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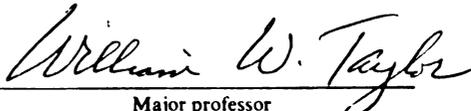
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**Role of Compensatory Mechanisms in the Population  
Dynamics of Lake Trout (Salvelinus namaycush)  
in the U.S. Waters of Lake Superior**

presented by

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has been accepted towards fulfillment  
of the requirements for

Ph.D. degree in **Fisheries/Wildlife**

  
Major professor

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**ROLE OF COMPENSATORY MECHANISMS IN THE POPULATION  
DYNAMICS OF LAKE TROUT (*SALVELINUS NAMAYCUSH*)  
IN THE U.S. WATERS OF LAKE SUPERIOR**

**By**

**Cecilia Paola Ferreri**

**A DISSERTATION**

**Submitted to  
Michigan State University  
in partial fulfillment of the requirements  
for the degree of**

**DOCTOR OF PHILOSOPHY**

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## **ABSTRACT**

### **ROLE OF COMPENSATORY MECHANISMS IN THE POPULATION DYNAMICS OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN THE U.S. WATERS OF LAKE SUPERIOR**

**By**

**Cecilia Paola Ferreri**

**Lake trout (*Salvelinus namaycush*) populations in Lake Superior have exhibited differing levels of abundance through time and thereby provide an opportunity in which to study the effects of compensation on population regulation. I explored the role of compensatory mechanisms in the population dynamics of lake trout in the Michigan and Wisconsin waters of Lake Superior during three time periods: the pre-sea lamprey period, prior to 1950 when lake trout were at a relatively high abundance and the fishery was the primary source of lake trout mortality; the sea lamprey dominant period, during the 1950s and 1960s when lake trout were at a very low abundance due to sea lamprey predation and over-exploitation; and currently, from 1985 to 1993 when wild lake trout abundance was at a moderate level.**

**The role of compensatory mechanisms was evaluated using a life table approach. Age-specific fecundity and survival schedules were incorporated into a Leslie projection matrix to calculate the finite rate of population increase ( $\lambda$ ). Individual growth, fecundity, and age-0 survival rates were calculated for each lake trout population and compared between time periods. Elasticity analyses were performed to determine the proportional contribution of each matrix parameter to the population growth rate during the three**

periods.

I found that individual growth rates, age-specific fecundity, and age-0 survival rates changed in response to the different levels of lake trout abundance during each of the study periods in both sites. Lake trout during the sea lamprey dominant period, which experienced the lowest abundance and highest mortality levels, exhibited the fastest individual growth rates, the highest age-specific fecundity, and the highest age-0 survival. These high rates contributed to the relatively high production potential exhibited by lake trout during the sea lamprey dominant period as compared to lake trout during the pre-sea lamprey or the current periods. Survival, particularly during the pre-reproductive ages, made a greater contribution than fecundity to the population growth rate of lake trout during the current time period. Reducing fishing mortality, which has its greatest impact on lake trout that are about to become mature, has a greater effect on the population growth rate than reducing sea lamprey induced mortality by an equal percentage.

## **DEDICATION**

**In memory of my grandparents, Ruben Valencia Carillo and Marjorie Mundy de Valencia, who through their love and by their example inspired me to strive for excellence.**

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## INTRODUCTION

Lake trout (*Salvelinus namaycush*) in Lake Superior had an important ecological role as a predator (Christie 1974, Ryder et al. 1981) and supported an important commercial fishery averaging two million kg annually until 1949 (Hile et al. 1951). Commercial yields of lake trout declined by 90% during the 1950s as a result of overexploitation and sea lamprey (*Petromyzon marinus*) predation (Pycha and King 1975). Efforts to rehabilitate lake trout populations in Lake Superior began in the 1950s with stocking of hatchery reared lake trout (Lawrie and Rahrer 1973) and chemical control of sea lampreys (Smith and Tibbles 1980). Additionally, severe harvest restrictions were placed on the commercial fishery in 1962 in an effort to reduce lake trout mortality (Krueger et al. 1986). Although progress toward rehabilitation of lake trout populations has been slow, abundance of wild lake trout in the Michigan and Wisconsin waters of Lake Superior has generally increased from 1970 to 1993 and is currently at moderate levels (Hansen 1994). Thus, lake trout in Lake Superior have experienced differing levels of abundance and mortality through time. Prior to 1950, lake trout were at a relatively high abundance, during the 1950s and 1960s, lake trout were at a very low abundance due to sea lamprey predation and over-exploitation, and currently, wild lake trout abundance is increasing toward historical levels (Figure 1). Because lake trout populations in Lake Superior have exhibited differing levels of abundance, they

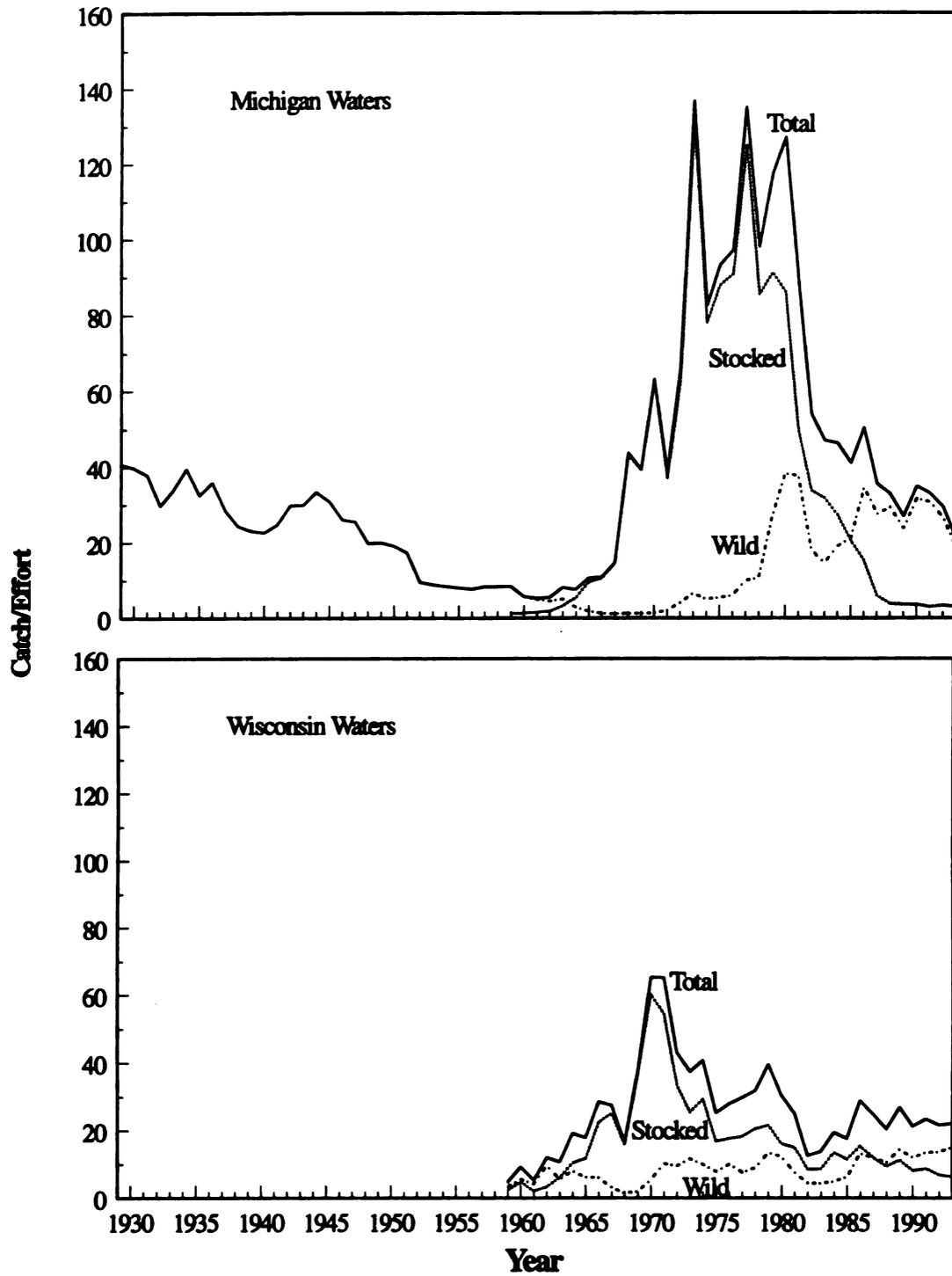


Figure 1. Relative contribution of stocked and wild fish to the total abundance of lake trout in the Michigan (1929-1993) and Wisconsin (1959-1993) waters of Lake Superior. Adapted from Hansen (1994).

provide an opportunity in which to study the effects of compensation on population regulation.

The idea of population compensation can be traced back to the first theories of population growth and regulation which are attributed to the observations of Malthus, who in 1798 observed that interactions between individuals at high densities limit population growth and lead to stability (McFadden 1977). These observations formed the foundation of the logistic model of population growth which implied that populations experience negative feedback mechanisms bounding growth between limits that are prescribed by the environment (Bellows 1981). Population compensation has been defined as “the sum of all density-dependent phenomena that act to stabilize a population” (Goodyear 1980). Thus, population compensation is mediated through density-dependent factors; processes that reduce population growth at higher population densities and increase growth at lower densities are compensatory (McFadden 1977). Compensatory mechanisms act through changes in growth, survival, and reproductive rates of the individuals in the population (Chen 1987). Each of these parameters has a range that is determined by the genetics of the individuals in the population (Phillipp et al. 1981, Weatherly and Rogers 1978). The expression of these rates in the population is modified by environmental conditions and determines population density. Density is a part of the environment which feeds back on growth, survival, and reproduction to mediate the expression of these rates within the range allowed by the population. Thus, when density is high, growth, survival, and reproduction should occur at lower rates than when density is low.

The continued existence and high levels of yield of fish populations undergoing

exploitation are often cited as evidence of compensatory mechanisms maintaining population viability (Goodyear 1977, 1980; McFadden 1977). However, there are limits to the compensatory capabilities of a fish species such that each fish population has an associated "compensatory reserve" which defines how much stress can be withstood by the population while remaining viable (Goodyear 1977). For example, there are limits as to how fast a fish may grow and to how fecund an individual may be. It is crucial to consider these limits, or the range of compensation available to the population, when assessing the impact of additional mortality on the population and how the population will respond (Goodyear 1977). A better understanding of the role that compensation plays in the regulation of fish populations will lead to better management of exploited populations (McFadden 1977).

The degree to which compensatory mechanisms are acting in a population can be determined by comparing the population to itself during periods of differing abundance levels. To achieve this comparison, a common unit is necessary that integrates the three agents of compensation, growth, survival, and reproduction, into a single measure. Lambda ( $\lambda$ ), the population's finite rate of growth, can serve as this common unit of comparison as it is sensitive to changes in the growth, survival, and reproductive rates of a population (Hayes and Taylor 1990). Lambda is commonly used to express the growth rate of a seasonally breeding population and is related to the population's intrinsic rate of increase,  $r$ , by:

$$\lambda = e^r$$

As a result, lambda greater than one indicates an increasing population, lambda equal to

one indicates a stable population, and lambda less than one indicates a decreasing population (Pielou 1977). One way to interpret lambda is in terms of a percent increase or decrease per year. For example, when  $\lambda = 1$ , there is no change per year. If  $\lambda = 1.2$ , the population is increasing at a rate of 20% per year, while if  $\lambda = 0.8$ , the population is decreasing at a rate of 20% per year.

Lambda is calculated from the Leslie projection matrix as the principle eigenvalue of the matrix (Pielou 1977, Caswell 1989). The Leslie matrix explicitly incorporates age-structure into the population (Pielou 1977) and allows for direct comparison of population growth or decline under a wide variety of conditions (Hayes and Taylor 1990). Further, the Leslie matrix allows for the determination of age-0 survival rates when post age-0 survival and fecundity rates are known (Vaughn and Saila 1976). Age-0 survival is difficult to measure in the field and is thus rarely measured for fish populations. However, the ability to calculate age-0 survival rates is important because many researchers believe that much of the compensation in fish populations, in terms of responding to large losses of adults, takes place at this stage (Sissenwine et al. 1988, Goodyear 1980). For instance, Ricker (1963) showed that even the slightest change in age-0 survival could lead to a large change in the abundance of the population at the time of recruitment.

The goal of this study was to evaluate the effect of compensatory mechanisms on the population dynamics of lake trout in Lake Superior. My specific objectives were to:

1. Determine, under different levels of abundance and mortality, if differences occur in individual growth rates, fecundity rates, and age-0 survival rates.

2. Evaluate the relative importance of fecundity and survival in determining the population growth rate of lake trout populations in Lake Superior.
  
3. Determine the effect of different management actions aimed at controlling mortality of current lake trout populations in Lake Superior on their population growth rate.

## **STUDY SITE AND TIME PERIODS**

I evaluated the effects of compensation on the population dynamics of lake trout in two areas of Lake Superior; one in the Michigan waters and one in the Wisconsin waters (Figure 2). The study areas overlap the following Lake Superior Management Zones: MI-4, MI-5, and MI-6 in Michigan waters and WI-2 in the Wisconsin waters (Hansen 1994). These areas of Lake Superior provided the long term data sets necessary to complete this study as they were sites of historically productive lake trout commercial fisheries (Baldwin 1979), and lake trout populations have been monitored in these areas by the National Biological Service for several decades (Hansen 1994). Additional information was available that allowed me to split the Wisconsin waters of Lake Superior into two distinct areas, the inshore and refuge areas, during the current time period only (Wisconsin State/Tribal Technical Committee 1990). This split was important because lake trout populations in the two areas have experienced different mortality rates as lake trout have been protected from fishing pressure in the offshore refuge area since 1976 (Schram et al. 1995). Although fishing was not allowed in the refuge area, these lake trout still experienced some fishing mortality due to straying out of the refuge area into neighboring waters where fishing was still allowed (Swanson 1974).

Three time periods were selected in which to evaluate the effects of compensation on the population dynamics of wild lake trout in Lake Superior (Figure 3). The study

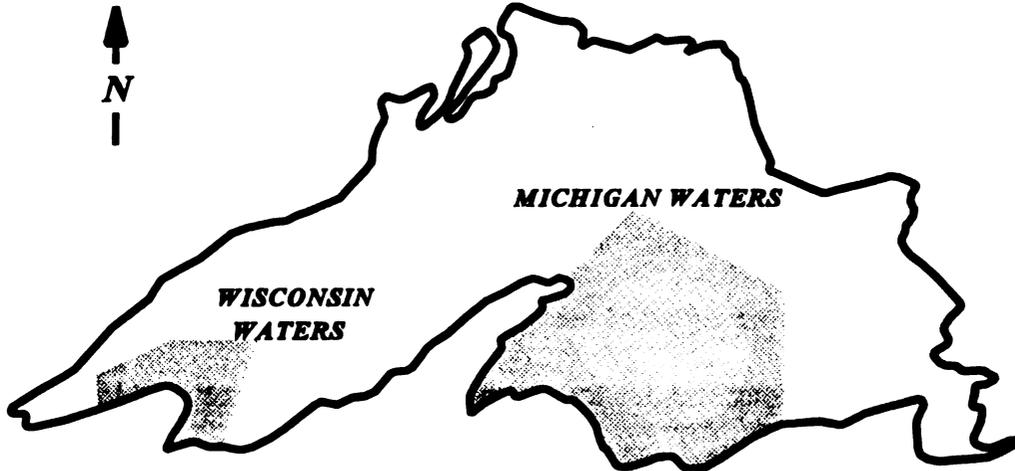


Figure 2. Lake Superior and the location of the study sites within the Michigan and Wisconsin waters.

periods were chosen to reflect different mortality regimes that resulted in different levels of lake trout abundance in both areas. Wild lake trout abundance in Lake Superior was at a relatively high level during the pre-sea lamprey period, 1929 to 1950. The commercial fishery was the primary source of adult lake trout mortality during this period (Hile et al. 1951, Pycha and King 1975). Sea lampreys were first recorded in Lake Superior in 1946, and by 1951, substantial numbers of spawning sea lampreys were captured in weirs located in tributaries to Lake Superior (Lawrie 1970). Further, a steep decline in lake trout yield was noted by 1951 as sea lampreys became abundant (Lawrie and Rahrer 1973). Thus, I selected 1951 as the beginning of the sea lamprey dominant period. Sea lamprey populations reached peak numbers in Lake Superior in 1961. However, in 1962, the number of sea lampreys declined by 86% as a result of the chemical control program which had started in 1958 (Smith and Tibbles 1980). As such, I chose 1961 as the ending of the sea lamprey dominant period. In an effort to rehabilitate lake trout populations that

had been decimated by a combination of the commercial fishery and the sea lamprey, lake trout stocking began in the early 1950s and was increased in 1958 (Krueger et al. 1986). By 1963 stocked fish began to dominate the total catch and continued to dominate the population dynamics of lake trout in Lake Superior until 1985 (Hansen 1994; see Figure 1). Hansen (1994) provided evidence that these hatchery-reared lake trout produced the wild fish that have dominated the population since 1985. Therefore, I chose the years from 1985 to 1993 to represent wild lake trout populations during the current time period.

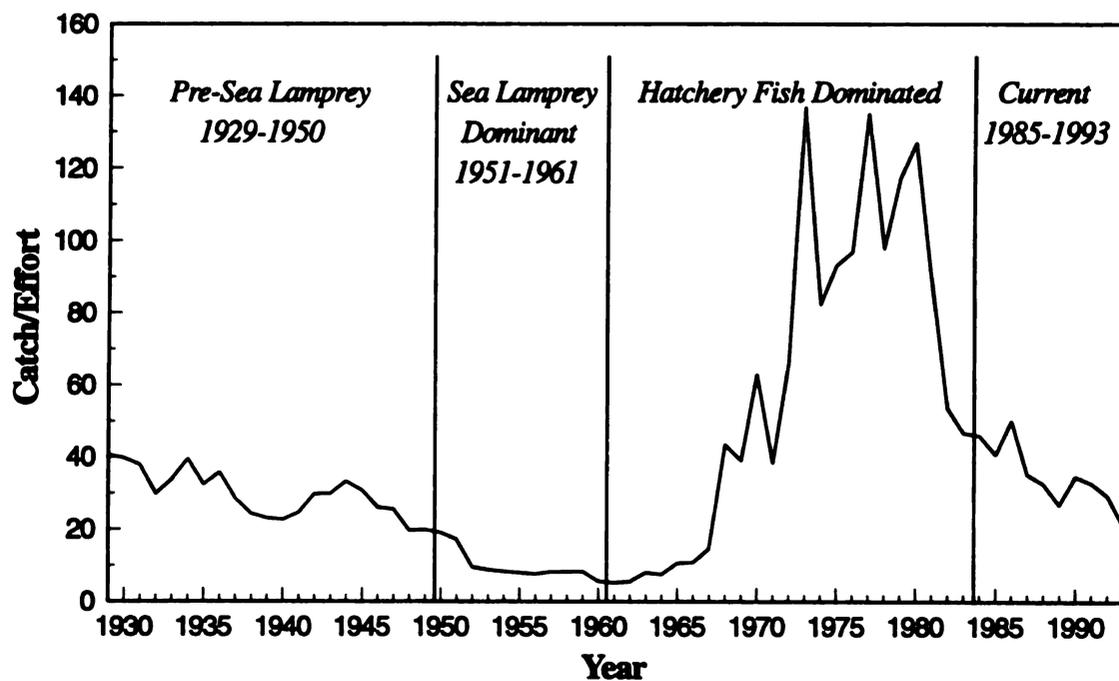


Figure 3. Three study periods chosen to evaluate the effects of compensation on the population dynamics of wild lake trout in Lake Superior. Assessment catch/effort in Michigan waters (adapted from Hansen 1994).

## METHODS

### *Leslie Matrix*

Leslie matrices were developed for wild lake trout in the Michigan and Wisconsin waters of Lake Superior for the three time periods. The Leslie matrix parameters, age-specific survival and fecundity rates, were estimated for each time period at each site from published literature and reports (Table 1). The probability of survival,  $P_x$ , from age  $x-1$  to age  $x$  was calculated as:

$$P_x = \frac{l_x}{l_{x-1}}$$

where  $l_x$  is the life table survivorship value at age  $x$  (Caswell 1989). Age-specific fecundity,  $F_x$ , was calculated as:

$$F_x = P_x m_x$$

where  $m_x$  is the life table age-specific fecundity rate (Caswell 1989). The finite rate of population growth,  $\lambda$ , was calculated as the principle eigenvalue of the Leslie matrix (Pielou 1977, Caswell 1989). I calculated  $\lambda$  for lake trout populations in the Michigan and Wisconsin waters of Lake Superior during the three study periods and used it to compare the growth rate of populations that exhibited different individual growth, survival, and reproduction rates.

Lake trout populations in both study sites had a different age structure in each of the time periods. Currently, lake trout in the Michigan waters live at least to age 24 while during the sea lamprey dominant period, few individuals lived beyond age 12. Thus, to facilitate comparison between time periods and sites, all matrices were extended to include 24 years. By extending the matrix to different ages and recalculating  $\lambda$ , I found that this extrapolation did not affect estimates of lambda because survival probabilities for the ages that did not appear in the population were so low that these ages did not contribute significantly to the population growth rate.

The first step necessary to estimate age-specific fecundity ( $F_x$ ) was to determine the individual growth rate experienced by the population. Size at age data, either weight at age or length at age, was extracted from the sources listed in Table 1. During the pre-sea lamprey and the sea lamprey dominant time periods, size at age was extrapolated to age 24 by fitting a power function to the data. The power function provided the highest coefficient of association for the two historical periods because lake trout were growing very quickly during these periods (Sakagawa and Pycha 1971). During the current time period, however, a logarithmic function had the best fit to the data provided by the sources in Table 1. Length-weight relationships published in the sources listed in Table 1 were used to estimate the corresponding length or weight at age. Finally, weight at age information was combined with published fecundity-weight relationships for Lake Superior lake trout to determine age-specific fecundity rates. This value was then multiplied by the percent of lake trout mature at that age to estimate the age-specific fecundity of the population. The growth, length-weight, and fecundity-weight functions used to construct the matrices are listed in Table 2.

**Table 1.** Sources of data used to construct the Leslie matrices for wild lake trout populations in the Michigan and Wisconsin waters of Lake Superior during the three study periods.

Time Period - Michigan Waters			
Matrix Parameter	Pre-Sea Lamprey	Sea Lamprey-Dominant	Current
Length at age	Sakagawa & Pycha 1971	Rahrer 1967	Ebener 1990
Length-weight	Sakagawa & Pycha 1971	Eschmeyer & Phillips 1965	Ebener 1990
Fecundity-weight	Eschmeyer 1955	Eschmeyer 1955	Peck 1988
Total mortality	Sakagawa & Pycha 1971	Pycha 1980	Ebener et al. 1989

Time Period - Wisconsin Waters			
Matrix Parameter	Pre-Sea Lamprey	Sea Lamprey-Dominant	Current
Length at age	Sakagawa & Pycha 1971	Rahrer 1967	WI Tech 1990
Length-weight	Sakagawa & Pycha 1971	Eschmeyer & Phillips 1965	Not Available
Fecundity-weight	Eschmeyer 1955	Eschmeyer 1955	Schram 1993
Total mortality	Swanson & Swedberg 1980	Swanson & Swedberg 1980	WI Tech 1990

Table 2. Mathematical functions used to estimate age specific length, weight, and fecundity in the Michigan and Wisconsin waters of Lake Superior.

Relationship	Michigan Waters	Wisconsin Waters
Size at age		
Pre-Sea Lamprey:	$W(\text{lbs}) = 3.1513\text{Age}^{0.8909}$	Same as Michigan
Sea Lamprey Dominant:	$L(\text{in}) = 4.2315\text{Age}^{0.8472}$	Same as Michigan
Current:	$L(\text{cm}) = 11.405\ln(\text{Age}) + 1.408$	$L(\text{cm}) = 8.692 \ln(\text{Age}) + 5.288$ $L(\text{cm}) = 10.894 \ln(\text{Age}) + 0.986$
	$R^2 = 0.9999$	$R^2 = 0.9792$ (inshore) $R^2 = 0.9926$ (refuge)
	$R^2 = 0.9923$	
	$R^2 = 0.9869$	
Length-weight		
Pre-Sea Lamprey:	$\log(W(\text{lb})) = -3.636 + 3.062\log(L(\text{in}))^A$	Same as Michigan
Sea Lamprey Dominant:	$\log(W(\text{lb})) = -3.765 + 3.191\log(L(\text{in}))^B$	Same as Michigan
Current:	$\log(W(\text{kg})) = -12.149 + 3.0917\log(L(\text{cm}))^C$	Not available
Fecundity-weight		
Pre-Sea Lamprey:	$F = -1923.39 + 823.23W(\text{lb})^D$	Same as Michigan
Sea Lamprey Dominant:	$F = -1923.39 + 823.23W(\text{lb})^D$	Same as Michigan
Current:	$F = -3400 + 2450W(\text{kg})^E$	$F = -12143.3 + 24.46L(\text{mm})^F$

<sup>A</sup>Sakagawa and Pycha 1971

<sup>B</sup>Eschmeyer and Phillips 1965

<sup>C</sup>Ebener 1990

<sup>D</sup>Eschmeyer 1955

<sup>E</sup>Peck 1988

<sup>F</sup>Schram 1993

Age-specific survival rates ( $P_x$ ) were determined as:

$$P_x = 1 - e^{-(M_x + F_x + L_x)}$$

where  $M_x$  is instantaneous natural mortality,  $F_x$  is instantaneous fishing mortality, and  $L_x$  is instantaneous sea lamprey mortality. These rates and total mortality were estimated by the sources listed in Table 1 using catch curve analysis (Ricker 1975). I assumed that natural mortality was the only mortality factor acting on fish that were not fully recruited to the fishery. Instantaneous natural mortality for lake trout in the Michigan and Wisconsin waters of Lake Superior was reported as 0.2 (Sakagawa and Pycha 1971), and this value was held constant for both sites during each period. Lake trout were fished using a 114 mm stretch mesh gillnet which reaches peak efficiency at 51 cm (20 in) in length (Pycha 1980). Thus, fishing mortality was assumed to begin significantly impacting populations when the fish reached 51 cm length. Fishing mortality was often determined by subtraction of the other mortality factors from a total mortality estimate. Sea lamprey induced mortality was assumed to be zero during the pre-sea lamprey period and was extracted from the sources listed in Table 1 for the other time periods. The parameters, age-specific length, weight, survival and fecundity, used to construct the Leslie matrix for lake trout populations in the Michigan waters for each study period are listed in Table 3. For lake trout populations in the Wisconsin waters, the Leslie matrix parameters of the historical time periods are listed in Table 4 and of the current time period are listed in Table 5. Refer to Appendix A for a detailed description of each matrix.

Table 3. Listing of parameters used to construct Leslie matrices for the Michigan waters of Lake Superior during the three study periods. Length is in cm, weight is in kg,  $P(x)$  is age specific survival, and  $F(x)$  is age specific fecundity.

age	Pre-Sea Lamprey			Sea Lamprey Dominant			Current			
	cm	kg	$P(x)$	cm	kg	$P(x)$	cm	kg	$P(x)$	$F(x)$
1	13.94	0.02	0.82	10.41	0.01	0.82	3.58	0.00	0.82	0.00
2	19.16	0.05	0.82	16.01	0.03	0.82	23.66	0.11	0.82	0.00
3	22.64	0.09	0.82	22.09	0.08	0.82	35.40	0.37	0.82	0.00
4	31.19	0.23	0.82	28.71	0.18	0.52	43.74	0.72	0.77	0.00
5	37.44	0.40	0.82	36.07	0.37	0.43	50.20	1.10	0.76	0.00
6	43.40	0.63	0.82	46.48	0.83	0.41	57.00	1.62	0.41	8.41
7	50.03	0.97	0.82	51.56	1.16	0.23	61.00	2.00	0.41	68.78
8	54.42	1.25	0.50	57.91	1.68	0.18	63.10	2.22	0.41	174.22
9	60.22	1.70	0.50	68.58	2.88	0.18	66.50	2.62	0.41	499.21
10	67.22	2.39	0.50	76.45	4.08	0.15	69.40	2.98	0.41	811.51
11	72.07	2.95	0.50	82.29	5.15	0.09	71.10	3.22	0.41	929.34
12	78.67	3.86	0.50	87.63	6.30	0.09	74.40	3.70	0.41	1175.46
13	84.62	4.83	0.50	94.42	7.99	0.08	78.10	4.30	0.41	1479.92
14	90.38	5.91	0.50	100.54	9.76	0.08	79.60	4.56	0.41	1612.29
15	95.98	7.10	0.50	106.59	11.77	0.08	83.10	5.21	0.41	1942.04
16	101.87	8.52	0.50	112.58	14.01	0.08	85.20	5.63	0.41	2154.38
17	107.44	10.03	0.50	118.51	16.50	0.08	86.30	5.86	0.41	2270.07
18	113.06	11.73	0.50	124.39	19.26	0.08	87.31	6.07	0.41	2378.68
19	118.63	13.59	0.50	130.22	22.29	0.08	88.87	6.41	0.41	2552.95
20	124.18	15.63	0.50	136.01	25.61	0.08	90.36	6.75	0.41	2724.33
21	129.70	17.86	0.50	141.75	29.22	0.08	91.77	7.08	0.41	2892.91
22	135.19	20.27	0.50	147.44	33.14	0.08	93.12	7.41	0.41	3058.78
23	140.65	22.89	0.50	153.11	37.37	0.08	94.41	7.73	0.41	3222.04
24	146.08	25.70	0.50	158.72	41.93	0.08	95.64	8.05	0.41	3382.78

Table 4. Listing of parameters used to construct Leslie matrices for the Wisconsin waters of Lake Superior during the two historical time periods. Length is in cm, weight is in kg,  $P(x)$  is age specific survival, and  $F(x)$  is age specific fecundity.

age	Pre-Sea Lamprey				Sea Lamprey Dominant			
	cm	kg	$P(x)$	$F(x)$	cm	kg	$P(x)$	$F(x)$
1	13.94	0.02	0.82	0.00	10.41	0.01	0.82	0.00
2	19.16	0.05	0.82	0.00	16.00	0.03	0.82	0.00
3	22.64	0.09	0.82	0.00	22.10	0.08	0.82	0.00
4	31.19	0.23	0.82	0.00	28.70	0.18	0.82	0.00
5	37.44	0.40	0.82	0.00	36.07	0.37	0.82	0.00
6	43.40	0.62	0.82	0.00	46.48	0.83	0.57	0.00
7	50.03	0.96	0.82	0.00	51.56	1.16	0.18	0.00
8	54.42	1.25	0.60	0.00	57.91	1.68	0.18	0.00
9	60.22	1.70	0.60	0.00	68.58	2.88	0.18	174.12
10	67.22	2.38	0.60	313.48	76.45	4.08	0.18	424.17
11	72.07	2.95	0.60	467.59	82.30	5.15	0.18	661.45
12	78.67	3.86	0.60	1289.57	87.63	6.30	0.18	845.73
13	84.62	4.82	0.60	1794.22	94.42	7.99	0.18	1118.57
14	90.38	5.90	0.60	2651.46	100.54	9.76	0.18	1404.19
15	95.98	7.09	0.60	3302.62	106.59	11.77	0.18	1726.78
16	101.87	8.51	0.60	4077.80	112.58	14.01	0.18	2088.16
17	107.44	10.02	0.60	4902.09	118.51	16.50	0.18	2490.15
18	113.06	11.71	0.60	5826.00	124.39	19.26	0.18	2934.50
19	118.63	13.57	0.60	6843.00	130.22	22.29	0.18	3422.97
20	124.18	15.61	0.60	7956.83	136.01	25.61	0.18	3957.25
21	129.70	17.83	0.60	9171.18	141.75	29.22	0.18	4539.03
22	135.19	20.25	0.60	10489.68	147.44	33.14	0.18	5169.98
23	140.65	22.86	0.60	11915.92	153.10	37.37	0.18	5851.72
24	146.08	25.67	0.60	13453.44	158.72	41.93	0.18	6585.87

**Table 5.** Listing of parameters used to construct Leslie matrices in the Wisconsin waters of Lake Superior during the current time period for the inshore and refuge areas. Length is in cm,  $P(x)$  is age specific survival, and  $F(x)$  is age specific fecundity; weight was not available for this time period.

age	Current - Inshore			Current - Refuge		
	cm	$P(x)$	$F(x)$	cm	$P(x)$	$F(x)$
1	13.43	0.82	0.00	2.50	0.82	0.00
2	28.73	0.82	0.00	21.68	0.82	0.00
3	37.68	0.82	0.00	32.90	0.82	0.00
4	44.04	0.80	0.00	40.86	0.82	0.00
5	49.40	0.78	0.00	47.83	0.79	0.00
6	51.77	0.40	0.00	51.84	0.52	0.00
7	56.37	0.40	23.03	55.42	0.52	25.47
8	60.49	0.40	74.32	60.30	0.52	93.95
9	62.85	0.40	129.24	63.50	0.52	174.54
10	62.65	0.40	477.39	65.41	0.52	744.52
11	66.84	0.40	841.50	68.48	0.52	1186.28
12	68.17	0.40	906.50	72.39	0.52	1432.67
13	70.06	0.40	998.84	73.48	0.52	1501.24
14	71.69	0.40	1078.90	75.53	0.52	1630.41
15	73.22	0.40	1153.43	77.44	0.52	1750.66
16	74.64	0.40	1223.15	79.22	0.52	1863.15
17	75.98	0.40	1288.65	80.90	0.52	1968.82
18	77.24	0.40	1350.40	82.48	0.52	2068.45
19	78.44	0.40	1408.81	83.98	0.52	2162.69
20	79.57	0.40	1464.22	85.40	0.52	2252.09
21	80.64	0.40	1516.93	86.75	0.52	2337.13
22	81.67	0.40	1567.19	88.04	0.52	2418.21
23	82.65	0.40	1615.21	89.27	0.52	2495.69
24	83.59	0.40	1661.19	90.44	0.52	2569.87

### *Growth Comparison*

A regression model was developed for each time period based on a natural log transformation of size at age in each matrix to facilitate comparison of size at age among the different sites and times. Using analysis of covariance with contrasts (Rawlings 1988), I compared the length and weight at age among the three time periods within the Michigan waters. I used the size at age data from the two historical periods in the Michigan waters to construct the historical matrices in the Wisconsin waters since historical age-specific length and weight information was lacking for Wisconsin lake trout. I was able to substitute Michigan growth data for Wisconsin lake trout because studies had indicated that lake trout in the two areas grew in a similar fashion. During the pre-sea lamprey period, Eschmeyer et al. (1953) indicated that the annual growth increment of adult lake trout in Wisconsin waters was similar to the growth rate exhibited in the Michigan waters - approximately 2.1 inches per year. Additionally, the age structure of lake trout collected in 1964, soon after the sea lamprey dominant period, using 114 mm stretch mesh gill nets in the Wisconsin waters reported by Swanson and Swedberg (1980) was similar to the age structure presented in Rahrer (1967) for lake trout collected with the same gear in the Michigan waters during the same period. Since I used the same growth data for the two sites during the pre-sea lamprey and the sea lamprey dominant periods, I was only able to compare length at age between the two sites during the current time period. In addition, length at age was calculated separately for lake trout in the inshore and refuge regions of the Wisconsin waters, and growth in both of these areas was compared to growth during the current time period in the Michigan waters.

### *Fecundity Comparison*

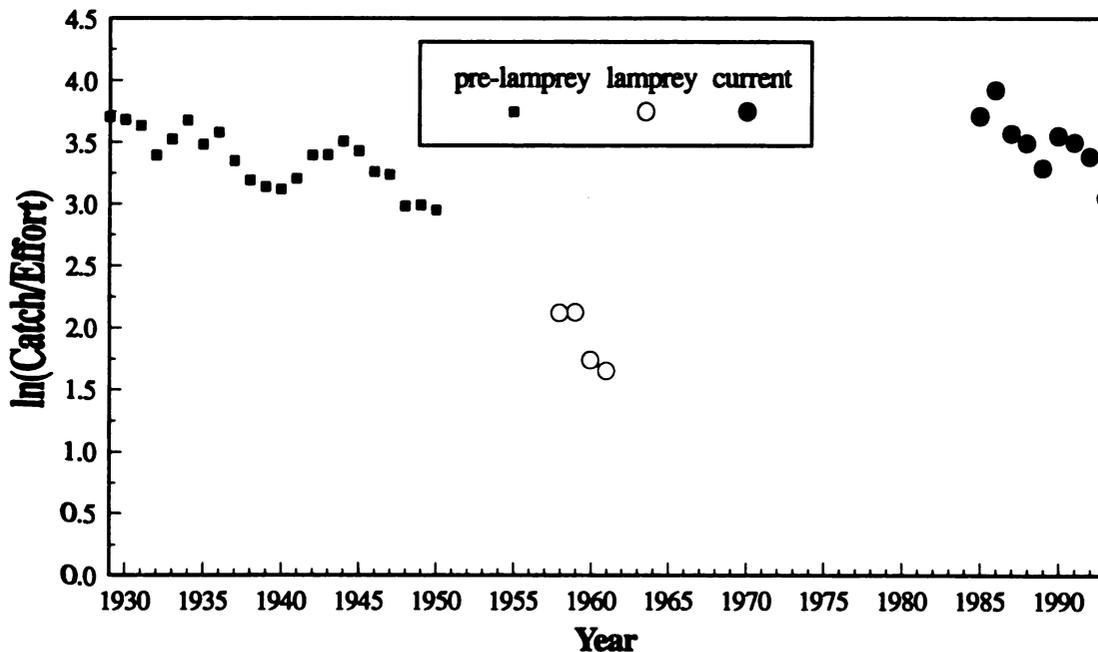
Fecundity-weight regressions had been developed for the current time period in the Michigan (Peck 1988) and Wisconsin (Schram 1993) waters and for the pre-sea lamprey period in the Michigan waters (Eschmeyer 1955). Using the data on number of eggs at weight presented in these publications, I recalculated the fecundity-weight regression for each data set and calculated the 95% confidence interval for the predicted values (Rawlings 1988) to test for differences in weight specific fecundity between the Michigan waters pre-sea lamprey and current time periods and Wisconsin current period.

To test for differences in age-specific fecundity between time periods and sites, I calculated age-specific fecundity using the fecundity-weight regression for those ages at which size was known. Using analysis of covariance with contrasts (Rawlings 1988), I compared the calculated fecundity at age of lake trout among the three time periods within the Michigan waters and the Wisconsin waters separately, and then compared the two areas within Wisconsin and the Michigan waters during the current time period.

### *Population Growth Rate Comparison*

In order to complete the Leslie matrix for each period, I estimated age-0 survival; that is, survival from egg deposition to age 1. Vaughn and Saila (1976) describe a method for calculating age-0 survival that requires an estimate of the finite rate of population growth ( $\lambda$ ) and a Leslie matrix that is complete except for the age-0 survival value. Hence, the first step in calculating age-0 survival was to estimate the population growth rate of lake trout populations in the Michigan and Wisconsin waters of Lake Superior during each of the time periods.

Hansen (1994) developed estimates of wild lake trout assessment catch per unit effort (cpe) in the Michigan waters of Lake Superior from 1929 to 1993. I used these data to calculate the instantaneous population growth rate for each period as the slope of the regression of the natural log of cpe against time (Figure 4; Pielou 1977). Only the years 1958 to 1961 were used to characterize the sea lamprey dominant period. As the average age of fish caught during these years was 6 to 7 years (Pycha 1980), these fish had been exposed to sea lamprey induced mortality for all of their life span making these years a better representation of the sea lamprey dominant time period than the entire time period.



**Figure 4.** Data points used in the regression of the natural log(cpe) on year to determine the finite rate of population growth in the Michigan waters of Lake Superior.

A time series of catch/effort such as Hansen (1994) developed in the Michigan waters was not available for the Wisconsin waters of Lake Superior. In fact, cpe data were not available for the historical time periods in Wisconsin waters. However, Pycha and King (1975) indicate that commercial catch/effort in Wisconsin waters during 1937-1948 was almost identical to that in the adjacent Michigan district MS-2. Therefore, I used lake trout commercial catch/effort recorded in MS-2 from 1929 to 1950 (Jensen and Buettner 1976) to represent cpe in the Wisconsin waters during the pre-sea lamprey period. Pycha and King (1975) developed an index of lake trout abundance in the Wisconsin waters of Lake Superior from 1949 to 1970. As in the Michigan waters, I used only the years from 1958 to 1961 to calculate the lake trout population growth rate for the sea lamprey dominant period. Hansen (1994) provided assessment cpe estimates for stocked and wild fish during the current time period in the Wisconsin waters. The Wisconsin State/Tribal Technical Committee (1990) reported that mortality rates calculated for wild lake trout best represent lake trout populations in the refuge area, while mortality rates calculated for stocked fish best represent the condition of lake trout populations outside the refuge area. Consequently, I used the cpe of stocked fish to represent the inshore waters where fishing was allowed, and the cpe of wild fish to represent the refuge area where fishing was not allowed. The instantaneous rate of population growth was determined as the slope of the regression of the natural log of cpe and the abundance index against time (Figure 5; Pielou 1977).

Finally, the finite rate of population growth ( $\lambda$ ) of lake trout in the Michigan and Wisconsin waters of Lake Superior during each time period was calculated as the antilog of the corresponding slope (Pielou 1977). A two-tailed Student's t test was used to

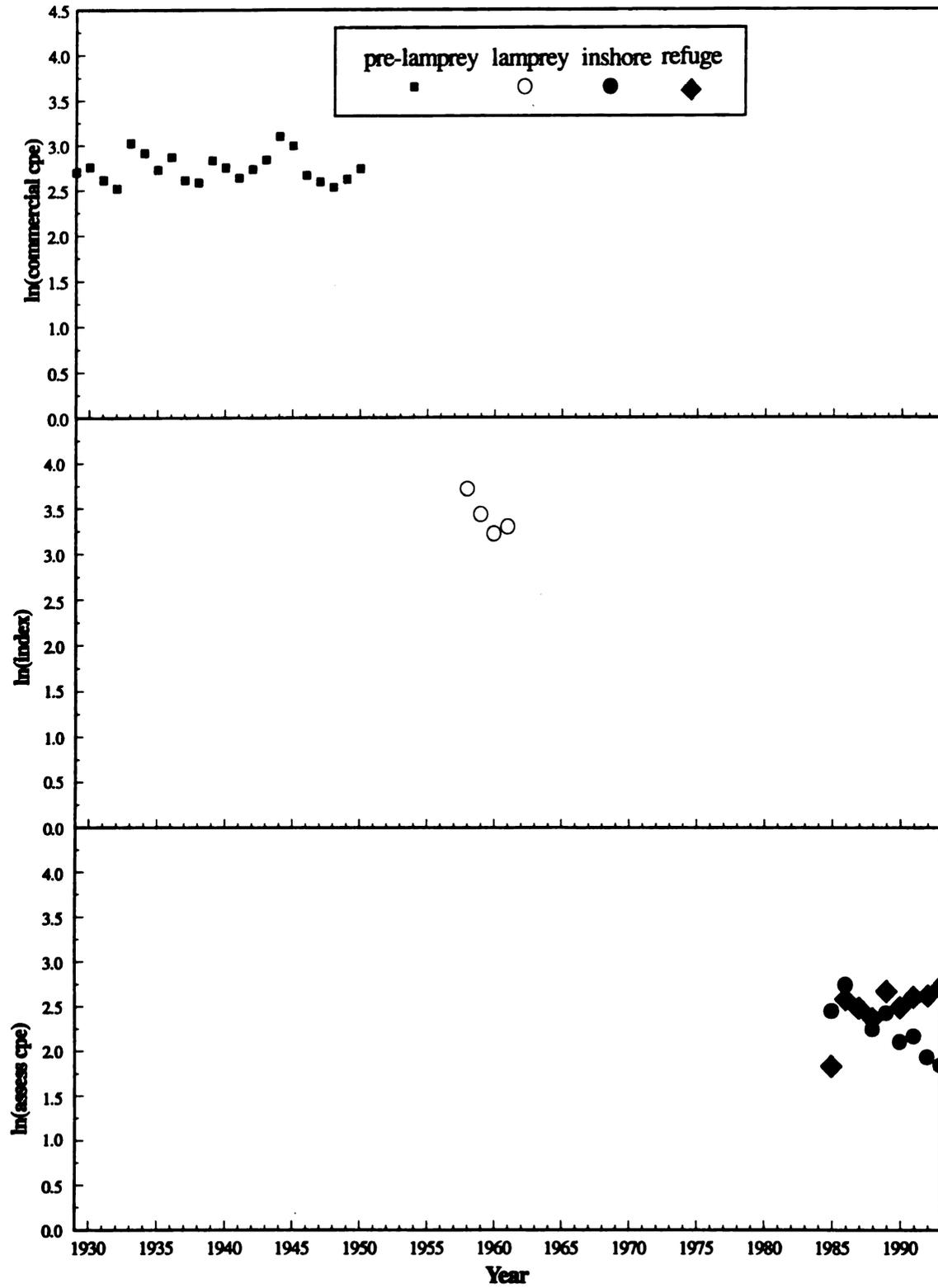


Figure 5. Data points used to determine the finite rate of population growth in the Wisconsin waters of Lake Superior for the three study periods.

determine if  $\lambda$  was significantly different from 1 (Rawlings 1988), a value which would indicate stable population numbers through time. I also calculated the 95% confidence interval of  $\lambda$  using the antilog<sub>e</sub> transformation of the upper and lower confidence limits for the slope. Analysis of covariance with contrasts (Rawlings 1988) was used to determine if the population growth rates corresponding to the different time periods were significantly different.

### *Age-0 Survival Estimates*

Using the estimates of  $\lambda$  and the parameterized Leslie matrix for each time period in both the Michigan and Wisconsin waters, age-0 survival ( $P_0$ ) was calculated using the equation:

$$P_0 = \frac{\lambda}{m_1 + \sum_{i=1}^{k-1} [(m_{i+1}/\lambda^i)(\prod_{j=1}^i P_j)]}$$

here  $\lambda$  is the finite rate of population growth,  $P_j$  is survival at age  $j$ , and  $m_i$  is fecundity at age  $i$ , and  $k$  is the longevity of the species (Vaughn and Saila 1976). The 95% confidence interval around  $P_0$  was approximated using the upper and lower bounds for  $\lambda$  in the equation for  $P_0$ .

### *Relative Contribution of $P_x$ and $F_x$*

Once the Leslie matrices were completed, I determined the sensitivity of the population growth rate to changes in age-specific survival and fecundity. I chose to use elasticity analysis, a type of sensitivity analysis that allows one to determine the

proportional change in the population growth rate in response to a proportional change in age-specific survival or fecundity (Caswell 1989). The calculated elasticities summed to 1 so that the relative contribution of matrix elements, age-specific survival and fecundity, to the population growth rate can be directly compared (deKroon et al. 1986, Caswell 1989). Thus, matrix elements (age specific survival and fecundity) associated with higher elasticities make a higher relative contribution to population growth rate than matrix elements associated with lower elasticity values. Comparison of elasticities allowed me to determine which factors were most important in determining the population growth. The elasticity ( $e_{ij}$ ) of  $\lambda$  with respect to the matrix element  $a_{ij}$  was calculated as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \left( \frac{v_i w_j}{\langle v, w \rangle} \right)$$

where  $w_i$  was the right eigenvector corresponding to  $\lambda$ ,  $v_i$  was the left eigenvector corresponding to  $\lambda$ , and  $\langle v, w \rangle$  was the scalar product of the two vectors (deKroon et al. 1986, Caswell 1989).

### *Fishing and Sea Lamprey Induced Mortality Tradeoff*

I evaluated the effect of different management scenarios aimed at controlling total mortality of current lake trout populations in the Michigan and Wisconsin waters of Lake Superior by changing either fishing or sea lamprey induced mortality to a specified percentage of the current value in the matrix and then recalculating  $\lambda$ . I allowed fishing mortality to vary from 0% to 200% of its current value and explored the effect of sea lamprey induced mortality at 0%, 50%, 100%, and 200% of the current sea lamprey

induced mortality rate. Additionally, by allowing both fishing and sea lamprey induced mortality to be zero and recalculating  $\lambda$  in this analysis, I was able to estimate the compensatory scope, or production potential, of these lake trout populations.

## RESULTS

### *Mortality Comparison*

In the Michigan waters of Lake Superior, sea lamprey induced mortality was very high during the sea lamprey dominant period and was still an important mortality factor during the current time period (Figure 6). Age specific fishing mortality did not vary greatly between the three time periods, but was an important mortality factor during each time period. Fishing and sea lamprey induced mortality rates were of similar magnitude during the current time period.

Sea lamprey induced mortality was not as extreme in the Wisconsin waters of Lake Superior as in the Michigan waters, but, as in the Michigan waters, it was higher during the sea lamprey dominant period than during the current period (Figure 7). Age specific fishing mortality in the Wisconsin waters was dramatically greater during the sea lamprey dominant period than during both the other periods in Wisconsin waters and the three periods in the Michigan waters. However, lake trout that resided in the refuge area of the Wisconsin waters during the current period experienced lower age specific fishing mortality and equal sea lamprey induced mortality than fish that were found in the inshore area.

Age specific fishing mortality exhibited a shift in the age of onset between the time periods in both sites. Since lake trout were fished using 114 mm (4.5 in) stretch mesh gill-nets that began catching fish efficiently at 51 cm (20 in; Pycha 1980) during the

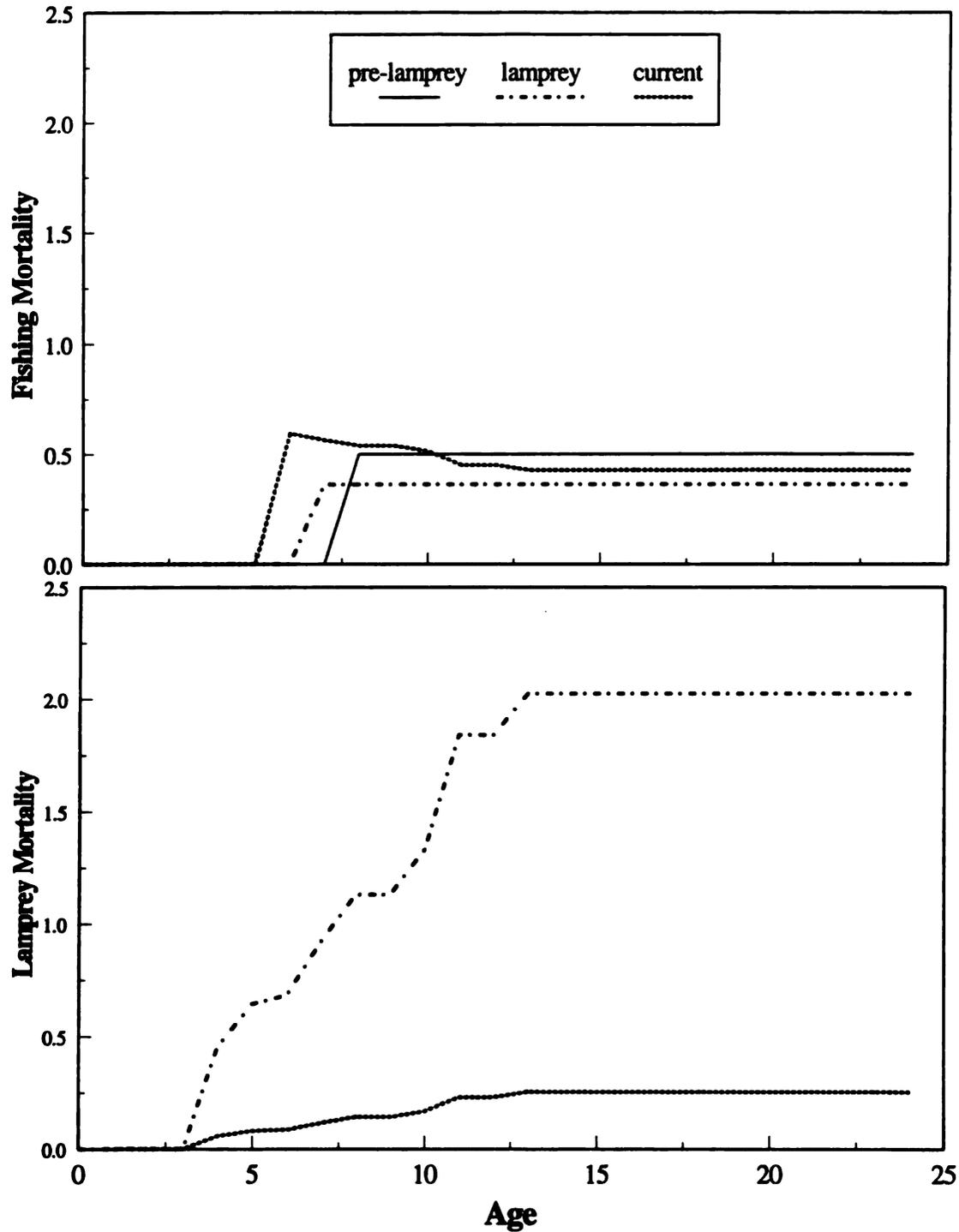


Figure 6. Age specific instantaneous fishing and sea lamprey mortality experienced by lake trout in the Michigan waters of Lake Superior during the three study periods.

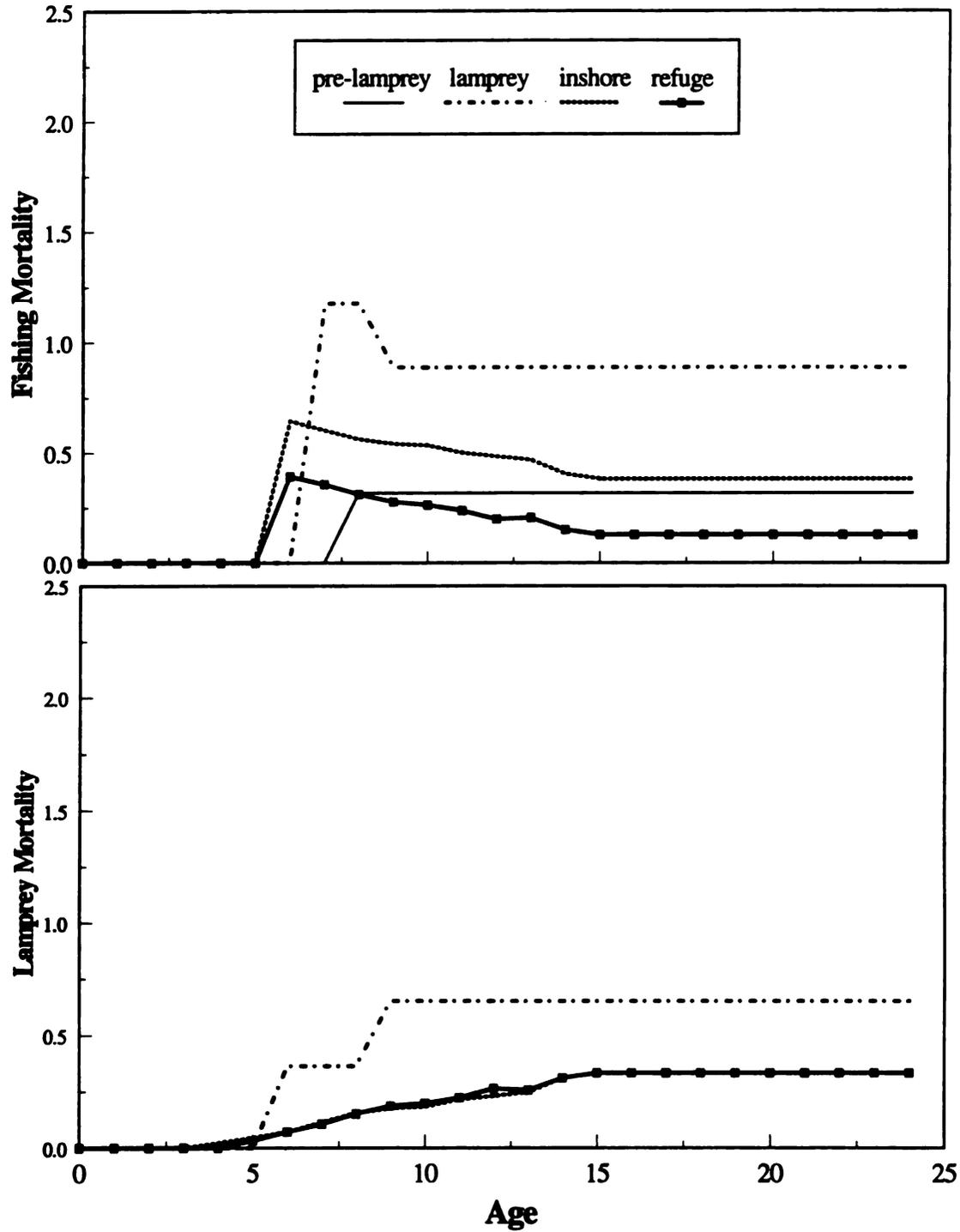


Figure 7. Age specific instantaneous fishing and sea lamprey mortality experienced by lake trout in the Wisconsin waters of Lake Superior during the three study periods.

three periods, the shift in age at which fishing mortality begins to take effect indicated that lake trout in each of the study periods reached a size of 51 cm (20 in) at different ages.

### *Growth Comparison*

Length and weight at age of lake trout in the Michigan waters of Lake Superior were significantly different during each time period ( $P=0.001$ ; Figure 8). Lake trout grew faster in both length and weight during the sea lamprey dominant period than during the pre-sea lamprey period. Further, current lake trout grew very differently than lake trout during either of the historical periods. Current lake trout grew faster until approximately age 8, but reached a much smaller ultimate adult size than lake trout during the historical time periods.

In the Wisconsin waters during the current time period, lake trout in the refuge area grew significantly longer at age than in the inshore area ( $P = 0.0116$ ; Figure 9). In addition, during the current time period, growth in length of lake trout in the Michigan waters was not significantly different than lake trout growth in the Wisconsin inshore area ( $P = 0.3058$ ), but was significantly different than lake trout growth in the Wisconsin refuge area ( $P = 0.0306$ ). This finding was probably due to the fact that lake trout are heavily fished in both the Michigan waters and the inshore area of the Wisconsin waters resulting in similar growth in the two areas.

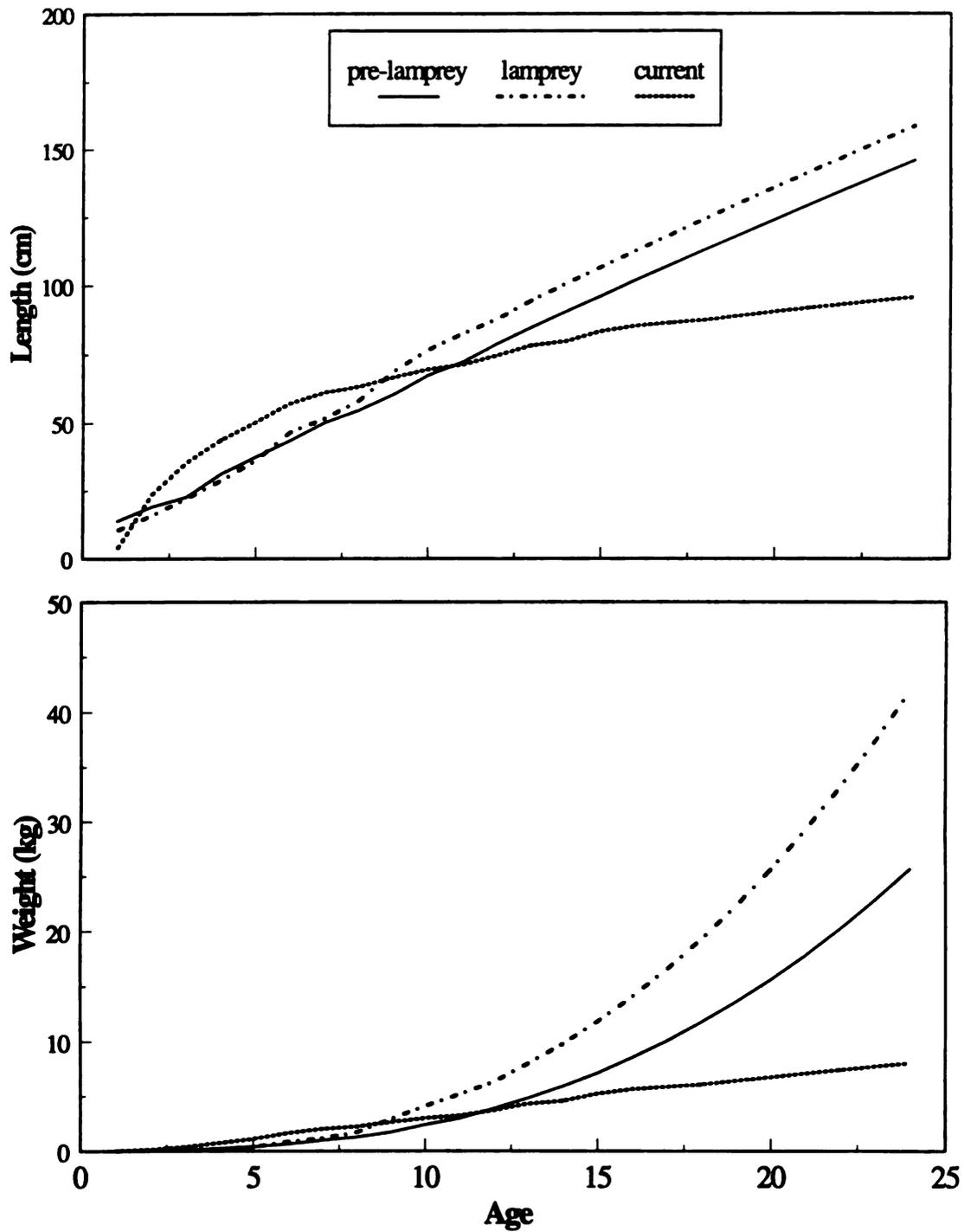


Figure 8. Comparison of length and weight at age of lake trout in the Michigan waters of Lake Superior during the three study periods.

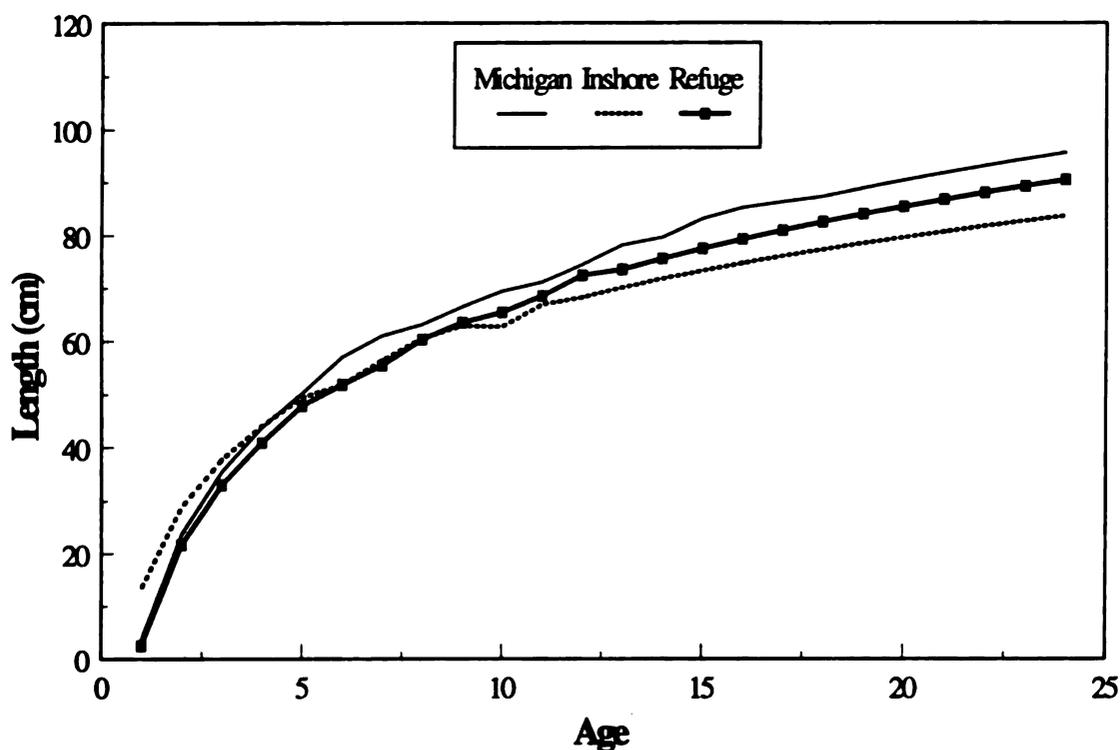


Figure 9. Length at age of lake trout in the Michigan and Wisconsin (inshore and refuge areas) waters of Lake Superior during the current time period.

#### *Fecundity Comparison*

Fecundity of lake trout between sites and time periods was compared in terms of both weight specific and age specific fecundity. I compared the weight specific fecundity of lake trout during the periods for which a fecundity-weight relationship was available: the pre-sea lamprey and the current periods in the Michigan waters, and the current period in Wisconsin waters. Weight specific fecundity was not significantly different as indicated by the overlap in the 95% confidence intervals on the predicted value of number of eggs at a given weight (Figure 10). Although the 95% confidence intervals for the two periods in the Michigan waters overlapped, current lake trout consistently have a higher

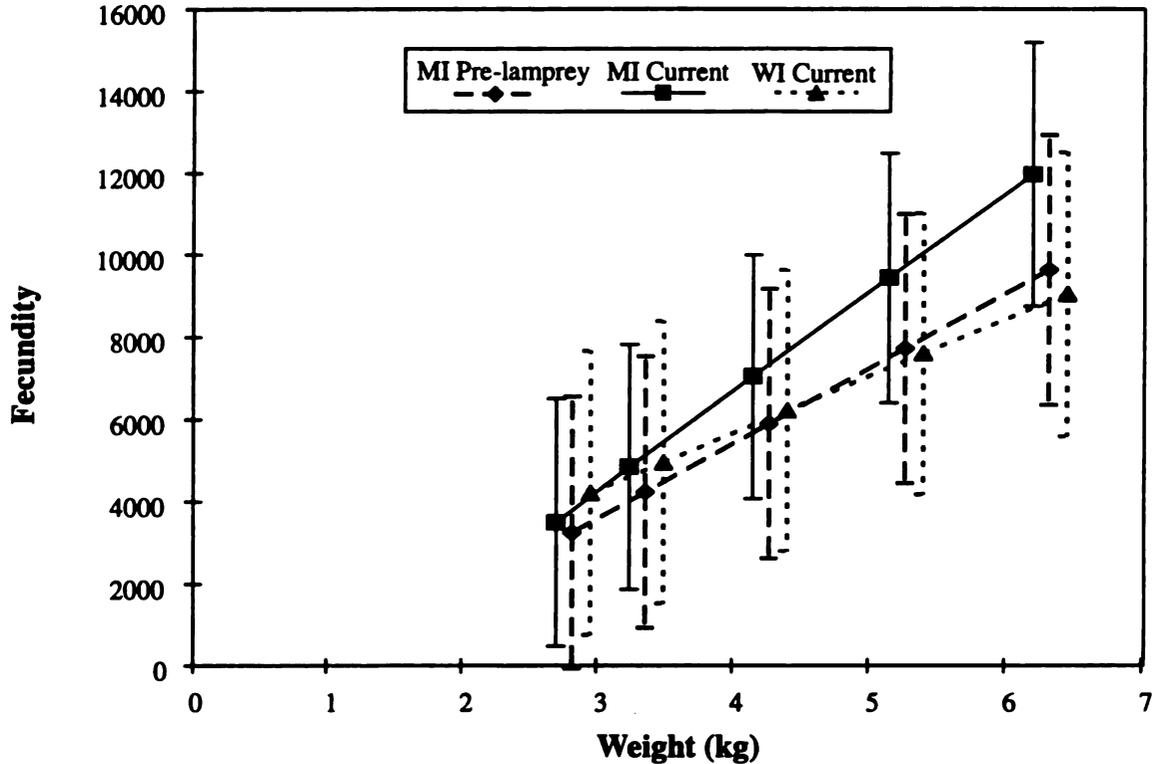


Figure 10. Comparison of weight specific fecundity of lake trout populations during the pre-sea lamprey and current time periods in the Michigan waters and during the current period in the Wisconsin waters of Lake Superior.

number of eggs at a given weight.

I compared age specific fecundity between the three time periods in both sites separately and between sites during the current time period. In the Michigan waters, age specific fecundity was not significantly different between the pre-sea lamprey period and the sea lamprey dominant period ( $P = 0.07$ ). However, age specific fecundity during the historical periods was significantly different from the current time period ( $P = 0.001$  for both comparisons; Figure 11). A similar pattern was evident in the Wisconsin waters where fecundity at age of lake trout during the pre-sea lamprey and the sea lamprey dominant periods were not significantly different from each other ( $P = 0.1612$ ; Figure

11). However, age specific fecundity in both historical time periods was significantly different from age specific fecundity calculated for both the refuge and the inshore areas during the current time period ( $P = 0.0004$  for the inshore area and  $P = 0.0016$  for the refuge area). Age specific fecundity of current lake trout populations in the Michigan waters was not significantly different from that of current lake trout populations in the inshore area of the Wisconsin waters ( $P = 0.5706$ ) or from lake trout in the Wisconsin refuge area ( $P = 0.4102$ ; Figure 12). Likewise, the fecundity at age of lake trout currently found in the inshore and refuge areas of the Wisconsin waters was not significantly different ( $P = 0.2939$ ).

The age at which members of the population became mature shifted between the three time periods in both sites. Lake trout during the pre-sea lamprey period became mature at age 10 in both sites, age 9 during the sea lamprey dominant period in both sites, and ages 6 and 7 during the current period in the Michigan and Wisconsin waters respectively.

#### *Population Growth Rate Comparison*

The finite population growth rates calculated for the pre-sea lamprey and current periods in the Michigan waters and for the inshore area of the current period in Wisconsin waters (Table 6) were all significantly less than 1 indicating that the population abundance was declining during these periods. The population growth rate calculated during the sea lamprey dominant period was not significantly different from 1 in either the Michigan ( $P=0.0726$ ) or the Wisconsin ( $P=0.1292$ ) waters. However, it is known from experience that lake trout populations collapsed in Lake Superior during this time

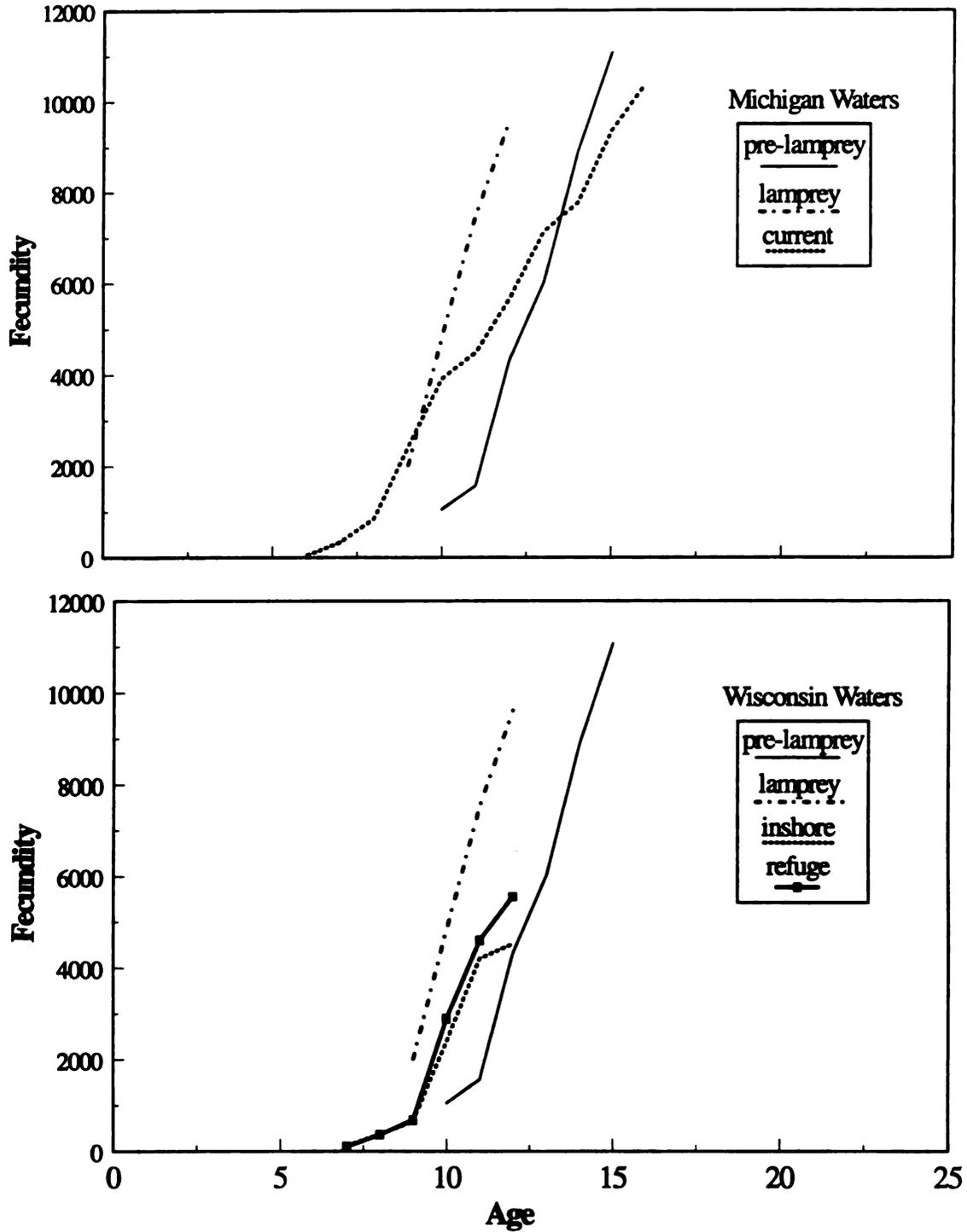


Figure 11. Comparison of age specific fecundity of lake trout populations in the Michigan and Wisconsin waters of Lake Superior during the three study periods.

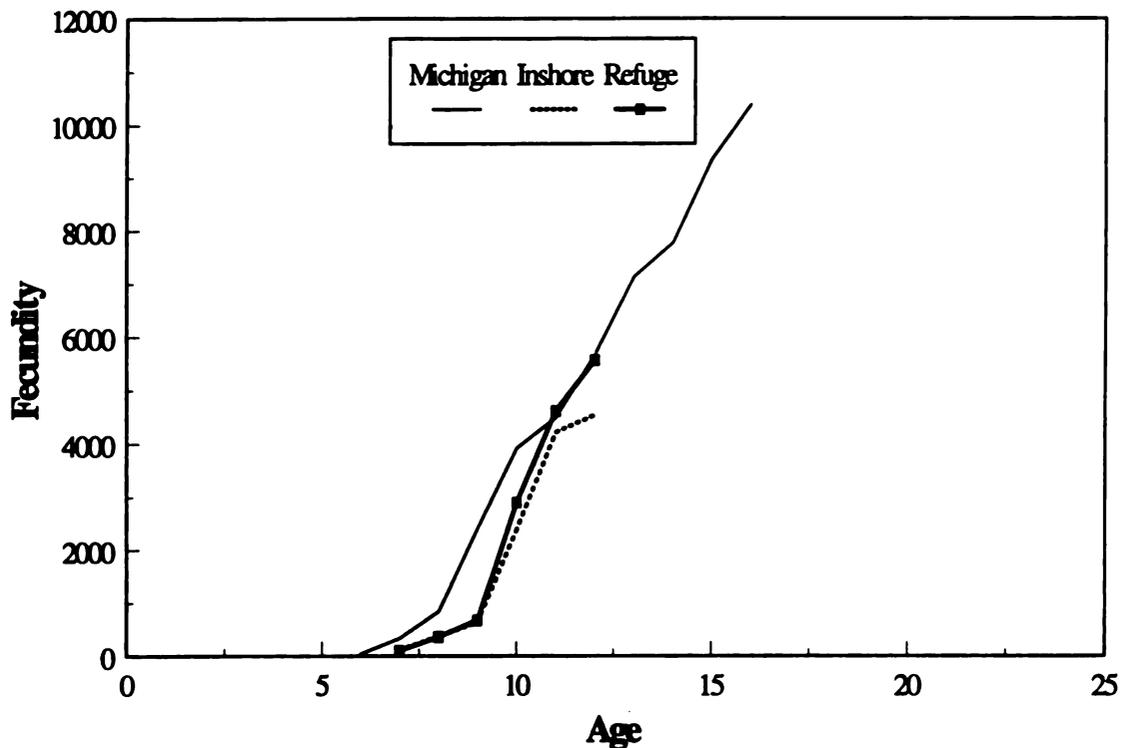


Figure 12. Comparison of age specific fecundity of current lake trout populations in the Michigan and Wisconsin (inshore and refuge areas) waters of Lake Superior.

period. The lack of statistical significance was probably the result of having such few data points included in the regression ( $N = 4$ ) and does not negate the biological significance of these population growth rates. The population growth rate calculated for the pre-sea lamprey period in the Wisconsin waters was not significantly different from 1 indicating that lake trout in the Wisconsin waters of Lake Superior had a relatively stable abundance before sea lamprey invaded the lake. In contrast, the population growth rate calculated for the current time period in the refuge area of the Wisconsin waters was significantly greater than 1 indicating that the population was increasing.

In the Michigan waters, the population growth rate during the pre-sea lamprey period was significantly greater than the population growth rates during the sea lamprey dominant ( $P=0.0335$ ) and current ( $P=0.0350$ ) periods. However, the population growth rates calculated for the current and sea lamprey dominant periods were not significantly different from each other ( $P=0.1400$ ). In the Wisconsin waters, the population growth rate calculated for the pre-sea lamprey period was significantly greater than the population growth rate of current lake trout in the inshore area ( $P=0.0002$ ), but was

Table 6. Estimates of finite rate of population growth ( $\lambda$ ) of wild lake trout in the Michigan and Wisconsin waters of Lake Superior, the bounds of the 95% confidence interval, and the probability of getting a larger value of  $t$  if the parameter was truly equal to 1 ( $H_0: \lambda=1$ ).

<b>Michigan Waters</b>					
Period	Years	$\lambda$	Lower 95%	Upper 95%	$P> t $
Pre-Sea Lamprey	1929-1950	0.972	0.962	0.983	0.000024
Sea Lamprey Dominant	1958-1961	0.836	0.671	1.041	0.072575
Current	1985-1993	0.930	0.886	0.976	0.009224
<b>Wisconsin Waters</b>					
Period	Years	$\lambda$	Lower 95%	Upper 95%	$P> t $
Pre-Sea Lamprey	1929-1950	0.998	0.987	1.010	0.840974
Sea Lamprey Dominant	1958-1961	0.863	0.671	1.111	0.129232
Current - Inshore	1985-1993	0.910	0.873	0.949	0.001108
Current - Refuge	1985-1993	1.069	1.004	1.130	0.040392

significantly less than the current population growth rate in the refuge area ( $P=0.0042$ ). However, the population growth rate for the pre-sea lamprey period was not significantly different from that during the sea lamprey dominant period ( $P=0.0598$ ). Further, the calculated population growth rate for the sea lamprey dominant period was significantly less than the current population growth rate in the refuge area ( $P=0.0093$ ), but was not significantly different from the population growth rate of lake trout in the inshore area ( $P=0.5017$ ).

I also compared the population growth rates during the current time period between the Michigan waters and the inshore and refuge areas of the Wisconsin waters of Lake Superior. The population growth rate in the Wisconsin refuge area was significantly greater than the population growth rate in the Wisconsin inshore area ( $P=0.0001$ ) and in the Michigan waters ( $P = 0.0002$ ); that is, the population in the Wisconsin refuge area was increasing while lake trout populations in the Wisconsin inshore area and in Michigan waters were declining. The population growth rates in the Michigan waters and the inshore area of the Wisconsin waters were not significantly different ( $P = 0.4918$ ).

#### *Age-0 Survival Estimates*

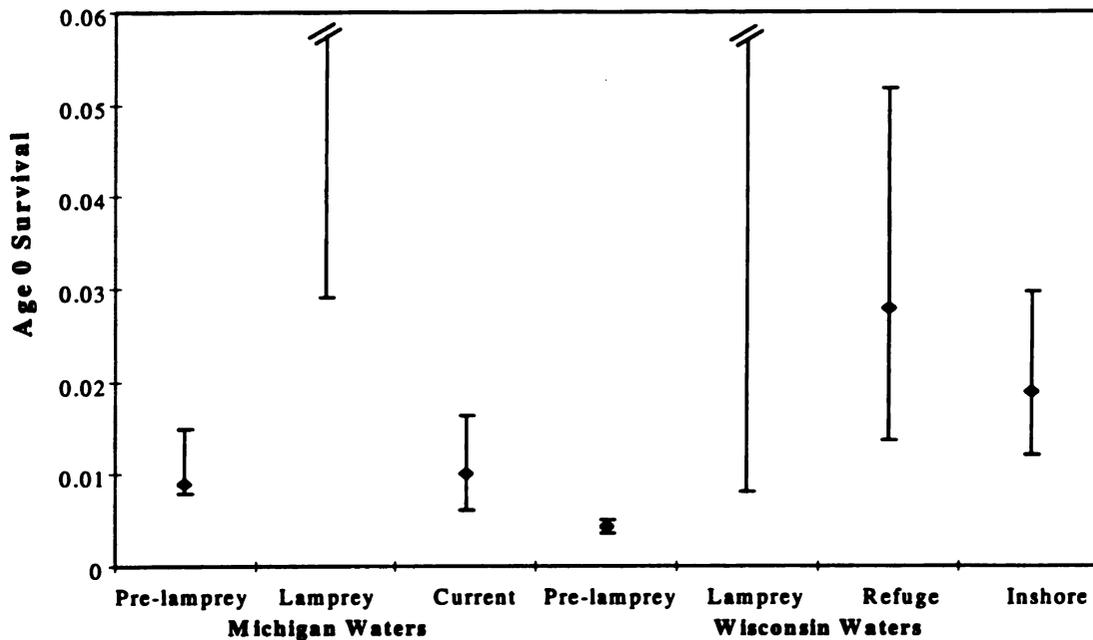
Estimates of average age-0 survival for lake trout ranged from 0.00907 to 0.288 in the Michigan waters and from 0.00430 to 0.119 in the Wisconsin waters (Table 7) of Lake Superior. In the Michigan waters, the lowest estimate of age-0 survival was obtained for the pre-sea lamprey period. The estimate of age-0 survival increased dramatically during the sea lamprey dominant period, but the estimate in the current time period was almost as low as the estimate for the pre-lamprey period. The confidence

Table 7. Estimates of age-0 survival and of the upper and lower 95% confidence interval bounds for wild lake trout in the Michigan and Wisconsin waters of Lake Superior during the three time periods.

<b>Michigan Waters</b>			
<b>Period</b>	<b>Age-0 Survival</b>	<b>Lower 95%</b>	<b>Upper 95%</b>
Pre-Sea Lamprey	0.00907	0.00784	0.0105
Sea Lamprey Dominant	0.288	0.0290	2.806
Current	0.0101	0.00619	0.0164
<b>Wisconsin Waters</b>			
<b>Period</b>	<b>Age-0 Survival</b>	<b>Lower 95%</b>	<b>Upper 95%</b>
Pre-Sea Lamprey	0.00430	0.00363	0.00510
Sea Lamprey Dominant	0.119	0.00808	1.694
Current - Inshore	0.0189	0.0120	0.0296
Current - Refuge	0.0279	0.0136	0.0517

intervals around the estimates of age-0 survival during the pre-sea lamprey and the current time periods in the Michigan waters overlap indicating that these estimates were not different (Figure 13). However, neither of the confidence intervals for the pre-lamprey or the current periods overlap the confidence interval for the estimate during the sea lamprey dominant era. That these confidence intervals did not overlap indicated that the estimates of age-0 survival during the pre-sea lamprey and the current periods were different from the estimate of age-0 survival during the sea lamprey dominant period.

The estimates of age-0 survival in the Wisconsin waters exhibit a similar trend to the estimates in the Michigan waters (Table 7). The lowest age-0 survival was estimated for the pre-sea lamprey period. The estimate increased dramatically for the sea lamprey



**Figure 13.** The 95% confidence intervals for estimates of age-0 survival in the Michigan and Wisconsin waters of Lake Superior during the three study periods. Only the lower 95% confidence limit is shown for the sea lamprey dominant period.

dominant period and decreased in both the inshore and refuge areas during the current time period. The confidence intervals for the estimates during the pre-sea lamprey and the sea lamprey dominant periods do not overlap indicating that age-0 survival during the sea lamprey dominant period was significantly higher (Figure 13). However, the confidence interval for the estimate of age-0 survival during the sea lamprey dominant period completely overlaps the confidence intervals around the estimates for the current period in both the inshore and refuge areas indicating that age-0 survival was not different during the sea lamprey dominant and the current periods. In contrast to the Michigan waters, the confidence intervals for the estimates during the pre-sea lamprey and the current periods do not overlap indicating that age-0 survival during the pre-sea lamprey

period was significantly lower than age-0 survival during the current period. In addition, the confidence intervals for estimates of age-0 survival in the Michigan waters and the inshore and refuge areas of the Wisconsin waters during the current time period overlap indicating that current lake trout populations exhibit similar age-0 survival rates in the three areas.

The age-0 survival rates estimated for the sea lamprey dominant period in the Michigan waters were very high. To determine the effect of age-0 survival on the growth rate of lake trout populations in the Michigan waters, the age-0 survival rates estimated for the current and pre-sea lamprey period were substituted into the Leslie matrix characterizing the sea lamprey dominant period and used to calculate  $\lambda$  (Figure 14). During the sea lamprey dominant period, lake trout populations were declining ( $\lambda = 0.8361$ ). If these fish had the same age-0 survival as lake trout in the pre-sea lamprey or current time periods, the population would have declined at a greater rate ( $\lambda = 0.6011$ ,  $0.6073$  respectively). Clearly, if age-0 survival rate had not increased in response to increased adult lake trout mortality during the sea lamprey dominant period, the population would have declined in a more precipitous manner than observed.

Using the population dynamics observed during the current time period in the Michigan waters, I examined the effect of increasing age-0 survival (Figure 14). Currently, lake trout populations in the Michigan waters of Lake Superior are declining ( $\lambda = 0.930$ ). If the current population had an age-0 survival equal to that of the sea lamprey dominant period, the current population would increase rather than decrease ( $\lambda = 1.319$ ). However, age-0 survival need only increase to 0.0208 from its current value of 0.0101 to achieve stable population growth ( $\lambda = 1$ ).

Similar effects of age-0 survival were observed in the Wisconsin waters of Lake Superior. Lake trout populations were declining quickly during the sea lamprey dominant period in the Wisconsin waters. As in the Michigan waters, if age-0 survival had not increased, lake trout populations would have declined at an even faster rate (Figure 15). Currently, lake trout populations in the Wisconsin waters are declining in the inshore area ( $\lambda = 0.910$ ) and are increasing in the refuge area ( $\lambda = 1.069$ ). If lake trout in the inshore area had an age-0 survival equal to those in the refuge area, then the population would be decreasing at a slower rate ( $\lambda = 0.944$ ; Figure 15). However, if the lake trout population in the inshore waters had an age-0 survival similar to lake trout populations during the pre-sea lamprey period, the population would decrease at an even faster rate ( $\lambda = 0.796$ ). If these lake trout had an age-0 survival as high as that estimated for the sea lamprey dominant period, the current inshore population would be increasing at a rate of approximately 9% per year ( $\lambda = 1.086$ ). However, to achieve stable population growth in the inshore area, the age-0 survival needs to increase from 0.0279 to 0.0511.

#### *Relative Contribution of $P_x$ and $F_x$*

Similar trends in the proportional sensitivity of the population growth rate to changes in age-specific survival and fecundity were observed in the Michigan and Wisconsin waters of Lake Superior. Lake trout populations in the Michigan and Wisconsin waters during the pre-sea lamprey period were at a relatively high level of abundance, but were declining due to heavy fishing exploitation. During this period, the relative contribution of survival to the population growth rate was greater than fecundity at all ages (Figure 16). Age at first maturity was reached at age 10 in both sites, and

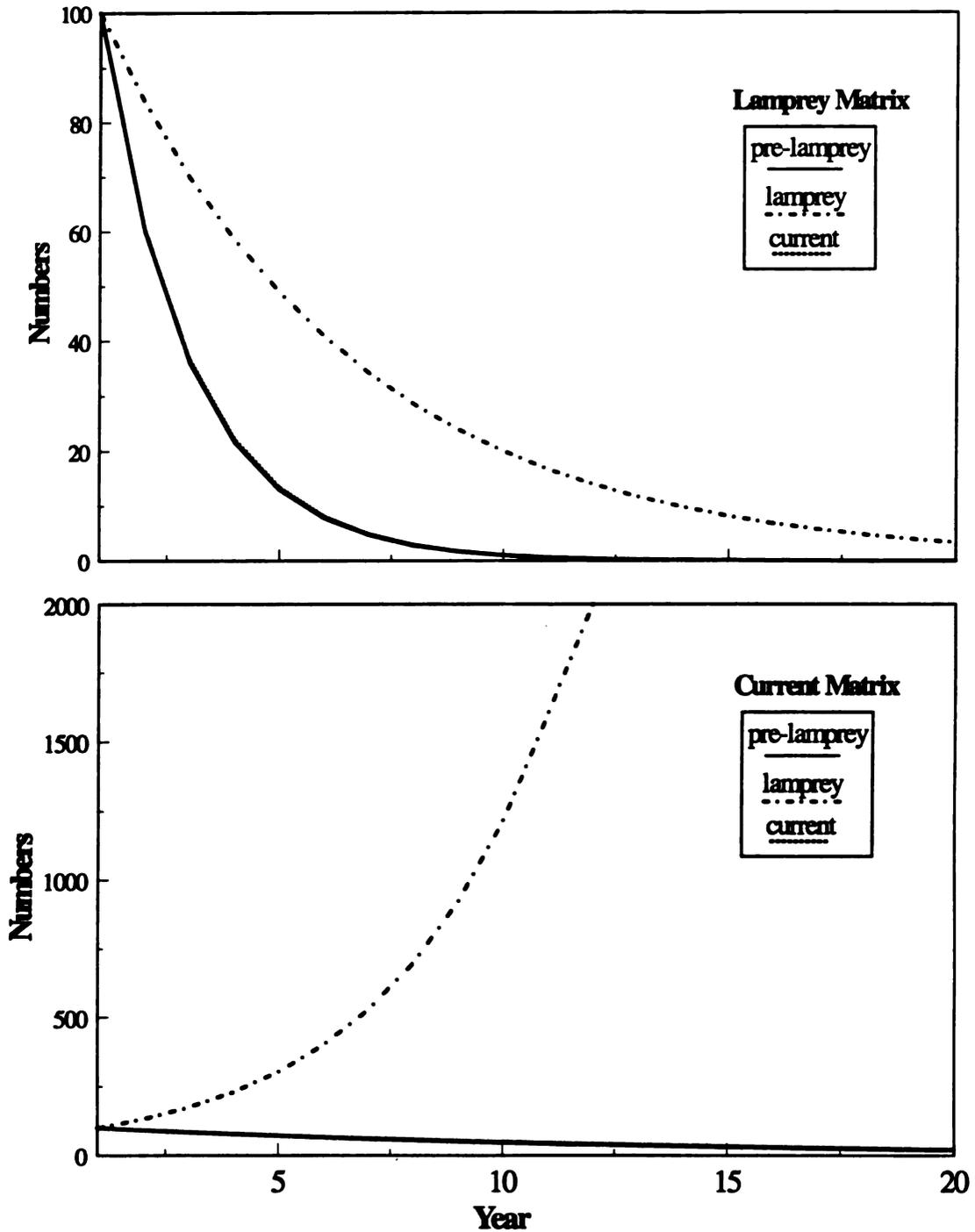


Figure 14. Projections of lake trout populations during the sea lamprey dominant (top) and the current (bottom) periods in the Michigan waters of Lake Superior using the age-0 survival corresponding to the three time periods ( $N = 100$  at year 1).



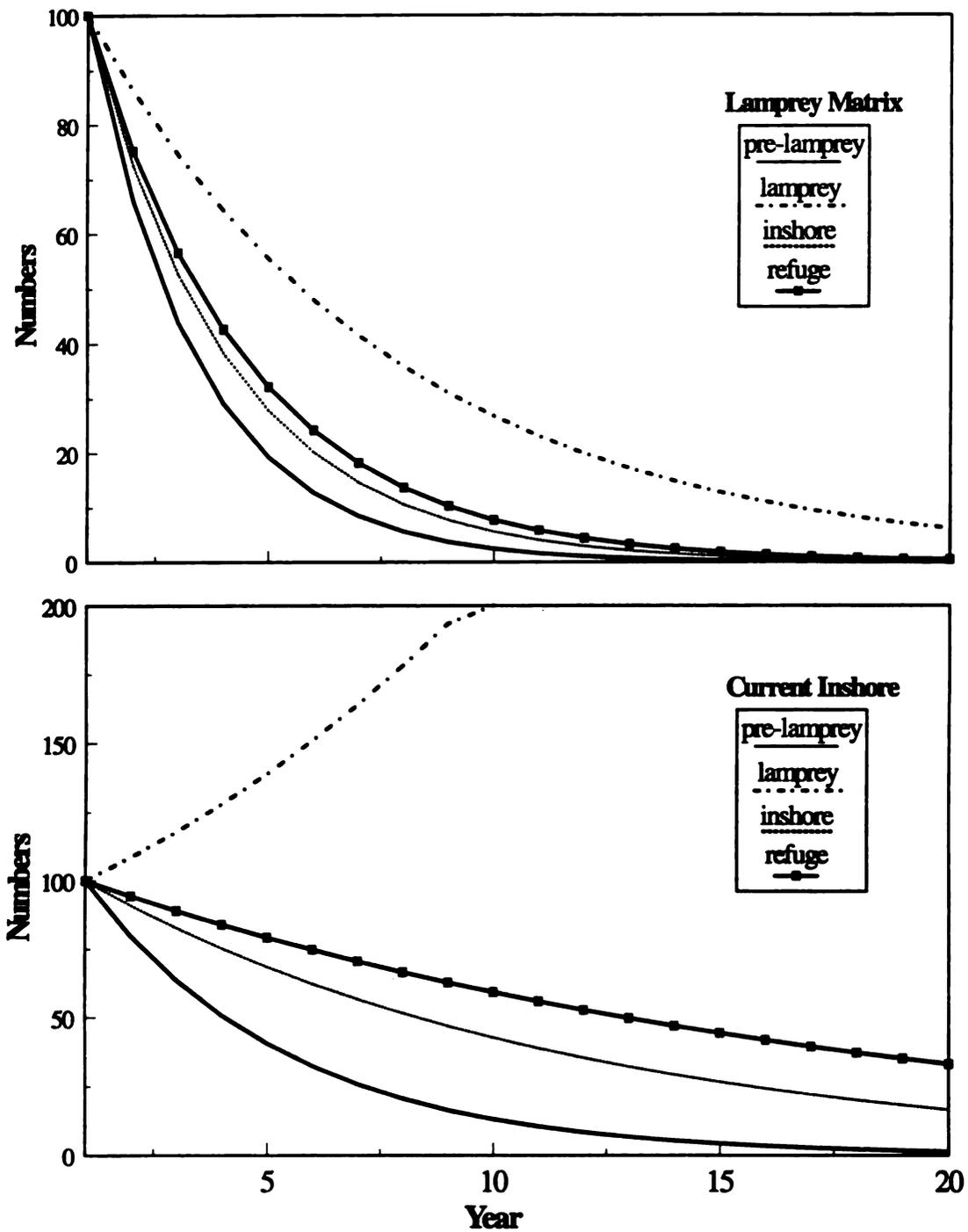


Figure 15. Projections of lake trout populations during the sea lamprey dominant (top) and the current (bottom) periods in the Wisconsin waters of Lake Superior using the age-0 survival corresponding to the three time periods ( $N = 100$  at year 1).

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survival during the pre-reproductive ages was the most significant factor contributing to the population growth rate. During the sea lamprey dominant period, lake trout populations declined at an even faster rate, and the age structure of the population was truncated with few individuals living beyond age 12 in the Michigan waters and age 13 in the Wisconsin waters (Figure 17). Age at first maturity was reached at age 9 in both sites during this time period, and survival during the pre-reproductive ages was still very important in contributing to the population growth rate. However, once the fish reached maturity, the relative contribution of fecundity to the population growth rate was much greater than survival at those ages.

During the current time period, lake trout populations in the Michigan waters and in the inshore area of the Wisconsin waters were declining, while they were increasing in the refuge area of the Wisconsin waters. Lake trout matured at a much earlier age than in the historical time periods in both sites, age 6 in the Michigan waters and age 7 in the Wisconsin waters (Figure 18). Survival of lake trout during the pre-reproductive ages still had the greatest relative contribution to population growth, and survival was more important than fecundity in determining population growth rate until age 11. The relative contribution of survival and fecundity of the older lake trout in the population was nearly identical, although it was much less than the relative contribution of either survival or fecundity at earlier ages.

### *Compensatory Scope*

I calculated the maximum possible population growth rate for lake trout populations during each time period assuming that all mortality factors, other than natural

Elasticity

Elasticity

Fig

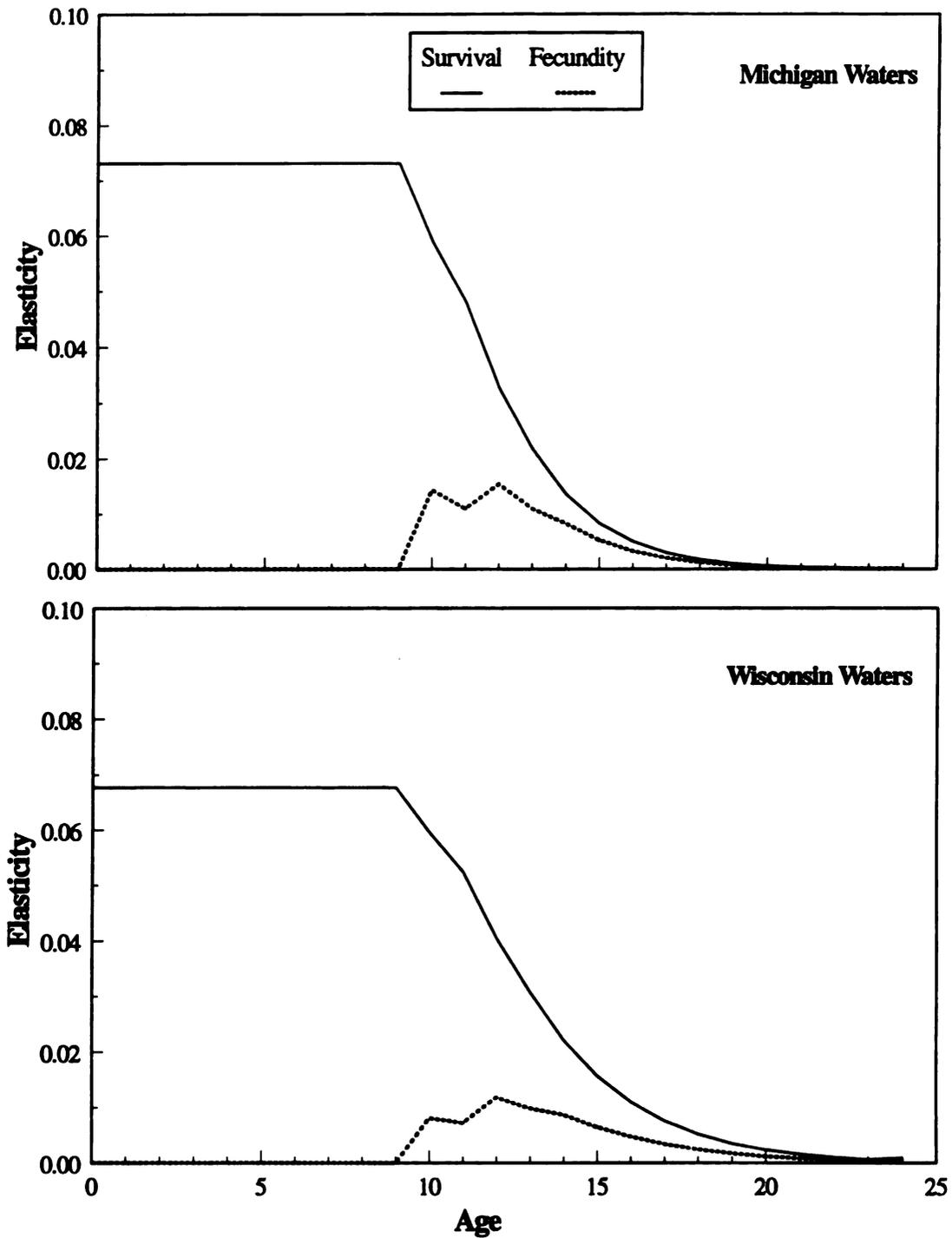
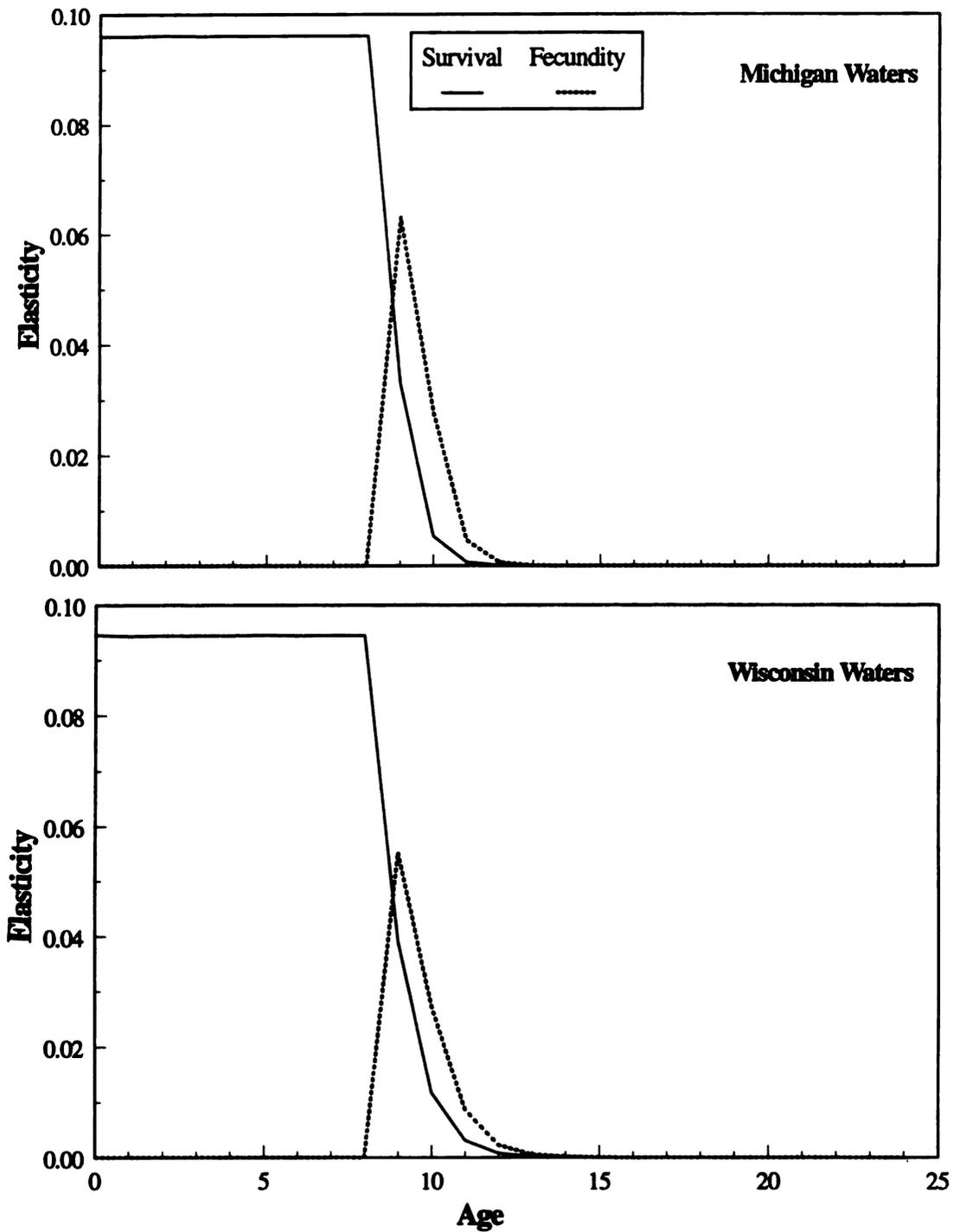


Figure 16. Elasticities (relative contribution) of age specific survival and fecundity rates to lake trout population growth during the pre-sea lamprey period in the Michigan and Wisconsin waters of Lake Superior.





**Figure 17.** Elasticities (relative contribution) of age specific survival and fecundity rates to lake trout population growth during the sea lamprey dominant period in the Michigan and Wisconsin waters of Lake Superior.

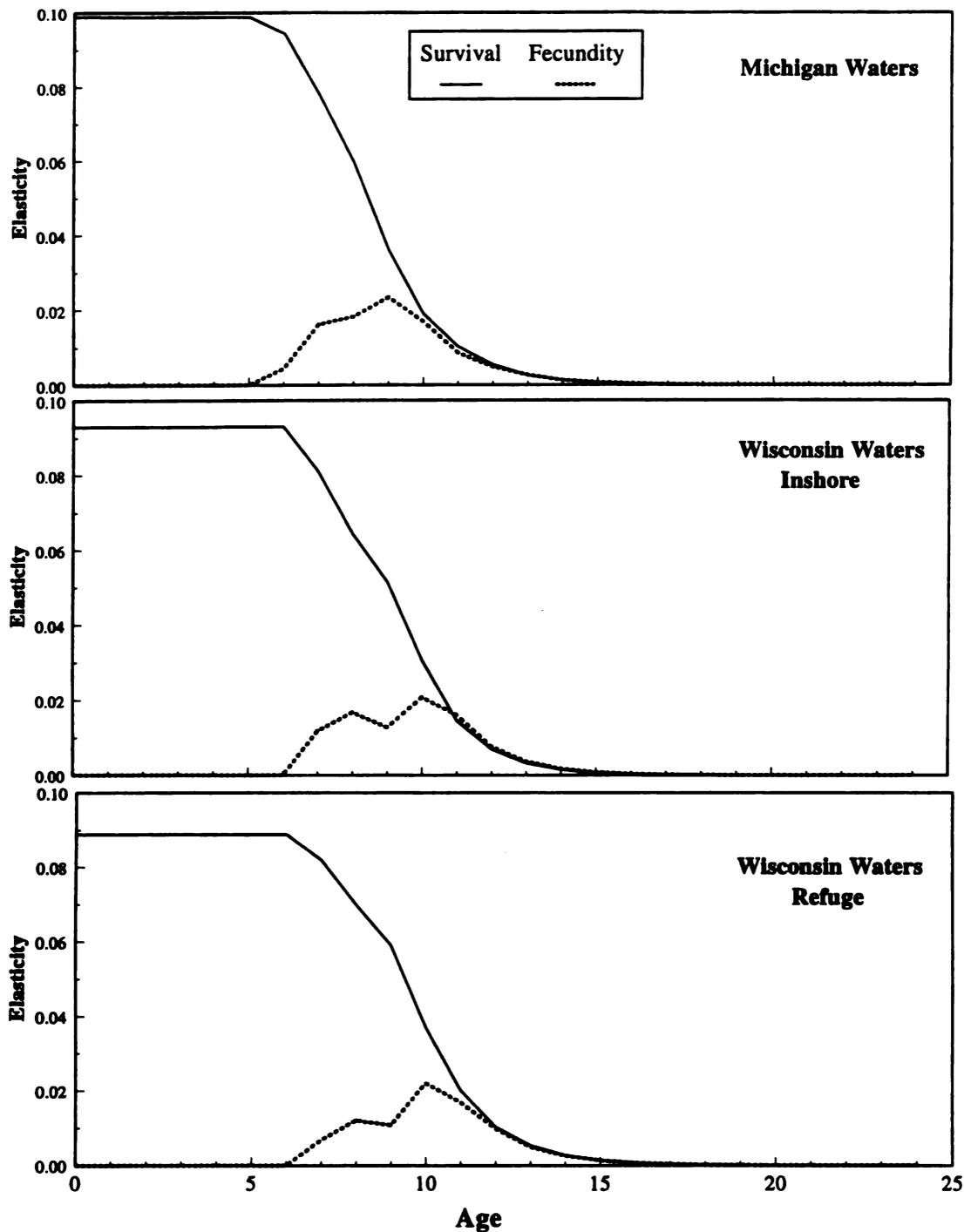


Figure 18. Elasticities (relative contribution) of age specific survival and fecundity rates to lake trout population growth during the current time period in the Michigan and Wisconsin waters of Lake Superior.

mortality, were removed to determine the compensatory scope of the population. The greatest production potential was exhibited by lake trout populations during the sea lamprey dominant period in both the Michigan and Wisconsin waters (Table 8). If both fishing and sea lamprey induced mortality were reduced to zero during the sea lamprey dominant period, lake trout populations had the potential to grow at 70% per year rather than decline at 16% per year in the Michigan waters and to grow at 59% per year rather than decline at 14% per year in the Wisconsin waters.

During the pre-sea lamprey period, lake trout populations had the potential to grow at 22% per year in the Michigan waters and at 17% per year in the Wisconsin waters if fishing mortality had been completely eliminated. The production potential of current lake trout populations in both areas was less than that of lake trout populations during the sea lamprey dominant period and greater than that of lake trout populations during the pre-sea lamprey period (Table 8). If both fishing and sea lamprey induced mortality could be eliminated completely, current lake trout populations could grow at a rate of 28% per year in the Michigan waters and at 29% annually in the inshore area of the Wisconsin waters rather than decline by 7% and 9% annually respectively. Eliminating fishing and sea lamprey induced mortality in the refuge area of the Wisconsin waters would allow the population to grow at a much faster rate, 35% per year rather than the current 7%.

### *Fishing and Sea Lamprey Induced Mortality Tradeoff*

I evaluated the tradeoff between fishing and sea lamprey induced mortality for current lake trout populations in the Michigan waters and the inshore and refuge areas of

**Table 8.** Comparison of the observed population growth rate during each time period and the calculated maximum possible population growth rate.

<b>Time Period &amp; Site</b>	<b>Observed <math>\lambda</math></b>	<b>Maximum <math>\lambda</math></b>
<b>Pre-Sea Lamprey</b>		
Michigan	0.972	1.221
Wisconsin	0.998	1.167
<b>Sea Lamprey Dominant</b>		
Michigan	0.836	1.705
Wisconsin	0.863	1.587
<b>Current</b>		
Michigan	0.930	1.283
Wisconsin - Inshore	0.910	1.293
Wisconsin - Refuge	1.069	1.347

the Wisconsin waters. In the Michigan waters, lake trout populations were declining at a rate of 7% per year ( $\lambda = 0.930$ ) given 100% of the current fishing mortality and 100% of the current sea lamprey induced mortality (Figure 19). Given the current level of sea lamprey induced mortality, if fishing mortality was allowed to increase further, the current population in the Michigan waters would decline at even faster rates. In fact, fishing mortality would need to be reduced by approximately 35% to achieve a stable population in the Michigan waters. In order to achieve a growing population in the Michigan waters, fishing would need to be reduced even further given the current rates of sea lamprey induced mortality. However, if sea lamprey induced mortality could be reduced to one-half of its current level, fishing would only need to be reduced by 20% in

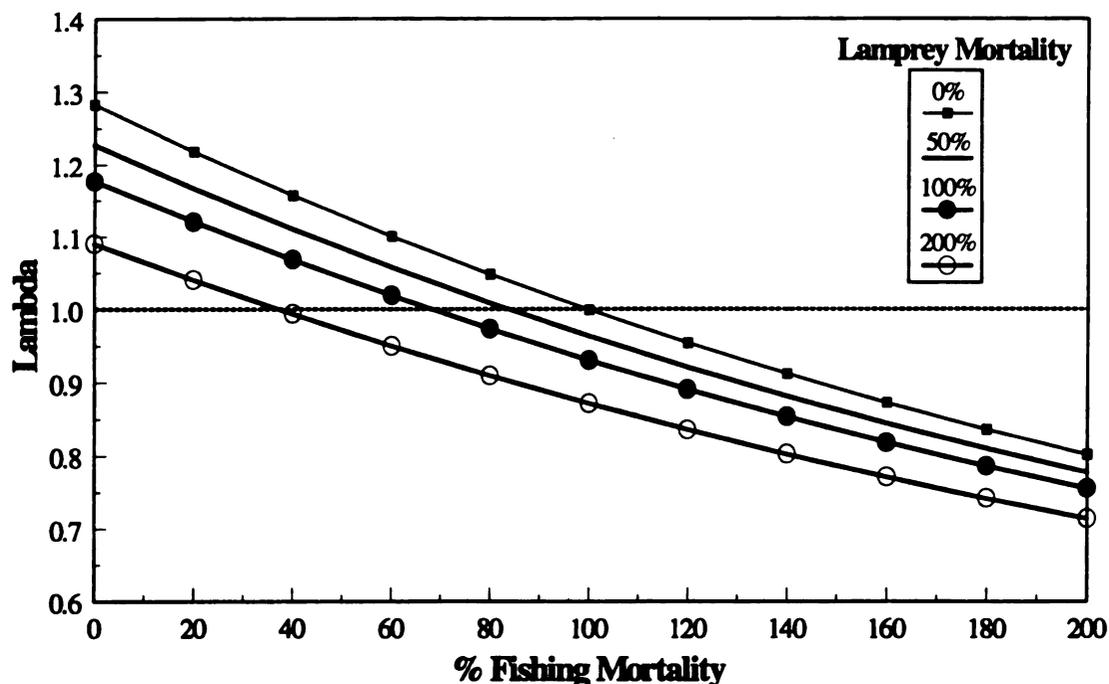


Figure 19. Tradeoff between fishing and sea lamprey induced mortality (expressed as a percent of the current value) for current lake trout populations in the Michigan waters of Lake Superior.

order to attain a stable population. Further, if sea lamprey induced mortality could be eliminated completely, fishing mortality would only need to be reduced by 1% or 2% in order to maintain a stable population. On the other hand, given current fishing mortality levels, if sea lamprey induced mortality doubled, the population would decrease at approximately 13% per year, a similar rate as observed during the sea lamprey dominant period. In order to achieve a stable population given 200% sea lamprey induced mortality, fishing mortality would have to be reduced by over 60%. Given the current individual growth and fecundity schedule of lake trout populations in the Michigan waters of Lake Superior, reducing fishing mortality had a greater effect on the population growth rate than reducing sea lamprey induced mortality. For example, if the current fishing mortality rate was reduced by 20% given the current sea lamprey induced

mortality,  $\lambda$  would increase to 0.973. On the other hand, if the current sea lamprey induced mortality was reduced by 20% given the current level of fishing mortality,  $\lambda$  only increases to 0.943 - 3% per year less than when fishing was reduced by the same percentage.

Similar trends were observed in the inshore area of the Wisconsin waters. Currently, given 100% of the current fishing and sea lamprey induced mortality, the lake trout population is decreasing at 9% per year (Figure 20). Given the current rate of sea lamprey induced mortality, fishing mortality would need to be reduced by 40% to achieve stable population growth and should be reduced even further if growing lake trout

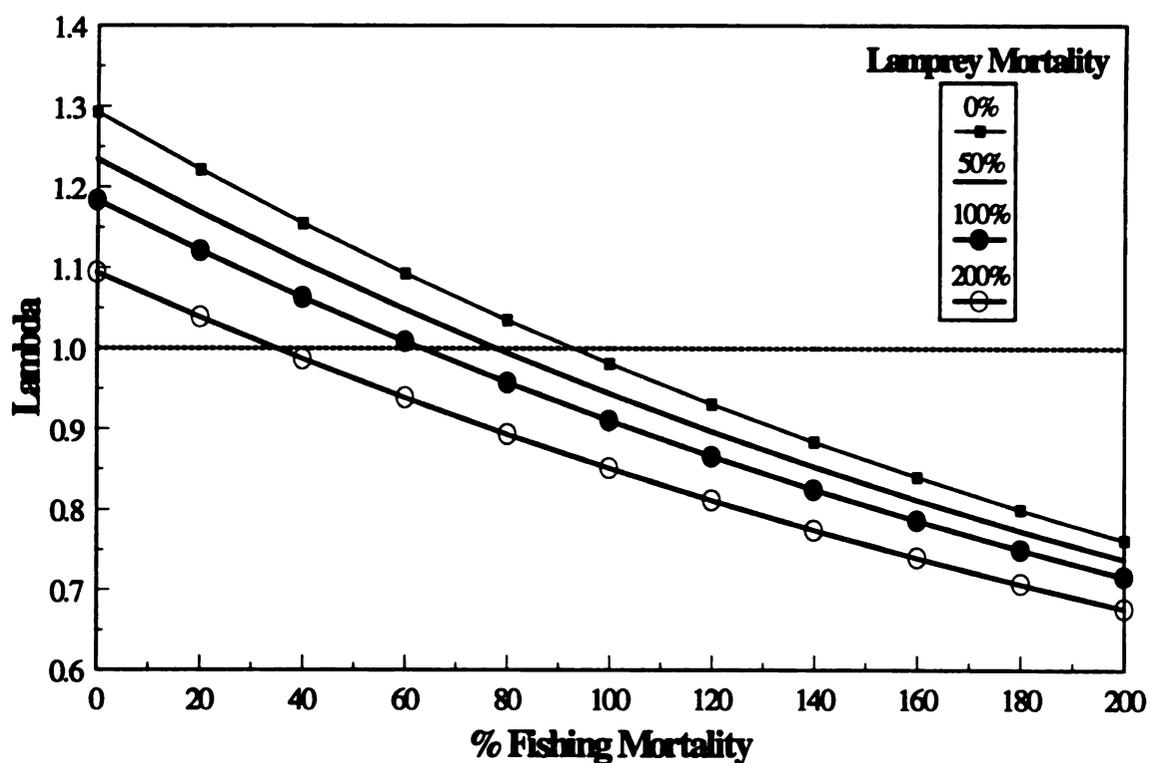


Figure 20. Tradeoff between fishing and sea lamprey induced mortality (expressed as a percent of the current value) for current lake trout populations in the inshore area of the Wisconsin waters of Lake Superior.

populations were desired. Any additional fishing pressure would cause the population to decrease at an even faster rate. If sea lamprey induced mortality could be reduced to half of its current rate, fishing would only need to be reduced by about 22% to allow stable population growth. Further, if sea lamprey induced mortality could be eliminated, fishing mortality would only need to be reduced by about 5% to achieve a stable population. As in the Michigan waters, if sea lamprey induced mortality was allowed to double, fishing mortality would need to be reduced by about 65% to achieve a stable population in the inshore area of the Wisconsin waters. Reducing fishing mortality had a greater effect on the population growth rate of lake trout in the inshore area of Wisconsin waters than reducing sea lamprey induced mortality. For example, a 20% reduction in current fishing mortality caused  $\lambda$  to increase to 0.958 whereas a 20% reduction in current sea lamprey induced mortality only caused  $\lambda$  to increase to 0.923.

Lake trout populations in the refuge area of the Wisconsin waters were increasing at 7% per year. Even though this area was considered a refuge, these fish still experience fishing mortality because they stray out of the refuge area into neighboring waters where fishing is still allowed (Swanson 1974). However, if fishing mortality could be eliminated completely on these fish, lake trout populations in the refuge could grow at 24% per year given the current level of sea lamprey induced mortality (Figure 21). If sea lamprey induced mortality could be eliminated as well, lake trout populations in the refuge could grow at 35% per year. As in the Michigan waters and the inshore area of Wisconsin waters, reductions in fishing mortality had more effect on the population growth rate than reductions in sea lamprey induced mortality. For example, reducing

fishing mortality by 20% caused  $\lambda$  to increase to 1.10 while an equal reduction in sea lamprey induced mortality caused  $\lambda$  to only increase to 1.08.

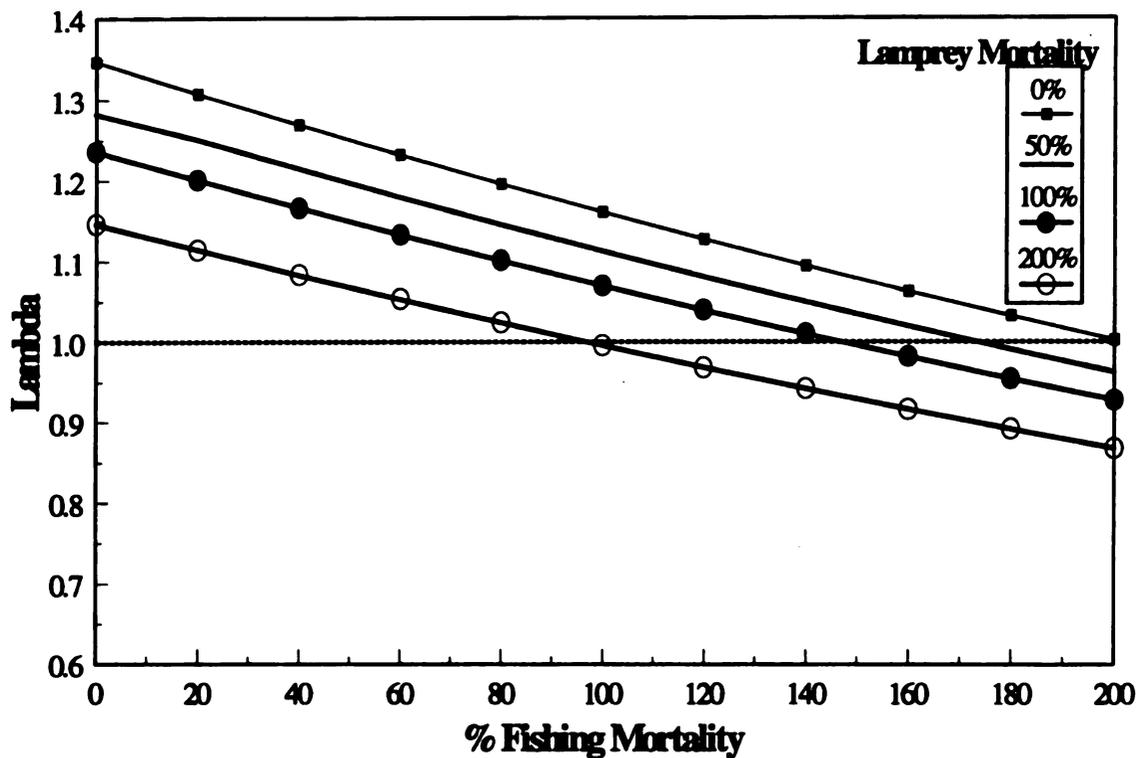
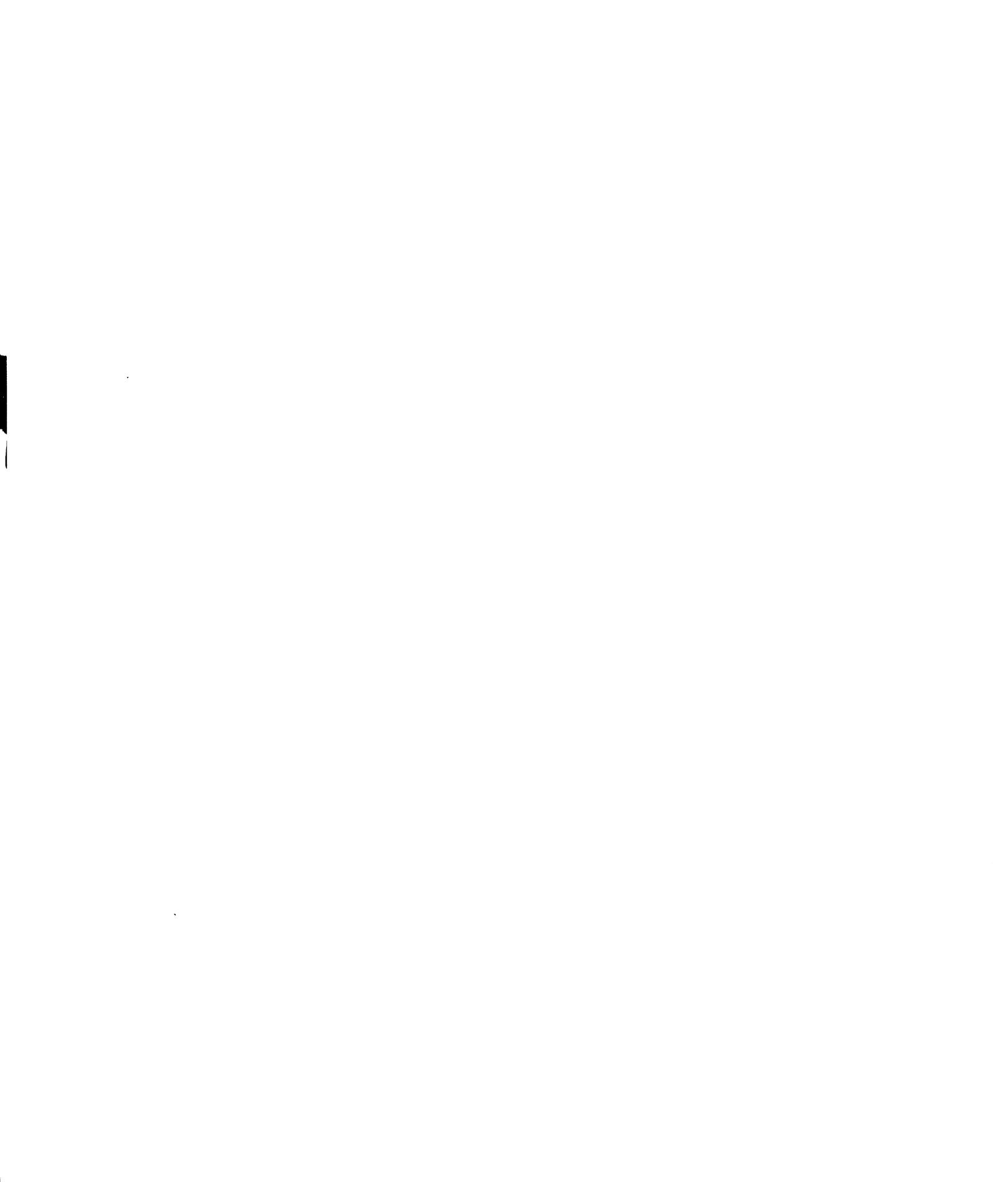


Figure 21. Tradeoff between fishing and sea lamprey induced mortality (expressed as a percent of the current value) for current lake trout populations in the refuge area of the Wisconsin waters of Lake Superior.



## DISCUSSION

Lake trout populations in the Michigan and Wisconsin waters of Lake Superior have experienced different levels of abundance through time (Hansen 1994). These different abundance levels were associated with different mortality regimes experienced by the populations. Lake trout during the pre-sea lamprey, sea lamprey dominant, and current periods responded to the differing levels of mortality and abundance through changes in the following agents of compensation: individual growth rate, age-specific fecundity, and age-0 survival.

### *Changes in Individual Growth*

Studies have indicated that individual growth in fish is highly flexible, and compensatory growth is probably the most commonly observed density-dependent process (Goodyear 1980). In an overview of individual growth rates, Healy (1978a) noted that growth rates of lake trout in the Great Lakes during 1950s were near the maximum rate observed for lake trout throughout its range. From this observation, he hypothesized that the rapid growth rates exhibited by these lake trout populations were a compensatory response to increased adult mortality resulting from sea lamprey predation and exploitation (Healy 1978a). In this study, I found that length at age of lake trout populations was significantly different between the three study periods in the Michigan

waters of Lake Superior. Lake trout during the pre-sea lamprey and the sea lamprey dominant periods grew in a similar manner. However, fish during the sea lamprey dominant period grew much faster and were significantly longer at age than lake trout during the pre-sea lamprey period. This increased growth in length of lake trout between the pre-sea lamprey and the sea lamprey dominant period could be classified as a density-dependent response. Lake trout during the sea lamprey dominant period experienced excessive adult mortality which led to a dramatic decline in abundance (Pycha and King 1975). With lower densities, more food resources can become available per individual leading to increased individual growth rates (Goodyear 1980). Thus, as lake trout abundance declined during the sea lamprey dominant period, the individuals that survived had more food resources available to them and were able to grow at a faster rate. A similar trend was evident in the weight at age of lake trout in the Michigan and Wisconsin waters of Lake Superior. Lake trout that experienced the lowest population abundance level, during the sea lamprey dominant period, were significantly heavier at age than lake trout that experienced higher population abundance levels during the pre-sea lamprey period.

Lake trout during the current time period grew in a significantly different form than lake trout of the pre-sea lamprey or the sea lamprey dominant periods. In general, current lake trout grew longer and heavier at age than historical lake trout until approximately eight years of age. Then, the growth rate of current lake trout slowed dramatically, and these fish reached a much smaller total length and weight than lake trout during the historical periods. Current lake trout in both the Michigan and Wisconsin waters exhibited this type of growth form that was significantly different from that of

individuals comprising historical lake trout populations.

Differences in length and weight at age between historical and current lake trout may be the result of a shift in the genetic make-up of lake trout populations inhabiting the Michigan and Wisconsin waters of Lake Superior. Hansen (1994) recently provided evidence that the wild fish currently found in the Michigan and Wisconsin waters of Lake Superior were the progeny of hatchery reared lake trout. Historically, Lake Superior was home for a rich variety of lake trout stocks that varied in both their appearance and in the habitats they inhabited (Krueger and Ihssen 1995, Goodier 1981). However, many of these stocks were lost during the 1950s and 1960s as a result of overfishing and sea lamprey predation (Goodier 1981). In an effort to rehabilitate lake trout populations, management agencies initiated stocking of hatchery reared lake trout into Lake Superior in the early 1950s (Lawrie and Rahrer 1973). Releases of hatchery reared fish into the United States waters of Lake Superior have been dominated by the Marquette hatchery strain since 1958; the Marquette strain originated from Lake Superior and has been used as the primary broodstock in the federal hatchery system (Hansen et al. 1995). The Marquette strain was developed in the early 1950s, after much of the genetic diversity of lake trout in Lake Superior was lost (Goodier 1981). Thus, the difference in growth form between current and historical lake trout in the Michigan and Wisconsin waters of Lake Superior may be a consequence of comparing different genetic strains that exhibit differences in individual growth.

On the other hand, individual growth can be as heavily influenced by environmental characteristics such as temperature and food as by genetics (Krueger and Ihssen 1995). Thus, the change in growth form between historical and current lake trout

populations may be a reflection of environmental changes that have taken place in Lake Superior. For example, the forage base in Lake Superior has changed dramatically since the early 1900s (Anderson and Smith 1971). Historically, lake herring and deepwater ciscoes were the primary prey of lake trout in Lake Superior. Lake herring abundance began to decline in the 1950s and rainbow smelt increased replacing the coregonines as the major food source of lake trout (Dryer et al. 1965). During the 1980s, rainbow smelt abundance declined while lake herring abundance increased. However, rainbow smelt remain the principal prey of lake trout in Lake Superior (Conner et al. 1993). Thus, the difference in growth form between current and historical lake trout may be the result of a shift in the quantity and quality of food resources available. Although it would be difficult to sort out how much influence the environment or genetics had in changing the individual growth pattern of current lake trout populations, it is clear that the individual growth pattern of current lake trout populations is significantly different than that of historical lake trout populations in the Michigan and Wisconsin waters of Lake Superior.

### *Changes in Fecundity*

Density-dependent processes can affect fecundity in several ways (Goodyear 1980). First, density can affect the number of eggs spawned by a female. In high density conditions where food is limiting, less energy is available for the production of mature ova. Lowering population density in this situation should lead to an increase in the number of eggs produced by surviving females. Second, since fecundity increases with the size of the individual fish, lower densities which lead to higher growth rates and

larger sizes at a given age can also lead to higher age-specific fecundity. Finally, another effect of increased growth on fecundity is a lowering of the age at which females can become mature. Increased growth rates resulting from lower densities leads to individuals reaching a larger size at an earlier age resulting in an earlier age at maturity (Goodyear 1980).

Healy (1978a) hypothesized that density-dependent changes in fecundity of lake trout populations may be an important compensatory response to increased exploitation of adult lake trout. To determine if density-dependent processes were affecting the number of eggs spawned by female lake trout, I compared weight specific fecundity of lake trout during the pre-sea lamprey and current periods in the Michigan waters and during the current period in Wisconsin waters of Lake Superior. If the number of eggs produced by females had changed, I would have expected the weight specific fecundity of lake trout from these three periods to be different. I found that weight specific fecundity was not significantly different between the pre-sea lamprey and current time periods in the Michigan and Wisconsin waters of Lake Superior. This finding was consistent with Healy's (1978b) finding that the average fecundity of a 55 cm lake trout from four different Canadian lakes that varied in the amount of lake trout exploitation was "remarkably consistent", ranging only from 2420 - 2436 eggs. In his study, Healy (1978b) was not able to establish a clear relationship between exploitation and changes in length specific fecundity. These findings seem to indicate that lake trout are genetically programmed to produce a certain number of eggs at a given size, and that this parameter is not very flexible and does not easily change in response to changing environmental conditions.

Unfortunately, I was not able to locate data concerning lake trout fecundity for the sea lamprey dominant period when lake trout mortality was at its highest and abundance was lowest to test for differences in weight specific fecundity. Neither total mortality levels or abundance levels were dramatically different between the pre-sea lamprey ( $Z = 0.70$ ) and the current ( $Z = 0.88$ ) time periods and may explain why weight specific fecundity was not significantly different between the two periods. However, like Peck (1988), I found that current lake trout in the Michigan waters have consistently higher fecundity than lake trout during the pre-sea lamprey period even though the difference was not statistically significant. Like the differences in growth form between current and historical lake trout, the slightly higher weight specific fecundity of current lake trout may be due to a shift in the genetic strain present in these waters of Lake Superior or to a change in the environmental conditions of Lake Superior since the historical time period.

To determine the effect of individual growth rates on fecundity, I compared age-specific fecundity of lake trout during each of the three time periods in both sites. In contrast to weight specific fecundity, age specific fecundity was significantly different during each of the time periods in both sites. This difference in age specific fecundity was a reflection of the different individual growth rates exhibited by lake trout during each period rather than a change in absolute fecundity. Lake trout during the sea lamprey dominant period, when lake trout abundance was lowest, exhibited the fastest individual growth, and hence the highest age-specific fecundity. Current lake trout, which grow faster than historical lake trout at early ages but then reach a smaller ultimate size, exhibited a higher age specific fecundity than pre-sea lamprey lake trout during earlier ages and a lower age specific fecundity at older ages. Thus, the effects of individual

growth rates on fecundity were marked, and the differences in age specific fecundity can be attributed to changes in individual growth rates.

Maturity of lake trout populations has been related to reaching a given size (Martin and Olver 1980). Thus, faster growing lake trout can mature at younger ages than slower growing lake trout. The shift at age of first maturity from age 9 during the pre-sea lamprey period to age 8 during the sea lamprey dominant period in both the Michigan and Wisconsin waters of Lake Superior was most likely a reflection of the different individual growth rates exhibited by these lake trout. Current lake trout in both sites begin to mature at a much younger ages than during either historical period. Currently, lake trout mature at age 6 in the Michigan waters of Lake Superior and at age 7 in the Wisconsin waters. Although the age at maturation has changed through time, the size at which approximately 50% of the population matures was relatively consistent between the pre-sea lamprey and the current periods (67 cm in Michigan pre-sea lamprey period, 61 cm in Michigan current period, and 63 cm and 65 cm in the inshore and refuge areas of current Wisconsin respectively). That size at maturation has remained relatively constant indicates that changes in individual growth rate are responsible for the shifting age at maturation.

#### *Changes in Age-0 Survival*

Increasing age-0 survival has been hypothesized to be an important compensatory response to increased adult mortality rates in fish populations (Sissenwine et al. 1988, Goodyear 1980). For example, decreases in adult population density in species that have

limited spawning habitat can lead to increased survival from egg to age 1 by eliminating bed overseeding as well as decreasing chances of cannibalism and disease (Goodyear 1980). Ricker (1963) and Sissenwine et al. (1988) showed that small changes age-0 survival can greatly influence the abundance of the recruited population in later years. Many factors have been hypothesized to affect age-0 survival of lake trout in the Great Lakes including the availability of suitable spawning and nursery habitat (Eshenroder et al. 1995, Marsden et al. 1995), behavioral selection of spawning habitat by stocked fish (Binkowski 1984), inadequate stock sizes (Selgeby et al. 1995), contaminants (Zint et al. 1995), and genetic strain differences (Krueger and Ihssen 1995). Researchers have measured survival of lake trout from egg deposition to swim-up fry (Perkins and Krueger 1995) but have been unable to quantify survival from egg deposition to age-1. I calculated age-0 survival of lake trout in the Michigan and Wisconsin waters of Lake Superior during the three study periods to determine if lake trout populations exhibited a compensatory change in age-0 survival related to changes in population abundance through time. The age-0 survival rate calculated using the Leslie matrix reflects the survival rate from egg deposition to age-1 necessary to maintain the population at a given rate of population growth (Vaughn and Saila 1976). The dramatic increase in the estimated age-0 survival between the pre-sea lamprey period, when lake trout populations were at relatively high levels of abundance, and the sea lamprey dominant period, when excessive adult mortality caused lake trout populations to collapse, in both the Michigan and Wisconsin waters of Lake Superior lends support to the theory that age-0 survival may have increased in response to increased adult mortality. The existence of this compensatory mechanism in lake trout populations was further supported by the fact that

substituting the age-0 survival rate estimated for either the pre-sea lamprey or the current time period into the sea lamprey dominant period matrix caused the population in both the Michigan and Wisconsin waters to decline even faster than was observed. Thus, although lake trout populations may have never reached an age-0 survival as high as that calculated for the sea lamprey dominant period, as evidenced by their continued rapid decline, age-0 survival must have increased substantially during the sea lamprey dominant period or the population would have declined even faster. Although these results support the theory, the evidence is not conclusive because of the variability in the estimates of age-0 survival and the lack of a mechanistic basis for these observations.

The age-0 survival rate estimated for current lake trout populations in the Michigan waters of Lake Superior was almost equal to that estimated for populations during the pre-sea lamprey period. In Wisconsin waters of Lake Superior, the age-0 survival rate estimated for current lake trout populations in the inshore and refuge areas were not significantly different from each other, but were significantly higher than that estimated for lake trout during the pre-sea lamprey period. If changes in age-0 survival were compensatory, it would be expected that as lake trout densities increased, age-0 survival would decrease. Thus, this return of current age-0 survival rates towards historical levels as lake trout abundance has increased lends further support to the theory that age-0 survival responds in a compensatory way to changes in population abundance and mortality regimes.

#### *Relative Contribution of $F_x$ and $P_x$*

Evaluation of the relative contribution of age-specific fecundity and survival

rates to the population growth rate can help guide the concentration of management efforts (Crouse et al. 1987). The elasticity analysis indicates that survival, especially during the pre-reproductive ages, was the most important factor contributing to the population growth rate of lake trout populations in the Michigan and Wisconsin waters of Lake Superior during the three study periods. The relative contribution of fecundity only became more important than the relative contribution of survival to the population growth rate during the sea lamprey dominant period in both sites. This shift was most likely a result of adult lake trout survival being so low during the sea lamprey dominant period that few individuals survived to maturity or beyond.

One of the assumptions used for this analysis was that natural mortality remained constant through all study periods. However, this assumption may not be accurate as natural mortality may act in a compensatory manner; that is, natural mortality may change in response to population density (Backiel and LeCren 1978). This assumption needs to be further investigated in lake trout populations. If natural mortality changes with population density, then the estimates of natural mortality used to construct the matrices should change accordingly. Future research should explore the implication of changes in natural mortality rate on the relative contribution of survival to the population growth rate.

### *Compensatory Scope*

I calculated the production potential of current lake trout populations during the three study periods in the Michigan and Wisconsin waters of Lake Superior by allowing fishing and sea lamprey induced mortality to be zero. This calculation allowed me to

compare the potential of these populations, in terms of individual growth and fecundity rates, to sustain themselves under different mortality regimes. The relatively high production potential of lake trout populations during the sea lamprey dominant period in both sites was due to the fast individual growth rate, the high age specific fecundity, and the high age-0 survival exhibited by these populations. Lake trout populations during that time period were growing and reproducing as fast as possible to sustain themselves in the face of heavy mortality regime experienced during the sea lamprey dominant period. Lake trout populations during the pre-sea lamprey period in both the Michigan and Wisconsin waters of Lake Superior were associated with the highest levels of abundance and exhibited the smallest compensatory scope. The agents of compensation, growth, survival, and reproduction were expressed at a much lower rate during the pre-sea lamprey period than during the sea lamprey dominant period. Finally, lake trout populations during current time period in both sites exhibited a compensatory scope that was intermediate between the compensatory scope exhibited during the other two periods. This intermediate production potential seems to indicate that current lake trout populations are recovering towards historical levels of abundance. Further, my results clearly indicated that if fishing and sea lamprey induced mortality were eliminated during any time period in either site, lake trout populations had the capacity to increase dramatically.

#### *Fishing and Sea Lamprey Induced Mortality Tradeoff*

Having established that survival was the key parameter driving the population growth rate of lake trout in the Michigan and Wisconsin waters of Lake Superior, I

determined how the population growth rate of current populations would change under different mortality regimes. In dealing with Great Lakes lake trout, managers have two choices to control lake trout mortality: they can regulate fishing induced mortality through fishing regulations or they can regulate sea lamprey induced mortality by altering the sea lamprey control program. The tradeoff analysis showed that greater gains, in terms of lake trout population growth, were made by reducing fishing mortality than by reducing sea lamprey induced mortality by equal percentages. This finding is most likely due to the fact that fishing mortality was greater than sea lamprey induced mortality during the years right before maturity in all three areas. Historical and current records indicate that lake trout tend to reach maturity at about 60 cm in length (Eschmeyer 1955, Ebener et al. 1989). Lake trout are fished using 114 mm stretch mesh gillnets which target lake trout that are approximately 51 cm in length (Pycha 1980). Sea lamprey, on the other hand, are size selective predators that target the largest prey item available (Swink 1991). Thus, fishing mortality is greatest during several of the pre-reproductive years when survival is most important in driving the population growth rate. As a result, reducing fishing mortality under the current scenario will have a greater impact on the population growth rate than reducing sea lamprey induced mortality.

Given the current levels of fishing mortality in the Michigan waters and the inshore area of the Wisconsin waters, sea lamprey induced mortality would have to be completely eliminated for lake trout to achieve stable population growth in these two areas. After 30 years of sea lamprey control efforts, it seems unlikely that eliminating sea lamprey from the Great Lakes is possible. In fact, sea lamprey populations in the Great Lakes are likely to increase rather than decrease. The Clean Water Act has improved

water quality in many tributaries to the Great Lakes allowing sea lamprey to use more habitat within each tributary to spawn as well as to colonize new streams (Zint et al. 1995, Moore and Lychwick 1980). In addition, current funding policies regarding the Great Lakes Fishery Commission's chemical control program has made it difficult for them to maintain an adequate sea lamprey control program and clearly will not allow them to enhance the program in response to increased sea lamprey abundances (Great Lakes Fishery Commission 1993). If sea lamprey abundance increases due to improved water quality in the Great Lakes, lake trout mortality can be expected to increase as well (Ferreri et al. 1995). In this case, fishing induced mortality will have to be reduced even further if lake trout populations are to achieve stable population growth.

In summary, I found that individual growth rates, age-specific fecundity, and age-0 survival rates changed in response to the different levels of lake trout abundance during each of the study periods in both sites. Lake trout during the sea lamprey dominant period, which experienced the lowest abundance and highest mortality levels, exhibited the fastest individual growth rates, the highest age-specific fecundity, and the highest age-0 survival. These high rates contributed to the relatively high production potential exhibited by lake trout during the sea lamprey dominant period as compared to lake trout during the pre-sea lamprey or the current periods. Survival, particularly during the pre-reproductive ages, makes a greater contribution than fecundity to the population growth rate of lake trout during the current time period. Reducing fishing mortality, which has its greatest impact on lake trout that are about to become mature, has a greater effect on the population growth rate than reducing sea lamprey induced mortality by an equal percentage.

## **MANAGEMENT IMPLICATIONS**

**This study demonstrates the importance of long-term databases to fisheries management. Without the 60 year time series of lake trout catch per effort in Lake Superior provided by Hansen (1994), it would have been impossible to discern changes in lake trout abundance through time. One of the major obstacles to completing this study was the lack of availability of historical biological data. It is critical that fisheries management agencies collect and maintain long term databases that at the very least include total catch, total effort, age, length, weight, and fecundity of individuals in the population. Without such historical background data, it is difficult to effectively evaluate the effect of management actions.**

**A major goal of lake trout rehabilitation in Lake Superior is the re-establishment of self-sustaining populations (Busiahn 1990). To achieve this goal, the population growth rate must be greater than or equal to 1 (Pielou 1977). This goal has been accomplished in the refuge area of the Wisconsin waters by limiting fishing mortality. The elasticity analysis showed that managers will gain the most benefit by concentrating their efforts and policies on increasing lake trout survival in the inshore area of the Wisconsin waters and in the Michigan waters. The tradeoff analysis where I evaluated the consequence of reducing either fishing or sea lamprey induced mortality indicated that managers should concentrate efforts first on reducing fishing mortality and then on**

reducing sea lamprey induced mortality. However, to achieve a stable lake trout population in either the Michigan or the inshore area of the Wisconsin waters, given current levels of sea lamprey induced mortality, fishing mortality would have to be reduced to 60% of its current rate. A reduction in fishing mortality of this magnitude may not be socially or politically acceptable. Thus, managers can use the Leslie matrix tradeoff framework to determine the optimal mix of fishing and sea lamprey control that will ensure the sustainability of lake trout populations in the Michigan and Wisconsin waters of Lake Superior.

The elasticity analysis showed that the population growth rate of lake trout in the Michigan and Wisconsin waters of Lake Superior was most sensitive to changes in the survival of lake trout to maturity. Currently, lake trout in these areas reach maturity at approximately 60 cm in length (Ebener et al. 1989), yet they can be legally harvested at 43.2 cm (Hansen et al. 1995). In addition, lake trout fisheries utilize 114 mm stretch mesh gillnets that are selective for lake trout that are 51 cm in length. With the current size limit and gear, many of the lake trout caught by the fishery are immature. One way to limit the impact of the fishery is to raise the minimum size limit of legally harvested lake trout to over 60 cm. This action would protect lake trout during the critical juvenile years until they reached maturity and spawned.

Another way in which managers may achieve stable lake trout populations in both the Michigan waters and the inshore area of the Wisconsin waters is through increasing the age-0 survival rate of these populations. My analysis showed that age-0 survival rate in both areas must essentially double in order to achieve stable populations. Stated in this manner, this increase seems impossible to achieve. However, the necessary increase

translates into one additional survivor to age 1 from every 100 eggs deposited in the Michigan waters and two additional survivors from every 100 eggs deposited in the inshore area of the Wisconsin waters. However, since current age-0 survival was not significantly different from the pre-sea lamprey period in the Michigan waters and was slightly higher than during the pre-sea lamprey period in the Wisconsin waters, it will be less fruitful for managers to concentrate their efforts on increasing age-0 survival than on limiting juvenile lake trout mortality.

## **APPENDIX**

## APPENDIX A: Lake Superior Lake Trout - Matrix Development

### *Michigan Waters - Pre-Sea Lamprey Period*

Sakagawa and Pycha (1971) analyzed lake trout scales collected in 1948 from the inshore waters of Lake Superior between the Keweenaw Peninsula and Munising, Michigan. I used the weight at age data for lake trout ages 3 -16 reported by Sakagawa and Pycha (1971) to estimate individual growth rates. Growth data for lake trout ages 0 - 2 was determined for fish collected between 1948-1952 in a study of lake trout early life history in the same area of Lake Superior (Eschmeyer 1956). I extrapolated weight at age to age 24 by fitting the following power function to the last four points in the series allowing me to capture the slowing trend in growth in weight for older ages of lake trout:

$$\text{Weight} = 3.1513 \text{ Age}^{0.8909} \quad R^2 = 0.9999$$

According to Sakagawa and Pycha (1971), a 20 year old lake trout should weigh approximately 28 lbs. I found, using the power function, that a 20 year old lake trout was estimated to weigh 27.5 lbs. Thus, the power function represented the weight at age trend well. Length at age was estimated using the length-weight relationship reported by Sakagawa and Pycha (1971):

$$\log(\text{Weight}) = -3.636 + 3.062 \log(\text{Length})$$

where *Weight* was in pounds and *Length* was in inches.

Weight-specific fecundity was estimated using data from Eschmeyer (1954) where he collected lake trout between 1950 to 1954 to compare the fecundity of lake trout

caught primarily east of the Keweenaw Peninsula in Lake Superior. I used this data to fit a regression line that described the weight-fecundity relationship for this lake trout population:

$$Fecundity = -1923.39 + 832.23Weight \quad R^2=0.7774$$

where *Weight* was the weight of the fish in pounds. I estimated the age-specific fecundity of lake trout in the Michigan waters of Lake Superior during the pre-sea lamprey period by combining the fecundity-weight relationship with the weight at age information. The estimated age-specific fecundity was then multiplied by a maturity schedule (percent mature at age), reported in Eschmeyer's (1954) fecundity study, to determine this population's expected age-specific fecundity.

Age-specific mortality was determined as the sum of the instantaneous rates of natural, sea lamprey, and fishing mortality. Sakagawa and Pycha (1971) estimated instantaneous natural ( $M=0.2$ ) and total mortality ( $Z=0.70$ ) for lake trout during the pre-sea lamprey period. Sea lamprey induced mortality was assumed to be zero during the pre-lamprey period. Lake trout were fished using a 114 mm stretch mesh gillnet which fished most efficiency at when the fish reached 51 cm (20 in) in length (Pycha 1980). Thus, fishing mortality was assumed to begin significantly impacting populations when the lake trout reached 51 cm length. Once fish reached this size, I estimated fishing mortality by subtracting natural mortality from the total mortality. The length, weight, fecundity, and survival at age used in the Leslie matrix to represent lake trout during the pre-sea lamprey period in the Michigan waters of Lake Superior are listed in Table 2.

*Michigan Waters - Sea Lamprey Dominant Period*

Lake trout growth during the period of peak sea lamprey abundance was estimated using data reported by Rahrer (1967). Fish were collected from the inshore waters of Lake Superior between the Keweenaw Peninsula and Grand Marais, Michigan in 1953 to determine the growth rate of lake trout in the presence of sea lamprey. I used back-calculated lengths for ages 1 - 12 presented in Rahrer (1967) to estimate length in inches at age for the sea lamprey dominant time period. I extrapolated length to age 24 by fitting the following power function to the last four years in the growth series to capture the slowing growth in length at older ages:

$$Length = 4.2315 Age^{0.8472} \quad R^2 = 0.9923$$

Weight at age was estimated using the length-weight relationship reported in Eschmeyer and Phillips (1965). The majority of lake trout analyzed in this study were collected from the inshore Michigan waters of Lake Superior between 1953 to 1956. The reported length-weight relationship for lake trout during this time period was:

$$\log(Weight) = -3.765 + 3.191 \log(Length)$$

where *Weight* was in pounds and *Length* was total length in inches.

I was not successful in locating fecundity data for this time period. Thus, I used the fecundity-weight relationship and the maturity schedule from the Michigan waters pre-sea lamprey period which was based on Eschmeyer's (1955) data. This seemed reasonable since I was examining fish populations from the same area only a few years later and since Eschmeyer's data was based on fish collected between 1950 and 1954, the

beginning of my sea lamprey dominant period. Further, in a study to determine if lake trout fecundity changed in response to varying levels of exploitation, Healy (1978b) found that the average fecundity of a 55 cm lake trout from four different Canadian lakes that varied in exploitation was remarkably consistent, ranging only from 2420 - 2436 eggs.

Age-specific mortality was determined as the sum of instantaneous rates of natural, sea lamprey induced, and fishing mortality. I assumed natural mortality was the same as during the pre-sea lamprey period ( $M=0.2$ , Sakagawa and Pycha 1971). The only estimate of total mortality for lake trout in the inshore Michigan waters of Lake Superior that I could find was in Pycha (1980). Using catch curve analysis for the years 1968 - 1978, he reported annual estimates of total mortality. I chose to use the total mortality estimate for the year 1968 ( $Z=2.31$ ) as a conservative estimate of total mortality experience by lake trout during the period of peak sea lamprey abundance. This was a conservative estimate because the chemical control program had been effective at significantly reducing sea lamprey abundance in Lake Superior by 1968, and total mortality experienced by lake trout populations in the late 1950s and early 1960s was probably even higher. Pycha (1980) also estimated fishing mortality during 1968 ( $F=0.362$ ). Sea lamprey induced mortality was assumed to account for the difference between total mortality and the sum of fishing and natural mortality. Since sea lamprey prefer larger prey (Johnson and Anderson 1980), there is a gradient of sea lamprey induced mortality with size/age of lake trout. I used the age-specific sea lamprey induced mortality schedule reported in Ebener et al. (1989) to distribute sea lamprey induced mortality to each age class. The length, weight, fecundity, and survival at age used in the

Leslie matrix to represent lake trout during the sea lamprey dominant period in the Michigan waters of Lake Superior are listed in Table 2.

*Michigan Waters - Current Period*

Lake trout length at age for the current time period was estimated using data reported in Ebener (1990). This report described the size composition of hatchery and wild lake trout captured around the Keweenaw Peninsula from 1987 to 1989. I used the mean length at age from ages 6 to 17 to fit a logarithmic function which allowed me to extrapolate length at age from age 1 to age 24. During this time period, the following logarithmic function provided a better fit to the younger age groups than a power function and still allowed me to capture the slowing trend in growth of older lake trout:

$$Length = 11.405 \ln(Age) + 1.408 \quad R^2 = 0.9869$$

where *Length* was in inches. Weight at age was estimated using the length-weight relationship determined on the same set of fish in Ebener (1990):

$$\ln(Weight) = -12.0149 + 3.0917 \ln(Length)$$

where *Weight* was in kg and *Length* was in cm.

Peck (1988) studied the fecundity of both hatchery and wild lake trout collected in the fall of 1977 - 1983 in the inshore waters of Lake Superior between the Keweenaw Peninsula and Munising, Michigan. He found no significant differences in weight-specific fecundity between hatchery and wild fish. Thus, I used the relationship reported by Peck (1988) to estimate weight-specific fecundity:

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$$Fecundity = -3400 + 2450 \text{ Weight} \quad R^2=0.7921$$

where *Fecundity* is the total number of eggs at a certain *Weight* in kg. I combined the weight-specific fecundity information with the weight at age information to determine age-specific fecundity. Then, I used the maturity schedule (percent mature at age) reported by Ebener et al. (1989) to multiply the estimated age-specific fecundity to determine the population's expected age-specific fecundity.

Age-specific mortality was determined as the sum of the instantaneous rates of natural, sea lamprey induced, and fishing mortality. I assumed natural mortality remained at the same level as the previous two periods ( $M=0.2$ , Sakagawa and Pycha 1971). Total mortality was averaged from 1986-1988 in the statistical district MI-4 which included most of the waters where fish had been collected from ( $Z=0.88$ , Ebener et al. 1989). I used the age-specific sea lamprey induced mortality calculated by Ebener (1990) for the sea lamprey component of total mortality. Finally, fishing mortality which began significantly impacting the population when the fish reached 51 cm in length (Pycha 1980) was determined by subtraction of natural and sea lamprey induced mortality from the total mortality. The length, weight, fecundity, and survival at age used in the Leslie matrix to represent lake trout during the current time period in the Michigan waters of Lake Superior are listed in Table 2.

#### *Wisconsin Waters - Pre-Sea Lamprey Period*

Data on size at age for lake trout in the Wisconsin waters of Lake Superior was not available for the pre-sea lamprey period. However, in a study of the movement of

marked lake trout in Lake Superior, Eschmeyer et al. (1953) indicated that the annual growth increment of adult lake trout in the Wisconsin waters was similar to the growth rate exhibited in the Michigan waters - approximately 2.1 inches per year. Thus, I used the data from the Michigan waters pre-lamprey matrix to estimate size at age for lake trout in the Wisconsin waters during this time period. I also used the same length-weight relationship as for lake trout in the Michigan waters.

Fecundity data was not available for this site either. As I assumed that the fish were growing in a similar manner, I used the fecundity-weight relationship and the maturity schedule from the matrix for the Michigan waters pre-sea lamprey period.

Age specific mortality was determined as the sum of natural, fishing, and sea lamprey induced mortality. Natural mortality was estimated as 0.2 (Sakagawa and Pycha 1971). To determine total mortality for this period, I constructed a catch curve from information on total number of lake trout caught at Gull Island Reef in 1957 and the age distribution of these fish (Swanson and Swedberg 1980). Total mortality was estimated from the catch curve as 0.5173. Since most of the fish caught in 1957 were seven years old or older, these lake trout had lived most of their lives during a period of low sea lamprey abundance as sea lamprey did not reach peak abundance in Lake Superior until the early 1960s (Lawrie and Rahrer 1973). Thus, sea lamprey induced mortality was assumed to be 0 during the pre-lamprey period. Fishing mortality was determined as the difference between total and natural mortality and was assumed to begin impacting the population when lake trout reached a length of 51 cm (Pycha 1980). The length, weight, fecundity, and survival at age used in the Leslie matrix to represent lake trout during the pre-sea lamprey period in the Wisconsin waters of Lake Superior are listed in Table 3.



*Wisconsin Waters - Sea Lamprey Dominant Period*

As with the pre-sea lamprey period, size at age data was lacking for lake trout during the sea lamprey dominant period in the Wisconsin waters of Lake Superior. However, Swanson and Swedberg (1980) reported the age structure of lake trout collected using 114 mm stretch mesh gill nets in the Wisconsin waters from 1964 to 1979. The age structure reported in that study was similar to the age structure presented in Rahrer (1967) for lake trout collected in 114 mm stretch mesh gill nets in the Michigan waters in 1953. Since the same type of gill net was used in both areas to collect lake trout, the same size selectivity was represented in the age structures reported indicating that lake trout in both areas were growing in a similar fashion. Thus, I used the length at age and the length-weight relationship for lake trout in the Michigan waters during the sea lamprey dominant period to characterize the growth of lake trout in the Wisconsin waters. For the same reasons, I also used the fecundity-weight relationship and the maturity schedule for lake trout in the Michigan waters during the sea lamprey dominant period to characterize lake trout in the Wisconsin waters. Dryer and King (1968) indicated that size at first maturity for lake trout in the Wisconsin waters of Lake Superior during the sea lamprey dominant period was approximately 25 inches, the same size that Eschmeyer (1955) reported for lake trout during the pre-lamprey period in the Michigan waters. This observation lends further support to the assumption that lake trout in the Michigan and Wisconsin waters were growing and maturing at similar rates during the pre-sea lamprey and the sea lamprey dominant periods.

Age specific mortality was determined as the sum of natural, fishing, and sea lamprey induced mortality. Natural mortality was estimated as 0.2 (Sakagawa and Pycha

1971). Total mortality ( $Z=1.7385$ ) was estimated from a catch curve of age classes caught in 1964 (Swanson and Swedberg 1980). Lake trout caught in 1964 were from 5 to 10 years of age and had been exposed to high sea lamprey abundances throughout their lives. Sea lamprey induced mortality during this time period was calculated in a series of steps. First, the percent of fish wounded by size category during 1960 (Swanson and Swedberg 1980) was used to determine the total number of marks by size category (Eshenroder and Koonce 1984):

$$\text{marks} = -\ln (1 - \%wounded)$$

Sea lamprey induced mortality ( $L$ ) was then calculated as (Eshenroder and Koonce 1984):

$$L = \frac{M (1-P)}{P}$$

where  $M$  was the number of marks by size category, and  $P$  was the probability of a lake trout surviving a sea lamprey attack ( $P=0.38$ ; Swink and Hanson 1986). Finally, fishing mortality started at 51 cm in length (Pycha 1980) and was calculated by subtraction of the natural and sea lamprey induced components from the total mortality. The length, weight, fecundity, and survival at age used in the Leslie matrix to represent lake trout during the sea lamprey dominant period in the Wisconsin waters of Lake Superior are listed in Table 3.

#### *Wisconsin Waters - Current Period*

The statistical district WI-2 is made up of two components, the inshore waters and the offshore lake trout refuge. Wild lake trout have been captured only in the refuge areas

where fishing has not been permitted (Wisconsin State/Tribal Technical Committee 1990). Further, the Wisconsin State/Tribal Technical Committee (1990) reported that mortality rates calculated for wild lake trout best represent lake trout populations in the refuge area, while mortality rates calculated for stocked fish best represent the condition of lake trout populations outside the refuge area. Thus, I chose to model lake trout in the inshore and refuge areas separately using data from stocked fish to represent the inshore areas and data from wild fish to represent the refuge area. Length at age for wild and hatchery reared lake trout during the current time period in the Wisconsin waters of Lake Superior was estimated from data reported by the Wisconsin State/Tribal Technical Committee (1990). I used mean length at age from ages 5 to 12 to fit a logarithmic function which allowed me to extrapolate length at age from age 1 to 24. The logarithmic function allowed me to capture the slowing trend in growth exhibited by older lake trout. The functions for the inshore and refuge areas were:

$$\begin{array}{ll} \textit{inshore:} & \textit{Length} = 8.692 \ln(\textit{Age}) + 5.288 & R^2 = 0.9792 \\ \textit{refuge:} & \textit{Length} = 10.894 \ln(\textit{Age}) + 0.986 & R^2 = 0.9926 \end{array}$$

where *Length* was the average length in cm. I could not locate length-weight information for these populations, so weight was not estimated.

Length-specific fecundity was estimated for both populations using the relationship reported by Schram (1993):

$$\textit{Fecundity} = -12143.3 + 24.46 \textit{Length} \quad R^2=0.55$$

where *Fecundity* is the total number of eggs produced by a fish of a certain *Length* in mm. This relationship was based on lake trout collected at Gull Island Shoal during 1985-

1989. The length-fecundity information was combined with the length at age data to estimate fecundity at age for both populations. I used the maturity schedule reported by the Wisconsin State/Tribal Technical Committee (1990) and the estimated age specific fecundity to estimate the population's expected age specific fecundity.

Age specific mortality was determined as the sum of the instantaneous rates of natural, sea lamprey induced, and fishing mortality in both areas. I assumed natural mortality remained at the same level as in the previous two periods ( $M=0.2$ , Sakagawa and Pycha 1971). Total mortality was reported by Hansen et al. (1994) for both hatchery and wild fish. I averaged the total mortality rate from 1985 to 1993 experienced by hatchery fish for the inshore waters ( $Z = 0.916$ ) and by the wild fish to represent the refuge area ( $Z = 0.664$ ). I used the age specific sea lamprey induced mortality calculated by the Wisconsin State/Tribal Technical Committee (1990) for hatchery and wild lake trout for the sea lamprey component of total mortality for the inshore and refuge populations respectively. Fishing mortality was assumed to be lower in the refuge area than in the inshore area. Although fishing was not allowed in the refuge area, these fish still experience fishing mortality because they stray out of the refuge area into neighboring waters where fishing is still allowed (Swanson 1974). In both areas, fishing mortality began impacting the population when the lake trout reached 51 cm in length (Pycha 1980) and was determined by subtraction of the natural and sea lamprey components from the total mortality. The length, fecundity, and survival at age used in the Leslie matrix to represent lake trout during the current time period in the inshore and refuge areas of the Wisconsin waters of Lake Superior are listed in Table 4.

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