# A MODEL TO LINK HABITAT SUPPLY TO POPULATION DYNAMICS FOR LAKE TROUT (*SALVELINUS NAMAYCUSH*) POPULATIONS IN WESTERN LAKE SUPERIOR

By

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# ABSTRACT

# A MODEL TO LINK HABITAT SUPPLY TO POPULATION DYNAMICS FOR LAKE TROUT (*SALVELINUS NAMAYCUSH*) POPULATIONS IN WESTERN LAKE SUPERIOR

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In Lake Superior, wild lake trout populations have increased since the low population levels of the 1950's. Although population growth has occurred throughout the lake, the degree and rate of restoration has varied by region and over time. The availability of detailed substrate data allows the comparisons of the physical attributes of areas within the lake and the simulation of population processes that are dependent upon habitat characteristics and spatial location. I developed a spatially explicit model that incorporates the interaction between habitat and environmental conditions to describe lake trout population dynamics in the Minnesota waters of Lake Superior. I then used this model to address hypotheses concerning lake trout rehabilitation in Lake Superior. Model predictions suggest that habitat conditions for lake trout vary along the Minnesota shore, and these differences can cause differences in the population growth rate and growth potential. The model also predicted that eggs deposited by shallower spawning hatchery reared lake trout realized lower survival than eggs deposited by wild fish.

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# INTRODUCTION

Societal recognition of the need for fish habitat restoration and protection has been increasing (Kelso and Hartig 1995). This icreasing focus on habitat management implies a need for methods that connect habitat conditions to fish population performance, so habitat manipulations can be evaluated in the context of what they were enacted to achieve. Defining the inter-relationships between habitat characteristics and fish populations can be a difficult task. Most of the traditional models developed for fisheries stock assessment and management (e.g. stock-recruit models) do not include interactions between populations and the components of their environment (Sissenwine et al. 1978). For example, these models usually do not explicitly consider the effects of environmental conditions (weather, hydrology) on populations, which can be a major influence on year-class strength (Cushing 1982; Crecco and Savoy 1984).

Since traditional fisheries models are not suited to determining the effects of habitat change on populations, managers have used other tools to develop fish community objectives based on measures of habitat quantity and quality. Habitat-yield models, such as the morphoedaphic index, use easily measured characteristics like mean depth and total dissolved solids of a water body to make predictions about potential fish yield from the system (Ryder 1965; Ryder et al. 1974). These models are easy to apply and rely on physical characteristics that are assumed to determine the productivity of the system (Oglesby 1982; Ryder 1965; Ryder 1982). By design, these models are general and can easily be applied to many bodies of water. However, these methods are not useful for investigating the interaction between specific habitat components and fish populations.

In contrast, Habitat-Suitability Index (HSI) models allow elucidation of the effects of individual habitat components on specific life stages of the species of concern (USFWS 1981). These models combine suitability curves for several habitat components to derive a single value as a measure of overall suitability over several life stages or for individual life stages (e.g., Raleigh 1982). HSI models are used to evaluate suitability and thus compare habitats, but they do not allow predictions of the demographic performance indicators (i.e., growth, abundance, and mortality) of a population as habitat suitability and availability changes, which limits their utility for forecasting the consequences of habitat restoration or loss.

To be able to investigate the role of habitat characteristics on fish populations, a more mechanistic approach is necessary that allows the flexibility to incorporate specific processes that affect the interaction between fish populations and their habitat. Hayes et al. (1996) provided an appealing framework for investigating how habitat features can affect fish populations. A key element of this approach is a broad definition of habitat that includes physical and biological characteristics. They make a distinction between habitat components whose effects on population processes are density dependent or independent and whose supply is or is not dynamically affected by the fish population. Available prey would represent a dynamically affected density dependent factor, and temperature would be a density independent unaffected factor. They argue that these distinctions have implications for forecasting the effects of habitat change on population dynamics.

Minns et al. (1996) developed an age-structured population model to explore the effects of changes in habitat supply on northern pike (*Esox lucius*) in Hamilton Harbor, Ontario, Canada. They developed the model by using pike habitat requirements and demographic parameters from the published literature to develop the habitat linkages for three separate life-stages: spawning/egg incubation, juvenile, and adult. By applying this model to habitat supply estimates from Hamilton Harbor, they were able to determine what life-stage specific habitat requirements were critical for limiting population performance. They concluded that juvenile rearing habitat was likely to be limiting pike populations, in contrast to the common perception that spawning habitat was in limited supply. This study illustrates how explicitly considering habitat interactions at separate life stages can lead to improved fish management through habitat manipulations.

Models of this type simulate the life history of individual units in the population (cohorts) allowing explicit consideration of the effect of habitat features on survival and growth at each life stage. Within these population models, process models can be included that translate observed environmental conditions into responses of fish populations (De Angelis and Cushman 1990). Therefore, these models draw upon empirical and theoretical work of others to try and simulate the processes by which habitat can affect survival, growth, or reproductive success. Process models are useful when empirical relationships for the influence of potentially important environmental factors on population performance do not exist (De Angelis and Cushman 1990). Process models allow us to simulate population responses by integrating analyses and observations relevant to the questions at hand into a mechanistic hypothesis, and have been widely used to model processes such as feeding and migration (Eggers 1977; Beyer and Laurence 1980). Furthermore, the mechanistic approach of these process models allows investigations of the interaction between environmental components. For example, Jones et al. (2003) incorporate the interaction of temperature and discharge to estimate the potential habitat quality for walleye (*Sander vitreus*) in the Sandusky River, Ohio based on the distance of potential spawning areas from nursery areas at the river mouth.

In this thesis, I describe the development of a habitat supply model for lake trout *(Salvelinus namaycush)* in the Minnesota waters of Lake Superior, and examine relevant issues concerning the relationship between habitat characteristics and lake trout population dynamics in Lake Superior. By looking at habitat needs for specific life stages of lake trout, it is possible to describe the effects of habitat supply and the mechanisms by which changes in habitat supply may influence lake trout population dynamics in Lake Superior. The Minnesota shore was selected as the study area because of the availability of substrate and bathymetry data, the heterogeneity of substrate types along the shoreline, and the management history of the area. The history of the fishery along the Minnesota shore is broadly consistent with the rest of the lake in that populations crashed in the 1950's, and re-established over the next several decades, but restoration has not been uniform throughout this area of the lake. Rates of restoration and habitat characteristics along the Minnesota shore vary by region. My analysis examines whether some of the spatial differences in restoration success can be explained by spatial differences in habitat features.

## History of lake trout fisheries in Lake Superior

Lake trout were the top predator in Lake Superior prior to the introduction of non-indigenous species (GLIFWC 2000), and played an integral role in the fish community structure (Edwards et al. 1990). Humans have also relied on Lake Superior lake trout as an important food source and an economic resource for centuries (Baldwin 2000; GLIFWC 2000). Several bands of Native Americans settled on the shores of Lake Superior and lived off the resources of the water and surrounding land (GLIFWC 2000). Fish were an important component of the diet and trading resources available to these bands. Tribal fishing techniques included setting willow bark nets from birch bark canoes and spearing fish through the ice.

In the late 1800's and early 1900's the non-Indian commercial fishery grew rapidly, and the fishing boom continued into the 1950's when populations and harvests were greatly reduced (Figure 1, data from Baldwin et al. 1979). The commercial lake trout fishery in Minnesota became established later than other fisheries in Lake Superior, but after establishment, trends in catch mirrored the lake as a whole (Figure 1). The population crash of the 1950's was largely due to over-fishing and the introduction of non-native sea lamprey (*Petromyzon marinus*), which preys on lake trout (Smith and Tibbles 1980). However, the increases in fishing pressure prior to the 1950's and the increases in fishing effectiveness through the introduction of nylon gillnets substantially reduced lake trout abundance in the lake prior to the establishment of sea lamprey populations (Wilberg 2002).

Sea lamprey entered Lake Erie through the Welland canal in the 1920's, and subsequently invaded the upper Great Lakes, where they increased in abundance until 1961 (Coble et al. 1990). The additional mortality on lake trout from sea lamprey predation caused abundance to continue to decline despite the reduction of fishing pressure during 1954-1961(Coble et al. 1990; Hansen et al. 1995). From 1954 to 1961, commercial harvest of lake trout in Lake Superior dropped from 4.1 million pounds to 380 thousand pounds; all commercial lake trout fisheries were closed in 1962 (Pycha and King 1975).

Restoration efforts in Lake Superior have focused on increasing production through hatchery releases and reducing mortality on lake trout populations through sea lamprey control and fishing restrictions (Hansen et al. 1995). Releases of hatchery fish began in the 1950's in Ontario, Michigan, and Wisconsin waters, and in 1962 in Minnesota waters (Figure 2, data from GLFC 2000; Lawrie and Rahrer 1972). Large scale stocking efforts began in 1953 when approximately 470,000 lake trout were released into the lake. The level of stocking increased substantially from the early 1950's to the 1960's; over 3 million fish were released in 1966 (Figure 2) Sea lamprey control began in 1953 by trying to block sea lamprey access to spawning streams. However, the restoration efforts of the 1950's were largely unsuccessful and stocks continued to decline into the 1960's (Hansen et al. 1995).

Restoration efforts began to show signs of success in the 1960's due to an increase in stocking efforts and reduction of sea lamprey mortality (Hansen et al. 1995). In 1958, the treatments of streams with the lampricide TFM began to effectively reduce lamprey populations in the lake (Smith et al. 1974). By the fall of 1961, the number of sea lamprey in Lake Superior decreased by 87% from its peak earlier in the same year (Smith et al. 1974;Hansen et al. 1995). The high levels of stocking from the 1960's to 80's produced a large population of hatchery reared lake trout in the lake that were able to reproduce. In Minnesota waters, stocking began when approximately 76,000 hatchery lake trout were released in 1962; stocking intensity increased rapidly and remained near

300,000 released annually from the 1970's to mid-1980's (Figure 3; GLFC 2000). No stocking took place near Isle Royale yet population increases mirrored those occurring in stocked areas of the lake (Figure 4) indicating that increased survival in the lake was an important component for restoration success in addition to increased hatchery plantings.

Populations of lake trout in Lake Superior have increased since the population crash (Hansen et al. 1995). For example, the Gull Island Shoal population has shown dramatic increases, but the lack of evidence for a density dependent effect on survival suggests that lake trout have not yet reached maximum population size for this area (Bronte et al. 1995a; Schram et al. 1995a). In Michigan waters, Wilberg et al. (2002) found that current gill-net catch per effort estimates approach the levels of 1929-43 when corrected for changes in fishing gear and under-reporting rates. Reduced growth rates (Sitar et al. unpublished data) and evidence for density dependence in stock recruitment relationships (Richards et al. 2004) suggest that populations are approaching or exceeding the carrying capacity in Michigan waters of Lake Superior. Peck and Schorfhaar (1991) and Richards et al. (2004) used assessment data to show that the composition of lake trout in the Michigan waters of Lake Superior has gone from mostly hatchery fish to mostly wild origin fish from 1970 to the present. In 1996, managers declared lake trout restoration in Lake Superior a partial success and agreed to greatly reduce stocking and rely on natural reproduction for further population growth (Hansen 1998).

On a large geographic scale, restoration efforts and effectiveness for the Minnesota shore are similar to patterns in the lake as a whole. Populations declined rapidly from the 1940's to 1961, and evidence of restoration success began in the early 1960's after sea lamprey numbers were reduced and levels of stocking were high (Baldwin 2000). The

Minnesota lake trout fishery is divided geographically into three management districts (MN1, MN2, MN3 – Figure 6). If we examine restoration progress along the Minnesota shore at a finer scale, we see that success has occurred all along the shore, but the degree and rate of restoration differs by region (D. Schreiner, Minnesota Department of Natural Resources, Duluth, MN, personal communication). MN-3 has realized the fastest rate of wild lake trout population growth. Although progress has been slower than MN3, wild lake trout populations have consistently grown in MN1 and MN2 (Figure 7). Survey CPE's have been similar in MN1 and MN2. MN1 has supported higher fishing pressure and adult mortality rates than the other two units, and has received a larger number of stocked fish.

No remnant wild populations along the Minnesota shore were believed to have survived the population crash, so presumably re-establishment of spawning populations has been due to successful spawning of stocked fish, or, possibly, wild fish straying from other areas.

## Potential habitat concerns

General habitat characteristics necessary for all life-stages of lake trout include high dissolved oxygen content and cold water. These conditions exist throughout Lake Superior and are not likely to impose limitations on the populations (Ebener 1998). However, differences in restoration success in various areas of Lake Superior suggest variability in other characteristics that influence population performance, such as management practices, habitat conditions other than oxygen and temperature, and fish community composition. Management practices can affect both recruitment (i.e.

stocking) and adult survival (i.e. fishing mortality) directly and indirectly. The stocking intensity in the three management zones of the Minnesota shoreline was similar until the 1990's when stocking levels in MN1 increased relative to the other units (Figure 5). Fishing mortality is highest in MN1 while MN2 and MN3 have similar mortality levels. In general, fishing mortality rates are low, and harvest from the restrictive fishery is not believed to drive population dynamics. Hansen et al. (1996) found lake trout recruitment to age-7 in Minnesota waters of Lake Superior from 1963 to 1986 to be more strongly influenced by abundance of adult wild lake trout than gillnet fishing effort or the combined abundance of wild and stocked lake trout, implying that recruitment is not being limited by gillnet fishing effort. Hypotheses regarding the role of specific habitat conditions on the survival of lake trout in Lake Superior have been presented (Bronte et al. 1995b; Burnham-Curtis et al. 1995; Eshenroder et al. 1995; Manny et al. 1995), but not thoroughly investigated (Burnham-Curtis et al. 1995).

Lake trout in Lake Superior rely on different habitat characteristics at different life-stages. To identify limitations imposed by habitat availability or the life-stage where habitat is potentially limiting, we must first identify the habitat characteristics necessary for lake trout within that life-stage. Good lake trout spawning/egg incubation habitat is generally described as porous substrate with interstitial spaces greater than 30 cm (Wagner 1982; Gunn 1995). Incubating eggs require porous substrates with deep interstitial spaces to provide protection from wave action and predators while allowing ventilation. Young of year lake trout reside in shallow areas for the first several weeks after emergence and gradually move to deeper water as the season progresses (Peck 1981, Bronte 1995). For this time period, lake trout rely on invertebrate prey that are abundant in sandy depositional areas (Carpenter et al. 1974). Lake trout continue to feed on invertebrates for their first few years of life; Mysis comprise a major diet component for lake trout less than 10 inches in Western Lake Superior (Anderson and Smith 1971), and are abundant in deep water over sandy substrate (Carpenter et al. 1974). Anderson and Smith (1971) found the diets of lake trout greater than ten inches to be dominated by fish prey. Piscivorous lean lake trout inhabit waters less than 80m in depth, requiring cold clean water and an abundance of forage fish (Burnham-Curtis and Bronte 1996).

The performance of egg incubation habitat measured by egg survival is determined in part by intrinsic qualities of the habitat such as percent fines, substrate composition, temperature, and oxygen concentration (Ostergaard 1987). In addition to these intrinsic characteristics, the performance of habitat in terms of affecting populations is also dependent upon the frequency of damaging climatological events and proximity to habitats required for subsequent life-stages. Eshenroder et al. (1995) hypothesize that the availability of spawning habitat may be limiting lake trout population in the Great Lakes despite the presence of large quantities of what would be considered quality spawning substrate. Their speculations are based on observations of climatological factors, such as violent wind events, reducing survival of eggs in areas with an abundance of otherwise suitable spawning habitats. They speculate that when including these extrinsic factors, the apparent supply of good lake trout spawning habitat may be much lower than previously thought (Eshenroder et al. 1995).

The characteristics of nearby habitat areas and their location relative to spawning sites can also affect egg survival on a spawning reef. Sly (1988) observed sources of sediment up current from spawning areas re-suspending and settling on incubating eggs causing suffocation.  These sediment sources that can be re-suspended tend to be more common in inshore areas, thereby decreasing incubation survival relative to offshore reefs.

Burnham-Curtis and Bronte (1995) and Bronte (1995b) identified the juxtaposition of nursery areas and spawning areas as a potentially important factor affecting recruitment of lake trout.  Lake trout fry will move to nursery areas where there is an adequate supply of invertebrates for food.  The availability of such nursery areas in proximity to spawning areas is another factor that may affect the ultimate survival of eggs emerging from spawning areas.

Another issue for lake trout restoration involves is the potential difference in habitat use by hatchery versus wild origin fish.  Hatchery lake trout in Lake Superior have lower rates of spawning success than wild fish (Schram et al. 1995a), tend to spawn earlier than wild lake trout and use available habitat differently, both temporally and spatially, than wild lake trout (Krueger et al. 1986; Ebener 1990a).   These differences may have consequences for the spawning success of hatchery lake trout.

To examine the potential influence of habitat factors on Lake Superior lake trout restoration, I constructed a model that would allow me to address relevant habitat issues in Minnesota waters of Lake Superior.  I constructed the model to investigate the effects of habitat supply and distribution on lake trout populations and, specifically, to simulate the interactions between physical, climatological, and ecological processes occurring along the Minnesota shore.  By defining the quality of habitat areas as being dependent on both their composition and their location relative to spatial patterns of environmental factors such as wind and currents, I attempted to assess the extent to which such habitat characteristics may account for differences in lake trout recovery in management zones along the Minnesota shore.

## METHODS

### Study Area

The Minnesota shoreline of Lake Superior was selected as the study area for this modeling exercise. The Minnesota shoreline spans approximately 240 kilometers and includes a wide range of bathymetric and substrate conditions (Richards and Bonde 1999). Three lake trout management units are delineated for the Minnesota waters of Lake Superior (Figure 6), and they differ in the composition of substrates and depth profile. The eastern most region (MN3) has a narrower shelf and high percentage of large rocky substrates while the western most region (MN1) has a higher composition of sandy substrates and a wide shelf; MN2 is intermediate between the other two zones in both respects. Both hatchery and wild origin lake trout populations exist in the three regions along the Minnesota shore although the ratio of wild to hatchery fish is not consistent between regions. As of 2002, MN3 had the highest ratio of wild to stocked fish (82%), MN2 had the second highest (62%), and MN1 had the lowest ratio of wild to stocked fish (43%) in the angler creel survey (D. Schreiner, MNDNR, Duluth, MN, unpublished data).

To explore the habitat issues relevant to lake trout population performance in Lake Superior, a spatially explicit summary of habitat types is necessary. Richards et al. (1999) mapped substrate composition and bathymetry for 65 km$^2$ of the approximately 185 km$^2$ of habitat along the Minnesota shore of Lake Superior with depths between 5 and 30 meters. These data, collected with a sonar-based ROXANN system, provide a spatial distribution of substrate types and depths that I used as the first component for identifying potential lake trout habitat.

The model represents the study area as a polygon coverage based on the ROXANN substrate classifications (Richards and Bonde 1999). I used the polygon coverage from Richards et al. (1999) and assumed that spawning sites should be amorphous and based on a single substrate classification. Because some of the mechanisms in the model are depth dependent, I further subdivided the polygons based on the intersection of 10 meter contour plots generated by the sonar transects to allow for consideration of different depths even though a single substrate derived polygon may cover the entire depth range. This manipulation of the spatial data yields a set of reasonably sized polygons classified by substrate type and depth with a maximum depth range of 10 meters within a polygon. This polygon coverage represents the primary spatial domain for the model; each polygon represents a habitat unit. Additional manipulations of the spatial data were made when necessary, and are described in the model descriptions for each life-stage. In the eastern most end of the mapped area the habitat coverage is not continuous, so I could not provide reasonable estimates of fry dispersal from spawning to down current nursery areas.

### Environmental data

Environmental data are crucial to the application of this model. The interaction of physical characteristics and climatic patterns affects the population dynamics of lake trout through a number of mechanisms. To approximate water temperatures in the spawning and nursery areas, I used the mean daily temperature from the 20m deep water intake at the French River Hatchery. To approximate the wind conditions along the Minnesota shore, I used the maximum sustained daily wind speed from the Devil's Island monitoring station in western Lake Superior as the daily wind speeds used in the model.

Model overview

I used a stage-structured cohort-based population model within a spatially explicit model structure to simulate the Minnesota lake trout population. Cohorts in the model were defined on the basis of age and spatial location. Initially, cohorts were distinguished by the location of egg incubation and day of emergence. As the lake trout aged, cohorts were aggregated until the adult life-stage when they were only designated by age. Cohorts were updated daily for the first year of life, and annually for subsequent years.

The population dynamics were described as:

$$N_{i,t} = N_{i-1,t-1}e^{-Z} \tag{1}$$

where, $N_{i,t}$ is the number of individuals age i at time t, and Z is total instantaneous mortality. Total mortality was subdivided into individual mortality components operating simultaneously,

$$Z = (M_a + M_b + \ldots\ldots M_l). \tag{2}$$

Modeling these components as functions of habitat conditions directly links specific habitat features to population performance.

The model was organized as a series of sub-models that represent life history stages of lake trout. The sub-model structure was designed to accommodate changing habitat requirements for lake trout at different ontogenetic stages and the movement of lake trout to areas with habitat characteristics required for each life stage.

### Spawning sub-model

Lake trout aggregate in spawning areas when temperatures decline in the fall and summer thermal stratification deteriorates (Martin and Olver 1980). Since lake trout spawn at night in inhospitable weather (Gunn 1995), there are few direct observations of the details of spawning behavior in the field, and what observations have been made are mostly from inland lakes ( Martin and Olver 1980; Gunn 1995; McAughey and Gunn 1995). Spawning lake trout have been reported to show little aggression among males (Martin and Baldwin 1960; Noakes 1980) and no distinct sexual dimorphism (Martin and Olver 1980). Unlike other salmonids, lake trout do not construct nests but deposit their eggs directly over porous substrate making no attempt to bury or guard the eggs (Martin and Olver 1980).

Lake trout appear to exhibit a high degree of spawning site fidelity, returning to the area where they emerged from the substrate as fry to spawn as adults (Martin and Olver 1980; MacLean et al. 1981). Although the level of site fidelity and straying rates are not known, it seems that straying rates are quite low. In Canadian inland lakes, McAughey and Gunn (1995) observed lake trout spawning in only a small amount of the available spawning habitat. When the spawning areas in the lake were made unavailable to lake trout, they spawned elsewhere successfully, suggesting that lake trout will continue to spawn on established shoals even when other available habitat remains unused. McAughey and Gunn's observations in inland lakes suggest that available spawning habitat is not limiting lake trout population growth in the lakes they studied, and the homing mechanism in lake trout is strong. My model incorporates homing to natal spawning grounds by distributing adult lake trout to spawning areas based on the proportion of recruits to the adult population that came from each spawning area.

Hatchery-origin lake trout do not have a spawning site to return to, and it is not known which habitat units in the study area are currently used by existing wild lake trout populations. To distribute hatchery fish and the initial population of wild fish among the habitat units, I used a mechanism that attempts to mimic the selection process for hatchery and straying lake trout and approximates where wild lake trout are likely to spawn based on observations of lake trout spawning areas in Lake Superior. A basic assumption of this approach is that lake trout spawning areas become established because they contain characteristics that are appealing to adult lake trout, and successful spawning has generated adult populations that return to those sites.

Eggs were distributed among the habitat units with a rule that attempts to simulate how females would select spawning areas based on the intrinsic habitat quality of a unit. In order to quantify the qualitative characteristics of the available habitat, a habitat selection value (*HSV*) was calculated for each habitat unit in the study area. The calculation is similar to the lake trout HSI (Marcus et al. 1984) where a simple multiplicative method is used to combine variables:

$$HSV = V_{Substrate} \text{ x } V_{Depth} \text{ x } V_{Density} \qquad (3)$$

where $V$ was the value for each respective variable used in calculating the $HSV$.

The distribution of values for the substrate variable ($V_{Substrate}$) was the same for hatchery and wild females and relies on the “good”, “average”, and “poor” spawning substrate identifications in Richards et al. (1999). Substrate consisting of hard porous substrates like cobbles and boulders were classified as good ($V_{Substrate} = 1.0$). Less desirable substrate types like mixtures of coarse substrates with sand and cracked bedrock were classified as average ($V_{Substrate} = 0.7$). Habitat units with substrates that were not considered lake trout spawning habitat, such as sand and smooth bedrock were classified as poor ($V_{Substrate} = 0.1$).

Hatchery lake trout in Lake Superior tend to spawn in shallower water than their wild counterparts (Ebener 1990b; Eshenroder et al. 1995). To simulate these differences in depth preference, I used different depth distributions for hatchery and wild fish to determine the $V_{depth}$ value for a habitat unit. Depth of capture data from Keweenaw Peninsula spawning assessments in 1989 (Ebener 1990a) were used to generate these values. I fit a normal probability density function (PDF) to the frequency distributions of catches at depth after normalizing the frequencies to a maximum of one (Figure 8). The $V_{depth}$ value for each habitat unit was computed from

$$\frac{1}{\sigma\sqrt{2\pi}}e^{-\frac{(d_i-d_{opt})^2}{2\sigma^2}} \tag{4}$$

where $d_i$ is the depth of the unit, $d_{opt}$ is the depth at the mean of the normal distribution, and $\sigma$ is the standard deviation.

I assumed the distribution was normal and the collected data included the mode of the distribution. The mean for the hatchery distribution was at 18 feet ($\sigma = 6$) while the mean for the wild distribution was 35 feet ($\sigma = 9$). The data indicate that hatchery fish show a much stronger depth preference. The hatchery distribution was very narrow around the minimum depth values, and the wild distribution indicates that wild fish spawn at a wide range of depths (Figure 8). In the Keweenaw assessments, catches of wild fish did not show a descending abundance with increasing depth presumably because nets were not set at depths beyond 55 feet. I adjusted the distribution by forcing it to reach its mode at the deepest depths recorded in the data. I truncated the low end of distributions at ten feet for both hatchery and wild lake trout, which was the lower limit of the Keweenaw assessments, and a minimum depth where I thought lake trout would be found spawning in Lake Superior.

To distribute the females to the habitat units and account for the affect of density on the *HSV*, all habitat units were first assigned to 1 of ten ranked bins based on $V_{depth}$ and $V_{substrate}$. Females were then randomly assigned to a bin using a skewed probability distribution that heavily favored the highest ranking bins (i.e., a female has a 90% chance of being assigned to the two highest bins). Females were then randomly assigned to one of the habitat units within the bin selected in the first step with all units in a bin having an equal probability of selection.

Although lake trout form large spawning aggregations, I assumed that above some threshold the density of spawners in a unit would be a deterrent to additional females using that location to spawn. Unfortunately, there are no empirical data on the effect of density on spawning site selection for lake trout, but it seems unreasonable to assume that lake trout would continue to spawn in an area where the density of spawners, and thus eggs, would lead to low egg survival. There are data on lake trout egg densities on spawning reefs. While females are distributed to the habitat units the *HSV* for each unit is continually adjusted based on the density of females in the habitat unit according to a negative logistic function. The inflection point for the logistic function was set at the maximum lake trout egg densities found in the literature.

The total number of eggs deposited in a habitat unit was calculated using the age-fecundity relationship from Schram et al. (1993):

$$E_H = \sum_{i=1}^{A} (-646.8 + 612.03i) \cdot N_{i,H} \cdot Mat_i \qquad (5)$$

where $E$ is the total number of eggs available for deposition in habitat unit $H$, $i$ is the age, $A$ is the maximum age, $N_i$ is the number of females in age-class i, and $Mat_i$ is the proportion of females in age-class $i$ that will spawn.

Lake trout move on to the spawning grounds when water temperatures decline in the fall (Gunn 1995; Martin and Olver 1980). Severe wind conditions and the breakdown of thermal stratification have also been observed as influencing the onset and duration of spawning (Martin 1957; McCrimmon 1958; Helm 1960; Deroche 1969). The factors that actually trigger lake trout to begin and stop spawning occur in the fall, and the actual dates vary throughout their range ( Loftus 1958; Payne et al. 1990;Gunn 1995). Eschmeyer (1955) reported the spawning season for stocks of Lake Superior lean lake trout to be between early October and mid-November, with the peak of spawning activity occurring from late October to early November.

Egg deposition in the model was distributed over time using a normal distribution spanning the time period in Eschmeyer (1955). The parameters and equation for this distribution are:

$$\mu = (d_s + d_e) / 2 \qquad (6)$$

$$\sigma = ((d_e - d_s)/2)/2.58 \tag{7}$$

$$E_d = \left(\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(d-\mu)^2}{2\sigma^2}}\right) E_H \tag{8}$$

where $E_d$ is the number of eggs deposited on day *d* within each habitat unit, $E_H$ is the total number of eggs deposited in habitat unit *H*, $d_s$ is the first day of spawning and $d_e$ is the last day of spawning.

Egg-incubation submodel

In the model, the mean daily temperature determines the rate of egg development through the accumulation of thermal units. One thermal unit is accumulated for each degree the daily mean temperature is above 0 °C. For example, a cohort of eggs would accumulate 2 thermal units for a day where the mean daily temperature was 2 °C. I used egg incubation data for lake trout from Casselman (1995) to develop a linear function that estimates the daily percentage of egg development:

$$Y = 0.1532\,T + 0.1886 \tag{9}$$

where Y is the percent development per day towards emergence and T is the mean daily incubation temperature (° C). The duration of the spawning period and water temperatures during incubation combine to determine the temporal distribution of lake trout emergence.

The egg incubation period for lake trout in Lake Superior is long. Spawning occurs in the fall, and eggs incubate through the winter and spring with emergence occurring from late spring through mid-summer (Peck 1981; Bronte et al. 1995b). During this extended period, the eggs are susceptible to predation from benthic predators, smothering by sediments, and physical disruptions (Eshenroder et al. 1995; Fitzsimons 1995; Manny et al. 1995).

Three sources of mortality were explicitly considered in this submodel: a base mortality for different substrates, a mortality due to direct physical shock from high wind events, and mortality caused by sedimentation (Figure 9). The base mortality was derived from literature values to represent realistic mortality rates in different substrate types that are not due to factors being modeled explicitly.

I used climate data from the Devil's Island monitoring station in western Lake Superior to determine the frequency of wind events that could cause additional mortality on the eggs through physical disruption. Lake trout eggs are in the substrate during late fall and winter when winds over the lake are strongest (Beletsky et al. 1999). High wind events can cause a decrease in egg incubation survival by delivering turbulence to the eggs incubating in the substrate ( Fitzsimons 1994; Eshenroder et al. 1995; Fitzsimons 1995). A direct physical shock can cause mortality especially if the shock is delivered while the eggs are in the critical stage of late epiboly (Fitzsimons 1994; ; Eshenroder et al. 1995; Manny et al. 1995). To determine if a wind shock event occurs, the model determines the period that the eggs are in the sensitive phase of late epiboly and then uses the wind data to determine if a critical wind event occurs during that time period. At the temperatures the eggs are exposed to in Lake Superior, this critical phase lasts between approximately 15 and 27 % of the development period (Balon 1980; Martin and Olver 1980).

I used wind data to calculate the maximal orbital velocity at the depths of incubating eggs, and compared this to an estimate of the orbital velocity at which egg survival would be affected. The orbital velocity near bottom was calculated for all habitat units with incubating eggs each day of the sensitive period. Methods described in Hallermeier (1981) were used to determine the orbital velocity at the water substrate interface for specific depths based on the wave height and wave period. The calculations of near bottom velocities were used for both the wind shock and sedimentation component (see Appendix A for details of calculations).

The maximum orbital velocity ($v_{max}$) at the water-substrate interface is

$$V_{max} = \frac{\omega H}{2\sinh(\frac{2\pi d}{L})} \qquad (10)$$

where H is the wave height, $\omega$ is the wave angular velocity, d is the local depth, and L is the wave length (Hallermeier 1981). To relate $v_{max}$ to survival of lake trout eggs, I developed an exponential relationship between maximum orbital velocity encountered and incubation survival from survival estimates from sites in Lake Ontario (Fitzsimons et al. 1995). Fitzsimons et al. (1995) developed a relationship between fetch and egg survival for sites in Lake Ontario. For the sites in Fitzsimons' study, I calculated the maximum $v_{max}$ encountered during the susceptible incubation period by running the model described above with the spatial locations, and depths of Fitzsimons' study sites, wind data from NOAA C-MAN station GLLN6 on Gallo Island, NY, and the high quality substrate value. I then used the maximum orbital velocity encountered during the time period of the study to reform the relationship between fetch and survival from

Fitzsimons' study to a relationship between maximum orbital velocity encountered and relative incubation survival, by fitting a regression line to the natural log transformed data ($r^2 = 0.63$). The resulting relationship is

$$S = 0.9113 \cdot e^{-0.283 v_{max}} \tag{11}$$

where S represents wind shock-related incubation survival and $v_{max}$ is the maximum orbital velocity encountered at the site.

Although lake trout will generally spawn in clean substrate with deep interstitial spaces, fine sediment can settle on the incubating eggs after egg deposition causing suffocation and, therefore, mortality (Manny et al. 1995). The sediment loads come from areas up current with fine substrates that become re-suspended during high wind events (Hallermeier 1981; Bennett 1987; Bailey and Hamilton 1997). A sediment re-suspension event occurs when wind conditions are strong enough for bottom orbital velocities to exceed those required to suspend substrate particles; motion of sand sized particles begins at 15.4cm/sec (Hallermeier 1981). If the orbital velocity at the substrate-water interface is high enough for a large sediment movement event, fine particles are re-suspended, travel with the currents, and are deposited in areas down current (see Appendix A). These sediments will ultimately be cleaned away by the predominant currents and deposited in depositional areas, but the temporary smothering of the eggs can cause anoxic conditions that lead to high egg mortality.

To simulate the sedimentation events in the model, a grid consisting of 20m X 20m cells was superimposed on top of the study area habitat units. When a sediment re-suspension event occurred, a simple particle settlement model was then used to simulate which spawning areas were covered with sediment. Since the current is relatively consistent along the Minnesota shoreline and data on daily current conditions are not available (Beletsky et al. 1999), I assumed that immediately following the re-suspension event the suspended mass drifted in the main current settling out at a rate determined by particle size. Fine substrates in the Minnesota shoreline GIS coverage are classified as a single category of sand and finer particles; therefore I used a single particle settling velocity of 9.2 mm/sec. which is for particles slightly smaller than sand (Everts 1981). The maximum range of the effect of the sediment re-suspension ($R_{max}$) is calculated by:

$$R_{max} = 0.75\, D\, V_c / V_s \qquad (12)$$

where $D$ is water depth, $V_s$ is the particle settling velocity, and $V_c$ is the current velocity.

The spread of sediment was modeled as a plume that starts as wide as the habitat unit and spreads out at an angle of 30° resulting in a trapezoidal shape that defines the affected area. All grid cells within the trapezoid were assumed to have a sediment-smothering event occur which results in higher egg mortality. I used the *in situ* incubation results from Manny et al. (1995) to estimate the effect of post-depositional sedimentation. An average mortality of 35% was attributed to the smothering effect when sedimentation occurred after egg deposition. I assumed the eggs were uniformly distributed within each habitat unit, and applied the additional mortality only to a proportion of the eggs equal to the number of grid cells affected divided by the total number of cells within the habitat unit.

### Emergence and early feeding submodel

Lake trout fry emerge from the spawning substrate shortly after hatching (Balon 1980;Martin and Olver 1980). Lake trout fry are capable swimmers and possess a large yolk sac allowing them to survive weeks without feeding, although they will generally begin feeding prior to complete yolk sac absorption (Martin and Olver 1980). For the first few weeks after emergence, lake trout fry are found in shallow nearshore areas that provide protection from predators and an abundant supply of invertebrate prey. The characteristics of these nearshore nursery areas differ according to the lake or region within a lake where spawning took place. In inland lakes, lake trout fry may remain in shallow rocky areas near the location of egg incubation (DeRoche 1969). In Presque Isle Harbor, Lake Superior, Peck (1981) found age-0 lake trout in shallow waters over rock or sand substrates; these fry remained within the harbor throughout the early summer season before moving to deeper water. In Western Lake Superior, sandy substrate areas are important rearing areas for young of year lake trout (Bronte et al. 1995b). The calm conditions of these depositional areas presumably allow lake trout to forage and grow, without being displaced by the current. While in these nursery areas, age-0 lake trout feed exclusively on the rich supply of invertebrate prey (Eschmyer 1955; Martin and Olver 1980; Hudson et al. 1995).

### Transport to nursery grounds

Bronte et al. (1995b) tracked the movement of lake trout fry from the primary spawning reefs in Gull Island Shoal in Western Lake Superior to the nursery areas off of Michigan Island, a distance of up to 11 kilometers. The authors propose a mechanism by which the predominant currents and wind conditions in the area deliver the fry to the nursery area. The physical processes that deliver fine materials to these depositional areas may also deliver lake trout fry and allow them to settle out of the current.

I assumed a mechanism similar to the one described by Bronte et al. (1995b) was responsible for transporting lake trout fry along the Minnesota shoreline. I developed a transport model that simulates the travel path of pelagic larvae. The ultimate destination of a pelagic larva in the water column is the result of diffusive and advective processes and the rate of settlement of fry from the water column (Possingham and Roughgarden 1990). For lake trout fry along the Minnesota shoreline, the current over the spawning area will advect fry in a predictable direction while at the same time the active swimming of fry against and across the current will give rise to diffusion from the path of the current.

Fry movement was modeled in a two-dimensional plane with the direction and speed of travel determined by the lake currents and a diffusion factor. To keep track of movements and to relate coordinate locations to habitat characteristics, a 20m X 20m grid was superimposed on top of the polygon spatial coverage with each grid cell linked to the habitat unit beneath the cell in the polygon coverage. I used the mean current data for the western shore of Lake Superior from Beletsky et al. (1999) for the speed and direction of travel from the current force. Dispersion was modeled by including movement in a random direction ($0^o$ to $360^o$) with a travel speed of up to 0.5 body lengths per second. The fry remained in the water column until they either entered a suitable nursery area or depleted their yolk sac reserves.

Direct observations of the amount of time lake trout can survive without exogenous food sources are not available. Twongo and MacCrimmon (1976) observed rainbow trout feeding shortly before complete absorption of the yolk sac after swim-up. Groups in the study that were deprived food 35 days past hatching suffered higher mortality than groups with food available before day 35. The elevated mortality of fry deprived of food for more than 35 days suggests that 35 days may represent the limit of yolk-sac reserves for rainbow trout fry at the study temperature (8.5°C) under laboratory conditions. I assumed that lake trout have similar yolk sac reserves as rainbow trout, and I converted days to thermal units to apply the mortality relationship with temperatures experienced by lake trout fry in the study area. If a fry did not reach a nursery area before acquiring 300 thermal units, the fry was assumed to die from starvation. Once fry arrived in a suitable nursery habitat unit, they were added to the population of that unit and did not continue to move downstream.

### Growth model

On the nursery grounds, age-0 lake trout are opportunistic feeders feeding on whatever prey are abundant and of the proper size (Martin and Olver 1980). Fry in western Lake Superior feed primarily on Mysis and dipteran larvae which are abundant in the sandy substrate areas (Carpenter et al. 1974; Johnson et al. 1998). I modeled the predator-prey interaction between lake trout and their prey in each habitat unit that contained post-dispersal lake trout fry to estimate feeding and growth rates. The predator population modeled was simply the number of lake trout fry in each habitat unit subdivided into weekly cohorts or age groups based on their week of arrival in the nursery area. Estimates of prey abundance in the nursery areas came from literature estimates of invertebrate production in Lake Superior (Carpenter et al. 1974; Johnson et al. 1998).

Mysis is the primary prey of age-0 lake trout on the nursery grounds and was modeled as a standing stock population. There would be no Mysis reproduction occurring while the lake trout are in the nursery areas, and I assumed the population was depleted as they were eaten by the juvenile lake trout (Carpenter et al. 1974). An additional prey category was included to represent dipteran larvae and copepods; this alternative prey type was fixed at a constant level and represented a relatively small proportion of the diet.

Prey consumption was calculated using a functional response model with a single predator and two prey categories. The instantaneous rate of attack of age-0 lake trout in cohort k on the prey type j was calculated as

$$A_{j,k} = \frac{a_{j,k}}{1 + \sum_{i} (a_{i,k} \cdot h_{i,k} \cdot N_{i})} \tag{13}$$

where $a_{j,k}$ is the search rate for prey type j by lake trout cohort k, and the terms in the denominator are search rates, handling times (h), and densities (N) for each of the (i = 1,2 here) alternative prey types.

I estimated maximum daily feeding rates ($C_{max}$) from hatchery feed trials (Reinitz 1980) assuming that the fry in this study were growing at a maximum rate and fed full rations. The units of consumption from Reinitz's study were converted to energy to allow application to wild prey sources. $C_{max}$ was adjusted for temperature with the algorithm from Thornton and Lessem (1978) to scale the foraging rate and growth to temperatures encountered in Lake Superior (Luecke et al. 1990). $C_{max}$ was then converted to grams of prey according to the invertebrate energy densities in the literature (Gardner et al. 1985; Cummins and Wuycheck 1971). $C_{max}$ represents the consumption required to grow at the maximum rate. The proportion of $C_{max}$ that lake trout are able to consume in a habitat unit determines the proportion of maximum growth achieved. Handling time was then calculated as

$$h = w_j / C_{max}, \tag{14}$$

the average weight of a prey item divided by the maximum daily ration.

I modeled search rates by assuming lake trout fry forage along the bottom yielding a two dimensional encounter field estimated by:

$$a_{j,k} = 2 \cdot r_{j,k} \cdot V \tag{15}$$

where $r_{j,k}$ is the reactive distance for prey type j by cohort k, and V is swimming speed which was assumed to equal 1 body length per second. No estimates of reactive distances for age-0 lake trout are available from the literature, so I used measured reactive distances for 10 cm lake trout feeding on invertebrate prey as observed by Kettle and O'Brien (1978). Kettle and O'Brien (1978) fit a regression line to develop an equation for predicting reactive distance of lake trout from prey size. I used the equations from their analysis, but transformed the absolute reactive distance to a proportion of predator body length. The resulting equation is

$$r_{j,k} = p_j \cdot L_k \tag{16}$$

where $L_k$ is the length of lake trout in cohort $k$ , and $p_j$ is the reactive distance for prey $j$ expressed as a proportion of prey body length

$$p_j = 0.0473L_j - 0.000021 \qquad (17)$$

I set the body length of Mysis at 3 mm – the modal length of new recruits in spring and summer sampling from Lake Superior (Carpenter et al. 1974). The alternative prey category can include copepods with lengths near 1 mm and invertebrate predators like *Chaoborous* that can reach several mm in length, I set the length of this category at 2 mm. I assumed that on average this alternative prey group would consist of prey slightly smaller than Mysis.

The mortality on each prey category in a habitat unit was set equal to the instantaneous rate of attack per predator times the number of predators summed over all weekly cohorts of predators.

$$Z_j = \sum A_{j,k} * N_k \qquad (18)$$

The actual consumption by each predator group was calculated as the sum of

$$C_k = \sum A_{j,k} / Z_j * (1 - e^{-Z}{}_j)*N_j * w_j \qquad (19)$$

over all prey types (Jones et al. 1993).

I modeled maximum growth as a linear process based on the daily growth increment of 0.38 mm observed in hatchery feed trials (Reinitz 1980). In the model, the lake trout growth rates were calculated as the ratio of the actual consumption over the potential maximum consumption ($C_{max}$) that was seen in these feed trials ($C_k/C_{max}$). The $C_{max}$

used in this ratio is not adjusted for temperature because growth would be slower in colder waters even if food was abundant.

Fish continued to feed and grow in the nursery areas until temperatures exceeded 15°C when the lake trout fry moved to deeper and colder water (Peck 1981).

### Juvenile and adult

After all lake trout moved out of the near-shore areas, they were pooled into an age-structured region-wide population that was updated at the end of each growing season.

$$N_{t+1,i+1} = N_{t,i} * e^{-Z_i} \tag{20}$$

where $Z$ is total annual instantaneous mortality, t is the year and $i$ is age class. I used mortality rates for ages 0-6 from Wisconsin management zones (Ebener et al. 1986). Mortality rates for ages 6-15 were management unit specific estimates derived from preliminary catch at age analysis conducted by Minnesota DNR (MNDNR 2005).

## SIMULATIONS

The model described above represents a synthesis of the limited information available regarding the role of habitat in the early life history of lake trout. With this model, I examine the direct effects of habitat conditions on population dynamics, and also investigate biological questions from a spatially explicit perspective. Below, I use the model to assess the available lake trout habitat along the Minnesota shoreline of Lake Superior and investigate hypotheses concerning the role of habitat in the recovery of wild lake trout in this region. I used the model to address six questions regarding the role of habitat in lake trout restoration in this region.

1. How does spawning habitat quality vary throughout the region?

   To address this question, I developed a map of egg survival rates (acting as a demographic indicator of habitat quality) for potential spawning sites within the substrate-mapped area of the Minnesota shore. To generate a survival index for each habitat unit, I simply set the number of eggs deposited in each unit at a constant density of 100 eggs per square meter. I ran the egg incubation sub-model for the years I compiled environment data (1983-1998), and calculated mean survival rates across all daily cohorts and years modeled for each habitat unit. These survival rates were used to generate a data layer for the GIS coverage of the study area. These simulations are independent of assumptions about how lake trout may select the available habitat and represent the quality of each habitat unit for supporting successful lake trout reproduction according to the model.

2. What, if any, are the differences in overall spawning habitat quality among the three management units?

   I also used the model to explore the influence of habitat conditions on population performance on a regional scale. For these simulations, I pooled the habitat units into the three management units along the Minnesota shore to examine how the supply of good spawning habitat might explain the observed differences in restoration success among the management units. For these simulations, I distributed a constant density of spawners across all substrate types that could possibly be used for spawning by lake trout. I distributed eggs to all habitat units with porous substrate at a constant density (100 eggs / $m^2$). Lake trout do not randomly distribute eggs across all porous substrates, but these simulations represent the average potential of spawning habitat in a unit independent of any site selection assumptions.

3. How do spawning habitat selection rules (hypotheses) affect the comparison of habitat quality among units?

The assignment of an overall measure of survival to an area that includes multiple habitat units is sensitive to the rules used for assigning females to these units. For example, if a region has a mix of high quality and low quality egg incubation habitat, the model would generate lower overall survival values if the model assumes all habitat will be used than if spawning is limited to just the high quality areas. To separate out the assumptions built into the model, I ran a series of simulations using differing assumptions about habitat use by lake trout. I ran one simulation similar to those run for the previous question except I limited egg deposition to high quality substrates of cobbles and boulders. This scenario eliminates substrate mortality as a factor, and since no density effect on habitat selection is incorporated it represents the maximum potential of the high quality substrate areas. Another set of simulations used the full density-dependent habitat selection rules of the spawning sub-model described earlier. These simulations attempt to distribute the females in a manner consistent with how we believe lake trout would use the habitat available in a given area. For these simulations, I ran the model with high and low initial spawner abundance levels to see how the management units would compare between the early stages of restoration (low spawner numbers) and a restored scenario (large spawning aggregations). For the low density simulations, I used the wild lake trout population estimates in 1989 from Negus (1995). Since 1989 was relatively early in the restoration process ( Figure 7), I thought these numbers would represent a low density situation. For the high density simulations, I multiplied the level of wild lake trout in Negus (1995) by 20.

4. How do the hypothesized differences between hatchery and wild fish habitat selection affect the assessment of habitat quality?

To address this question with the model, I ran simulations at high and low densities of spawners using the density-dependent habitat selection rules and compared incubation survival rates between wild- and hatchery-produced cohorts. For the low density levels, I set the number of adult lake trout at the abundance level of wild lake trout in 1989 as estimated in Negus (1995) (Table 1). For the high density level, I set the number of adult lake trout at the combined abundance level of hatchery and wild lake trout in 1989 as estimated by Negus (1995) multiplied by 2 (Table 1). These simulations test for the potential for depth preferences, which are presumed to differ between hatchery and wild fish, to affect lake trout reproductive success given the habitat conditions along the Minnesota shoreline.

5. Under what conditions (e.g., spawner/egg abundances) could fry rearing habitat become limiting?

Most discussions of lake trout habitat in the Great Lakes focus on the supply and quality of spawning habitat. I wanted to use this model to help determine if nursery habitat has the potential to limit lake trout population growth. For the western portion of the management units, I ran simulations assuming high quality substrate was filled at the rate of 500 eggs/$m^2$. I consider this scenario a high or maximum productivity level for the spawning areas in MN1 (west) and MN2 (central). To model egg deposition rates that are scaled to a reasonable level for the Minnesota shore, I used the combined stocked and wild lake trout abundance at age estimates from Negus (1995) and distributed the eggs that could be produced by this population to all high quality substrate in the mapped areas of MN1 and MN2. The estimates in Negus (1995) are for the entire Minnesota shoreline, so by concentrating them in just MN1 and MN2 I allowed for some error and for population growth beyond the current estimated level. I then generated the feeding rates and growth of fry in the nursery and compared growth rates from these simulations to growth rates when prey abundance is not limiting.

6. How do the predicted rates of restoration (growth of wild populations) compare among the three management units, and is this comparison consistent with observed patterns?

In order to address this question, I used my model to simulate population growth of wild lake trout for each of the management units along the Minnesota shore. Since I wanted to compare these simulations to observed indices of population growth, I used the relative survival results from my early life history sub-model, the stocking history along the Minnesota shore, and published mortality rates to project wild population growth. I started the simulations with no wild fish in the population assuming that along the Minnesota shore the initial establishment of wild populations was driven by successful reproduction of hatchery fish. I built up a hatchery spawning stock by applying mortality rates to the fish stocked into each of the management units. I then used my model to estimate wild recruitment at age-0 from eggs deposited by hatchery spawners. I tracked the abundance of hatchery and wild origin lake trout in the simulation, but both populations contributed to production of wild recruits according to the spawning site selection rules described for the spawning sub-model. For years prior to 1983 and after 1998, I randomly selected a set of environmental conditions observed from 1983-1998. These simulations result in projected wild populations that I compared to indices of population abundance from the Minnesota DNR assessment program.

## RESULTS

### Spatial variation in spawning habitat quality

Habitat unit-specific survival rates for deposited eggs (my indicator of habitat quality) vary widely throughout the region (Maps 1 -14). Individual units with high survival rates exist across the entire shoreline of Minnesota. The easternmost areas (in MN3) have a higher proportion of the habitat units with high survival values (Table 2). There are several units with high survival in MN1 and MN2, but they represent a smaller proportion of the mapped area in these two management units (Table 2). The easternmost area also has relatively few habitat units with very low (< 0.1) survival rates, while a large part of the mapped area in MN1 has low survival levels (Table 2).

### Comparisons of overall survival among management units

Across all years, the estimated survival was consistently higher in MN3 than the other management units when I assumed all hard substrate types were used for spawning (Table 3). In this scenario, the consistent difference between MN3 and the other management units was due to greater relative availability of lower quality but potentially suitable substrates like cracked bed rock in MN1 and MN2. For these simulations, predicted egg survival was higher in MN3 for all years simulated. Predicted survival for MN2 was higher than MN1 in 13 of the 15 years simulated, but the magnitude of difference was small (< 0.01) (Table 3).

When I limited the available spawning habitat to only high quality substrates of cobble and boulder, the relative difference between management units changed slightly. Predicted survival rates were higher for all management units compared to the previous simulations. Predicted survival in MN3 was still higher than MN1 and MN2 in most years (MN1 was higher than MN3 in 2 years) (Table 4). In these simulations, MN1 survival rates were higher than MN2 predicted survival rates in all years, and the magnitude of the difference was meaningful (> 0.03).

When I invoked the density dependent wild fish distribution rules to determine what habitat units would be used for spawning, the survival estimates for all management units were intermediate between the simulations with only high quality substrate being used and those where all porous substrates were used (Table 5 ). The model predicted higher survival rates in MN3 than the other two management units in nearly all years and, the mean differences between MN3 and MN1 and MN2 were 0.08 and 0.07 respectively (Table 5). The differences amongst the management units were similar between the high and low density simulations (Table 5). MN2 showed the strongest density dependence effect, but the mean difference in incubation survival (over all years) between these high and low density levels was small (0.006).

Wind-induced mortality was highest in MN3, followed by MN2, and MN1 had the lowest overall wind mortality (Figure 10). In contrast, MN2 consistently had the highest level of sediment induced mortality, while this source of mortality was consistently zero or close to zero in MN3 (Figure 10). No management unit had the lowest survival for all the mortality types. MN1 had the lowest wind induced mortality, but had fairly high sediment induced mortality. MN2 had fairly high sediment and wind induced mortality which combine to make projected egg survival low in this area.

### Egg survival of hatchery vs. wild lake trout

The distribution of spawning fish generated by the model show some degree of overlap between hatchery and wild fish (Figure 11 and 12). In general though, differences in the patterns do exist between hatchery and wild fish. Wild fish tend to spawn deeper wherever there is available spawning substrate in deeper water along the Minnesota shore. The depth distributions of hatchery and wild fish are nearly completely separate under the low density simulations, but under the high density simulations, a larger proportion of the spawners spawned in deeper water. Some wild fish will spawn in shallow water and some hatchery fish will spawn in deeper water, but the wild spawning distributions show higher densities in deeper water versus shallow water than the hatchery spawner distributions. In general, the simulations that used the hatchery spawner distribution rules predicted a lower egg incubation survival than eggs distributed according to the wild site selection rules (Table 6 and 7) for both the high and low density simulations although variation existed between management units (Figure 13). The eggs distributed with the hatchery distribution rules realized a higher predicted egg survival in MN1 than the eggs distributed with the wild distribution rules under the low density simulations although the difference was small (0.005). In MN2, eggs distributed under the hatchery distribution rules realized higher survival at high spawner densities than at low spawner densities. The depth distribution of spawners in MN2 changed dramatically when spawner densities were increased. Under the low density simulations, 90% of the eggs were deposited in the 16 to 20 foot depth range while under the high density simulations the eggs were spread out between 10 and 25 feet (Figure 12).

### Habitat limitations at the fry stage

The dispersal model resulted with fry being well distributed among the sandy nursery areas. Several units received no fry, while a few had extremely high densities of fry. The latter tended to be small units so the absolute number of fry in these units was low and had little influence on mean values for the management unit. The travel times for lake trout to reach nursery areas were all short. Most fish arrived at a nursery area within 5 days and the maximum travel time was 16 days, so no cohorts died because of starvation before reaching a nursery area.

Mean length in the nursery areas increased slowly for the first few weeks as new cohorts arrived in the nursery area and temperatures remained cool. Growth then increased and continued at a fairly steady rate until the nursery feeding period ended in early fall. Predicted growth rates for the high egg density scenario were lower than the growth rate that would be expected if the fry were able to eat at the maximum level in both MN1 and MN2 nursery areas (Figures 14 and 15). Final length of fry at the moderate egg deposition level were also below the maximum level, and the mean size at the end of the feeding period was 11% less than the ultimate length if feeding rates were not limiting lake trout growth during this period.

### Predicted rates of population restoration

The full life-cycle simulations resulted with wild populations in all three units becoming established shortly after stocked fish reached maturity. Figure 16 shows the estimated populations of age 3 to 6 lake trout for each management unit. I chose to plot age 3 to 6 lake trout because these are the age groups targeted in the small mesh gill net survey conducted by MNDNR and lake trout age data is limited for this survey. The model estimated that the population in MN3 grew the fastest followed by MN-2, and MN-1 had the slowest overall population growth. The MN-1 and MN-2 populations increased at similar rates until 1985 when MN-2 began to increase at a faster rate than MN-1. MN-3 grew at a faster rate than the other two units as soon as the lake trout planted from the first stocking events reached maturity. Small mesh gill net catches of wild lake trout along the Minnesota shore indicate that wild lake trout populations in MN3 have increased faster than the other two units and that wild lake trout densities are highest in this unit (Figure 7).

## DISCUSSION

Potential lake trout habitat along the Minnesota shore is spatially variable with regard to wave exposure, sedimentation rates, and substrate composition. When I simulated the early life history of lake trout under varying population conditions, it became apparent that spatial heterogeneity could influence the patterns in lake trout restoration along the Minnesota shore.

I assembled egg survival estimates for potential lake trout spawning areas along the Minnesota shore. These values go beyond the availability of suitable substrate, and incorporate additional climatic and spatial components that determine the suitability of a location for producing lake trout fry. Being able to determine which locations are most important to protect for lake trout reproduction increases the probability of maintaining adequate spawning sites in the presence of other activities that could alter habitat, such as dredging for harbors and shipping channels.

The eastern most area of the Minnesota shoreline (MN3) has an abundance of locations that could be considered high quality spawning habitat. These sites have suitable substrate and low levels of sediment mortality. The deeper areas are of the highest overall quality because of the lower levels of wind induced mortality than in the shallow areas. The central area (MN2) has only a small amount of substrate that could be considered high quality spawning habitat. If maintaining a lake trout population in this region is important, more care must be taken to protect the limited high quality spawning habitat that is available than in the other units.

When the individual habitat units are aggregated to the level of management unit we notice some distinct patterns with regards to egg incubation survival. Across all of the egg incubation simulations I ran, predicted survival was consistently higher in MN3 than the other units. A major reason for the higher levels of predicted survival in MN3 is the large amount of hard porous substrate and the low level of sediment sources in the area. Large areas of sand and smaller particles are common in MN1 and MN2, but almost completely absent in MN3 which results in higher egg survival rates in this management unit. My model predicted higher egg survival rates in MN3 than the other management units under low spawning densities and when eggs were distributed to only high quality substrate areas. When eggs were distributed to only the high quality substrate areas, the differences in survival were due to factors other than the quantity of available spawning substrate. In my analysis, exposure to wave events and proximity to sediment sources affected the overall quality of spawning site in addition to the presence of substrate with deep interstitial spaces.

Our understanding of where lake trout will choose to spawn is limited as is our knowledge of what areas supported lake trout spawning prior to the lake trout population crash. The assumptions we make about how lake trout will determine where to spawn influence the potential egg survival rates. We cannot just assume that lake trout will spawn in areas with the highest potential for egg survival because some of the factors that influence egg survival are not observable when spawning site selection occurs. In fact, I do not believe we can even assume that lake trout will select the best spawning substrate available. In my simulations using the wild spawner distribution rules, predicted egg survival was lower than in the simulations where spawning was limited to the highest quality substrate even when spawner densities were extremely low. My model does not include and egg density effect on survival, so the differences in predicted survival are due to spawning site selection.

In my simulations of wild lake trout, increasing spawner density reduced overall egg survival in each management unit although the effect was small. I assumed that at higher densities lake trout would disperse to other, potentially less desirable spawning sites. Although I think this approach is reasonable and defensible, it is not clear how lake trout would respond to increasing densities. In inland lakes, lake trout will maintain large spawning aggregations and not use all of the potential spawning areas available (Gunn 1995, Kelso 1995). If lake trout in the Great Lakes behave in a similar manner, it relates to my analysis in two ways. I may underestimate the density dependent effect since the only density dependent mechanism I include is that lake trout will move to other, potentially less suitable, spawning locations when density increases. It is possible that lake trout will deposit an excess of eggs in an area that will lead to higher levels of mortality directly. Mechanisms for the reduction in survival could be loss of egg retention if interstitial spaces are filled or increased fungal growth or anoxic conditions due to the high egg densities. Additionally, I think the work in inland lakes indicates that we have a limited understanding of why lake trout select certain areas for spawning. Gunn (1995) blocked access to historic spawning areas; the lake trout spawners eventually found other places to spawn and realized equivalent levels of incubation survival. There may be factors in addition to spawning substrate and depth that determine where lake trout spawn, so, potentially, my analysis may have included potential spawning sites that lake trout would not use for spawning and underestimated the influence of increasing density.

Some data and analysis suggests that other factors could limit lake trout populations in Lake Superior. Survival of stocked lake trout throughout Lake Superior and Minnesota waters has been decreasing (Hansen et al 1994, MNDNR 2004). Hatchery reared lake trout are stocked as yearlings, and are not affected by any of the survival factors I explicitly consider in my model. Observed decreases in growth rates (Sitar et al. 2003) and the decline of the smelt forage base suggest that factors other than spawning habitat may limit lake trout populations (Bronte 2003).

Several analyses in Lake Superior have suggested that wild lake trout contribute more to recruitment than stocked lake trout (Schram et al. 1995b; Hansen et al. 1997). Wild lake trout also tend to select deeper water for spawning than hatchery lake trout. I tested the hypothesis that the differences in spawning site selection between hatchery and wild lake trout can cause the observed differences in reproductive success. In nearly all cases, eggs deposited by wild spawners realized equal or higher survival than eggs deposited by hatchery fish. The site selection rules integrate substrate, depth, and spawner density to determine where lake trout will deposit eggs. Wild lake trout use a depth distribution that favors deeper water than hatchery fish. The spatial distribution of spawning habitat selection generated from my model shows some degree of overlap between hatchery and wild fish, but where deeper sites are available wild fish on average spawned in deeper water than hatchery fish.

Because they incubate in deeper water, the eggs deposited by wild fish incur lower wind-shock mortality (orbital velocity at the substrate-water interface is a function of water depth). The rules for spawning site selection, wind patterns, and depth distribution of suitable substrate all combine to yield higher survival values for eggs deposited by wild fish in the model. The higher relative survival of wild eggs is consistent across all of the management units, but is greatest in MN3. The reason for the largest degree of difference in MN3 is that wind shock mortality comprises a larger percentage of the total incubation mortality than in the other management units, and potential spawning sites with suitable substrates exist throughout the depth range of the mapped area.

The depth preference criteria in the model are based on the depth of capture of mature lake trout on spawning reefs. The reason wild lake trout use deeper sites is not completely clear. It could be that hatchery lake trout, based on their rearing, seek out shallow areas for spawning (Foster 1984), whereas wild lake trout have search preference for deep water. An alternative hypothesis is based on the spawning site fidelity of lake trout. Lake trout throughout their range tend to spawn in shallow water where wave action cleans sediment off of the gravel and cobbles (Gunn 1995). Lake trout seek areas with clean rock and deep interstitial spaces. In the Great Lakes, however, very shallow areas are not suitable for incubating eggs because of ice scour and wind induced wave disturbance (Fitzsimons 1994; Eshenroder 1995). Wave disturbance is more substantial in these deep lakes with long open water fetches. Assuming strong site fidelity by lake trout, wild reared lake trout may simply be returning to where they successfully emerged. Since survival is ultimately higher in deeper water, we will generally see wild lake trout return to deeper water than fish that did not emerge from the gravel and are using innate spawning site preferences. If this latter hypothesis is correct, my model could be underestimating the difference in survival between hatchery and wild fish since it only uses a depth rule for differentiating site selection between wild and hatchery fish. Wild fish should actually be selecting sites that have had success at producing fry, and the densities are likely to be proportional to the relative survival of each site.

In MN2, my estimates of survival for eggs deposited by hatchery fish increased with increasing density. Since egg survival is a function of depth, it appears that as density increased the spawner distribution rules caused the lake trout to seek out additional areas for spawning. In MN2, this resulted in spawners being distributed to sites with depths on the edges of hatchery spawner depth preference curve (Figure 7). This result suggests that the potential for hatchery fish to produce wild fry will increase as adult densities increase.

The fry transport and early feeding simulations I ran for the western areas of the Minnesota shore used a high level of egg density in spawning sites and assumed high survival for the lake trout fry after emergence. In these simulations, most of the cohorts in the nursery areas were still able to feed at the maximum rate once the maximum feeding rate was adjusted for temperature for the first several weeks in the nursery area. As the fry grew in the nursery area, their feeding demands increased and growth decreased below the maximum growth level. The moderate egg density level, which is still a high estimate for the region, produced fry that grew close to the maximum rate and the weight of these fry ended up being nearly 90% of fry allowed to consume a maximum ration.

Several conditions account for the low predation pressure relative to the prey availability in the nursery areas. One reason is the vast amount of sandy substrate along the western Minnesota shoreline. Several large tracts of sand are present in this area, so very little of the total area consists of small isolated habitat units that would be more prone to harboring high densities of fry. The lake trout fry are very small when they arrive in these nearshore nursery areas and only remain for a limited amount of time. The temperatures in these nursery areas are low; I set the maximum ration from feed trials conducted at 11° and the temperature in the nursery area when lake trout arrive rarely exceeds 6°C. As the season progresses, the water warms and lake trout grow, increasing their energetic demands. Lake trout do not remain in the nursery areas for very long; as the fall approaches, they move to deeper water and will probably move deeper earlier if temperatures and thus growth are higher. We do not have detailed data on the substrate composition beyond the range of the mapped area, but it is possible that there are sandy-bottomed areas that are greater in magnitude than the near-shore area. Mysis populations also become denser in deeper water. Carpenter (1971) estimated Mysis populations exceeding 200 /m$^2$ in Lake Superior waters greater than 100 meters deep. The size of Mysis offshore and later in the season will also be greater than the shallow areas in the spring.

My model indicates that the potential exists for Mysis densities in shallow areas to be depleted by lake trout predation and result in a density dependent growth response in the soft bottomed nursery areas. However, I think it is reasonable to consider that if lake trout move to deeper water near the end of the summer, they may also move deeper if food was not available in the shallow nursery areas. If they are able to move earlier than the end of summer, and the invertebrate densities are much higher in deeper water, then it is unlikely that lake trout populations along the Minnesota shoreline will be limited by the availability of nursery habitat. If the fish do remain in shallow areas despite food limitations, conditions could exist that would result in slower growth in the nursery areas.

If the size of age of age 0 lake trout is limited by food supply, then they could be more vulnerable to predation and over-winter mortality than they would be if they reached their maximum growth potential.

The full life cycle simulations run with this model project that wild population growth rates vary by management unit. In order to provide realistic simulations it was necessary to have data on the stocking history and adult mortality rates in each of the management units. My model projected that the MN3 population would grow the fastest due to low adult mortality rates and higher levels of egg survival than the other management units. This result is consistent with the trends seen in the lake trout assessments along the Minnesota shore. The model also predicted that MN1 and MN2 would have similar rehabilitation rates, until MN2 started to grow faster than MN1. My model estimates higher egg survival in MN1 than MN2 when I use the hatchery spawner distribution rules at low densities. MN1 has experienced higher fishing mortality rates which has slowed the rate of rehabilitation relative to the other units.

My model predicted that the wild lake trout populations would grow immediately after the first stocked fish reached maturity. The model predicts a faster rate of recovery than the assessment data indicate. This model tries to account for the role habitat and climate conditions in the rate of population growth. Jonas et al. (2005) show that egg predators can cause high mortality on lake trout eggs in Lake Michigan. Furthermore, they found a saturation level for predators suggesting that the importance of egg predation is higher when egg densities are low. If egg predation is also important in Lake Superior, then rehabilitation would be slower initially because of low egg densities until hatchery stocks grew from many years of stocking. I also do not include any requirements for accumulating large spawning aggregations for successful spawning. When spawner numbers are low, reproduction could be depressed because of low fertilization rates and potentially higher egg predation rates.

I used this model to explore the possibility that the difference in the rate of restoration between the management units along the Minnesota shore could be explained by differences in the habitat supply in these management units. My model predicts population performance as a function of habitat. References in the fisheries literature to quality lake trout spawning habitat tend to focus on substrate type. The substrate characteristics and population trends along the Minnesota shore of Lake Superior suggest that additional factors must affect lake trout population trends. The conditions of substrate along the Minnesota shoreline run from large amounts of fine sediment in the west along a continuum to primarily hard substrate types in the eastern most area. Population trends, however, have not followed this continuum. The eastern most area (MN3) has realized the fastest population growth; the central area (MN2) and western area (MN1) have realized similar rates of population growth well below the rate seen in MN3 (figure 7). Furthermore, the differences in population growth show up almost immediately in the restoration process. If the rate of population growth were simply a function of the amount of cobble and boulder substrate, we wouldn’t expect to see a difference in rates of population growth at low population densities because the few lake trout that were in the area would not be sufficient to saturate the available high quality substrate and need to use less desirable spawning substrate. The patterns in restoration and the immediate difference indicate that something else is affecting population performance, and can cause a difference in reproductive success even though the substrate at spawning sites is similar.

The scenarios I ran to explore this hypothesis suggest that geographic location and proximity to sediment sources can affect the survival of incubating lake trout eggs and, therefore, the rate of population growth. Under all of the scenarios run, the eastern most habitat units had higher predicted egg survival values. One reason for this result is the absence of a source of fine sediment near the potential spawning sites. The difference was greatest when spawners were limited to only the highest quality substrates, which is where we would expect lake trout to spawn under low population densities.

## Incorporating spatial elements into biological models

In fisheries management, we are ultimately concerned with biological processes such as growth, recruitment, and mortality. These processes, however, are often dependent upon or driven by non-biological factors, such as physical processes, geology, and climatic conditions.

For this thesis, I've developed a modeling framework for incorporating spatially explicit habitat data into a model of lake trout recruitment dynamics and population performance. This model has allowed me to address hypotheses regarding the patterns in lake trout restoration seen along the Minnesota shoreline of Lake Superior. This approach differs from much of the habitat modeling work that has been done in fisheries in that I directly link habitat features to population processes (i.e., survival ), and incorporate spatial location as a characteristic of the available habitat. The spatially explicit structure of the model allows for the inclusion of factors that affect habitat quality, but are not intrinsic qualities of the actual spawning site. I attempted to include climatological phenomena that only appear when the eggs are actually incubating. This model also allows us to consider the importance of habitat conditions near the spawning area.

Lake trout rehabilitation in the Great lakes other than Lake Superior has been largely unsuccessful. Our current understanding suggests that mortality between egg deposition and the first year of life is likely responsible for recruitment failures (Jones et al. 1995, Savino et al. 1999). Despite this understanding, very few attempts have been made to develop a framework for integrating potentially important factors into an understanding of mortality and the potential for successful lake trout rehabilitation (Jonas et al 2005). This modeling exercise attempts to develop such a structure to integrate the information on biological processes, physical processes, and habitat availability on the recruitment dynamics for Lake Superior.

Unfortunately, the ultimate value of this type of approach is limited by our understanding in each of these areas. In this exercise, I simulate potential mechanisms that could determine the reproductive potential of areas along the Minnesota shore. In several instances in this exercise I have been confronted with limted information on biological responses. For example, I used a literature estimate of 35% to estimate the impact of a temporary smothering event. Certainly the degree of mortality will vary and in some cases could be as low as 0% survival. The impact of windshock mortality was similar. Although several references refer to the existence of windshock mortality (Eshenroder et al. 1995, Fitzsimons et al. 1994), only one study in Lake Ontario tried to quantify the mortality level. I believe these shortcomings are part of the research process. As we compile more specific quantitative information we will be able to make better use of tools that integrate multiple sources of information. At the same time, we must continue to develop our tools to make better use of the available information and to help determine what information is necessary to improve our understanding of biological systems.

# APPENDIX A.  TABLES AND FIGURES

Table 1. Annual mortality rates (MNDNR 2004) and estimated abundance of stocked and wild lake trout (Negus 1995) along the Minnesota shore of Lake Superior

| | **Annual Mortality Rate** | | | **Population Abundance** | |
|---|---|---|---|---|---|
| **Age** | **MN1** | **MN2** | **MN3** | **Wild** | **Stocked** |
| 0 | 0.9 | 0.9 | 0.9 | 1,107,767 | 54,000 |
| 1 | 0.24 | 0.24 | 0.24 | 114,100 | 371,000 |
| 2 | 0.12 | 0.12 | 0.12 | 36,860 | 160,360 |
| 3 | 0.12 | 0.12 | 0.12 | 14,647 | 60,861 |
| 4 | 0.12 | 0.12 | 0.14 | 31,664 | 242,314 |
| 5 | 0.15 | 0.15 | 0.17 | 24,860 | 183,487 |
| 6 | 0.19 | 0.19 | 0.19 | 8,740 | 68,225 |
| 7 | 0.43 | 0.28 | 0.30 | 9,842 | 139,162 |
| 8 | 0.43 | 0.28 | 0.30 | 2,096 | 50,388 |
| 9 | 0.43 | 0.28 | 0.30 | 1,670 | 20,147 |
| 10 | 0.43 | 0.28 | 0.30 | 551 | 14,936 |
| 11 | 0.43 | 0.28 | 0.30 | 124 | 6,690 |
| 12 | 0.43 | 0.28 | 0.30 | 133 | 3,777 |
| 13 | 0.43 | 0.28 | 0.30 | 62 | 1,865 |
| 14 | 0.43 | 0.28 | 0.30 | 49 | 918 |
| 15 | 0.43 | 0.28 | 0.30 | 23 | 448 |

Table 2. Proportion of area of potential spawning substrates in survival categories for each management unit along the Minnesota shore.

| | **Management Unit** | | |
|---|---|---|---|
| **Egg Survival Index** | **MN1** | **MN2** | **MN3** |
| < 0.6 | 0.05 | 0.11 | 0.03 |
| 0.06 -0.12 | 0.50 | 0.34 | 0.18 |
| 0.12 - 0.18 | 0.18 | 0.09 | 0.16 |
| 0.18 - 0.24 | 0.00 | 0.01 | 0.00 |
| 0.24 - 0.30 | 0.02 | 0.13 | 0.29 |
| 0.30 - 0.36 | 0.05 | 0.11 | 0.00 |
| 0.36 - 0.42 | 0.00 | 0.02 | 0.00 |
| 0.42 - 0.48 | 0.01 | 0.02 | 0.05 |
| >= 0.48 | 0.18 | 0.16 | 0.29 |

Table 3. Mean egg survival index for Minnesota management units in Lake Superior when eggs were distributed at a constant density amongst all porous substrates.

| | Management Unit | | |
|---|---|---|---|
| Spawning Year | **MN1** | **MN2** | **MN3** |
| 1983 | 0.268 | 0.275 | 0.335 |
| 1984 | 0.304 | 0.308 | 0.337 |
| 1985 | 0.301 | 0.310 | 0.339 |
| 1986 | 0.277 | 0.284 | 0.317 |
| 1987 | 0.295 | 0.302 | 0.331 |
| 1988 | 0.291 | 0.297 | 0.324 |
| 1989 | 0.296 | 0.301 | 0.307 |
| 1990 | 0.302 | 0.308 | 0.333 |
| 1991 | 0.303 | 0.307 | 0.347 |
| 1992 | 0.275 | 0.280 | 0.346 |
| 1993 | 0.277 | 0.286 | 0.327 |
| 1994 | 0.299 | 0.305 | 0.335 |
| 1995 | 0.288 | 0.296 | 0.331 |
| 1997 | 0.299 | 0.298 | 0.315 |
| 1998 | 0.289 | 0.290 | 0.338 |
| **Mean** | **0.291** | **0.296** | **0.331** |

Table 4. Mean egg survival index for Minnesota management units in Lake Superior when eggs were distributed at a constant density to substrates of cobbles and boulders.

| | Management Unit | | |
|---|---|---|---|
| **Spawning Year** | **MN1** | **MN2** | **MN3** |
| 1983 | 0.423 | 0.397 | 0.503 |
| 1984 | 0.495 | 0.451 | 0.506 |
| 1985 | 0.488 | 0.453 | 0.509 |
| 1986 | 0.440 | 0.412 | 0.471 |
| 1987 | 0.489 | 0.447 | 0.501 |
| 1988 | 0.482 | 0.438 | 0.491 |
| 1989 | 0.488 | 0.445 | 0.462 |
| 1990 | 0.491 | 0.451 | 0.498 |
| 1991 | 0.492 | 0.450 | 0.523 |
| 1992 | 0.437 | 0.405 | 0.522 |
| 1993 | 0.441 | 0.413 | 0.487 |
| 1994 | 0.486 | 0.447 | 0.503 |
| 1995 | 0.463 | 0.431 | 0.494 |
| 1997 | 0.485 | 0.435 | 0.468 |
| 1998 | 0.465 | 0.421 | 0.508 |
| **Mean** | **0.471** | **0.433** | **0.496** |

Table 5. Index of egg survival for eggs distributed following the wild spawner distributions rules at high and low densities.

| | Low Density | | | High Density | | |
|---|---|---|---|---|---|---|
| **Spawning Year** | **MN1** | **MN2** | **MN3** | **MN1** | **MN2** | **MN3** |
| 1983 | 0.362 | 0.359 | 0.485 | 0.344 | 0.357 | 0.480 |
| 1984 | 0.425 | 0.450 | 0.494 | 0.423 | 0.440 | 0.496 |
| 1985 | 0.416 | 0.437 | 0.504 | 0.423 | 0.437 | 0.493 |
| 1986 | 0.318 | 0.384 | 0.451 | 0.369 | 0.378 | 0.451 |
| 1987 | 0.409 | 0.411 | 0.490 | 0.410 | 0.428 | 0.489 |
| 1988 | 0.407 | 0.387 | 0.483 | 0.408 | 0.413 | 0.475 |
| 1989 | 0.393 | 0.438 | 0.458 | 0.418 | 0.424 | 0.437 |
| 1990 | 0.444 | 0.461 | 0.485 | 0.416 | 0.442 | 0.487 |
| 1991 | 0.453 | 0.466 | 0.517 | 0.422 | 0.435 | 0.515 |
| 1992 | 0.355 | 0.389 | 0.513 | 0.359 | 0.370 | 0.507 |
| 1993 | 0.364 | 0.353 | 0.490 | 0.359 | 0.368 | 0.465 |
| 1994 | 0.431 | 0.435 | 0.487 | 0.412 | 0.437 | 0.488 |
| 1995 | 0.428 | 0.398 | 0.481 | 0.392 | 0.401 | 0.478 |
| 1997 | 0.392 | 0.412 | 0.393 | 0.411 | 0.405 | 0.447 |
| 1998 | 0.388 | 0.430 | 0.493 | 0.396 | 0.385 | 0.495 |
| **Mean** | **0.399** | **0.414** | **0.482** | **0.397** | **0.408** | **0.480** |

Table 6. Index of egg survival for eggs distributed following the wild vs. hatchery spawner distributions rules at low densities. Spawner density for these simulations was set equal to the estimates of wild fish from Negus (1995).

| | Wild Distribution Rules | | | Hatchery Distribution Rules | | |
|---|---|---|---|---|---|---|
| **Spawning Year** | **MN1** | **MN2** | **MN3** | **MN1** | **MN2** | **MN3** |
| 1983 | 0.362 | 0.359 | 0.485 | 0.333 | 0.248 | 0.446 |
| 1984 | 0.425 | 0.450 | 0.494 | 0.445 | 0.321 | 0.442 |
| 1985 | 0.416 | 0.437 | 0.504 | 0.419 | 0.314 | 0.455 |
| 1986 | 0.318 | 0.384 | 0.451 | 0.346 | 0.253 | 0.393 |
| 1987 | 0.409 | 0.411 | 0.490 | 0.434 | 0.306 | 0.437 |
| 1988 | 0.407 | 0.387 | 0.483 | 0.419 | 0.293 | 0.423 |
| 1989 | 0.393 | 0.438 | 0.458 | 0.414 | 0.279 | 0.379 |
| 1990 | 0.444 | 0.461 | 0.485 | 0.446 | 0.324 | 0.432 |
| 1991 | 0.453 | 0.466 | 0.517 | 0.449 | 0.310 | 0.473 |
| 1992 | 0.355 | 0.389 | 0.513 | 0.352 | 0.260 | 0.452 |
| 1993 | 0.364 | 0.353 | 0.490 | 0.352 | 0.250 | 0.413 |
| 1994 | 0.431 | 0.435 | 0.487 | 0.441 | 0.322 | 0.440 |
| 1995 | 0.428 | 0.398 | 0.481 | 0.394 | 0.297 | 0.418 |
| 1997 | 0.392 | 0.412 | 0.393 | 0.432 | 0.309 | 0.387 |
| 1998 | 0.388 | 0.430 | 0.493 | 0.390 | 0.279 | 0.470 |
| **Mean** | **0.399** | **0.414** | **0.482** | **0.404** | **0.291** | **0.431** |

Table 7. Index of egg survival for eggs distributed following the wild vs. hatchery spawner distributions rules at high densities. Spawner density for these simulations was set equal to the estimates of hatchery fish from Negus (1995) multiplied by two.

| | **Wild Distribution Rules** | | | **Hatchery Distribution Rules** | | |
|---|---|---|---|---|---|---|
| **Spawning Year** | **MN1** | **MN2** | **MN3** | **MN1** | **MN2** | **MN3** |
| 1983 | 0.347 | 0.359 | 0.485 | 0.288 | 0.304 | 0.446 |
| 1984 | 0.439 | 0.434 | 0.488 | 0.388 | 0.392 | 0.446 |
| 1985 | 0.426 | 0.429 | 0.490 | 0.352 | 0.366 | 0.449 |
| 1986 | 0.358 | 0.369 | 0.450 | 0.300 | 0.314 | 0.383 |
| 1987 | 0.413 | 0.423 | 0.486 | 0.373 | 0.375 | 0.438 |
| 1988 | 0.410 | 0.403 | 0.468 | 0.366 | 0.355 | 0.411 |
| 1989 | 0.427 | 0.420 | 0.437 | 0.378 | 0.349 | 0.380 |
| 1990 | 0.422 | 0.439 | 0.479 | 0.397 | 0.407 | 0.417 |
| 1991 | 0.431 | 0.429 | 0.509 | 0.380 | 0.383 | 0.459 |
| 1992 | 0.364 | 0.374 | 0.503 | 0.303 | 0.311 | 0.462 |
| 1993 | 0.367 | 0.369 | 0.467 | 0.304 | 0.319 | 0.403 |
| 1994 | 0.416 | 0.424 | 0.484 | 0.372 | 0.363 | 0.428 |
| 1995 | 0.387 | 0.402 | 0.471 | 0.350 | 0.349 | 0.393 |
| 1997 | 0.417 | 0.405 | 0.449 | 0.377 | 0.354 | 0.372 |
| 1998 | 0.390 | 0.388 | 0.497 | 0.346 | 0.330 | 0.456 |
| **Mean** | **0.401** | **0.404** | **0.477** | **0.352** | **0.351** | **0.423** |

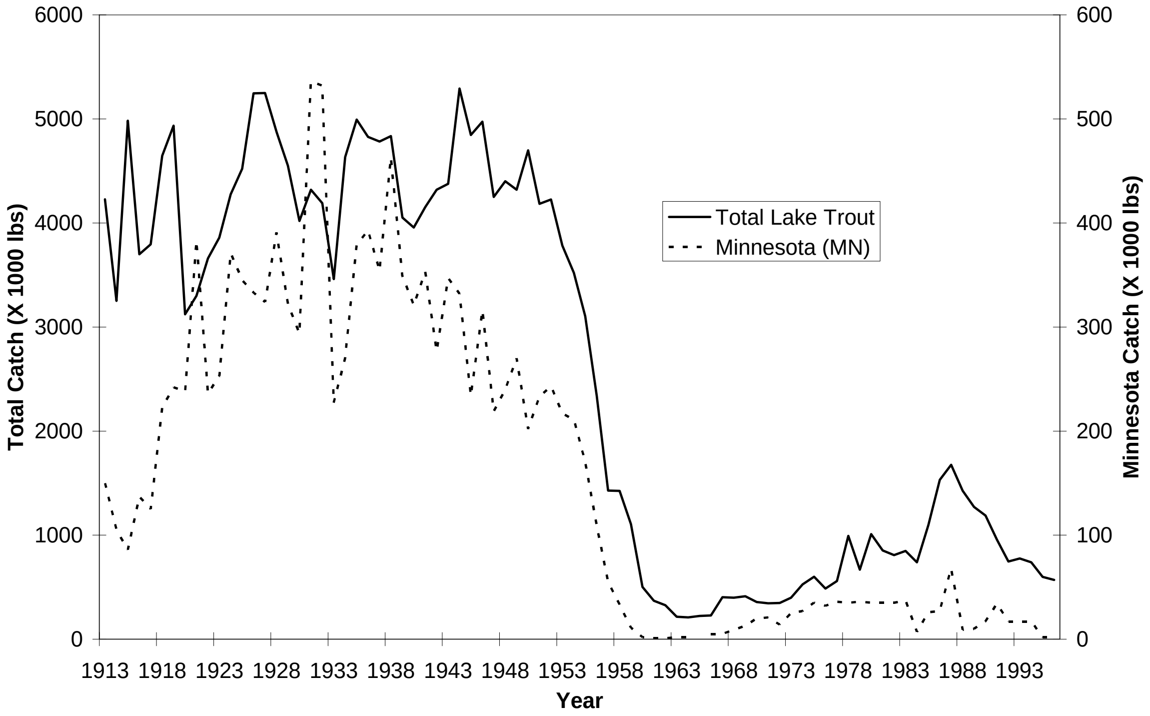


Figure 1. Total commercial catch of lake trout in all of Lake Superior and the Minnesota waters of Lake Superior from 1913 to to 1996. Total catch includes United States and Canadian reported landings.

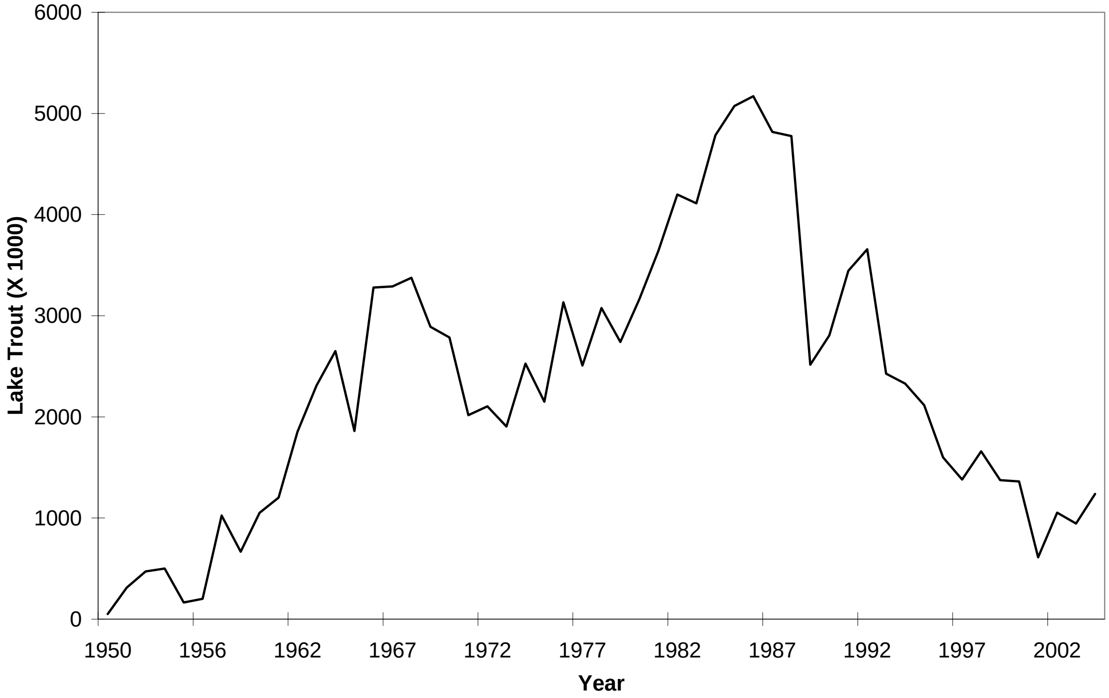


Figure 2. Number of lake trout stocked into Lake Superior.

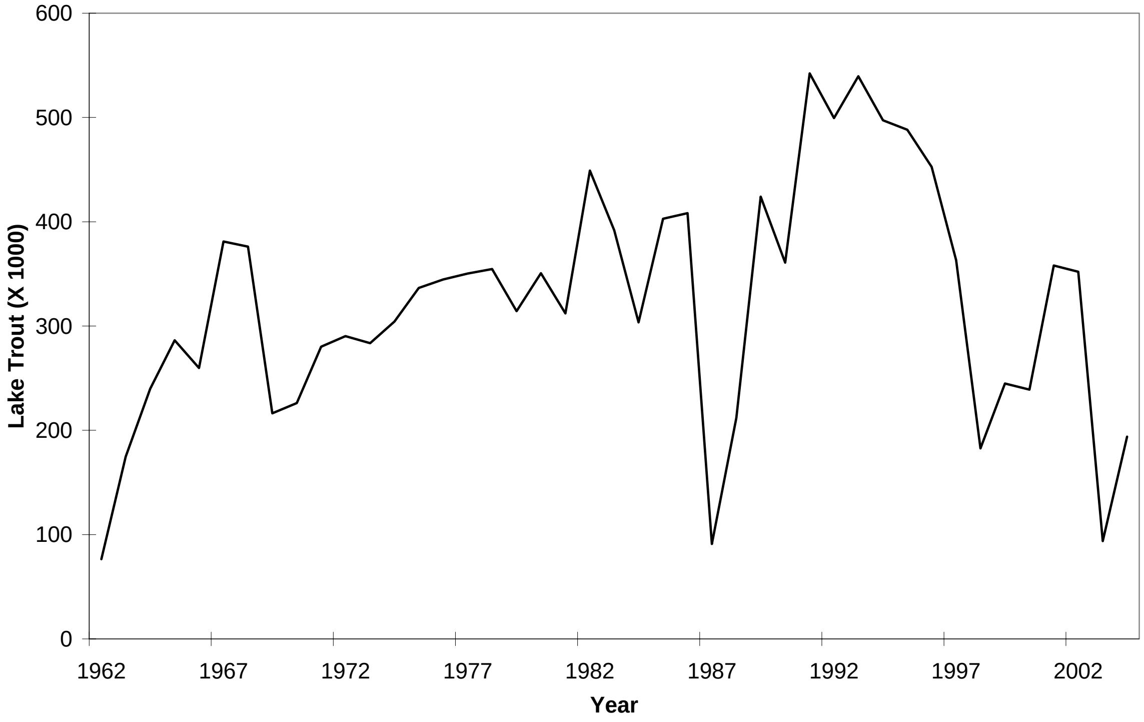


Figure 3. Number of lake trout stocked into the Minnesota waters of Lake Superior.

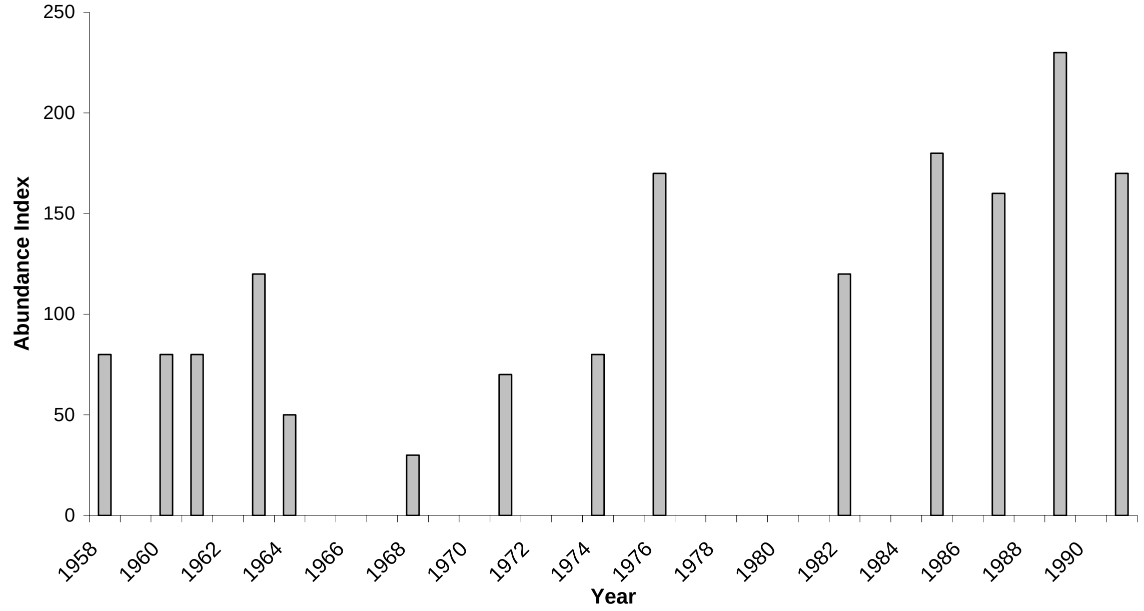


Figure 4. Index of abundance of juvenile lake trout (fish per km of small graded mesh gillnet) off of Isle Royale(Hansen et al. 1992). No stocking of lake trout took place in this area.

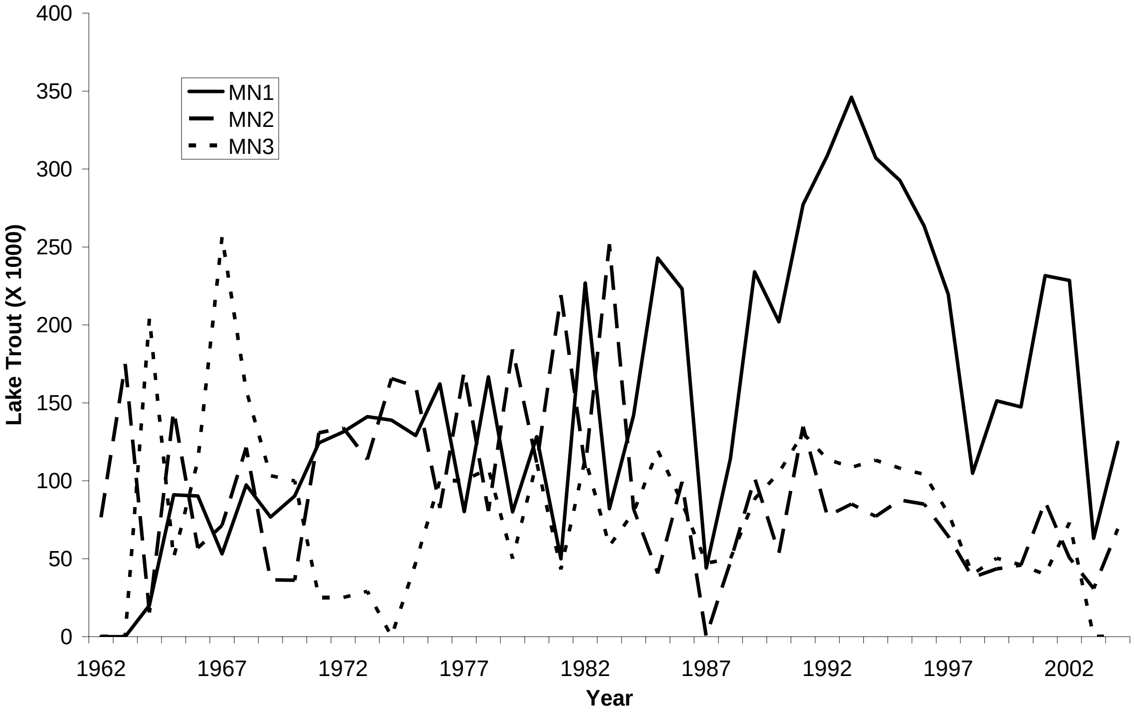


Figure 5. Number of lake trout stocked into the Minnesota management units of Lake Superior.

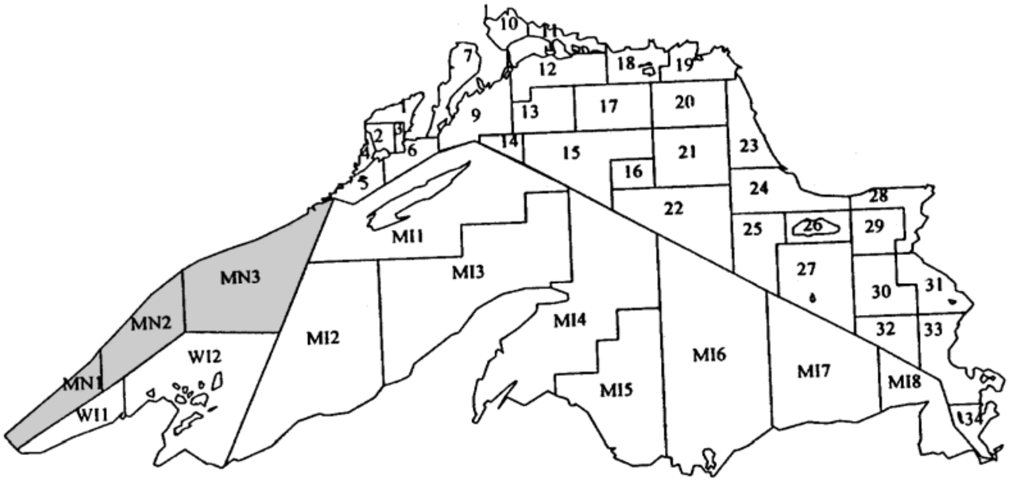


Figure 6. Lake trout management units for Lake Superior. This study addresses the Minnesota management units which are highlighted in gray.

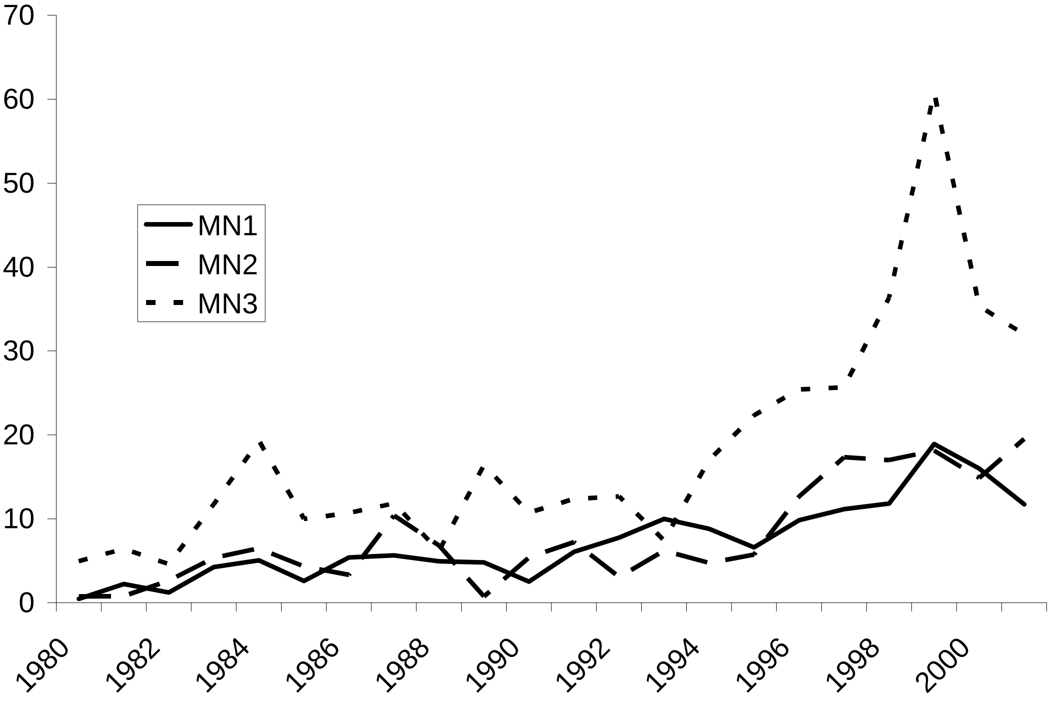


Figure 7. Smallmesh gillnet CPE of wild lake trout for management units in Minnesota waters of Lake Superior.

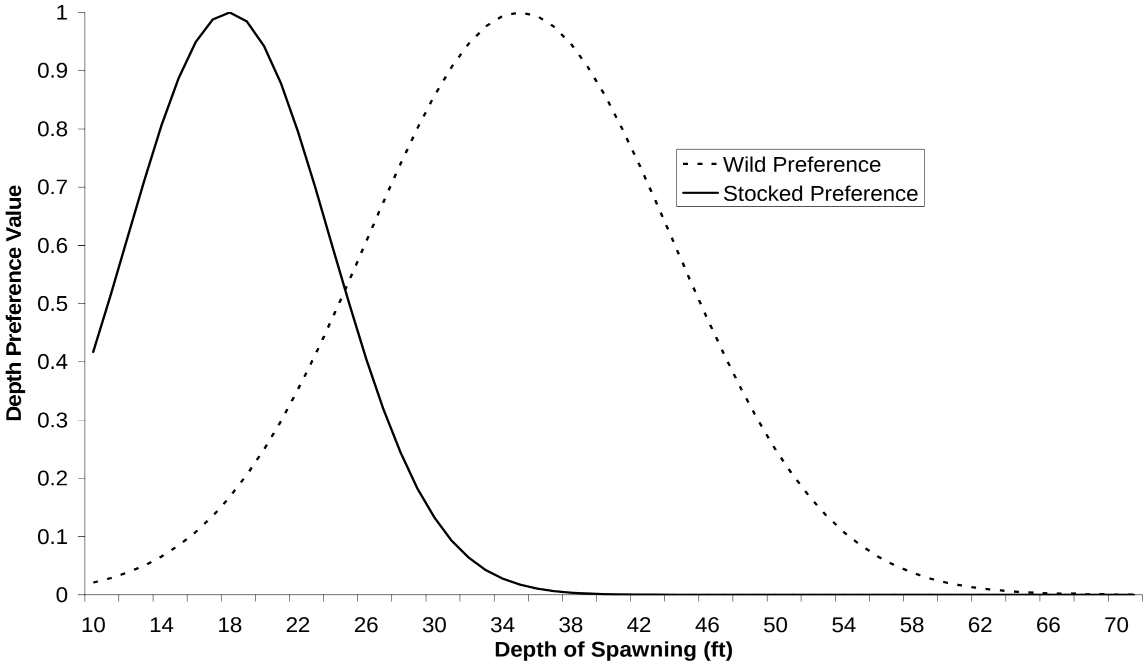


Figure 8. Depth factor of the habitat selection value of a potential spawning habitat. The curves were fit to data from the Keweenaw Peninsula area of Lake Superior (Ebener et al. 1990) with adjustments made to the wild distribution to account for the limited depth distribution of the data.

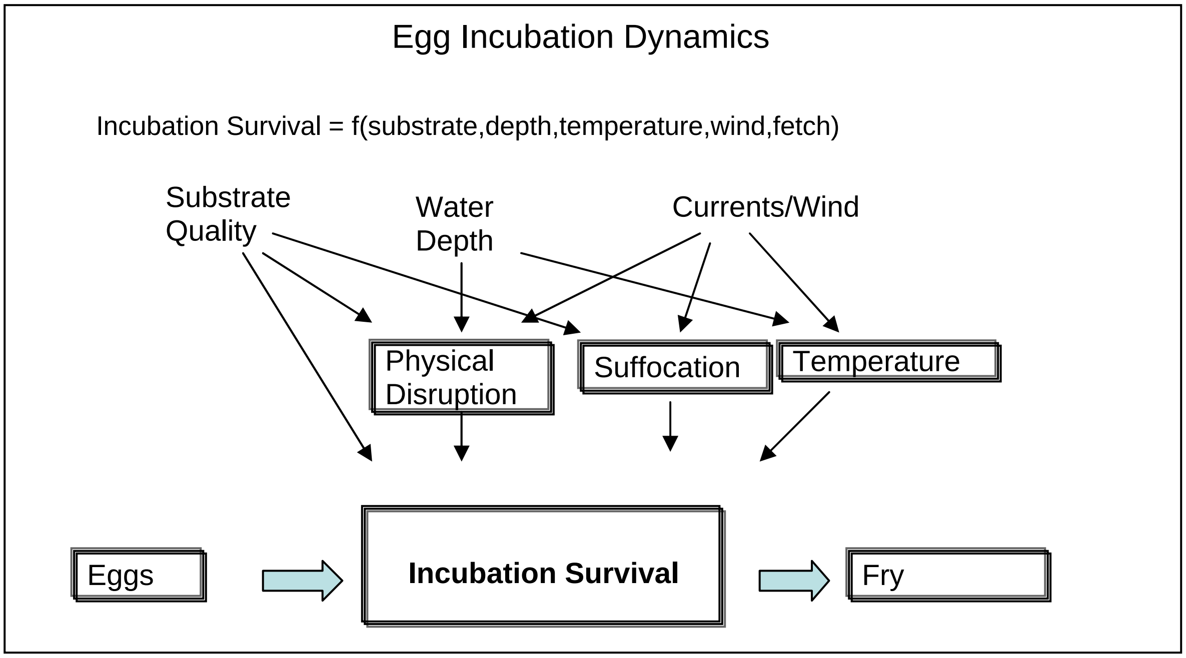


Figure 9. Schematic showing the physical factors affecting incubation survival and the interactions incorporated into the model.

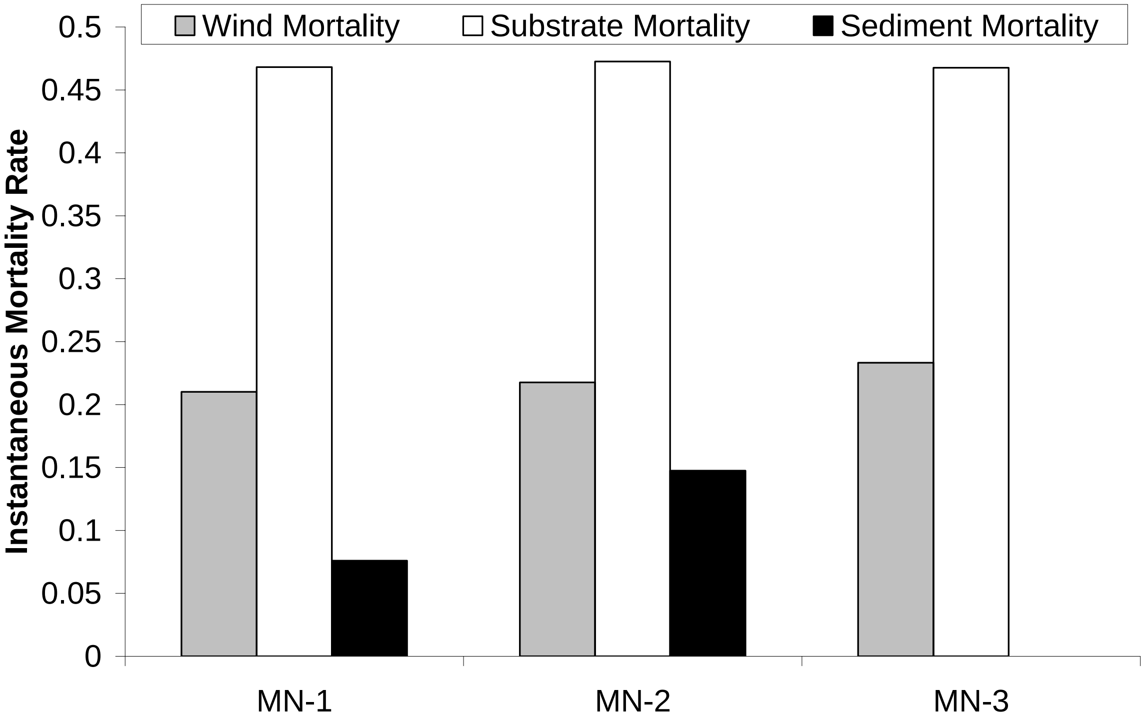


Figure 10. Egg incubation mortality components for each management unit along the Minnesota shore. For these simulations, eggs were distributed at a uniform density to substrates of cobble and boulder.

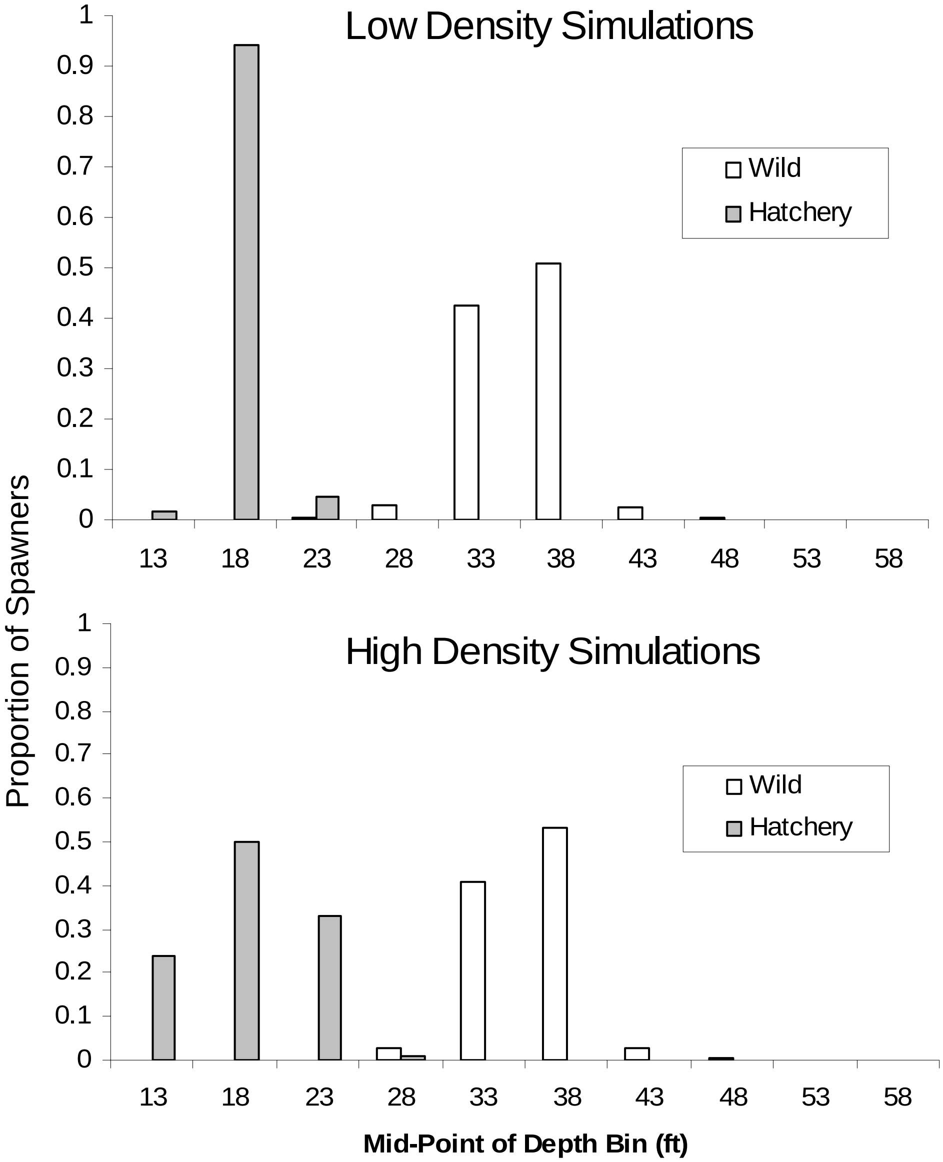


Figure 11. Depth distribution of hatchery and wild spawning lake trout averaged across the entire Minnesota shoreline.

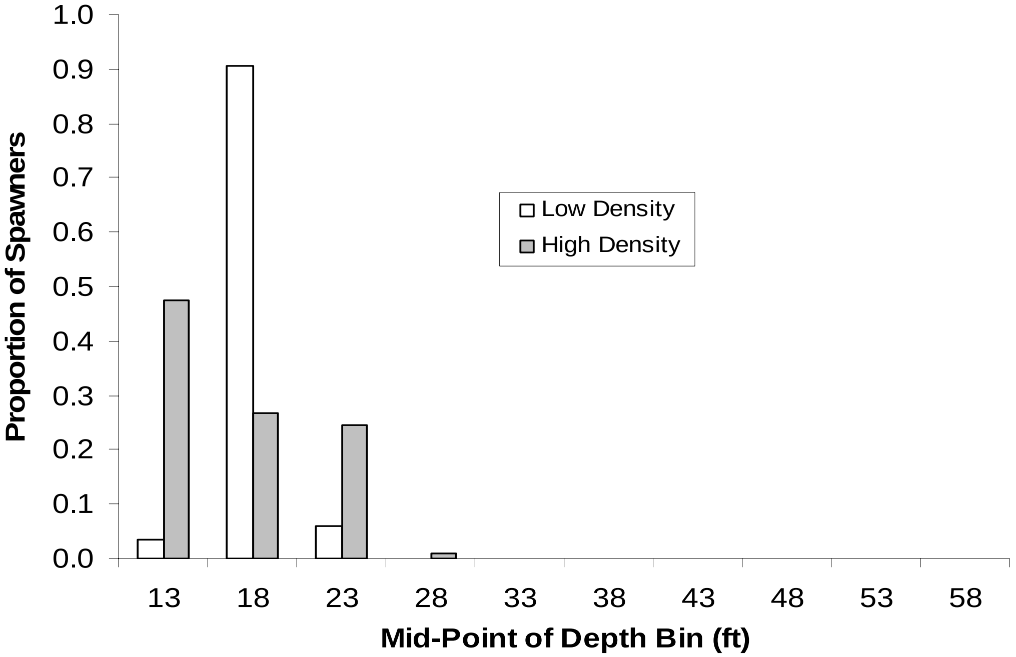


Figure 12. Comparison of the depth distribution of hatchery spawners in MN2 between high and low spawner densities

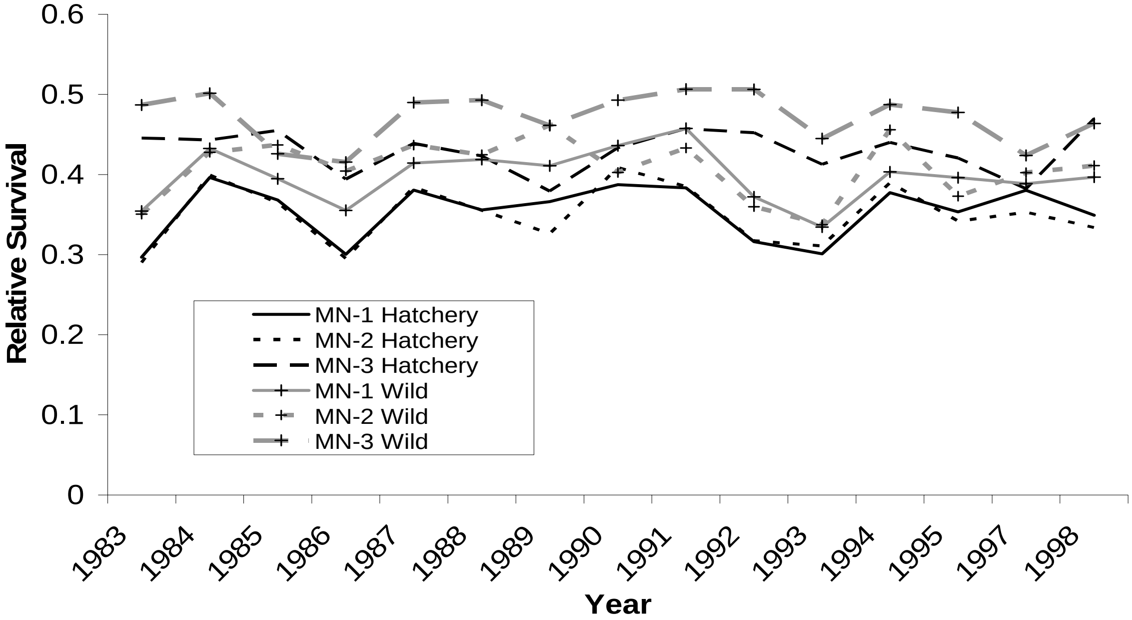


Figure 13. Overall survival values for habitat units in the three management units in Minnesota waters of Lake Superior for lake trout eggs distributed according to the hatchery and wild distribution rules.

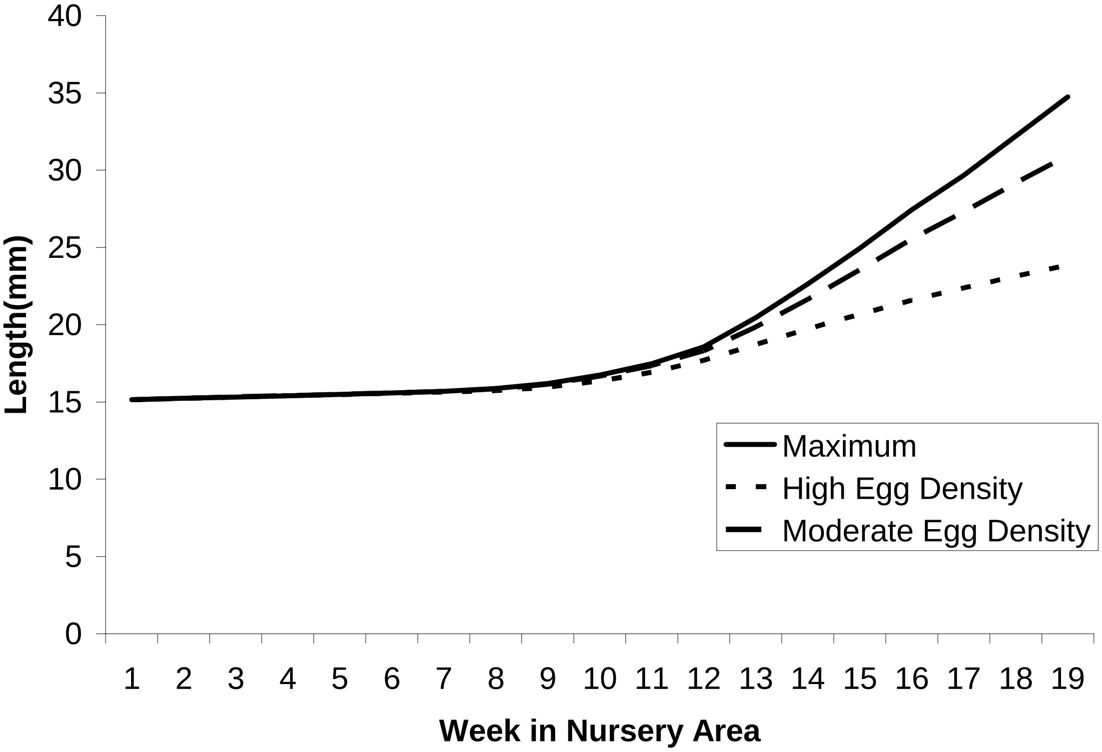


Figure 14. Projected length of lake trout fry in the nursery areas of MN-1. Maximum represents the growth level when fry area ble t consume their maximum daily ration. High egg density assumes egg deposition rates of 500 eggs per meter squared, and moderate egg density is equivalent to the eggs produced by the entire Minnesota populaion from Negus (1995). Both scenarios assume all cobble and boulder substrates are used for spawning.

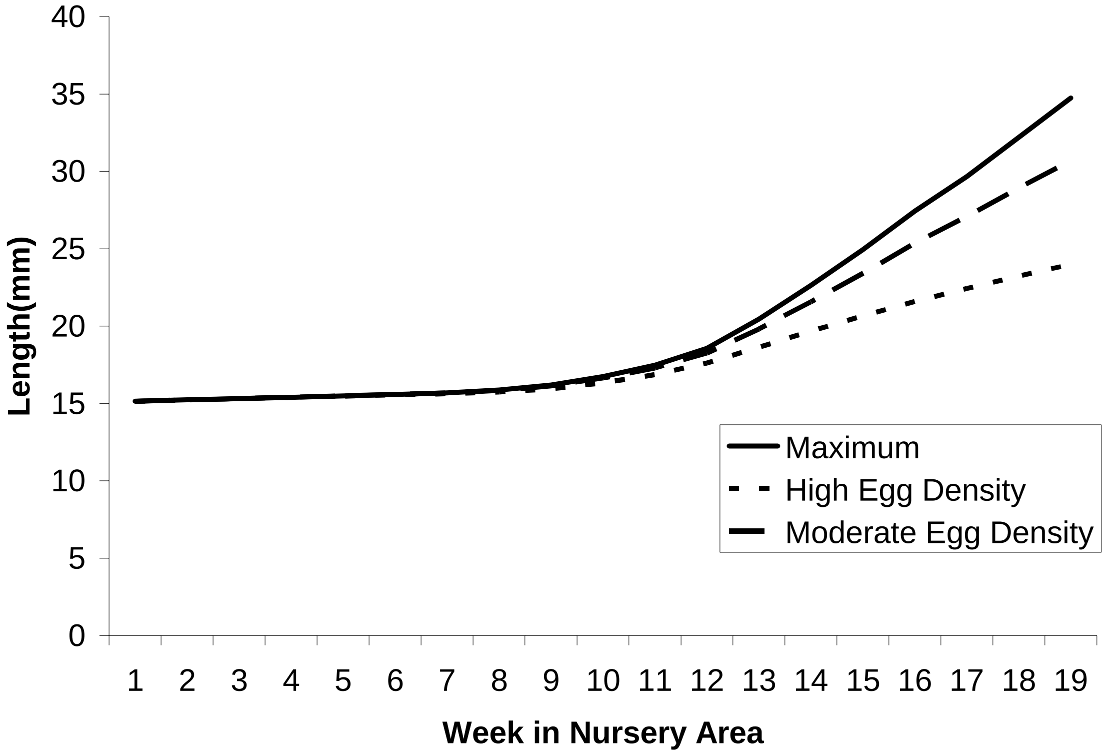


Figure 15. Projected length of lake trout fry in the nursery areas of MN-2. Maximum represents the growth level when fry area ble t consume their maximum daily ration. High egg density assumes egg deposition rates of 500 eggs per meter squared, and moderate egg density is equivalent to the eggs produced by the entire Minnesota populaion from Negus (1995). Both scenarios assume all cobble and boulder substrates are used for spawning.

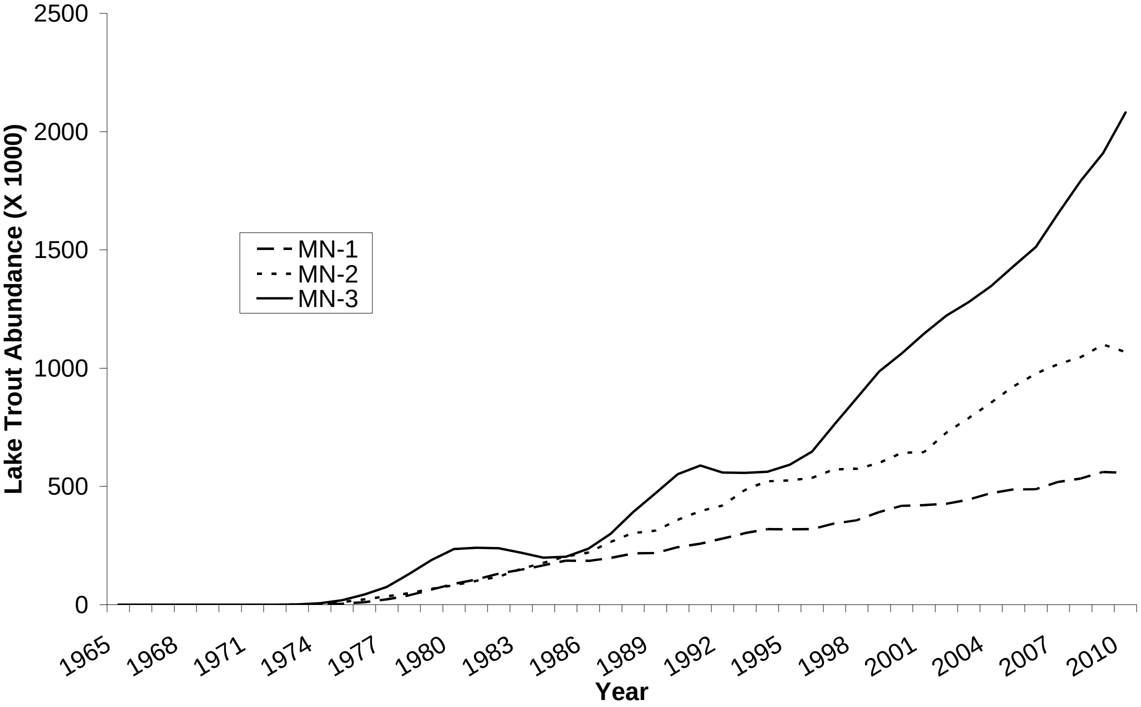


Figure 16. Model predicted wild lake trout population abundance (Ages 3-6).

# APPENDIX B.  PHYSICAL MODELING

Methods for estimating orbital velocity from wind speed

To determine if the wind conditions are sufficient to damage eggs incubating in a habitat unit, I needed to calculate the conditions at the water substrate interface as a function of windspeed and physical conditions. The maximum fluid velocity ($v_{max}$) at the water-substrate interface is

$$V_{\max} = \frac{\omega H}{2\sinh(\frac{2\pi d}{L})} \qquad (1)$$

where H is the wave height, ω is the angular velocity, d is the local depth, and L is the wave length (Hallermeier 1981). Wave conditions are monitored in the basin of Lake Superior by unmanned offshore buoys. These stations, however, do not operate during the winter months when lake trout eggs are incubating in the substrate; therefore, I estimated wave height from

$$H_S = \left[ 0.283 \tanh\left( 0.53 \left( \frac{gD}{U^2} \right)^{0.75} \right) \tanh\left( \frac{0.0125 \left( \frac{gF}{U^2} \right)^{0.42}}{\tanh\left( 0.53 \left( \frac{gD}{U^2} \right)^{0.75} \right)} \right) \right] * \frac{U^2}{g} \qquad (2)$$

where $H_S$ is the significant wave height, U is the wind speed, F is the open water fetch, D is the mean depth along the fetch length, and g is gravitational acceleration(Kang et al. 1982). The significant wave height is the average height of the one third largest waves in a wave train, and is commonly used to represent the conditions of a wave train. Wind speed (U) measurements were from the NOAA climate station DISW-3 on Devil's island. Open water fetch (F) is estimated in the model by an algorithm that essentially draws a line from the habitat unit into the wind direction and records the distance to where that line crosses the Lake Superior shoreline. The Euclidean distance between the points is calculated using the equation:

$$\sqrt{(x_1 - x_2) + (y_1 - y_2)} \tag{3}$$

The function for $H_S$ asymptotes with increasing depth; any wind blowing over Lake Superior to the Minnesota shore is not going to be depth limited. Wind that does not blow from the east is going to come overland and be fetch limited. Therefore, I set D as a constant at a high value so that depth would not limit wave development.

The angular wave frequency ω is equal to 2π / T, where T is the wave period. Wave period can also be estimated from wind conditions using the equation from Kang et al. (1982):

$$T_S = \left[ 1.2 \tanh\left( 0.833 \left( \frac{gD}{U^2} \right)^{0.375} \right) \tanh\left( \frac{0.0125 \left( \frac{gF}{U^2} \right)^{0.25}}{\tanh\left( 0.833 \left( \frac{gD}{U^2} \right)^{0.375} \right)} \right) \right] * \frac{2\pi U}{g} \tag{4}$$

Wave length (L) cannot be directly estimated. Kang et al. (1982), however, show that

$$L = L_o \tanh(\frac{2\pi d}{L}) \tag{5}$$

where:

$$L_o = \frac{gT^2}{2\pi}. \tag{6}$$

An iterative method is used to find the value of L that meets these constraints.

To relate water velocity conditions to the survival of lake trout eggs, I used observations of lake trout egg survival in Lake Ontario (Fitzsimons et al. 1995) and the water velocity calculations described above. Fitzsimons et al. (1995) measured the survival of lake trout eggs on spawning reefs in Lake Ontario. Using the mean depth and fetch from each location, and the maximum wind speed encountered during the eggs' susceptible phase of development, I calculated the maximum orbital velocity encountered by the eggs in each unit, and plotted this against the survival values from Fitzsimons et al. (1995) after removing the mortality due to other factors yielding the following relationship

$$S = 0.9113e^{-0.283v_{max}} \tag{7}$$

where S is egg survival through epiboly and $v_{max}$ is the maximum orbital velocity encountered at the water-substrate interface during the period the eggs were in their susceptible stage of development.

Methods for determining if sediment deposition occurs in a habitat unit

Wind induced turbulence can cause the resuspension of sediments from the substrate (Bailey and Hamilton 1997 ; Bennett 1987 ;Lick et al. 1994).
Hallermeir (1981) used the principles described above to derive the following equation for determining the critical wave conditions necessary to cause motion of substrate particles:

$$H_{min} = \frac{2v_s \sinh(\frac{2\pi d}{L})}{\omega} \tag{8}$$

where $H_{min}$ is the minimum wave height to cause resuspension of particles of size s. I calculated $H_{min}$ and $H_S$ for each habitat unit containing fine substrates. If $H_S > H_{min}$, a resuspension event is assumed to take place and areas down current are covered with sediment. The maximum range of the effect of the sediment re-suspension is calculated by:

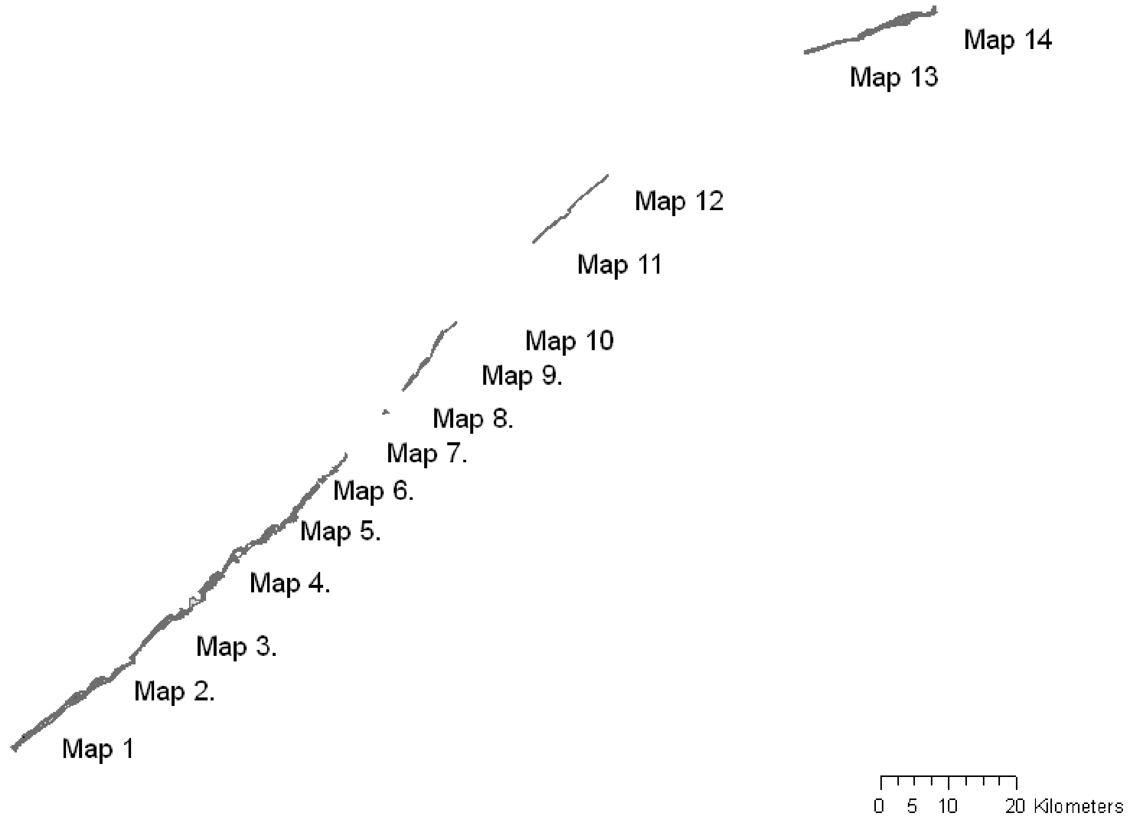
$$T = 0.75 * D/V_p \tag{9}$$

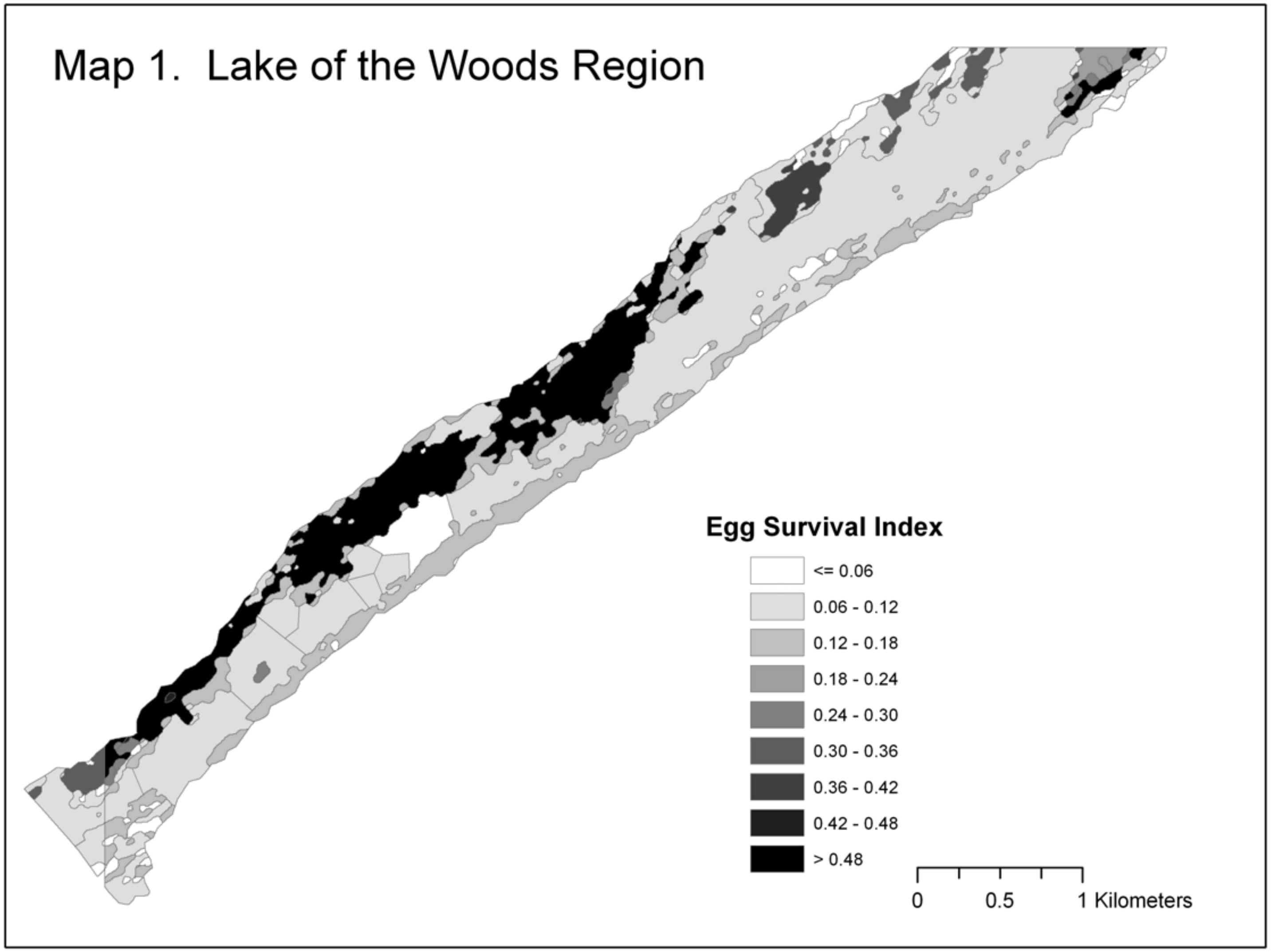
$$\text{Distance} = T * V_c \tag{10}$$

where D is water depth, T is the time the particles are traveling in suspension, $V_p$ is the particle settling velocity, $V_c$ is the current velocity. The spread of sediment is modeled as a plume that results in a triangle covering all of the affected areas. All grid cells within that triangle are assumed to have a sediment-smothering event occur which results in higher egg mortality.

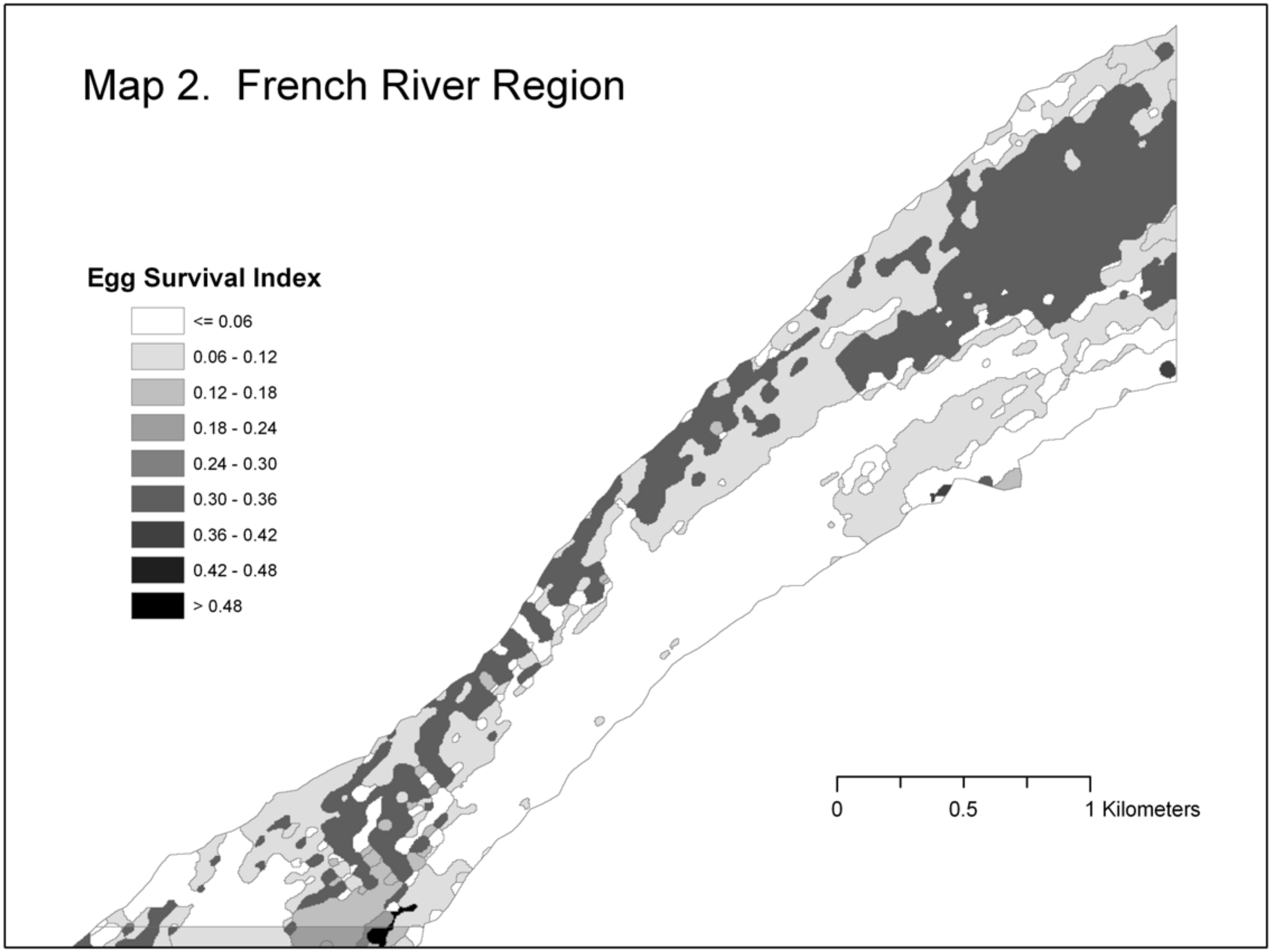
# APPENDIX C. EGG SURVIVAL MAPS FOR MINNESOTA SHORE

## Index of regional maps for Minnesota Shore of Lake Superior

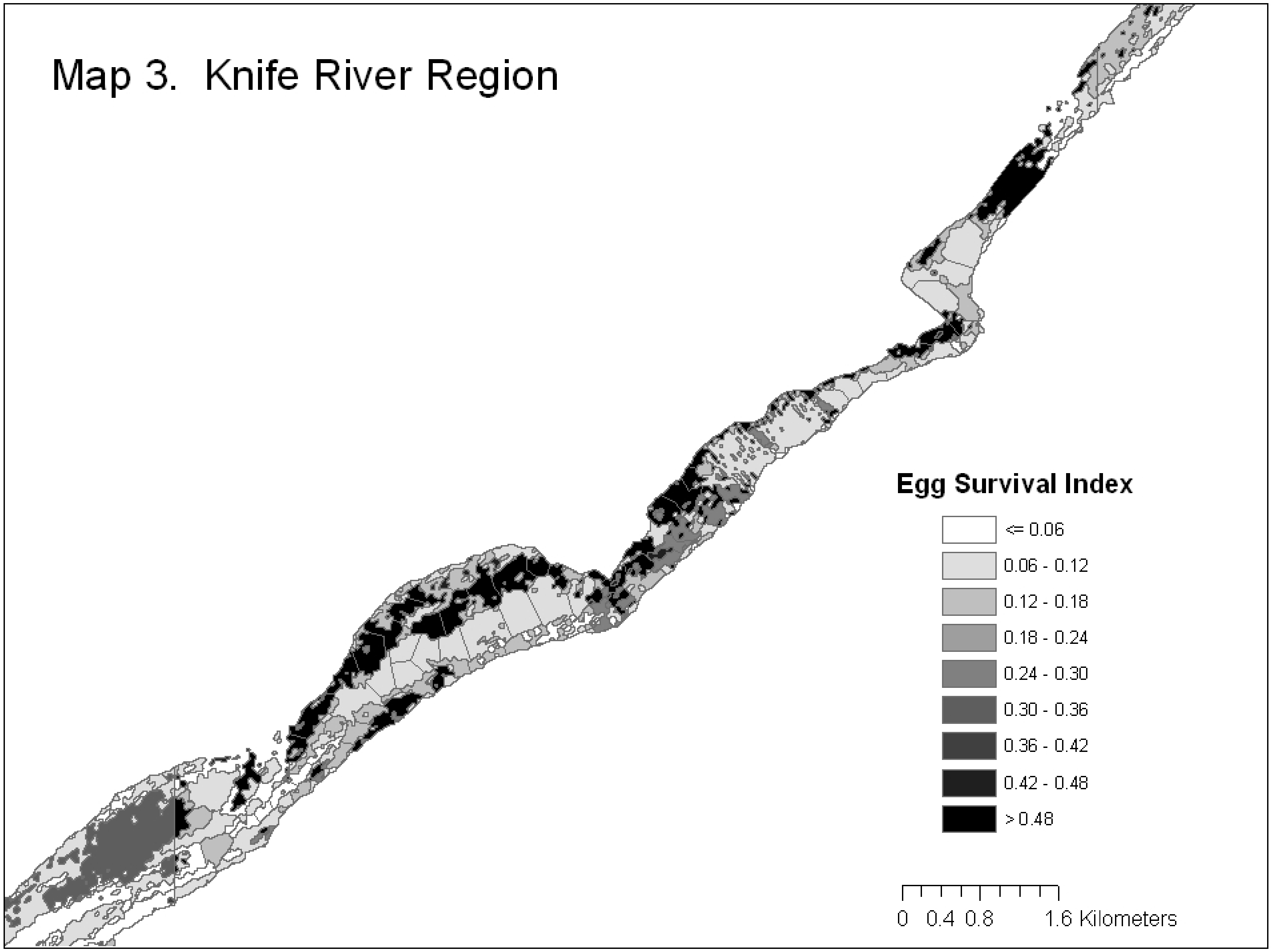




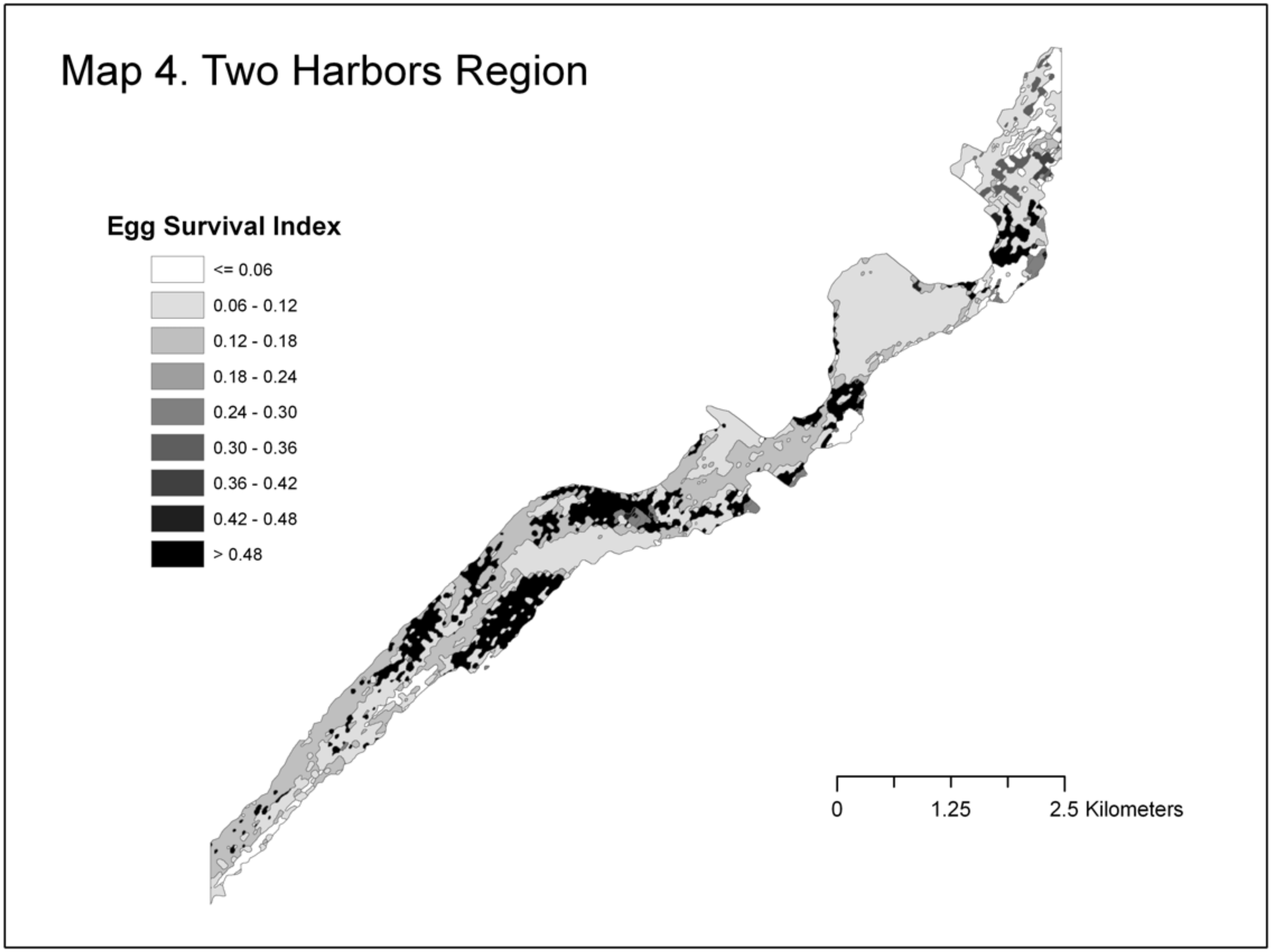
Map 1. Lake of the Woods Region



Map 2. French River Region

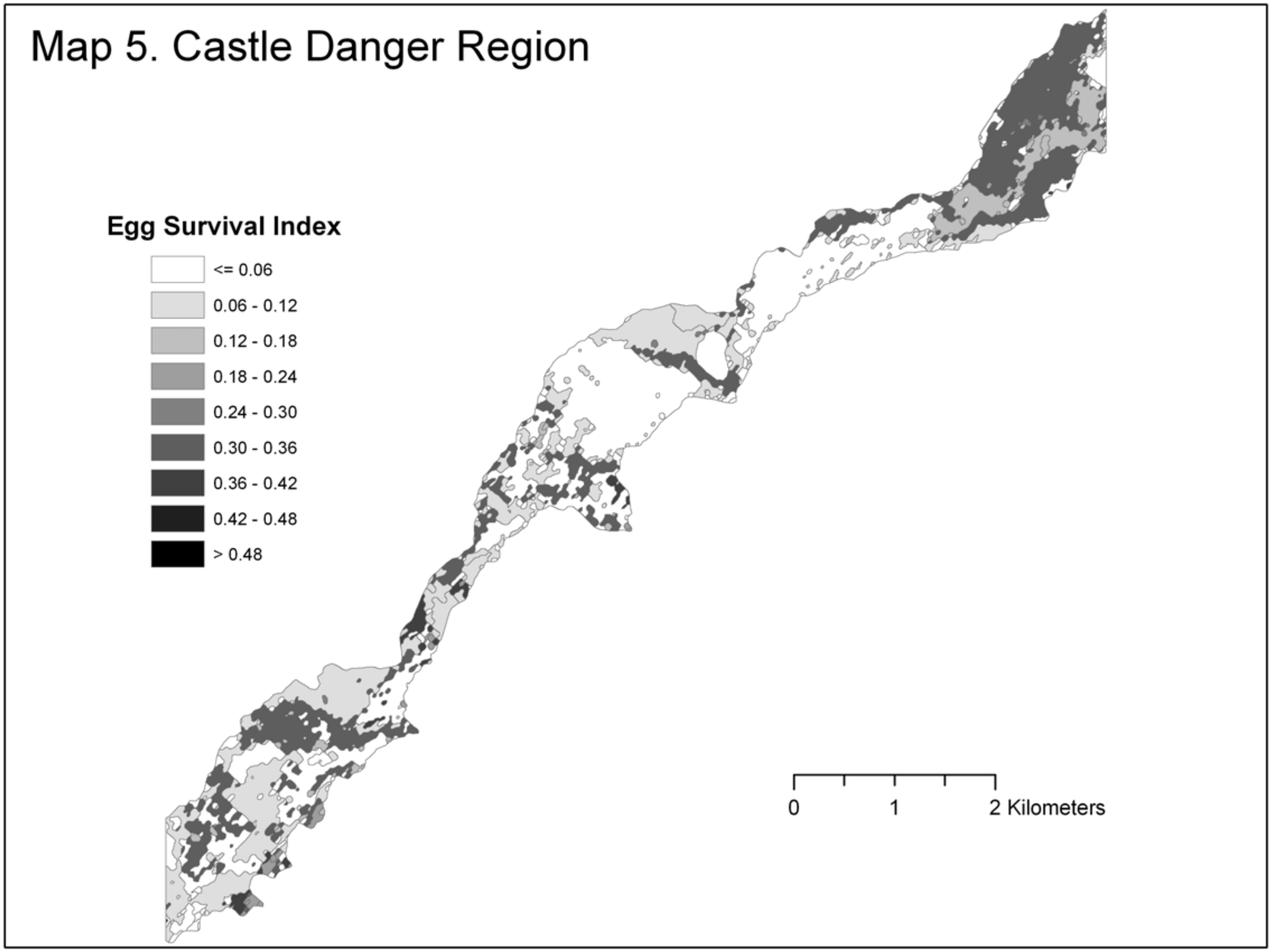


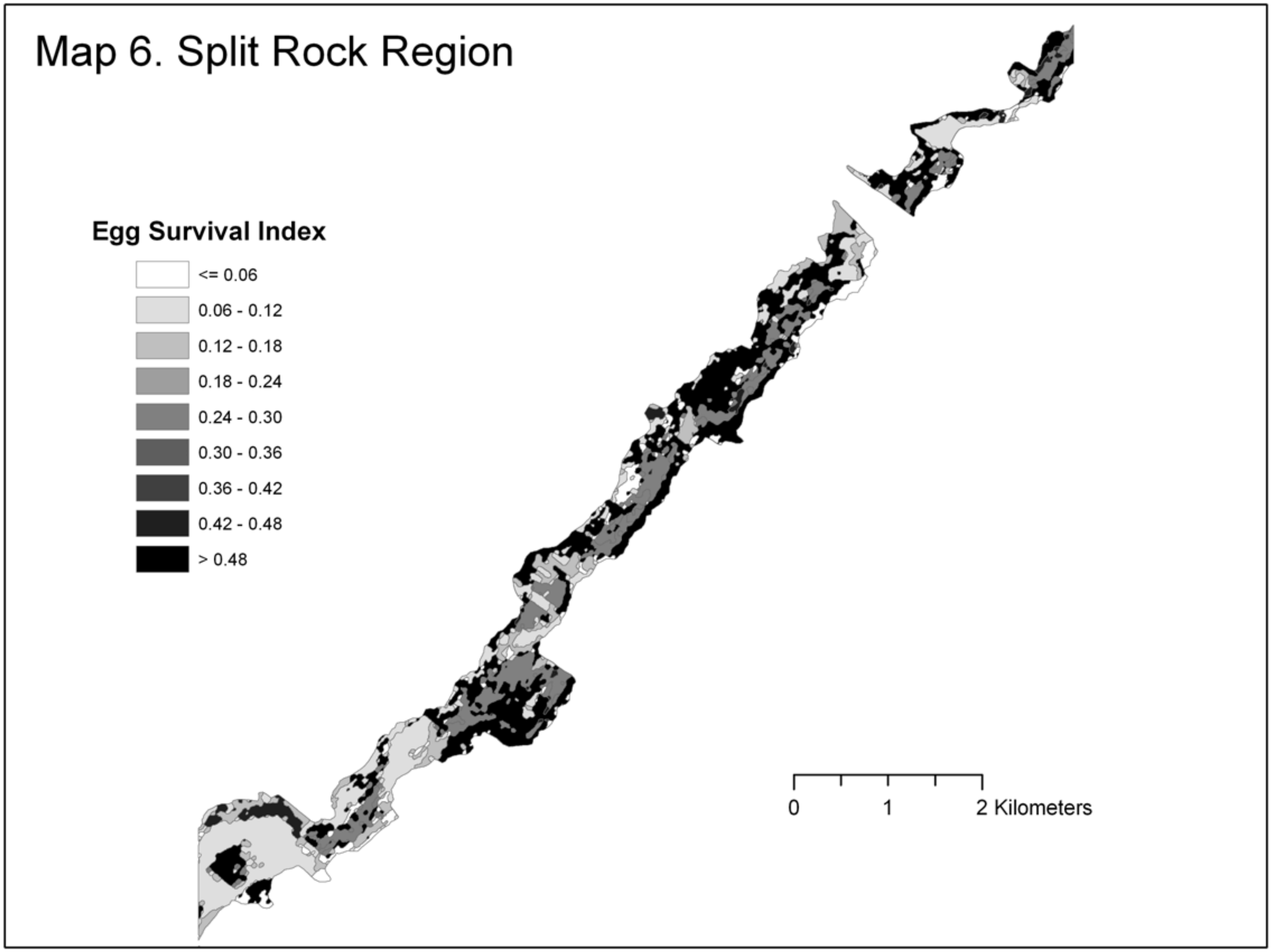
Map 3. Knife River Region



Map 4. Two Harbors Region

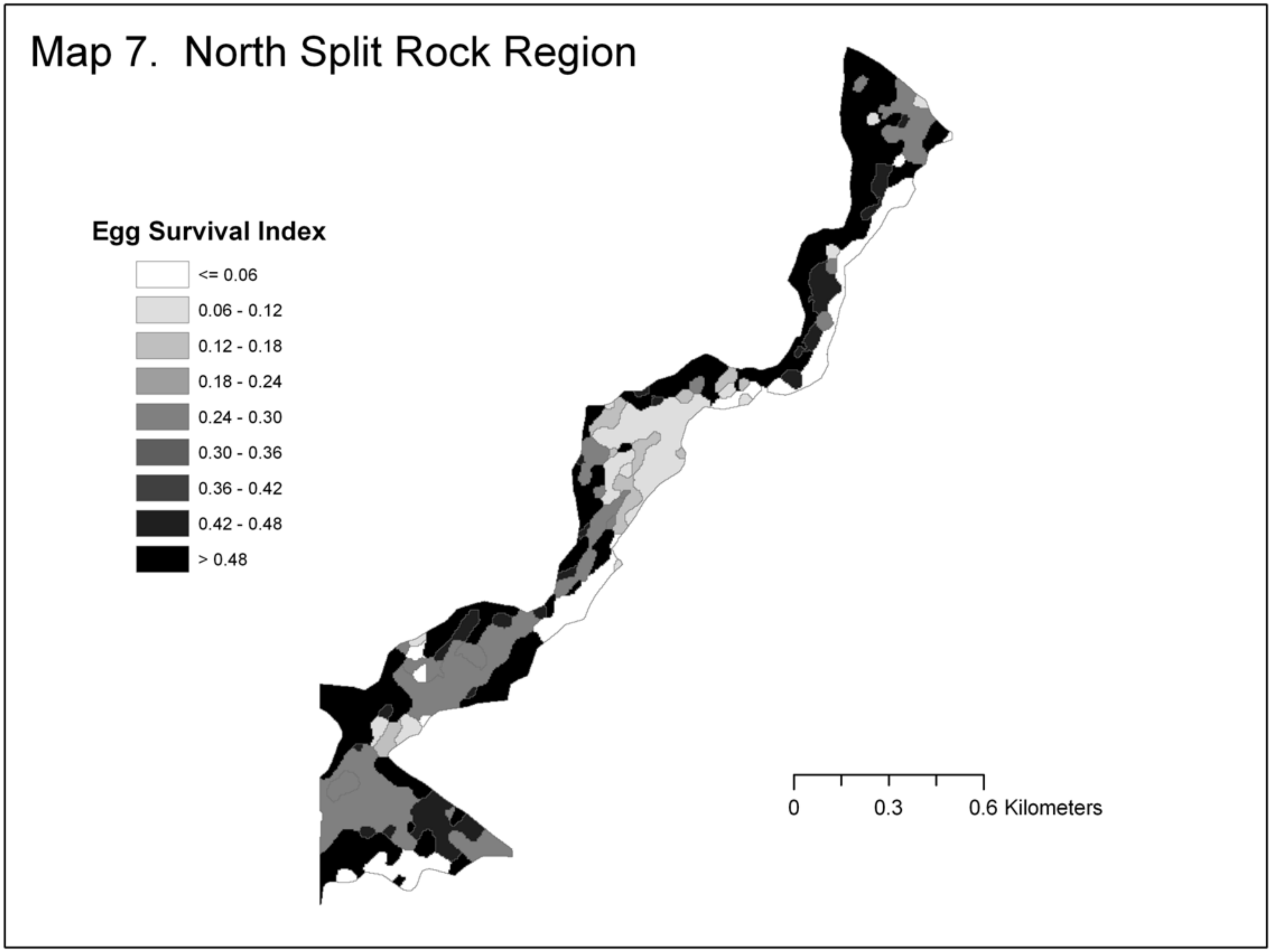
## Map 5. Castle Danger Region



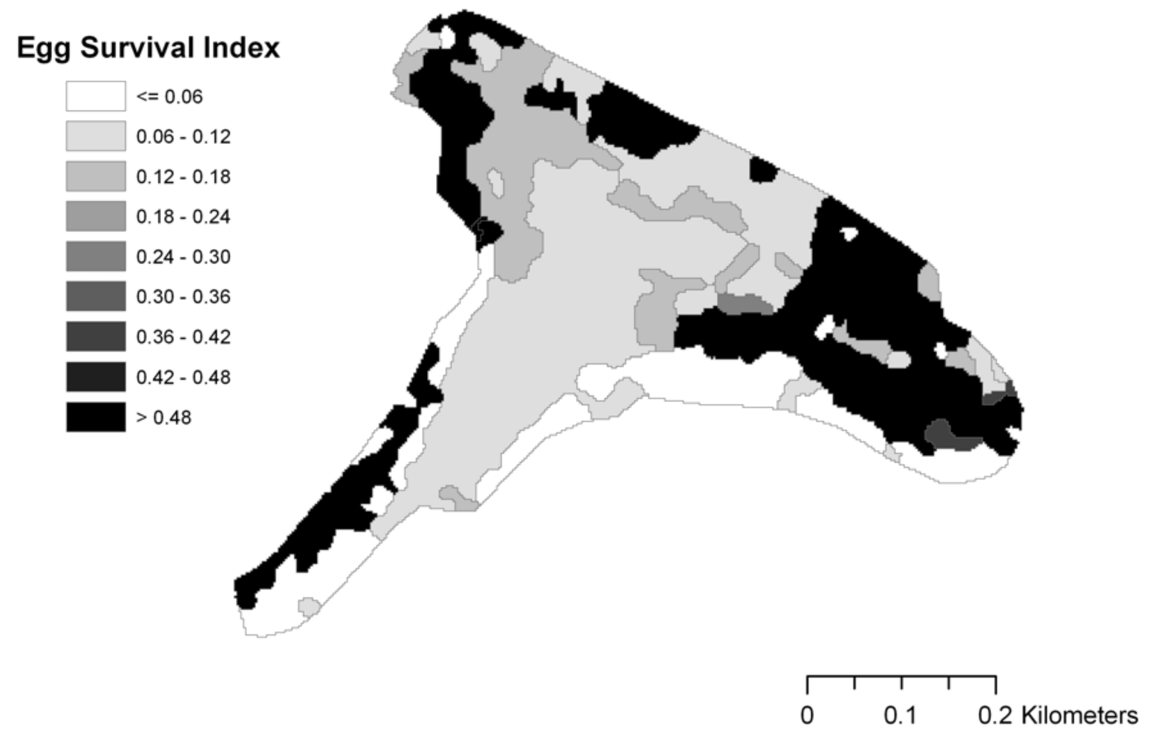


Map 6. Split Rock Region

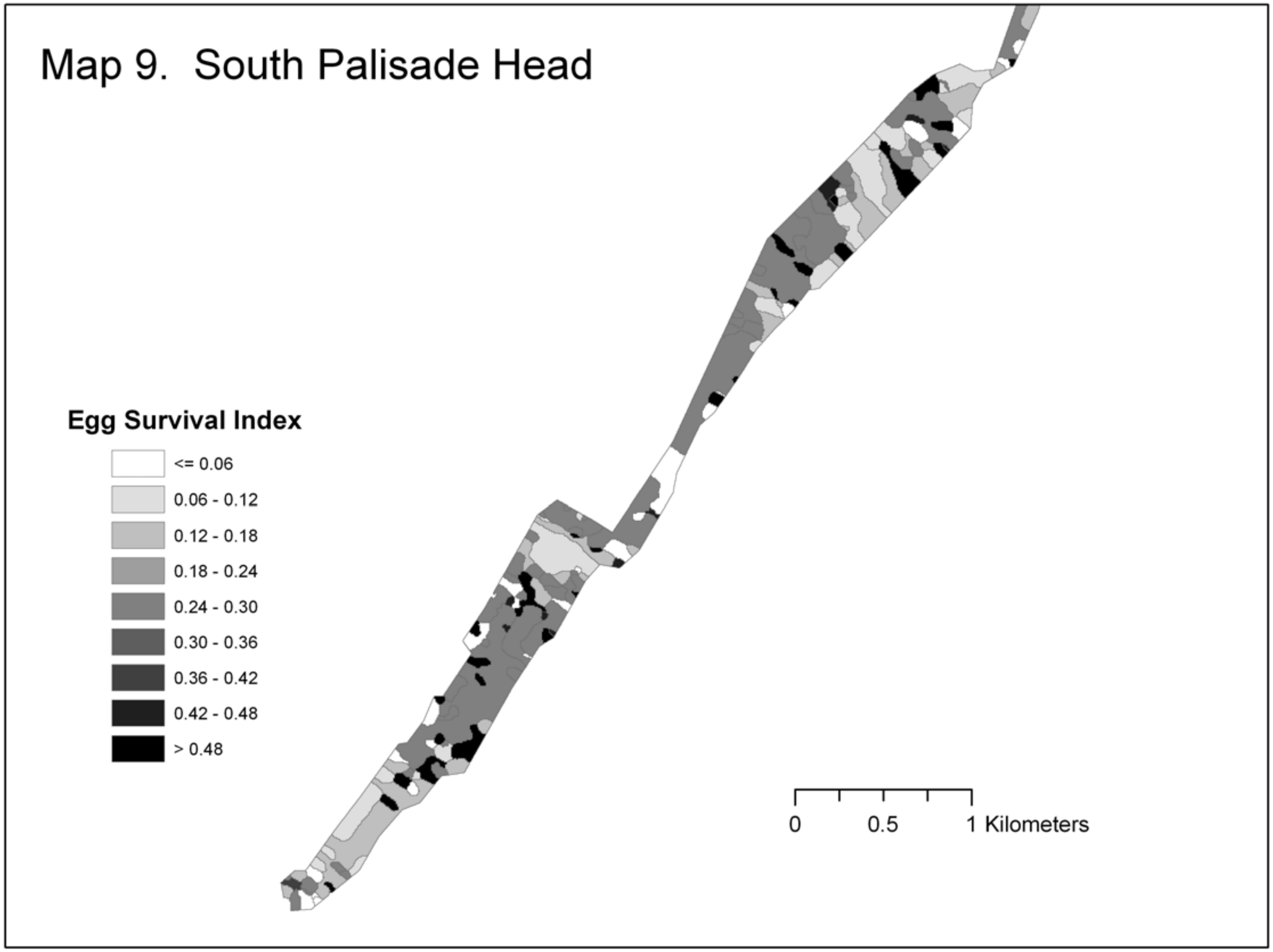
# Map 7. North Split Rock Region

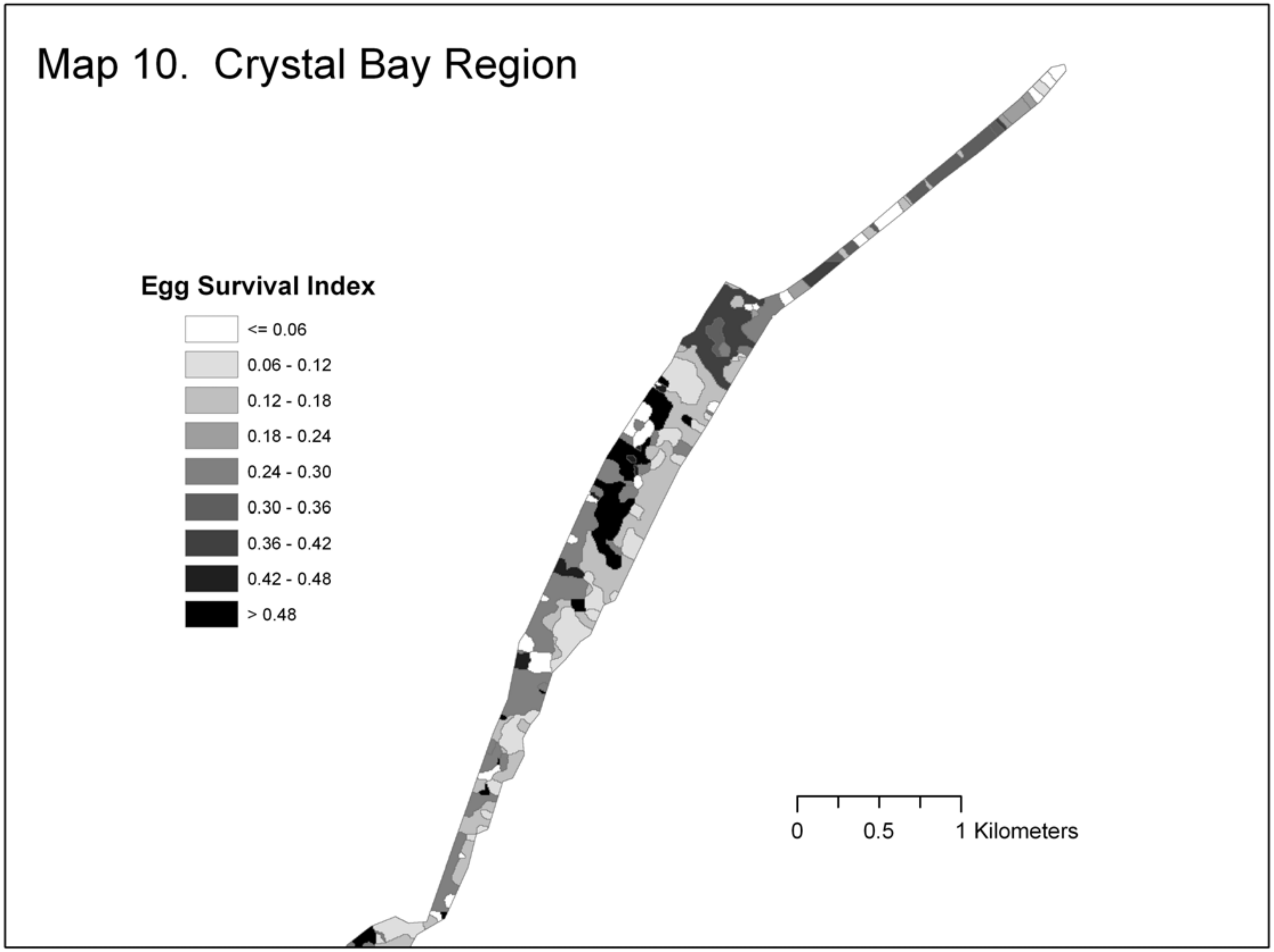


## Map 8. Light Pellet Island Region

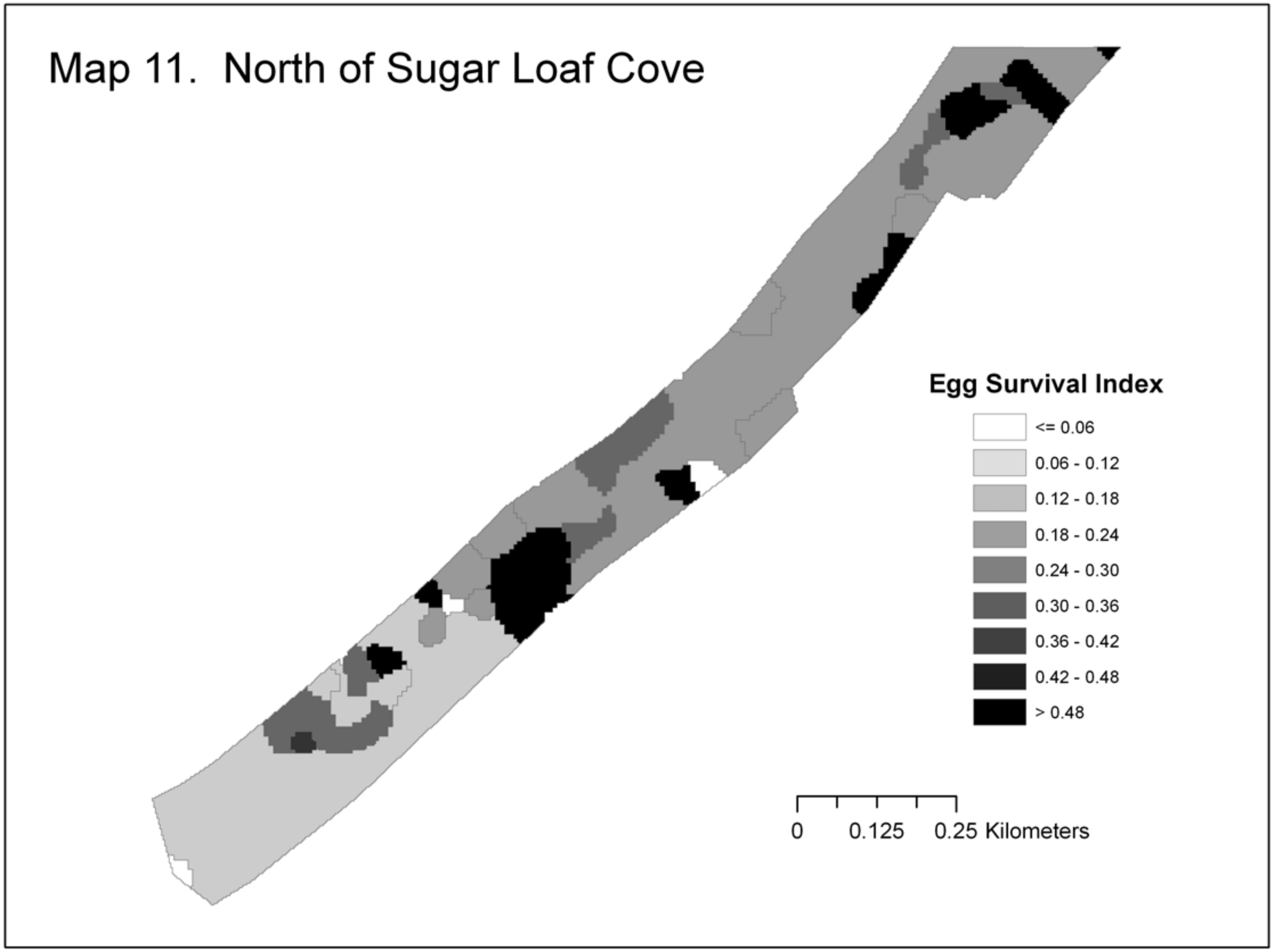


## Map 9. South Palisade Head



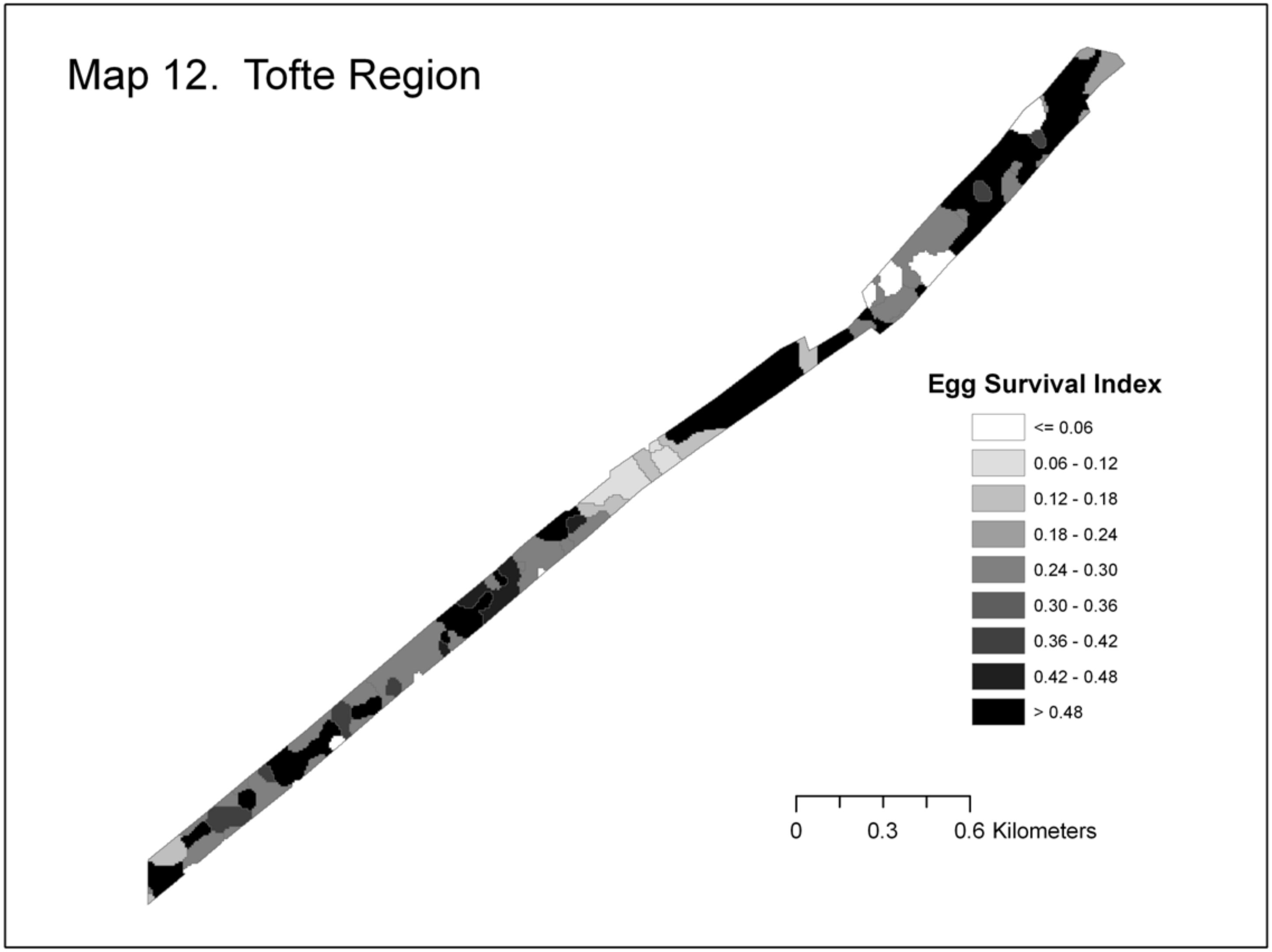


## Map 10. Crystal Bay Region

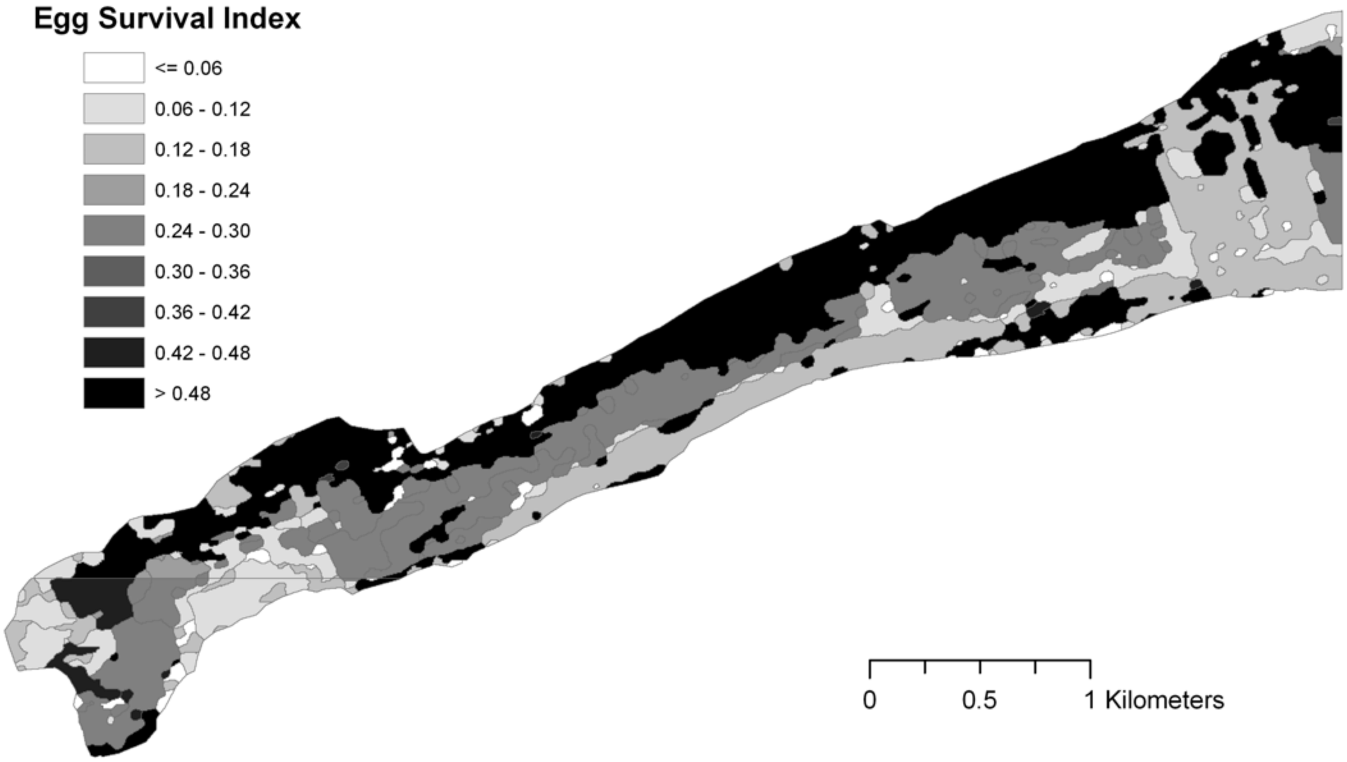


Map 11. North of Sugar Loaf Cove

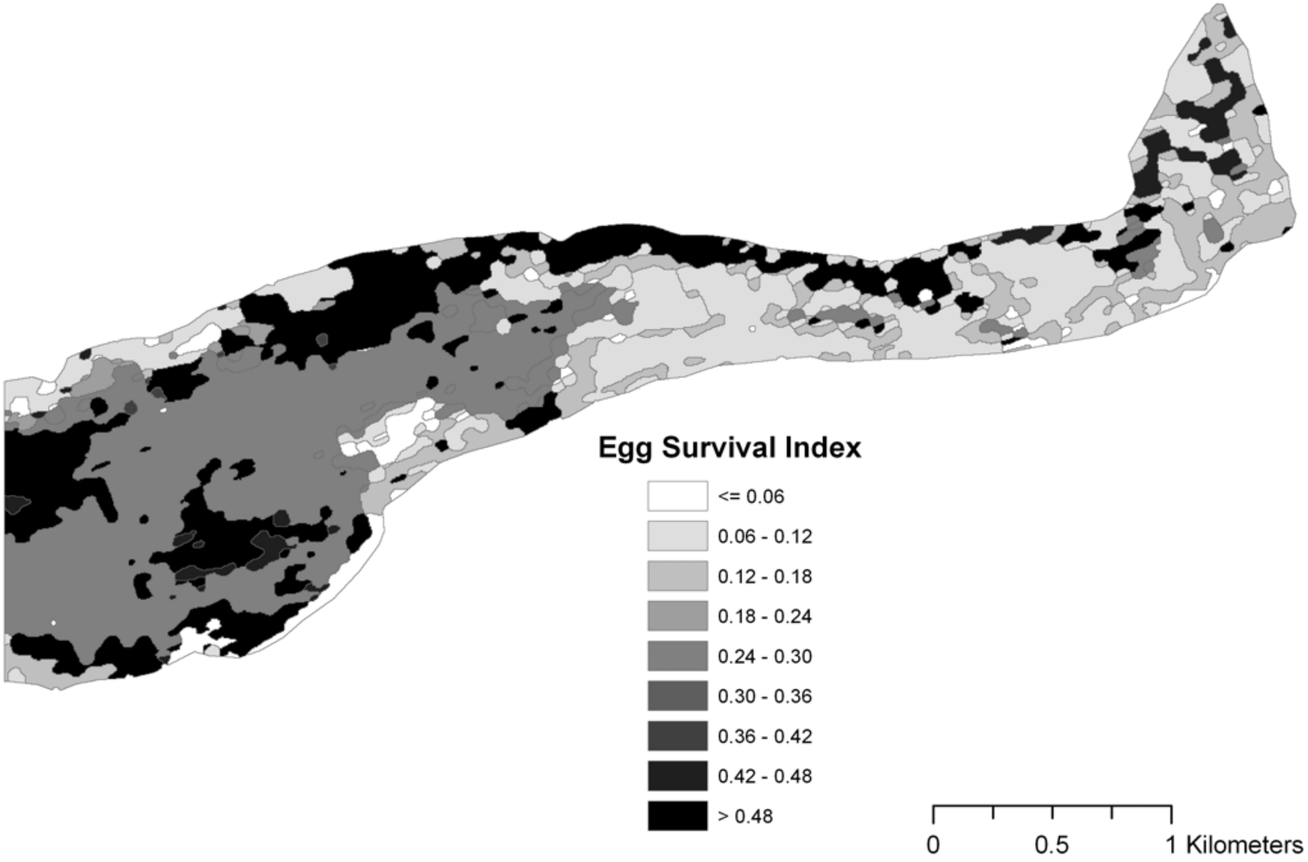
Map 12.  Tofte Region



Map 13. Grand Marais Region



Map 14.  Kadunce River Region



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