters are divided into lake trout management zones (Figure 1). This study will focus on the management units within the United States. Wisconsin's waters of Lake Superior are divided into two management zones, WI-1 and WI-2. The WI-2 management zone that includes the Apostle Islands region is characterized by shallow, rocky reefs along the shoreline of the mainland and the islands. Minnesota's waters are divided into three management zones, MN-3, MN-2, and MN-1 moving from west to east (Figure 1). These zones include confirmed inshore spawning habitat for lake trout, but little offshore habitat (Goodyear et al. 1982). Michigan's waters are divided into eight management units. MI-1 is Isle Royale and



was not included in this study. Michigan's waters contain a wide range of habitats that include inshore and offshore spawning habitat (Goodyear et al. 1982, Edsall and Kennedy 1995).

### ***Model Structure***

Sustainability of wild lake trout stocks in U.S. waters of Lake Superior was evaluated using a dynamic, age-structured simulation model. The simulation model included sub-population models for individual stocks (one for each management area) that were integrated into a meta-population model through estimated movement rates among management areas.

Each sub-population model was parameterized from SCAA model estimates for wild lake trout in each management area. The SCAA model used age-specific recreational and commercial fishery harvest and fishery independent survey catch/effort to estimate abundance-at-age, age- and year-specific mortality, age-specific gear selectivity, and year-specific catchability for age-4-and-older lake trout during 1980–2001 (Linton et al. 2007). The model was adapted and updated through at least 2010 for each management area. A SCAA model was not developed for WI-1, so I estimated abundance in WI-1 by multiplying abundance in MN-1 times the ratio of fishery independent survey CPE in WI-1 to MN-1 during 1987-2010, and then adding abundance in the two areas together. Each sub-population model (management unit) was age-structured and parameterized using recruitment, growth, and mortality sub-models (Table 1; Figure 2).

Beginning with abundance at age  $j$  in the most recent year  $i$ , the initial abundance-at-age  $N_{ij}$  (Table 1) was used to estimate 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 and year to the next age class and year, and  $Z_{ij}$  represents the total rate of instantaneous mortality for each age class  $j$  in year  $i$ . Total instantaneous mortality was partitioned into total instantaneous natural mortality  $M$  (assumed constant over all ages and years), total instantaneous sea lamprey mortality ( $M_{Lij}$  for age class  $j$  in year  $i$ ), and total instantaneous fishing mortality ( $F_{ij}$  for age class  $j$  in year  $i$ ):

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

The instantaneous natural mortality rate was estimated using Pauly's equation (Quinn and Deriso 1999) for each lake trout management stock:

$$\text{Log}_e M = -0.0152 - 0.279 \text{log}_e L_\infty + 0.6543 \text{log}_e K + 0.4634 \text{log}_e T$$

where  $L_\infty$  is the average asymptotic length from the von Bertalanffy growth equation,  $K$  is the rate at which length approaches  $L_\infty$ , and  $T$  is the average annual temperature. Instantaneous natural mortality rate was held constant, but varied among management zones (Table 1).

Instantaneous sea lamprey mortality was estimated separately for each lake trout management zone as a simple random variable based on the mean and standard deviation of fully-selected sea lamprey mortality estimated from the SCAA model for each zone (Table 1), estimated from the average wounding rate of a lake trout of length  $l$  in year  $y$ :

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

where  $s_j$  was the relative selectivity of sea lamprey mortality for each age class  $j$  derived from the average of the ratios of sea lamprey mortality on each age class to the fully selected sea lamprey mortality rate (Table 2),  $b_0$  was the mean fully-selected sea lamprey mortality rate during the SCAA reference period, and  $\varepsilon$  was the standard deviation of the fully-selected sea lamprey mortality rate during the SCAA reference period. Instantaneous sea lamprey mortality on age-

15-and-older lake trout was estimated as the fully-selected sea lamprey mortality rate because sea lamprey mortality increases with lake trout size to a maximum at age 15-and-older (Swink 1991, 2003).

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

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

Instantaneous fishing mortality  $F_{ij}$  of age  $j$  lake trout in year  $i$  was an input in the model from selectivity curves for each fishery (Figure 3). For the commercial 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  $s_{Cj}$  was the relative selectivity of commercial gill nets for age class  $j$  estimated using a gamma or double-logistic function (Figure 3). Instantaneous recreational fishing mortality was estimated the same as instantaneous commercial fishing mortality.

The number of recruits was predicted using a Ricker stock-recruitment model (Ricker 1975) with parameter uncertainty and process error:

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

Where  $N_{i,j=0}$  is the number of age-0 lake trout to enter into the population in year  $i$ ,  $\alpha$  is the number of recruits produced by spawning lake trout at low abundance,  $N_{i,j=8+}$  is the abundance of age-8-and-older lake trout in year  $i$ ,  $\beta$  is the decline in recruitment as parental abundance increases, and  $\varepsilon$  is the multiplicative process error. The Ricker stock-recruit equation used for

this model was based on eastern waters of Lake Superior (Nieland et al. 2008). A recruitment scalar for each management zone was used to scale recruitment in the simulation model to a level that reproduced average abundance in each area during the SCAA reference period (Tables 1–2). Recruitment scalars were calculated by minimizing differences across all management units between median abundance between estimated year-specific abundance from SCAA models and simulated abundance in years 51–200 of the simulation model.

Each sub-population was integrated into a meta-population model using estimates of lake trout movement rates among management areas previously estimated through mark-recapture (Kapusinski et al. 2005). For movement rates among management areas not previously estimated, an average rate of movement between adjacent zones was used (Table 3).

### *Simulations*

Median abundance, probability of extinction, and time to extinction were used to evaluate sustainability over a range of total instantaneous fishing mortality rates (Table 4). Fishing mortality rates were only varied in WI-2 and were held constant at the base rate for other management units to test the effect of varying fishing mortality rates in WI-2 on the rest of the lake, with and without movement among management units. Median abundance of age-4, age-4-and-older, and age-8-and-older lake trout was computed from year 51 to year 200 for 1,000 simulations of the model. Reporting of results began with year 51 to allow for a burn-in period to allow stabilization of the model. Confidence limits were computed as the 2.5-and 97.5-percentiles of 1,000 simulations in the model. The probability of extinction was calculated as the proportion of 1,000 simulations where abundance fell below 10% of abundance estimates from the SCAA period. A 95% confidence interval was calculated for the probability of extinction using the upper and lower 95% confidence limits for a binomial proportion (Zar 1999). Time to

extinction was calculated as the median number of years until age-4-and-older lake trout abundance declined to zero. 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

Median abundance of age-4 lake trout in WI-2 was higher with movement than without movement, and abundance declined steeply as fishing mortality increased to  $F = 0.5$  in the absence of movement, but not with movement (Figure 4). Median age-4 lake trout abundance was lower with movement than without movement in MN-3, MI-3, and MI-6, so these zones were sources of lake trout for other zones. Median age-4 lake trout abundance was higher with movement than without movement in MN1-WI1, MI-2, and MI-7, so these zones were sinks for lake trout from other zones, and would have few lake trout without movement from other zones. Median age-4 lake trout abundance in management zones MN2, MI-4, and MI-5 was not greatly affected by movement, so these zones were neither sources nor sinks for other zones (Figure 4).

Median abundance of age-4-and-older lake trout in WI-2 was higher with movement than without movement, and abundance declined steeply as fishing mortality increased to  $F = 0.5$  in the absence of movement, but not with movement. Median age-4-and-older lake trout abundance was lower with movement than without movement in MN-3, MI-3, and MI-6, suggesting these zones were sources of lake trout for other zones. Median age-4-and-older lake trout abundance was higher with movement than without movement in MN1-WI1, MI-2, MI-5, and MI-7, so these zones were sinks for lake trout from other zones, and would have few lake trout without movement from other zones. Median age-4-and-older lake trout abundance in management zones MN2 and MI4 was not greatly affected by movement, so these zones were neither sources nor sinks for other zones (Figure 5).

Median abundance of age-8-and-older lake trout in WI-2 was higher with movement than without movement, and abundance declined steeply as fishing mortality increased to  $F = 0.5$  in the absence of movement, but not without movement. Median age-8-and-older lake trout

abundance was lower with movement than without movement in MN-3, so this zone was a source of lake trout for other zones. Median age-4-and-older lake trout abundance was higher with movement than without movement in MN-2, MN1-WI-1, MI-2, MI-5, and MI-7, so these zones were sinks for lake trout from other zones, and would have few lake trout without movement from other zones. Median age-8-and-older lake trout abundance in management zones MN2, MI3, MI4, and MI6 was not greatly affected by movement, so these zones were neither sources nor sinks for other zones (Figure 7).

Movement of lake trout among management zones prevented extinctions within 200 years across a wide range of fishing mortality rates in all U.S. management zones of Lake Superior. Without movement, time to extinction declined from 200 years to less than 100 years as fishing mortality increased above  $F = 0.6$  for the lake trout population in WI-2 (Figure 7) and MI-2, but not in any other management zone. Similarly, without movement, the probability of extinction increased from 0.00 to 1.00 as fishing mortality increased from  $F = 0.6$  to  $F = 0.7$  for the lake trout population in WI-2 and MI-2, but not in any other management zone.

## DISCUSSION

I found that abundance of lake trout in eastern Wisconsin waters of Lake Superior was higher and protected from extinction by movement from other areas of the lake, but without movement, abundance was lower and declined to extinction in less than 100 years at  $F = 0.6$ , which suggests the area may function as an ecological trap (Delibes et al. 2001; Novaro et al. 2001; Battin 2004; Robinson et al. 2008). The WI-2 management zone contains ideal habitat (the Apostle Islands), ideal spawning grounds (e.g. Gull Island Shoal), and an abundant prey base, but exploitation in this zone is high (Table 1). Therefore, this area may be functioning as an ecological trap, thereby explaining the rapid decline in lake trout abundance as fishing mortality increased. An ecological trap is traditionally defined as a habitat patch that animals prefer over superior habitats (Battin 2004). A similar concept is an “attractive sink”, defined as habitat patches of disparate mortality that would otherwise be attractive to animals because of their abundant food and habitat resources (Delibes et al. 2001; Robinson et al. 2008). When animals in a population prefer an ecological trap over more “ideal” habitats, the effect on the result of the population can be dramatic (Robinson et al. 2008). My results show a dramatic effect of increased total instantaneous fishing mortality in WI-2 on an adjacent area: when fish occupying WI-2 are harvested at high rates, not enough fish migrate to the adjacent MI-2 management zone to maintain the population in that zone. Furthermore, Minnesota management zones do not contain habitat that is any more ideal for lake trout than WI-2, so MN-3 may be acting as a source for WI-2 because of low lake trout exploitation rates in Minnesota. These results are similar to a study that found non-hunted areas acted as a source for hunted areas when those animals moved from non-hunted areas to a hunted area (Novaro et al. 2001).



I found average abundance in some units increased when movement was included in simulations, thereby suggesting the presence of sink stocks as was found in other studies of animal metapopulations (Murphy 2002; Caudill 2003; Perkins et al. 2003; Robinson et al. 2008; Andreasen et al. 2012; Peery et al. 2006). For example, movement of mountain lions between Nevada and the Sierra Nevada mountain range led to the identification of sink populations in areas of decreased movement because of low-quality habitat (Andreasen et al. 2012). Similarly, a study of Florida grasshopper sparrows identified sinks in the population based on a model (Perkins et al. 2003), and a demographic model showed that a declining population of eastern kingbird *Tyrannus tyrannus* in central New York was partly caused by populations in upland and floodplain habitats that functioned as sink habitats (Murphy 2002). Estimating rates of immigration and emigration and using them in population models led to the identification of sink populations in marbled murrelets *Brachyramphus marmoratus* in California (Peery et al. 2006). A metapopulation of mayflies *Callibaetis ferrugineus hageni* showed the presence of sink populations (Caudill 2003). A study of cougars found that hunting pressure that was not evenly distributed across a landscape in which the population interacts induced source-sink population dynamics (Robinson et al. 2008).

I found average abundance in some units decreased when movement was included in simulations, thereby suggesting the presence of source stocks as was found in other studies of animal metapopulations (Ware and Schweigert 2001; Inchausti and Weimerskirch 2002; Caudill 2003; Andreasen et al. 2012; Peery et al. 2006). For example, the same study that identified sink populations of mountain lions between Nevada and the Sierra Nevada mountain range also identified source populations (Andreasen et al. 2012). Similarly, the same study that identified sink populations for female mayflies also found sources of female mayflies in high quality ponds

(and ones that contained no predators) that supplemented the sink populations (Caudill 2003). The same study that identified sink populations in marbled murrelets also identified source populations (Peery et al. 2006). In addition, models of Pacific herring movement showed that herring that strayed (moved away from their natal population) allowed for higher persistence of less productive herring populations (Ware and Schweigert 2001). Last, a study of wandering albatross *Diomedea exulans chionoptera* found that for small to medium size populations with a large source population nearby, migration decreased the probability of a decline in abundance (Inchausti and Weimerskirch 2002).

I found that some management zones functioned as sources and sinks for different age classes of lake trout, like other studies of metapopulations (Hill et al. 2003; Perkins et al. 2003). For example, MI-3 functioned as a source for age-4 and age-4-and-older lake trout, but not for age-8-and-older lake trout, with or without movement (Perkins et al. 2003). Presence of spawning and rearing habitat could cause a particular area to function as a source of young fish, whereas old fish may be drawn to the area to forage, so the same area functions as a sink for old fish. MI-3 does contain spawning habitat for lake trout but is less productive for adult fish than other areas (Goodyear et al. 1982). Further, long-term dynamics of source-sink populations can be unclear, because source populations can vary in habitat or forage quality among years, so some populations act as a source in some years and a sink in other years, like a study of Florida grasshopper sparrows that found a site functioned as a source for 2 years of study and a sink for another year of study (Perkins et al. 2003). Local populations can act as both sources and sinks by continually moving small numbers of animals among sub-populations (Hill et al. 2002). In my study, commercial and recreational fisheries were focused less on adult fish in MI-2 and MI-3, thereby leaving younger fish to maintain the population. The only management unit that

remained a source for age-8-and-older fish was MN-3, where fishing mortality was low.

Similarly, although habitat and forage quality in WI-2 has not declined, increased fishing mortality is likely the reason why WI-2 is functioning as a sink, rather than a source, even with the presence of the Gull Island Shoal refuge.

Estimated rates of movement used in my study showed movement of lake trout typically averaging around 42 km, with movement to other management units decreasing with distance from the tagged unit (Kapusinski et al. 2005), like other studies of lake trout movement in the Laurentian Great Lakes (Smith and Van Oosten 1939; Eschmeyer et al. 1953; Swanson 1973; McCullough 1996; Schmalz et al. 2002). For example, tagged lake trout in Lake Michigan dispersed 57–68 km, with 74% of lake trout tagged in fall and 73% of lake trout tagged in spring recaptured in the same location where they were tagged (Schmalz et al. 2002). Similarly, 77% of lake trout tagged in western Lake Michigan were caught within 80 km of the tagging location (Smith and Van Oosten 1939) and 90% of lake trout tagged in the Apostle Islands region were caught within 50 km of the tagging location (Eschmeyer et al. 1953). I found that WI-2 was likely acting as a source of fish for MI-2, like a previous study of lake trout movement that found one of three fish tagged on spawning grounds in Wisconsin migrated to Michigan (Swanson 1973). Low movement buffers populations against extinction and population crashes (McCullough 1996). Further, conditions necessary for persistence of metapopulations include (1) breeding populations that occur in discrete habitat patches, (2) local population dynamics that do not cause simultaneous extinction of all local populations, and (3) movement rates that would not facilitate the population to function as one (Kerr et al. 2010). In other words, sub-populations are separated by distances that species are capable of traveling, but do not usually do so (McCullough 1996).

## MANAGEMENT IMPLICATIONS

My findings suggest that movement should be taken into account in assessment models because lake trout stocks are not isolated from each other, thereby violating the assumption of stock-based assessment that immigration and emigration are negligible (Goethel et al. 2011; Kell et al. 2009). Accounting for movement in existing models would enable more accurate estimates of sustainable harvest levels for lake trout. For example, metapopulation dynamics seem to prevent the lake trout stock in WI-2 from declining, across a very broad range of fishing mortality. In addition, relatively high fishing mortality in WI-2 seems to draw fish into the area, perhaps as a density dependent response. If fishing mortality was lower, abundant lake trout spawning habitat in WI-2 would seem likely to produce enough fish for WI-2 to serve as a source, rather than a sink. This would also result in higher abundances of lake trout in MN-3 and MI-2, as in a study of albatross that showed localized impacts of long-line fisheries shifted the source-sink relation among populations (Inchausti and Weimerskirch 2002). Migration of wandering albatross between island populations contributed to a “rescue effect” in that migrating albatross would supplement populations in which bycatch due to long-line fisheries was higher, but the potential for the “rescue effect” to take place was reduced by shifting fishery activity (Inchausti and Weimerskirch 2002).

If stock assessment models do not account for movement, overharvest in multiple management zones could lead to destabilization and eventual collapse of populations (Sweanor et al. 2001). Although fishing mortality was only varied in one management unit in my study, at least one sub-population could not sustain itself without immigration of individuals from WI-2. Grouping multiple populations into one assessment model without considering subpopulation dynamics such as recruitment can lead to underestimation of extinction risk (Kell et al. 2009).

For example, when catches from two simulated fish populations were mixed, the collapse of one population of herring was undetected (Kell et al. 2009). Although the results of my study showed, in some cases, only small differences in abundance with or without movement in some management zones, fishing mortality was low across most of the lake. If fishing mortality increases and lake trout stocks continue to be managed as if movement is negligible, the risk of extinction of sink stocks would increase and some populations that currently serve as sources may not be able to do so under higher fishing pressure. Considering spatial structure in harvest policies is important for population productivity (Wilberg et al. 2008). Furthermore, fisheries should not be managed as though effects of management are contained. For example, high fishing mortality in WI-2 affects sustainability of fish in MI-2. Therefore, accounting for movement in existing lake trout stock-assessment models would reduce extinction risk by enabling tracking of dynamics among multiple populations.

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Table 1. Age-specific abundance ( $N_j$ , for age  $j$ ), instantaneous natural mortality rate ( $M$ ), instantaneous sea lamprey mortality rate ( $M_L$ ;  $M_L$  error = SE), instantaneous fishing mortality rate ( $F$ ), and recruitment scalar for a lake trout simulation model for U.S. waters of Lake Superior.

Parameter	Management Unit									
	MN-3	MN-2	MN-1/WI-1	WI-2	MI-2	MI-3	MI-4	MI-5	MI-6	MI-7
Starting year	2011	2009	2009	2011	2010	2010	2010	2011	2011	2011
$N_0$	555,835	52,461	55,399	154,337	8,779	634,130	1,946,703	415,144	1,893,448	1,552,218
$N_1$	501,352	56,793	29,987	111,762	28,377	763,789	5,238,691	1,587,205	2,062,567	754,616
$N_2$	352,502	15,607	31,044	165,124	28,023	193,397	766,302	816,346	814,215	396,811
$N_3$	135,933	25,547	82,984	303,798	37,781	38,126	277,754	1,188,089	1,067,282	517,400
$N_4$	115,783	21,756	70,676	88,081	31,398	30,950	225,488	149,382	119,853	66,041
$N_5$	98,358	18,465	59,869	313,058	10,683	18,423	140,686	68,368	101,076	54,071
$N_6$	58,359	10,911	23,815	3,122	6,005	13,079	86,535	168,643	90,864	103,713
$N_7$	29,555	7,543	17,840	64,897	2,550	9,196	73,336	92,362	75,920	36,624
$N_8$	16,510	4,729	11,517	102,913	2,281	8,245	54,317	59,038	40,586	24,399
$N_9$	11,589	2,912	7,223	681	1,962	6,368	46,789	47,449	41,037	14,873
$N_{10}$	6,091	1,582	4,298	23,403	2,044	5,184	29,044	37,062	22,079	10,765
$N_{11}$	4,075	1,409	3,937	3,554	937	3,730	21,361	30,512	18,383	3,966
$N_{12}$	2,844	1,076	2,777	6,992	533	2,392	27,159	19,660	8,461	7,452
$N_{13}$	3,184	697	1,682	4,216	206	1,507	16,892	29,976	16,281	1,428
$N_{14}$	2,576	450	1,059	16,923	80	678	10,151	22,570	15,223	2,756
$N_{15}$	1,832	461	1,074	494	2,559	2,579	10,094	9,232	6,935	2,215
$N_{16}$	4,637	740	3,866	1,638	6,037	2,754	6,182	8,699	2,329	1,299
$N_{17}$	2,693	819	2,329	1,672	4,815	2,128	4,545	5,391	1,651	1,002
$N_{18}$	1,485	830	2,888	1,544	4,236	1,664	3,205	3,651	542	374
$N_{19}$	821	668	2,178	1,014	3,158	1,196	2,151	2,675	378	262
$N_{20}$	574	397	1,312	876	2,367	942	1,711	1,822	219	154
$N_{21}$	424	307	1,056	661	1,888	840	1,640	1,450	186	131
$N_{22}$	290	340	1,006	485	1,742	567	869	1,343	160	115
$N_{23}$	217	213	683	391	1,005	378	676	769	79	55
$N_{24}$	189	173	540	287	795	286	472	569	56	40
$N_{25}$	129	195	601	210	560	233	433	406	39	27
$N_{26}$	103	173	542	161	503	227	434	358	35	26
$N_{27}$	110	122	379	165	511	193	328	356	34	25
$N_{28}$	98	116	343	151	400	143	235	279	24	17
$N_{29}$	70	103	307	110	289	119	215	202	17	12
$N_{30}$	63	67	201	92	262	98	163	179	16	12
$M$	0.16	0.16	0.16	0.11	0.12	0.2	0.19	283,649	0.15	0.18
$ML$ mean	0.14	0.11	0.15	0.12	0.1	0.13	0.11	0.18	0.2	0.2
$ML$ error	0.038	0.031	0.04	0.068	0.067	0.086	0.048	0.072	0.09	0.095
Starting $F$	0.09	0.05	0.09	1.2	0.27	0.16	0.05	0.02	0.02	0.07
Recruitment Scalar	1.89369	0.18409	0.34664	1.05012	0.26208	0.38244	2.19819	3.48342	14.42586	29.89283

Table 2. Relative selectivity of sea lamprey mortality for a lake trout simulation model for U.S. waters of Lake Superior.

Parameter	Management Unit									
	MN-3	MN-2	MN-1/WI-1	WI-2	MI-2	MI-3	MI-4	MI-5	MI-6	MI-7
<b>Starting year</b>	<b>2011</b>	<b>2009</b>	<b>2009</b>	<b>2011</b>	<b>2010</b>	<b>2010</b>	<b>2010</b>	<b>2011</b>	<b>2011</b>	<b>2011</b>
$N_0$	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
$N_1$	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
$N_2$	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
$N_3$	0.000	0.000	0.000	0.000	0.053	0.000	0.017	0.000	0.000	0.000
$N_4$	0.001	0.002	0.004	0.005	0.081	0.001	0.027	0.004	0.015	0.018
$N_5$	0.025	0.004	0.009	0.009	0.113	0.004	0.038	0.010	0.035	0.037
$N_6$	0.036	0.018	0.041	0.014	0.096	0.010	0.049	0.019	0.060	0.061
$N_7$	0.052	0.043	0.093	0.021	0.116	0.018	0.059	0.032	0.085	0.085
$N_8$	0.051	0.054	0.110	0.019	0.132	0.028	0.069	0.046	0.108	0.106
$N_9$	0.086	0.100	0.179	0.026	0.146	0.037	0.077	0.062	0.127	0.125
$N_{10}$	0.101	0.126	0.214	0.034	0.157	0.045	0.085	0.079	0.142	0.140
$N_{11}$	0.110	0.091	0.150	0.042	0.166	0.052	0.091	0.094	0.155	0.152
$N_{12}$	0.089	0.113	0.175	0.034	0.173	0.057	0.096	0.108	0.165	0.162
$N_{13}$	0.069	0.080	0.137	0.040	0.178	0.061	0.101	0.121	0.173	0.170
$N_{14}$	0.063	0.070	0.125	0.045	0.183	0.064	0.105	0.132	0.179	0.177
$N_{15-30}$	0.107	0.151	0.209	0.045	0.183	0.064	0.105	0.132	0.179	0.177



Table 3. Parameters of a stock-recruit model used in a lake trout simulation model for U.S. waters of Lake Superior (common to all management zones). The stock-recruit model was scaled to productivity of each management zone using recruitment scalars shown in Table 1.

$$\begin{aligned}
 \mathbf{Ln}(\alpha) &= N(2.005770051, 0.305113466086763) \\
 \beta &= -2.14632796734542 \times 10^{-06} + \\
 &\quad 2.91722535110464 \times 10^{-06} * \alpha + \\
 &\quad N(0, 7.94065477011281 \times 10^{-07}) \\
 \varepsilon &= N(-1.1426583745, 0.168796352349042)
 \end{aligned}$$

Table 4. Movement rates of lake trout among management units in U.S. waters of Lake Superior 1973–2001 (modified from Kapuscinski et al. 2005).

<b>Recapture</b> Unit	<b>Tagging Unit</b>									
	MN-3	MN-2	MN-1/WI-1	WI-2	MI-2	MI-3	MI-4	MI-5	MI-6	MI-7
<b>MI-1</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>MN-3</b>	66.63	16.04	0.00	3.62	0.98	1.49	0.72	0.00	0.00	0.00
<b>MN-2</b>	8.90	66.63	6.91	2.42	0.00	0.00	0.00	0.00	0.00	0.00
<b>MN-1/WI-1</b>	1.72	8.90	80.25	34.97	1.74	7.46	0.00	0.00	0.00	0.00
<b>WI-2</b>	2.91	1.72	8.97	41.98	6.23	2.29	2.04	0.05	0.37	0.24
<b>MI-2</b>	0.32	2.91	1.36	9.64	77.66	21.91	1.05	18.65	0.26	0.37
<b>MI-3</b>	0.56	0.32	0.58	2.31	8.10	46.43	8.41	2.29	7.04	0.26
<b>MI-4</b>	0.00	0.56	0.23	4.63	1.48	6.92	63.84	21.44	1.84	7.04
<b>MI-5</b>	0.00	0.00	1.69	0.43	3.51	13.50	21.60	56.86	14.50	1.84
<b>MI-6</b>	0.00	0.00	0.00	0.00	0.30	0.00	0.96	0.54	61.20	14.50
<b>MI-7</b>	0.00	0.00	0.00	0.00	0.00	0.00	1.39	0.16	9.29	61.20
<b>Sum</b>	97	98	100	100	100	100	100	100	99	95

Table 5. Movement and total instantaneous fishing mortality rates (for WI-2 only) simulated for lake trout in U.S. waters of Lake Superior.

<b>Movement Scenarios</b>			<b>Fishing Mortality</b>
			<b>Rates</b>
<b>Scenario</b>	<b>Movement Rate</b>	<b>Scenario Description</b>	<b>Total F</b>
1	0	No Movement	0.05 - 1.4
2	variable	Observed Movement Rates	0.05 - 1.4

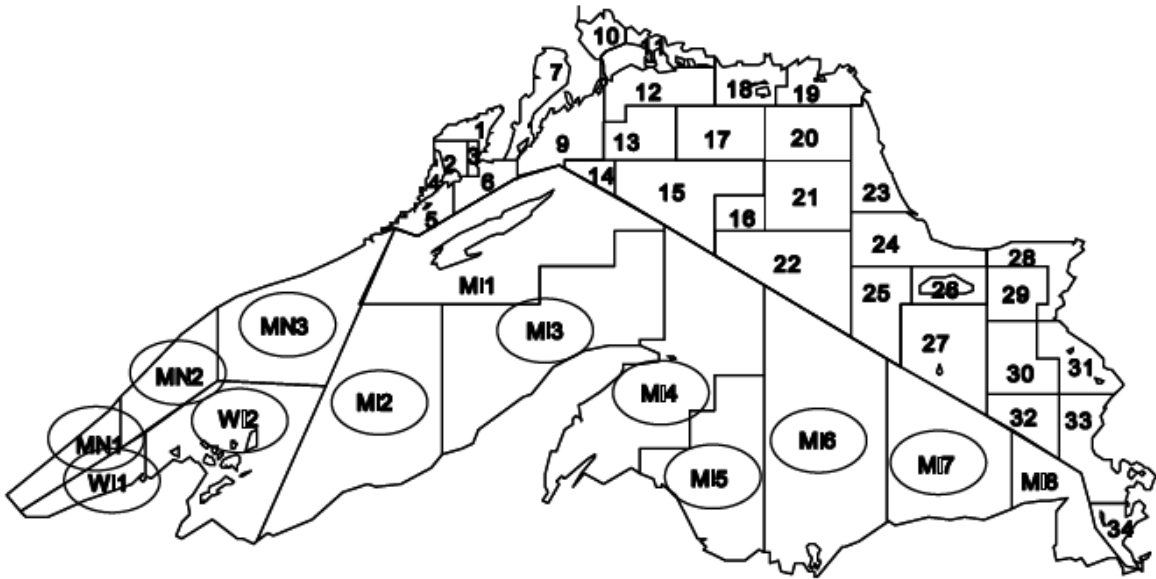


Figure 1. Lake trout management areas in Lake Superior. Jurisdictions in U.S. waters are denoted by alpha-numeric codes (MN = Minnesota; WI = Wisconsin, and MI = Michigan). Jurisdictions in Canada are denoted by numbers only. Ovals encircle the U.S. management zones for which stocks were integrated into the meta-population model.

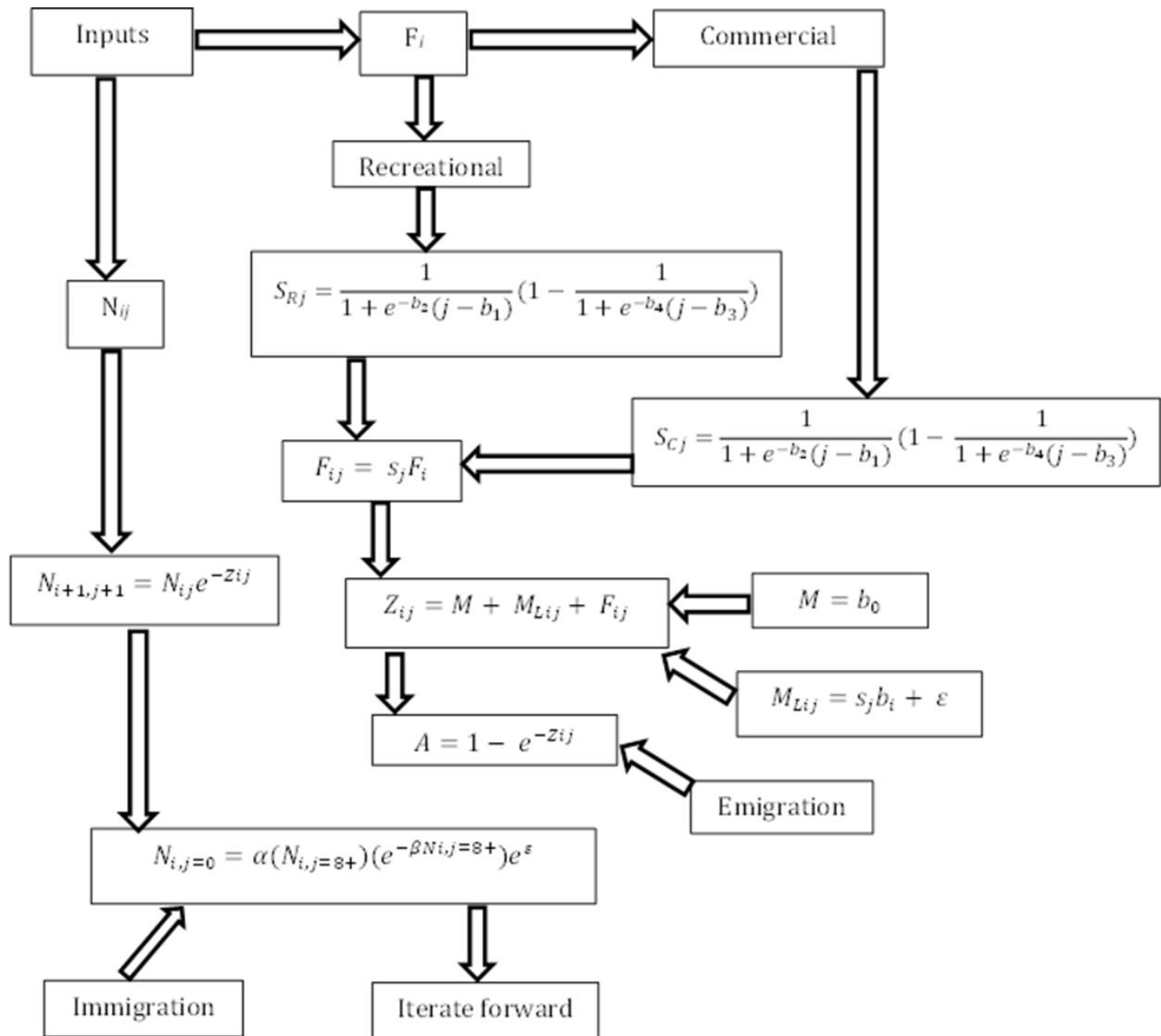


Figure 2. A schematic diagram of a simulation model for lake trout in Lake Superior, where  $i$  is year,  $j$  is age, and inputs are the total instantaneous fishing mortality rate  $F_i$  in year  $i$  and the initial abundance  $N_{ij}$  in year  $i$  for age  $j$ . In the model, each management zone in Figure 1 was linked to other management zones using immigration and emigration rates in Table 3.

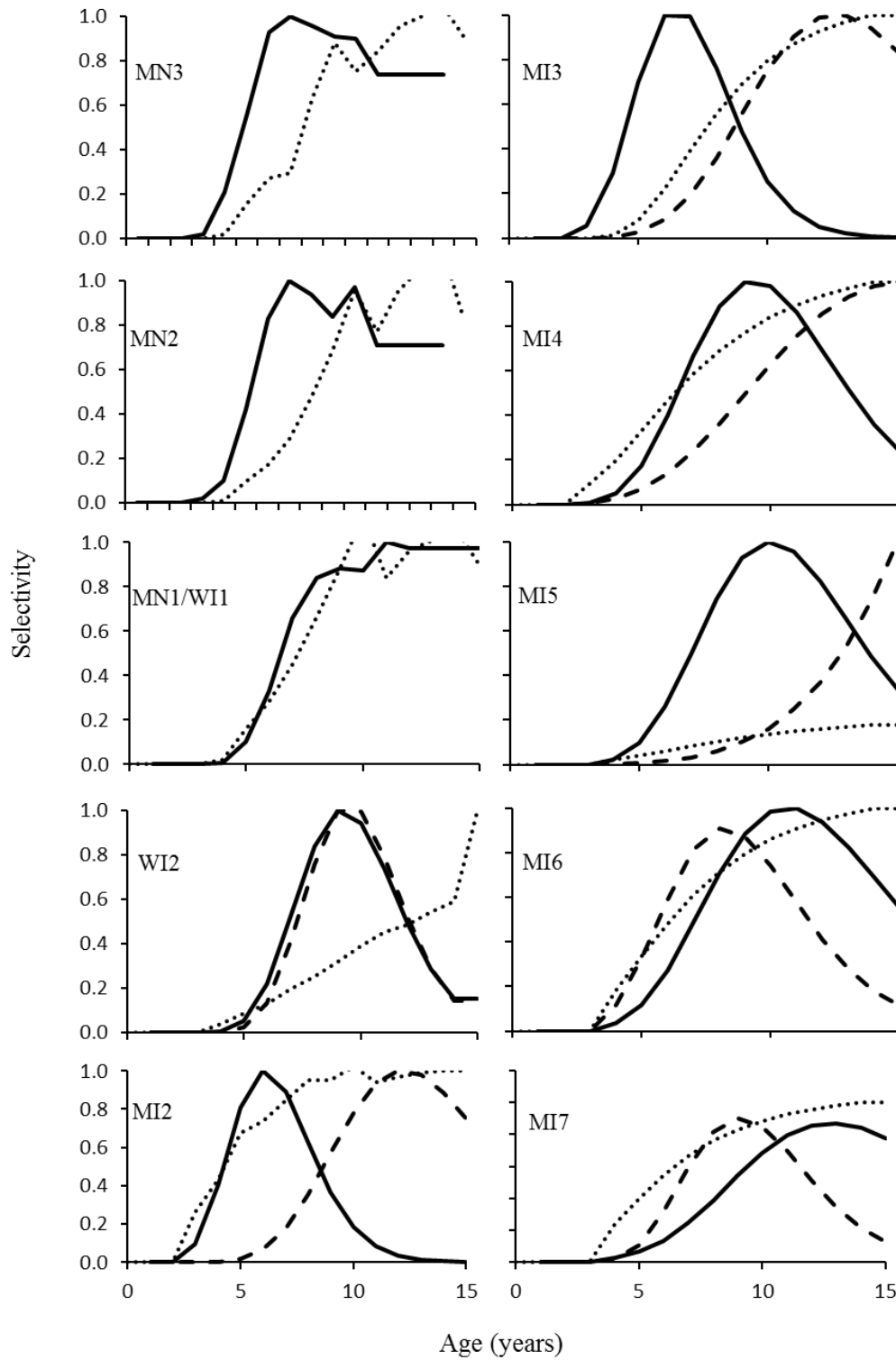


Figure 3. Age-specific selectivity of commercial gill-net fisheries (dashed lines), recreational angling fisheries (solid lines), and sea lamprey mortality (dotted lines) for lake trout in U.S. waters of Lake Superior.

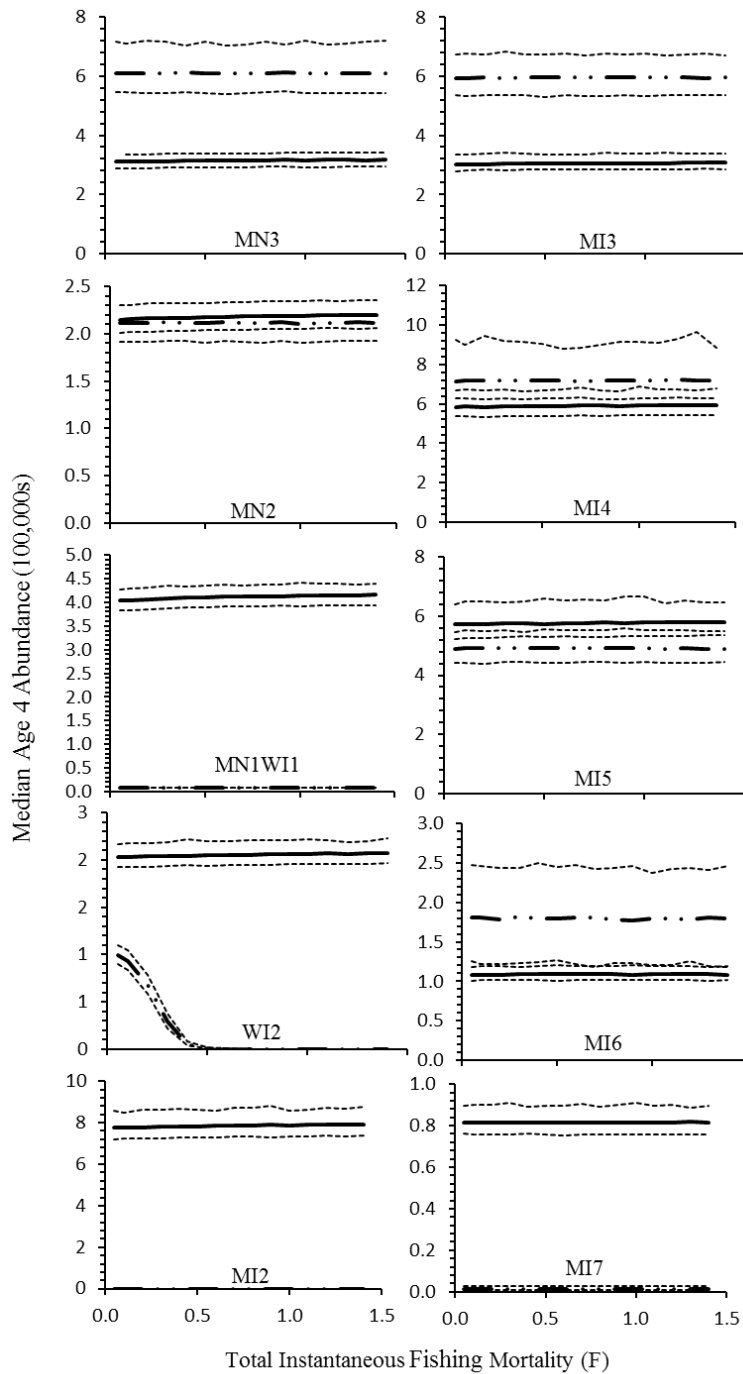


Figure 4. Median age-4 abundance of lake trout in relation to total instantaneous fishing mortality without movement (dashed line) and with movement rates (solid line) in U.S. management units of Lake Superior.

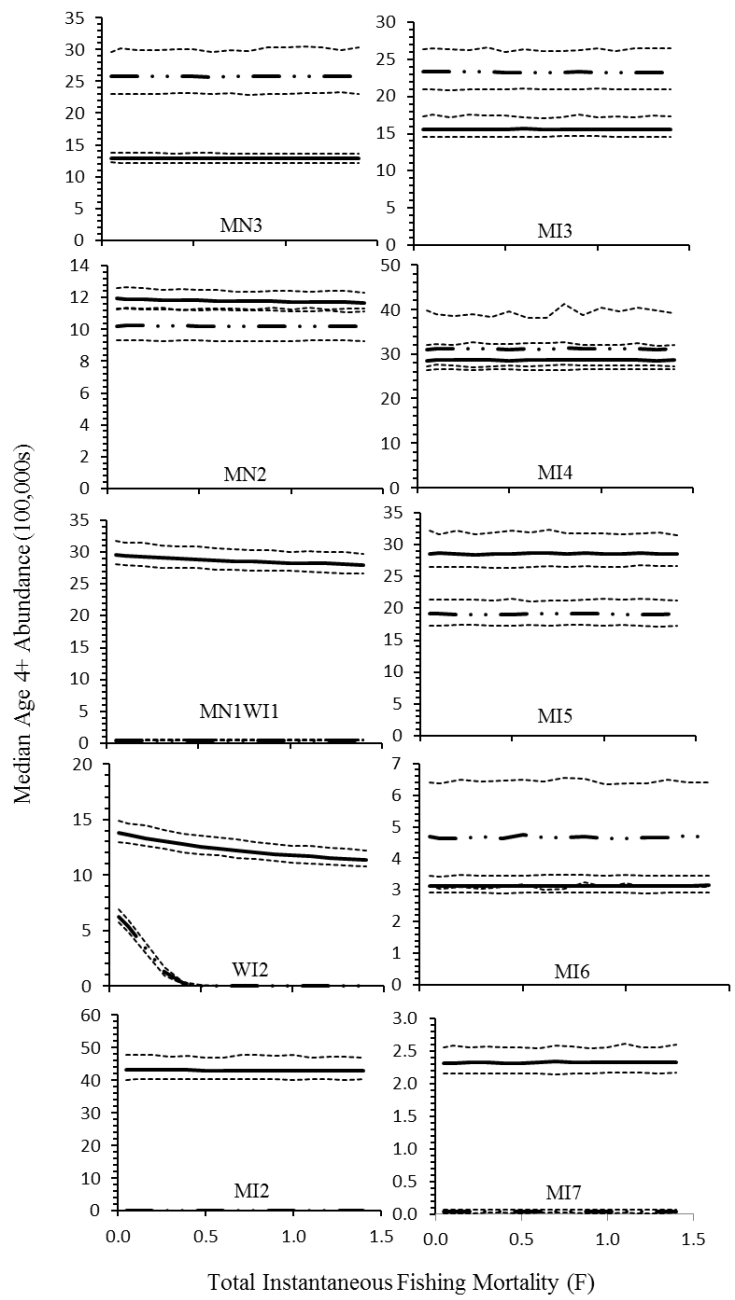


Figure 5. Median age-4+ abundance of lake trout in relation to total instantaneous fishing mortality without movement (dashed line) and with movement rates (solid line) in U.S. management units of Lake Superior.



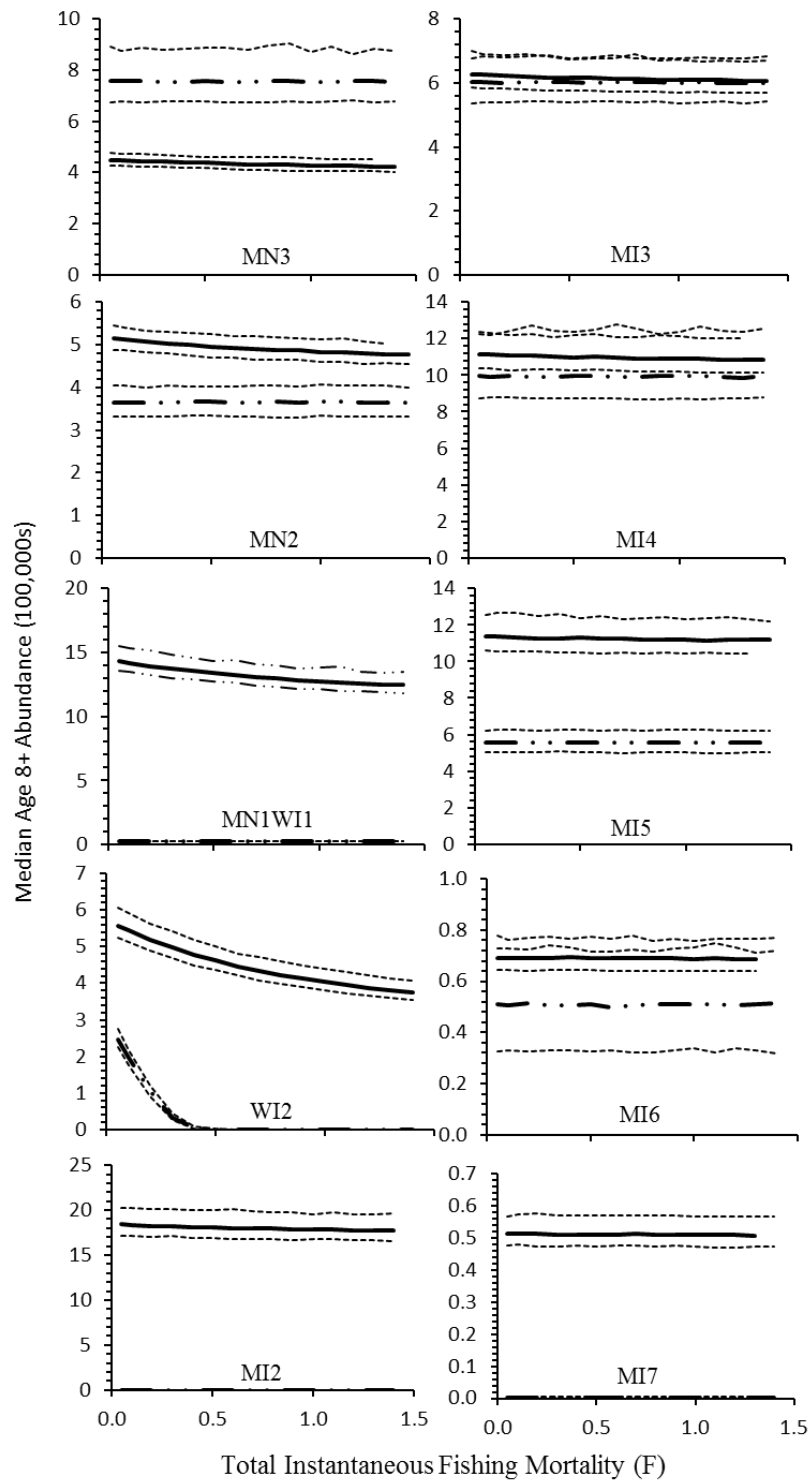


Figure 6. Median age 8+ abundance of lake trout in relation to total instantaneous fishing mortality without movement (dashed line) and with movement rates (solid line) in U.S. management units of Lake Superior.

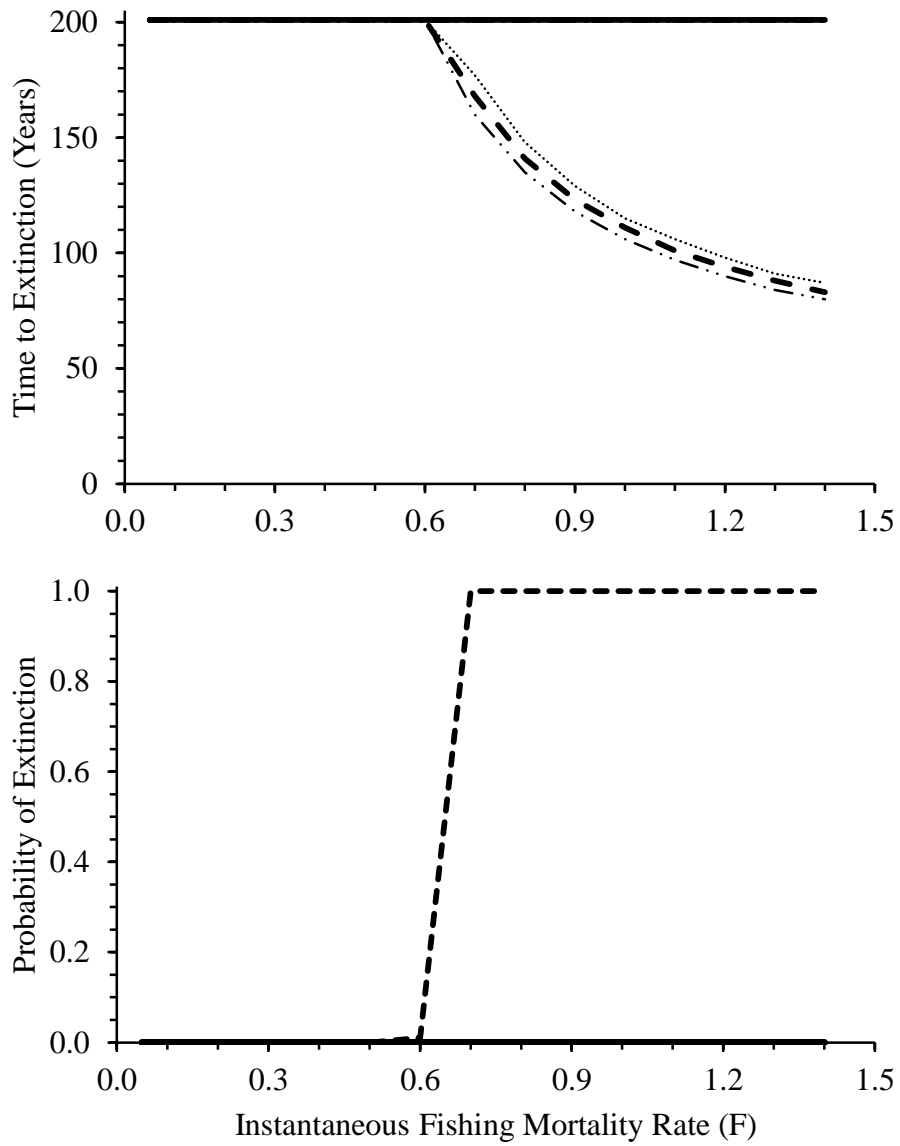


Figure 7. Time to extinction (years; upper panel) and probability of extinction (lower panel) in relation to the total instantaneous fishing mortality rate without movement (dashed line) and with movement (solid line) in eastern Wisconsin waters of Lake Superior.