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Dynamics of the Recovery of Lake Trout

(Salvelinus namaycush) in U.S. Waters of Lake Superior

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Michael Jay Hansen

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DYNAMICS OF THE RECOVERY OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN U.S. WATERS OF LAKE SUPERIOR

By

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ABSTRACT

DYNAMICS OF THE RECOVERY OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN U.S. WATERS OF LAKE SUPERIOR

By

Michael Jay Hansen

Lake trout (*Salvelinus namaycush*) were nearly extirpated from Lake Superior during the 1950s due to fishery exploitation and sea lamprey (*Petromyzon marinus*) predation. Reproducing populations of lake trout were reestablished in most areas of Lake Superior by stocking yearlings, controlling sea lampreys, and regulating fisheries. This dissertation evaluated relative contributions of stocked and wild adult lake trout to population recoveries and causes of declining survival of stocked lake trout, and compared current and historic population densities.

In Michigan and Minnesota, stocked lake trout were more strongly correlated to wild recruitment than wild lake trout. In Wisconsin, stocked and wild lake trout were both weakly correlated to wild recruitment. I conclude that stocked lake trout reproduced in Michigan and Minnesota because spawning grounds are inshore where inexperienced stocked spawners migrate during spawning. I conclude that stocked lake trout reproduced less successfully in Wisconsin because spawning shoals are offshore, and require homing ability not possessed by stocked fish.

In Michigan and Wisconsin, survival of stocked lake trout was strongly correlated to large-mesh gill-net fishing effort and to stocking. In Minnesota, survival of stocked lake trout was strongly correlated to density of wild lake trout and to stocking. I conclude that lake trout survival in Michigan and Wisconsin was limited

by fishing mortality, and may be enhanced if large-mesh gill-net fisheries are better controlled. I conclude that lake trout survival in Minnesota was limited by predation, and will be more difficult to enhance.

Historic lake trout densities in Michigan, previously thought to be stable prior to 1939, were declining as early as 1929 in some areas. Wild lake trout densities exceeded historic densities in some areas during the 1980s, but fell below historic densities in all areas during the 1990s. I conclude that lake trout restoration targets should be based on modern carrying capacity rather than historic yields or densities and that further progress in restoration can only be achieved if wild lake trout stocks are better protected from sea lamprey predation and fishery exploitation.

DEDICATION

For my father, George William Hansen, who planted the seed in me, as a young boy, that would later sprout into a desire to know about fish and to seek their conservation. My greatest honor in life is in knowing that he would be proud of the path that I chose.

ACKNOWLEDGMENTS

I am indebted to my program chair, William W. Taylor, and my supervisors, Jon G. Stanley (1991-94) and David W. Walsh (1994), who made my doctoral program a reality in spite of the difficulties imposed by my full-time job. Ivan L. Mao, Carl W. Ramm, and Scott R. Winterstein, the members of my guidance committee, contributed immensely to my ability to conduct the research, both in their classrooms and in their individual instruction. Many past and present members of the Lake Superior Technical Committee, a technical fisheries advisory committee organized under the auspices of the Great Lakes Fishery Commission, contributed to discussions that furthered this research. In particular, Mark P. Ebener, Richard G. Schorfhaar, Donald R. Schreiner, Stephen T. Schram, and James H. Selgeby enlightened me beyond my years about lake trout in Lake Superior and provided the data used herein. Richard L. Pycha conducted much of the early work that was the genesis for this research. Wayne R. MacCallum provided the map of Lake Superior lake trout management areas. Collection of the data used in this work was supported in part by funds from the United States Federal Aid in Sport Fish Restoration Act. Joan E. Bratley and Mary T. Halvorsen provided invaluable support in data management. Connie R. Hansen, my wife, made it all possible, through her endless support and patiencee—words cannot do justice to her contribution.

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INTRODUCTION

The Laurentian Great Lakes collectively arose from several glacial advances and retreats during the Pleistocene, and their fish faunas are therefore geologically young (Lawrie and Rahrer 1973). There are 174 species of fish in 71 genera and 28 families in the Great Lakes (Bailey and Smith 1981). The genus *Coregonus* differentiated into the greatest number of species (Todd and Smith 1980; Smith and Todd 1984), but the lake trout (*Salvelinus namaycush*) differentiated into the greatest number of distinct morphological forms (Khan and Qadri 1970; Goodier 1981). The taxonomic status of these morphological forms of lake trout in Lake Superior has been debated for decades (Khan and Qadri 1970), but there has been little dispute that lake trout formed discrete spawning stocks that used many offshore shoals, rocky shorelines, and tributary streams (Lawrie and Rahrer 1973).

Three forms of lake trout are still present in Lake Superior, including the "lean" lake trout that inhabits most deep, cold lakes in North America, and the "siscowet" and "humper" lake trout that occur only in Lake Superior (Khan and Qadri 1970; Goodier 1981; Burnham-Curtis 1993; Burnham-Curtis and Smith 1994). Lean lake trout are slender, have a low body fat content and straight, pointed snouts, and inhabit inshore waters less than 70 m deep. Siscowet lake trout are deep-bodied, have a high body fat content and blunt snouts, and inhabit offshore waters 50-150 m deep. Humper lake trout are intermediate in body depth, have an intermediate body fat content, and inhabit offshore shoals that are surrounded by waters greater than 100 m deep. Lake trout restoration in Lake Superior was limited to the lean form, so I will restrict further discussion and all of my analyses to lean lake trout.

Lean lake trout spawn in Lake Superior from October through early November (Eschmeyer 1955; Peck 1986; Ebener 1990). Males first mature at 7-8 years of age while females mature at 9-11 (Rahrer 1967; Peck 1979; Ebener 1990). Females produce 1,400-1,500 eggs per kg of body weight (Eschmeyer 1955; Peck 1988; Schram 1993), and annual recruitment of yearling lake trout was 3.6-10.1 million when fishery yields averaged 2 million kg annually (Sakagawa and Pycha 1971). Lake trout generally reside within an 80 km home range (90% of marked fish are returned within this distance, regardless of size at release and length of time at large), though some individuals move several hundred km (Eschmeyer *et al.* 1953; Loftus 1958; Buettner 1961; Pycha *et al.* 1965; Rahrer 1968; Swanson 1973; Ebener 1990).

History and Causes of Stock Collapse

Fisheries developed in Lake Superior in increasingly opportunistic pursuit of new grounds (Goodier 1982), a process known as *fishing up* that probably occurred throughout the 1800s and 1900s (Goodier 1989). The annual harvest of lake trout was less than 1 million kg in 1879 when lakewide harvest statistics were first available, peaked at 3 million kg in 1903, and averaged 2 million kg per year (CV=13%) during 1913-50 (Baldwin *et al.* 1979). The persistence of lake trout harvest during 1913-50 suggested that 2 million kg was a sustainable annual yield, but yield was sustained during the 1940s in Michigan by increased fishing intensity, in spite of declining abundance (Hile *et al.* 1951) (Figure 1). Efficiency of gill nets doubled during the late 1940s as nets were converted from cotton and linen twines to nylon (Pycha 1962) and fishermen enhanced their ability to locate fish using depth sounders (Hile *et al.* 1951).

Hile *et al.* (1951) warned that lake trout in Michigan waters of Lake Superior in 1949 were "fast nearing a dangerously low level and in poor condition to withstand the impending ravages of a growing population of sea lampreys" (*Petromyzon marinus*). During 1949-52, fishing intensity doubled, and sustained yield in spite of a 50% decline in abundance (Pycha and King 1975) (Figure 1). Fishing intensity, yield, and abundance then declined during 1953-61, as sea lampreys invaded Lake Superior, increased in abundance, and preyed on remaining lake trout (Dryer and King 1968). The combined effects of intensive fishing exploitation and sea lamprey predation were too much for lake trout to sustain, so stocks had essentially collapsed by 1962 when sea lampreys were reduced and lake trout fisheries were closed (Pycha and King 1975; Swanson and Swedberg 1980). Coble *et al.* (1990) found that the decline of lake trout in Michigan waters began in 1939, while Hile *et al.* (1951), Pycha and King (1975), and Jensen (1978) found that the decline began in 1945. In any case, lake trout abundance declined well before sea lampreys reached abundances that could otherwise have caused the decline.

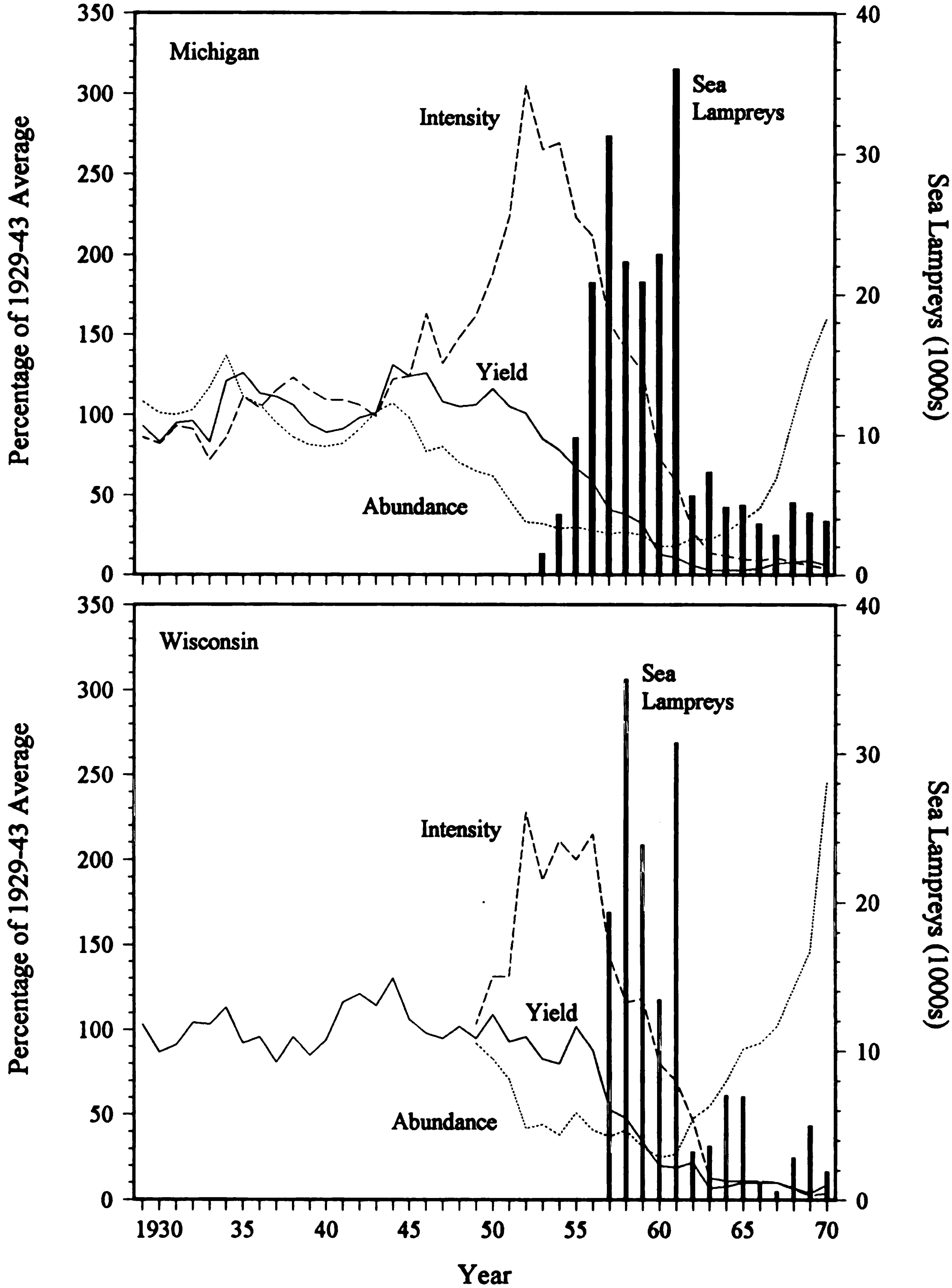

Figure 1. Lake trout fishery statistics and sea lampreys caught at electrical weirs in Michigan and Wisconsin waters of Lake Superior during 1929-70 (from Hile *et al.* 1951; Pycha and King 1975).

History and Causes of Stock Recovery

The primary strategy for restoring lake trout into Lake Superior was to increase recruitment by stocking, and to reduce mortality by controlling sea lampreys and regulating fisheries (Lawrie and Rahrer 1972, 1973; Pycha and King 1975; Lawrie 1978; LSLTTC 1986). Stocking of lake trout into Lake Superior was begun during 1950. Yearlings composed 88% of the 94 million stocked through 1992 because they survived 4-10 times better than fingerlings (Buettner 1961; Pycha and King 1967) (Table 1). Yearling releases increased during 1950-59, but still ranged much lower during 1960-92 (1.1-3.7 million/year) than the production of wild yearlings in years prior to stock collapse (3.6-10.1 million/year) (Sakagawa and Pycha 1971). Yearling plantings nonetheless still produced spawner densities in inshore Michigan waters similar to lightly exploited, offshore lean lake trout at Michipicoten Island, Superior Shoal, and the Caribou Islands prior to the invasion of sea lampreys (Lawrie 1978).

Sea lampreys invaded Lake Superior during the early 1940s, and reached an average abundance in the United States of 296,000 (± 80,000) during 1958-61 (Klar and Weise 1994) (Figure 2). Control subsequently reduced their numbers to an average of only 44,000 (± 22,000) during 1962-92 (Klar and Weise 1994). Sea lampreys reproduced widely, as larvae have been found in 90 United States and 64 Canadian streams since 1950, but most are produced in 19 United States and 9 Canadian streams that have suitable spawning and larval habitat, and adequate flow (Smith *et al.* 1974; Smith and Tibbles 1980; Klar and Weise 1994). Sea lampreys are controlled by killing larvae with selective chemicals, 3-trifluoromethyl-4-nitrophenol

Table 1. Thousands of fin-clipped lake trout stocked in the four jurisdictional areas of Lake Superior (updated and modified from Lawrie 1978; fry and age-2-and-older stockings excluded).

Year	Minnesota		Wisconsin		Michigan		Ontario		Total	
Class	Age 0	Age 1	Age 0	Age 1	Age 0	Age 1	Age 0	Age 1	Age 0	Age 1
1950	0	0	0	0	0	0	50	0	50	0
1951	0	0	0	102	0	0	0	0	0	102
1952	0	0	145	80	65	69	0	0	210	150
1953	0	0	133	102	139	134	50	0	322	236
1954	0	0	142	103	121	61	0	0	264	164
1955	0	0	0	201	0	0	0	0	0	201
1956	0	0	0	0	0	0	0	0	0	0
1957	0	0	0	184	0	298	0	538	0	1,020
1958	0	0	0	151	0	11	0	473	0	635
1959	0	0	0	161	0	393	0	396	0	950
1960	0	0	50	314	0	393	50	434	100	1,141
1961	0	0	0	256	0	705	60	508	60	1,469
1962	77	0	0	311	70	1,186	0	477	147	1,974
1963	175	182	0	745	162	1,196	0	472	337	2,596
1964	38	102	0	447	0	659	0	468	38	1,675
1965	150	108	0	352	0	2,218	0	450	150	3,128
1966	151	227	0	235	0	2,059	0	500	151	3,022
1967	154	223	0	239	0	2,260	0	500	154	3,222
1968	153	216	0	254	0	1,860	0	562	153	2,892
1969	0	226	0	204	0	1,916	0	438	0	2,785
1970	0	280	0	206	0	1,055	0	475	0	2,016
1971	0	290	0	259	0	1,063	0	371	0	1,983
1972	0	284	0	227	0	894	121	500	121	1,904
1973	0	304	0	436	0	887	0	465	0	2,092
1974	0	337	0	194	0	774	0	510	0	1,814
1975	0	345	0	551	24	785	0	520	24	2,200
1976	0	350	205	368	0	677	0	677	205	2,072
1977	0	355	183	440	101	731	0	629	284	2,155
1978	0	314	181	297	124	789	0	525	305	1,925
1979	0	351	211	342	228	578	0	548	439	1,818
1980	0	312	180	351	200	561	206	811	586	2,035
1981	0	288	287	242	153	676	203	990	644	2,195
1982	161	392	266	274	218	834	206	980	852	2,480
1983	0	212	175	131	0	472	272	1,290	447	2,105
1984	94	358	118	408	779	1,552	292	930	1,282	3,249
1985	45	408	222	312	76	1,045	303	1,337	646	3,102
1986	0	91	40	75	120	863	300	1,567	460	2,596
1987	0	212	160	180	0	394	300	1,685	460	2,471
1988	0	370	0	211	150	523	300	1,854	450	2,957
1989	54	361	0	173	150	0	467	1,252	671	1,786
1990	0	542	0	391	150	592	425	2,079	575	3,605
1991	0	499	0	417	150	682	300	2,096	450	3,694
1992	0	540	0	225	150	477	0	1,960	150	3,203
Subtotal	1,250	9,081	2,699	11,154	3,331	32,320	3,905	30,264	11,186	82,819
Total		10,331		13,853		35,651		34,169		94,005

(TFM) (Smith 1971), and Bayer-73 (Smith *et al.* 1974). Low-head barrier dams have also been built on four United States and six Ontario streams to block spawning sea lampreys without blocking other species.

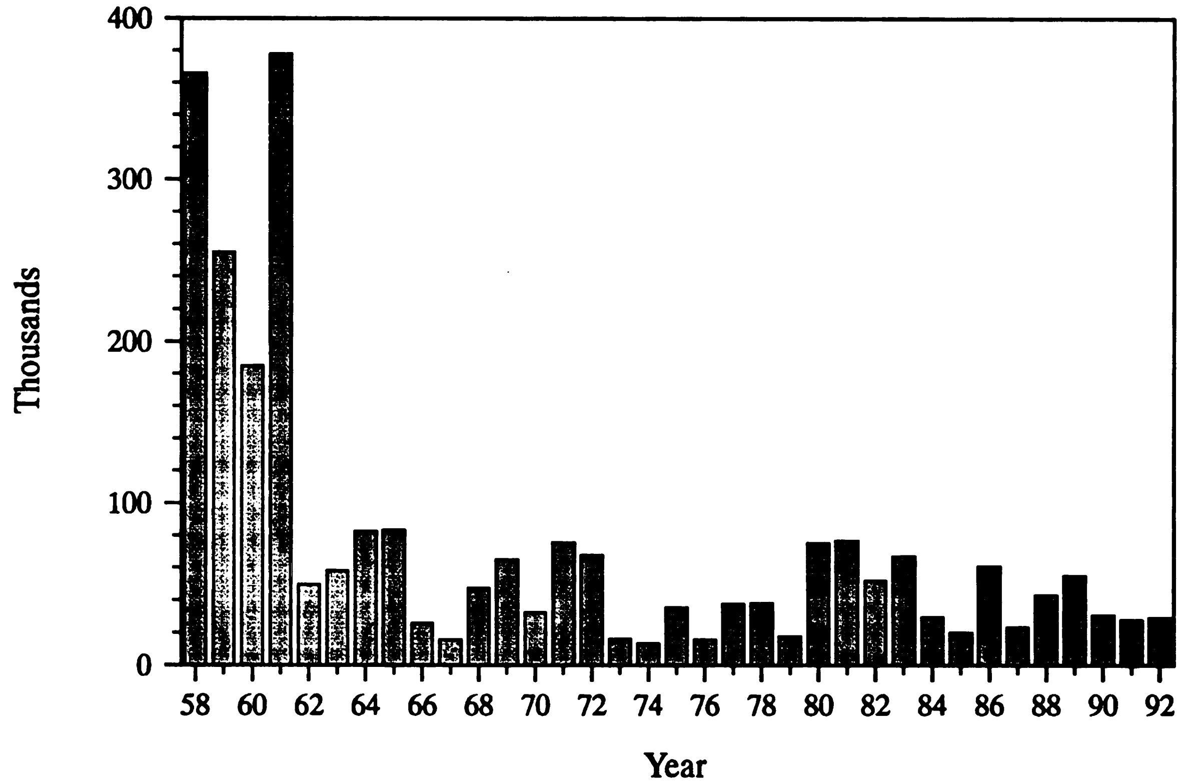

Figure 2. Estimated numbers of spawning sea lampreys in United States tributaries of Lake Superior during 1958-92 (from Klar and Weise 1994).

Sport and commercial fisheries for lake trout were closed in 1962 (Pycha and King 1975), but management agencies reopened restricted sport and commercial fisheries as lake trout stocks began to recover. Numerous regulations were intended to limit fishing mortality on lake trout, but were inconsistently applied in the various jurisdictions. Regulations that were intended to reduce fishing mortality on lake trout included: (1) limiting the number of commercial fishing licenses, (2) restricting gill netting for other species to depths that minimized the incidental kill of lake trout, (3) setting quotas on the commercial harvest and creel limits on the angling harvest, (4) establishing a refuge around the Gull Island Shoal lean lake trout spawning stock, (5) closing the lake trout spawning season to fishing, (6) converting to entrapment gear that allows higher survival of released lake trout, and (7) limiting gill-net effort.

Sea lampreys and fisheries have been reduced in Lake Superior, but continue to exert excessive mortality on lake trout. Sea lampreys caused mortality of 20-82% on lake trout (age 7 and older) during 1968-78 (instantaneous rates of 0.21 to 1.70), while fishing mortality was only 16-34% (instantaneous rates of 0.17 to 0.42) and natural mortality was only 23% (instantaneous rate of 0.26) (Pycha 1980). Consequently, sea lampreys consumed more of the available lake trout production than humans during 1968-78 when sea lampreys were at only 15% of their peak abundance. During 1990-92, sea lampreys consumed 41.6% of the total lake trout yield in United States waters west of the Keweenaw Peninsula and 17.9% from waters east of the Keweenaw Peninsula (Hansen *et al.* 1994b).

Hypotheses About Lake Trout Recovery

Interagency management of lake trout restoration is coordinated under the aegis of the Great Lakes Fishery Commission (GLFC 1980). Interagency committees of fishery researchers and managers developed a plan for restoring lake trout in Lake Superior (LSLTTC 1986), objectives for managing the entire fish community (Busiahn 1990), and reports of progress toward the goals and objectives (Hansen 1990, 1994).

These reports raised three questions, based on trends in lake trout abundance since 1970 (Figure 3). First, to what extent did stocked lake trout contribute to recruitment of wild lake trout? Second, why did abundance of stocked lake trout invariably decline, often to the point where stocking no longer enhanced abundance of spawning stocks? Third, how does the abundance of current lake trout stocks compare to that of historic lake trout stocks?

I will address each of these questions in this dissertation. In Chapter I, I will model the contribution of stocked lake trout to the recruitment of wild lake trout that became vulnerable to the assessment fishery in Michigan after 1970 and Minnesota after 1980 (Figure 3). In Chapter II, I will model potential causes of declining abundance of stocked lake trout that occurred in Michigan during the 1980s, Wisconsin during the 1970s; and Minnesota during the late 1980s. In Chapter III, I will evaluate the current status of lake trout stocks by developing a means to directly compare the abundance of lake trout during the 1990s with the abundance of lake trout during the 1929-43 historic reference period.

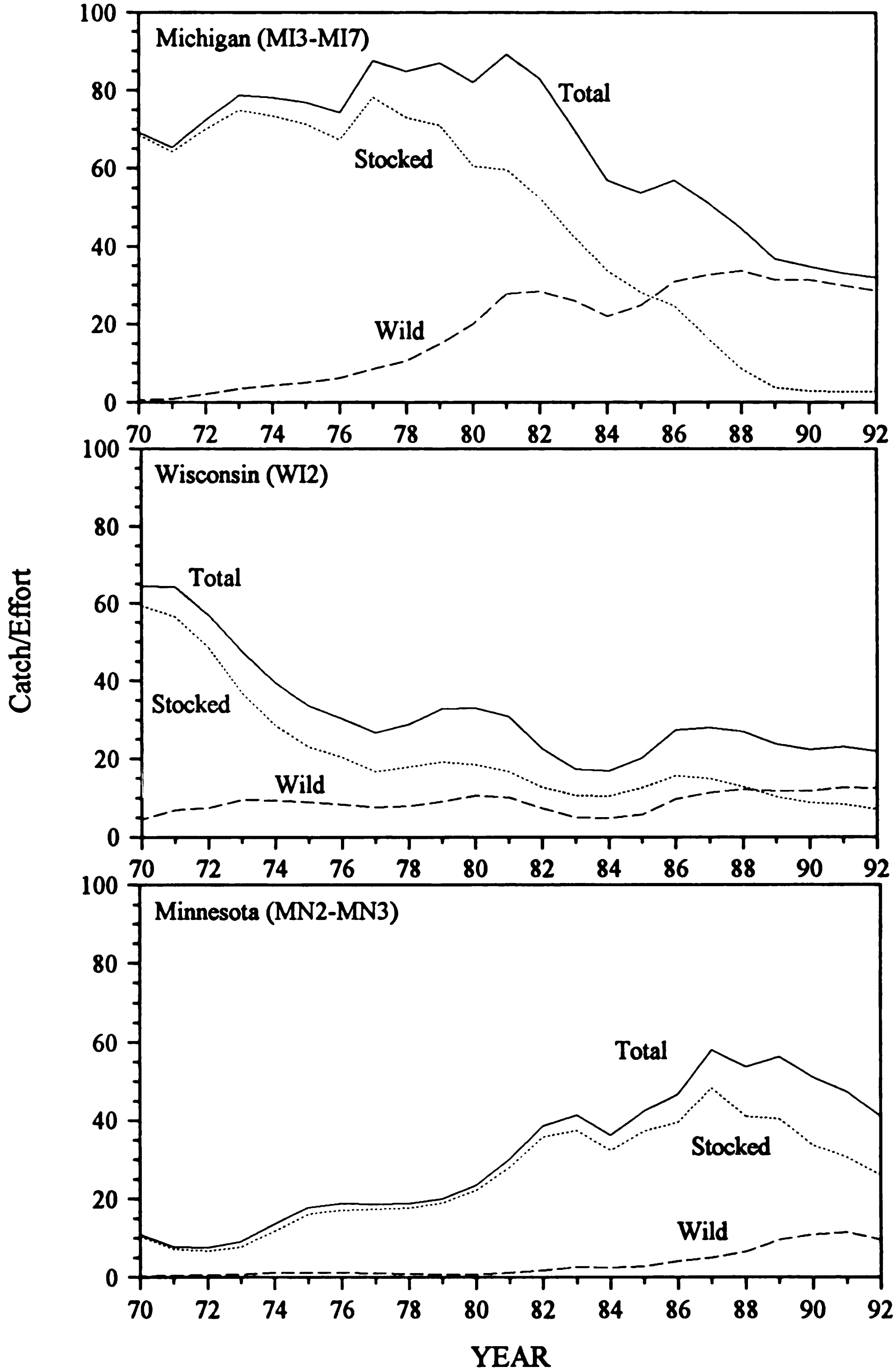

Figure 3. Spring abundance of wild and planted lake trout in U.S. waters of Lake Superior during 1970-92 (3-year moving averages of geometric mean number per km of 114-mm stretch-measure gill net) (from Hansen *et al.* 1994b).

CHAPTER I:

IMPORTANCE OF STOCKED LAKE TROUT TO RECRUITMENT IN U.S. WATERS OF LAKE SUPERIOR

Abstract.—Lake trout (*Salvelinus namaycush*) sustained an average annual yield of 2 million kg during 1913-50 in Lake Superior, but collapsed to near-extinction during 1951-62 because of excessive fishery exploitation and sea lamprey (*Petromyzon marinus*) predation. Hatchery-reared, juvenile lake trout were stocked, in conjunction with controls on sea lampreys and fisheries, to reestablish lake trout in the lake. The contribution of wild and stocked parents on recruitment were evaluated by regressing catch per effort (CPE) of the two potential parental stocks on CPE of wild recruits. Data were from lake trout catches in 114-mm assessment gill nets set each spring during 1959-93 in United States waters of Lake Superior. Stocked lake trout explained much of the variation in recruitment in Michigan (66%) and Minnesota (63%). In contrast, wild lake trout explained little of the variation in recruitment in either Michigan (9%) or Minnesota (14%). In Wisconsin, stocked and wild lake trout explained much less of the variation in recruitment (29% and 1%, respectively) than in either Michigan or Minnesota. I conclude that stocked lake trout reproduced in Michigan and Minnesota because they could easily locate the inshore spawning grounds there, and were largely responsible for stock recoveries in both states. I conclude that stocked lake trout reproduced less effectively in Wisconsin because they could not easily locate the offshore spawning grounds there, and were less responsible for stock recovery there.

Introduction

Lake trout (*Salvelinus namaycush*) sustained an average annual yield of 2 million kg (*CV*=13%) during 1913-50 in Lake Superior (Baldwin *et al.* 1979), but collapsed nearly to extinction during 1951-62 because of excessive fishery exploitation and sea lamprey (*Petromyzon marinus*) predation (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990). Hatchery-reared, juvenile lake trout were stocked, in conjunction with controls on sea lampreys and fisheries, to restore lake trout into the lake (Lawrie and Rahrer 1972, 1973; Pycha and King 1975). Stocking has been nearly continuous since 1951 in Wisconsin, 1952 in Michigan, 1957 in Ontario, and 1962 in Minnesota (Lawrie and Rahrer 1972, 1973; Pycha and King 1975; Lawrie 1978). Sea lampreys peaked in abundance during 1958-61, and were reduced 87% from 1961 to 1962 using chemicals, barrier dams, and traps (Smith 1971; Smith *et al.* 1974; Smith and Tibbles 1980; Klar and Weise 1994). Lake trout fisheries were closed lakewide in 1962, and reopened later (Pycha and King 1975).

The contribution of stocked lake trout to population recovery in Lake Superior has been the subject of considerable debate. Dryer and King (1968) predicted optimistically that the build-up of spawning stocks during 1958-66 and subsequent reproduction during 1964-66 (the first since 1959) at Gull Island Shoal, Wisconsin, would soon replace hatchery stockings. They noted, however, that stocked lake trout generally attempted to spawn near release sites, rather than on offshore reefs where spawning historically occurred. Pycha and King (1975) also noted that stocked lake trout tended to spawn inshore near stocking sites in Wisconsin where reproduction had not occurred historically, and suggested that stocking nearer suitable spawning grounds was needed to imprint the stocked fish to those sites. Wild spawners produced significantly more young lake trout than stocked spawners in the Apostle Islands because stocked fish were less able to locate offshore spawning reefs (Krueger *et al.* 1986). Stocked fish were substantially more abundant in Michigan than in Wisconsin, and aggregated in densities rivaling those at Gull Island Shoal on most historically important offshore spawning reefs (Peck 1979; Peck and Schorfhaar 1991).

The presence of residual native lake trout in most areas of Lake Superior confounded determination of the importance of stocked lake trout to recruitment (Lawrie 1978). Wild lake trout were extremely rare but were nonetheless responsible for recovery of the Gull Island Shoal stock (Swanson and Swedberg 1980). The presence of even a few wild lake trout in Lake Superior confounded interpretation of the importance of stocked fish on recruitment. Eshenroder *et al.* (1983) stated that "the Lake Superior example of success may not be appropriate for the situation in the other lakes where native stocks are believed to be extinct." The only study that has quantified the relative contributions of stocked and wild lake trout to recruitment in Lake Superior confirmed that stocked fish were reproductively ineffective compared to wild fish (Krueger *et al.* 1986). A conventional wisdom emerged, that stocked lake trout were impaired in their ability to find suitable spawning grounds, and spawned on sites that were inappropriate for reproduction (Eshenroder *et al.* 1983).

The contribution of stocked lake trout to recruitment has only been tested for a single spawning population in one area of Lake Superior (Sand Cut Reef, Wisconsin) (Krueger *et al.* 1986). A similar analysis across more areas would determine whether the results of the analysis by Krueger *et al.* (1986) apply to different spawning habitat distributions (e.g. inshore in Michigan and Minnesota, versus offshore in Wisconsin; Coberly and Horrall 1980; Goodyear *et al.* 1982; Thibodeau and Kelso 1990) and spawning stock densities (e.g. high in Michigan, versus low in Wisconsin and Minnesota; Hansen *et al.* 1994b). My objective was to determine the relative importance of stocked and wild adult lake trout to wild recruitment in different areas of Lake Superior. The null hypothesis for my analysis will be that stocked lake trout had no association with recruitment of wild lake trout in that area one generation later.

Methods

Study Area

Stock assessment of lake trout in Lake Superior is carried out in accordance with an inter-agency rehabilitation plan that specifies management areas for reporting progress in lake trout stock restoration (LSLTTC 1986) (Figure 4). The lake trout management areas in Michigan, Minnesota, and Wisconsin were modified from areas described by Hile (1962) for reporting commercial fishery statistics. Large statistical districts were divided into smaller management areas because of movement studies that showed 90% of marked lake trout were generally recaptured within 80 km, regardless of the size at release or length of time at large (Eschmeyer *et al.* 1953; Buettner 1961; Pycha *et al.* 1965; Rahrer 1968; Swanson 1973; Ebener 1990; Peck and Schorfhaar 1991). Management areas in Ontario are used for managing lake whitefish commercial fishery quotas, and bear no resemblance to former statistical districts.

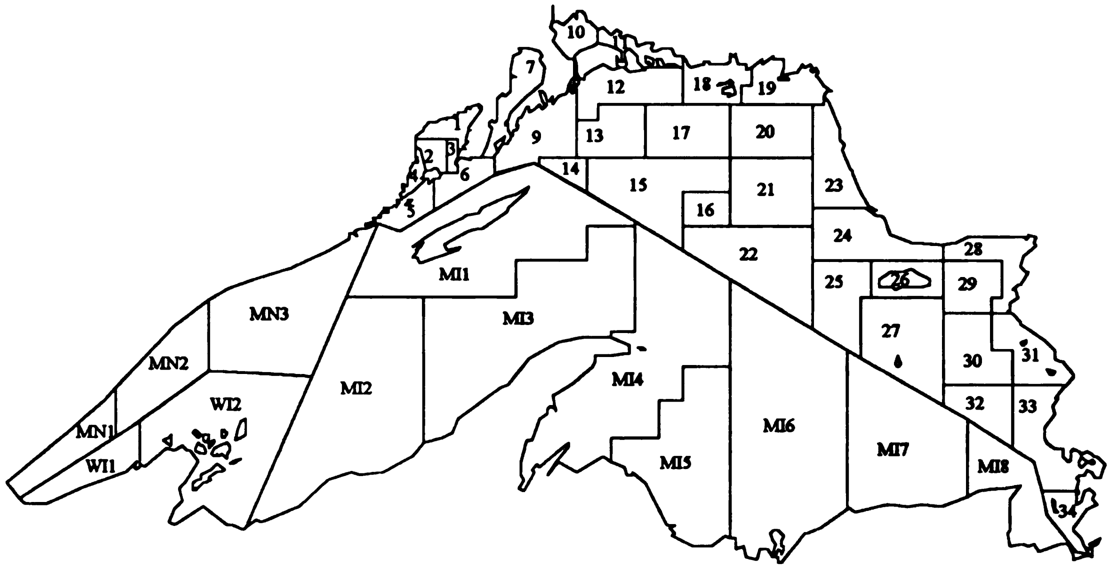

Figure 4. Lake Superior lake trout management areas. U.S. management areas are denoted by state: MI, Michigan; MN, Minnesota; WI, Wisconsin. Areas marked by numbers only are in Canadian waters.

Abundance

Trends in relative abundance of lake trout were monitored with assessment gill-nets fished in each lake trout management area during 1959-93 in Michigan and Wisconsin and 1963-93 in Minnesota. Nets were of 114-mm stretched-mesh, 210/2 multifilament nylon twine, 18 meshes deep, and hung on the 1/2 basis. Fishing was conducted from late April to early June, a period when availability was relatively high and uniform compared to other seasons (Sakagawa 1967). Nets were of non-uniform length, so catch per effort (CPE) was defined as the number of fish caught per km of net. Sets were also of non-uniform duration, particularly during 1959-69, so CPE was standardized to net-nights using corrections derived from an experiment during 1970: net-nights=1.00 for sets of one night duration, 1.52 for sets of two nights duration, and

1.80 for sets of three or more nights duration (Curtis *et al.*, in press).

Hatchery-reared lake trout were all marked by removal of a fin before stocking (Bailey 1965), so the CPE of unclipped lake trout was assumed to be of wild fish and the CPE of clipped lake trout was assumed to be of stocked fish. The mean CPEs of wild and stocked lake trout were distributed log-normally, with heteroscedastic variances, so one was added to each CPE to account for zero catches and transformed to natural logarithms for analysis (Sokal and Rohlf 1981). Means and standard errors were computed for each area and year, then transformed back into geometric means (Sokal and Rohlf 1981). Assessment fisheries in MI2, MN1, and WI1 were only begun in the 1980s, so CPEs from these areas were not analyzed further.

Statistical Analysis

Multiple linear regression was used to evaluate the relative contribution of stocked and wild lake trout to subsequent recruitment. The CPEs of stocked and wild lake trout in spring assessment fisheries were used as indices of parental and recruited stock sizes because previous movement studies showed that spawning stocks generally remained within 80 km of the spawning site. Total catches of stocked and wild lake trout were used because age-specific catches were not available across all areas and years. I assumed that the CPE of each parental stock would be related to the CPE of wild recruits eight years later (one generation) if that parental stock was reproductively important (Krueger *et al.* 1986). A generation time of eight years was used because age 7 is the modal age in 114-mm stretch-measure gill nets, and growth has not changed enough during the interval of analysis to alter either the modal age or the age of maturity (Hansen *et al.* 1994b). The model was:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \varepsilon. \tag{1}$$

where $y = \log_e$ catch per effort of wild recruits (CPE_R),

$x_1 = \log_e$ catch per effort of stocked parents (CPE_S),

$x_2 = \log_e$ catch per effort of wild parents (CPE_W), and

ε = residual variance unexplained by the regression.

Overall model fit was assessed using adjusted multiple coefficients of determination (R^2). Magnitudes of squared, standardized partial regression coefficients from the regression model (r^2) were used to assess the relative importance of stocked and wild parents (CPE_S and CPE_W) on recruits (CPE_R) in each management area. Covariance analyses were used to determine if area-specific relationships were homogeneous across management areas (N=9). I assumed that homogeneous slope coefficients indicated similar relationships for the areas tested. The results of covariance analyses were used to consolidate homogeneous sets of management areas into models describing stock-recruitment relationships across larger areas. Models were diagnosed for collinearity among predictor variables, and residual errors were diagnosed for normality, homogeneity of variance, independence, and linearity (Draper and Smith 1981; Systat, Inc. 1992; Kirby 1993).

Results

Abundance

Stocked lake trout were more abundant during 1959-1993 in western Michigan (MI3-MI5), than in eastern Michigan (MI6-MI8), Minnesota (MN2 and MN3), or Wisconsin (WI2). In western Michigan, stocked fish increased during the late 1960s, remained abundant during the 1970s, declined sharply during the 1980s, and remained scarce after 1988 (Figure 5; Appendix A, Tables 6-8). In eastern Michigan, stocked fish also increased during the late 1960s, but then declined quickly during the early 1970s, more slowly during the late 1970s and early 1980s, and were scarce after 1985 (Figure 6; Appendix A, Tables 9-11). In Wisconsin, stocked fish abundance followed a similar pattern as in eastern Michigan, but in Minnesota, stocked fish increased slowly during the 1970s, remained high during the 1980s, and declined thereafter (Figure 7; Appendix A, Tables 12-16). During the 1990s, stocked fish were extremely rare throughout Michigan, and were declining elsewhere.

Wild lake trout were generally more numerous in Michigan than in Minnesota or Wisconsin during 1959-1993, though wild fish were always present in Wisconsin and nearly absent in Michigan during the late 1960s and Minnesota during the 1960s and 1970s. In western Michigan, wild fish increased steadily during the 1970s and early 1980s, and declined slowly thereafter (Figure 5; Appendix A, Tables 6-8). In eastern Michigan, wild fish increased steadily after 1970, but declined in Whitefish Bay (MI8) where lake trout restoration was deferred in favor of gill-net fishing for lake whitefish (Figure 6; Appendix A, Tables 9-11). Wild fish were rare in Wisconsin

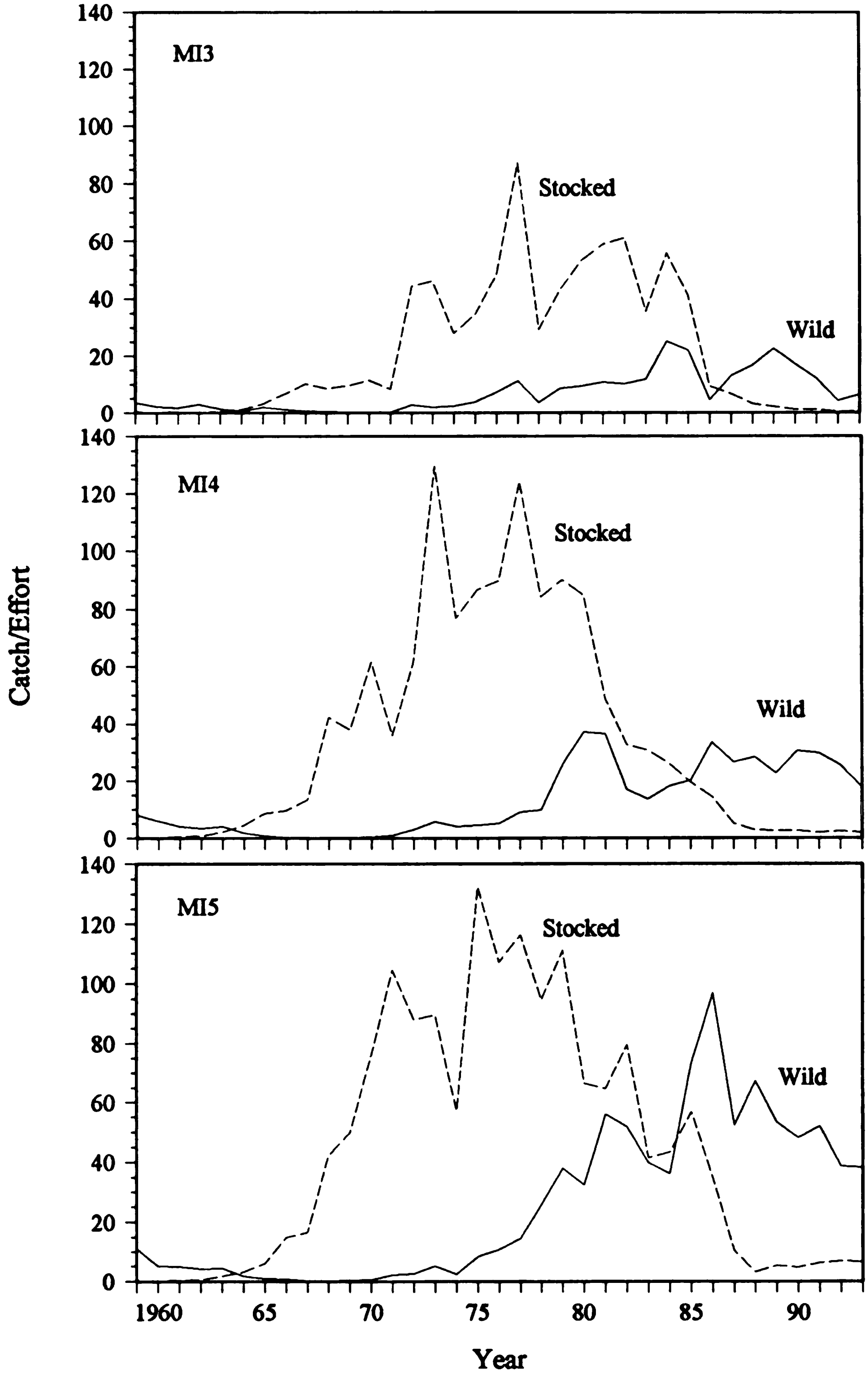

Figure 5. Catch/effort of lake trout in spring gillnet assessment fisheries at the western Keweenaw Peninsula (MI3), Keweenaw Bay (MI4), and Marquette (MI5), Michigan waters of Lake Superior during 1959-93.

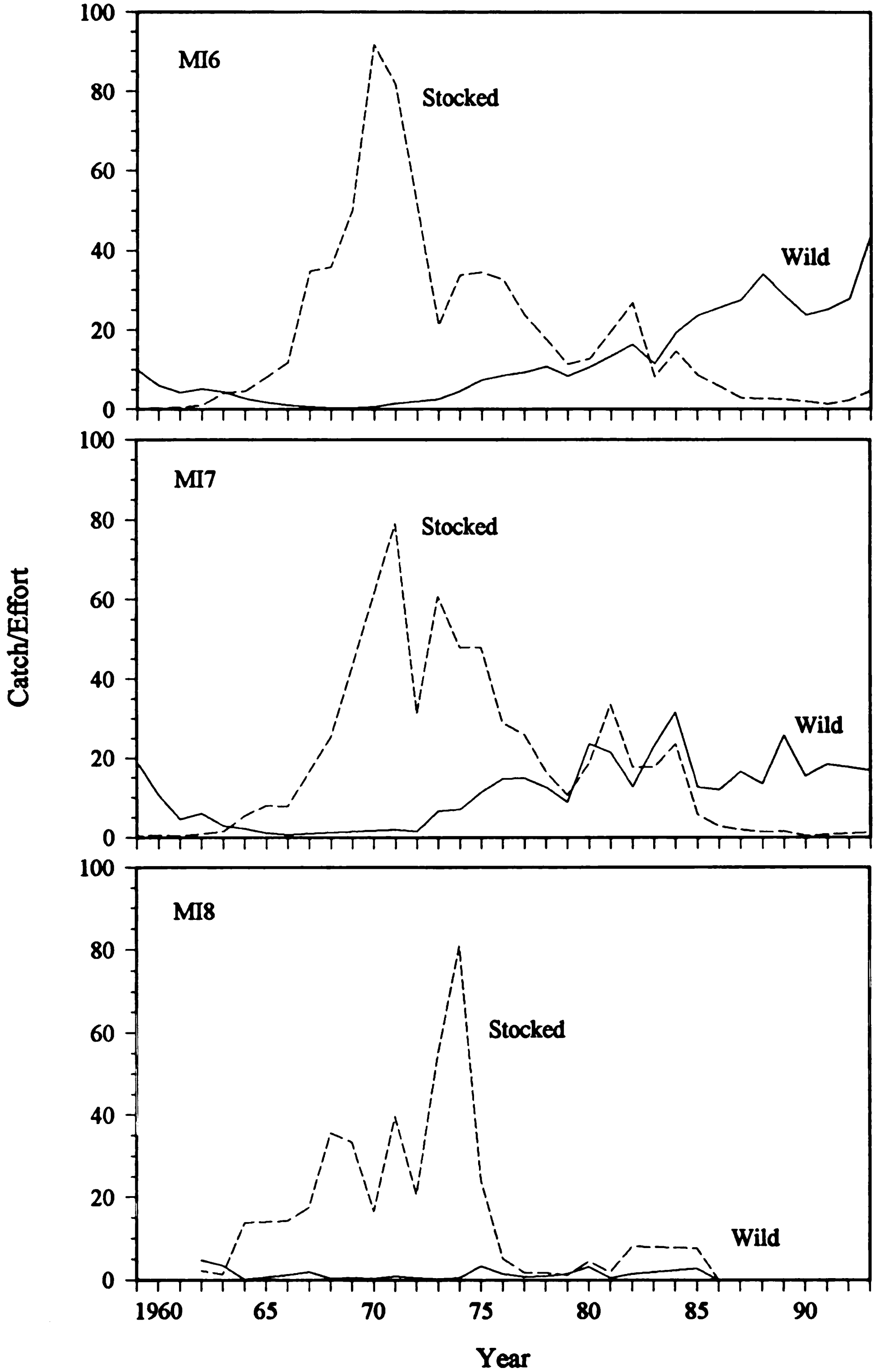

Figure 6. Catch/effort of lake trout in spring gillnet assessment fisheries at Munising (MI6), Grand Marais (MI7), and Whitefish Bay (MI8), Michigan waters of Lake Superior during 1959-93.

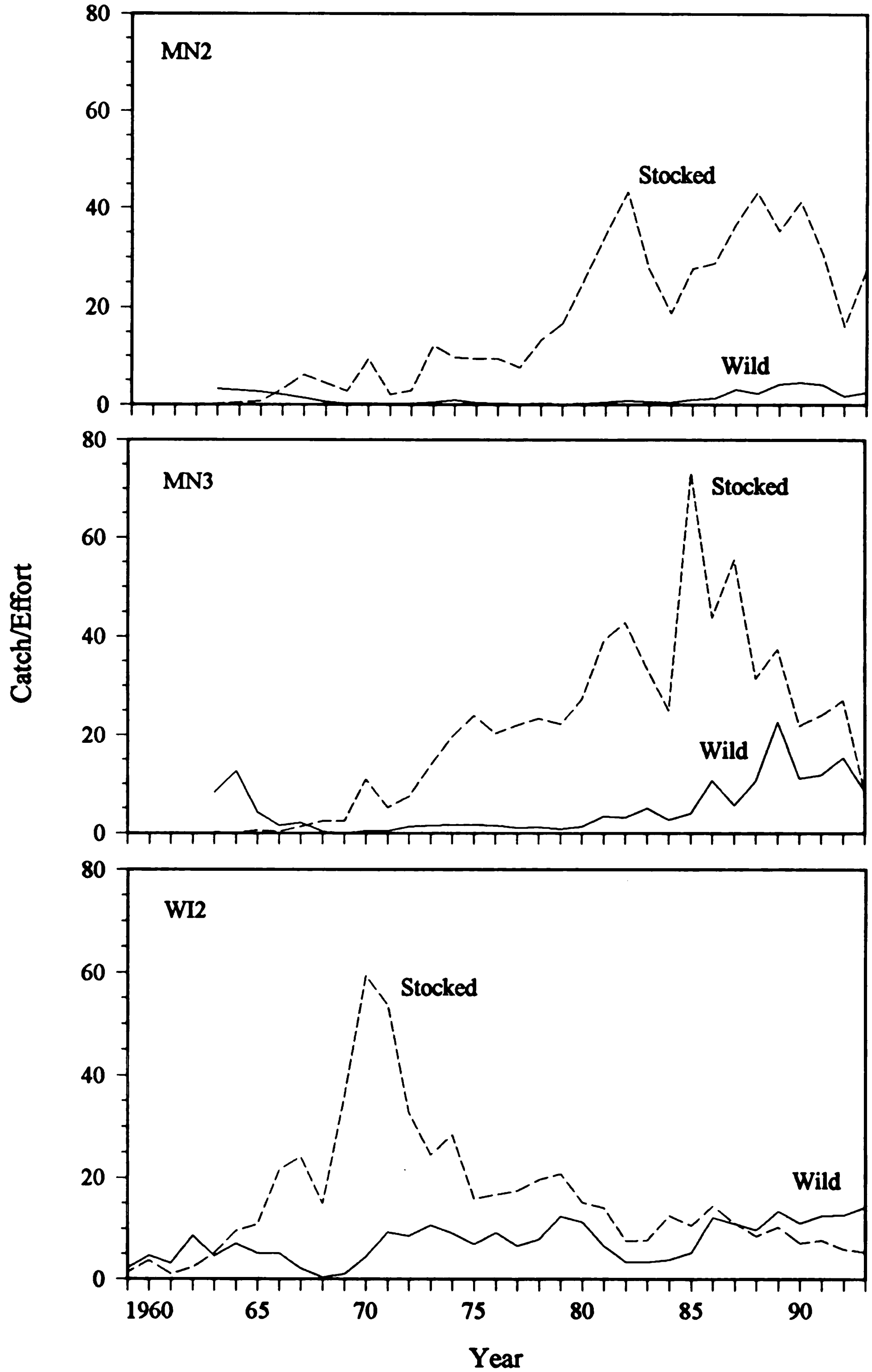

Figure 7. Catch/effort of lake trout in spring gillnet assessment fisheries in western (MN2) and eastern Minnesota (MN3), and eastern Wisconsin (WI2) waters of Lake Superior during 1959-93.

during the 1960s and Minnesota during the 1960s and 1970s, but increased slowly thereafter in each area (Figure 7; Appendix A, Tables 12-16). During the 1990s, wild fish outnumbered stocked lake trout in all areas except Minnesota and Whitefish Bay.

Sources of Recruitment

Stocked adult lake trout were significantly correlated to recruitment in all areas except MI8, whereas wild adult lake trout were significantly correlated to recruitment only in areas MI4-MI7 and MN3 (Figure 8). Stock-recruitment relationships were significantly different among management areas for both stocked (F=4.14; df=9, 196; P<0.001) and wild (F=2.43; df=9, 196; P=0.012) parents. However, stock-recruitment relationships were similar among Michigan areas MI4-MI7 for both wild (F=1.61; df=3, 95; P=0.19) and stocked (F=1.81; df=3, 95; P=0.15) parents, and average CPEs were similar among areas (F=1.39; df=3, 101; P=0.25). Stock-recruitment relationships were also similar among Minnesota areas MN2-MN3 for both wild (F=1.39; df=1, 40; P=0.25) and stocked parents (F=0.13; df=1, 40; P=0.72), but average CPEs were significantly different among areas (F=27.33; df=1, 42; P<0.001).

Variation in the CPEs of stocked and wild lake trout parents explained much of the variation in CPE of recruits eight years later (from R^2=0.54 in MI6 to R^2=0.94 in MI5) (Figure 9). Variation in the CPE of stocked parents explained the majority of variation in the CPE of recruits (r^2=0.67-1.00), whereas wild parents explained little variation (r^2=0.02-0.19). In Michigan areas MI4 through MI7, the combined CPEs of stocked and wild lake trout explained the majority of the variation in CPE of progeny (R^2=0.79), of which most was explained by stocked parents (r^2=0.66) and little was

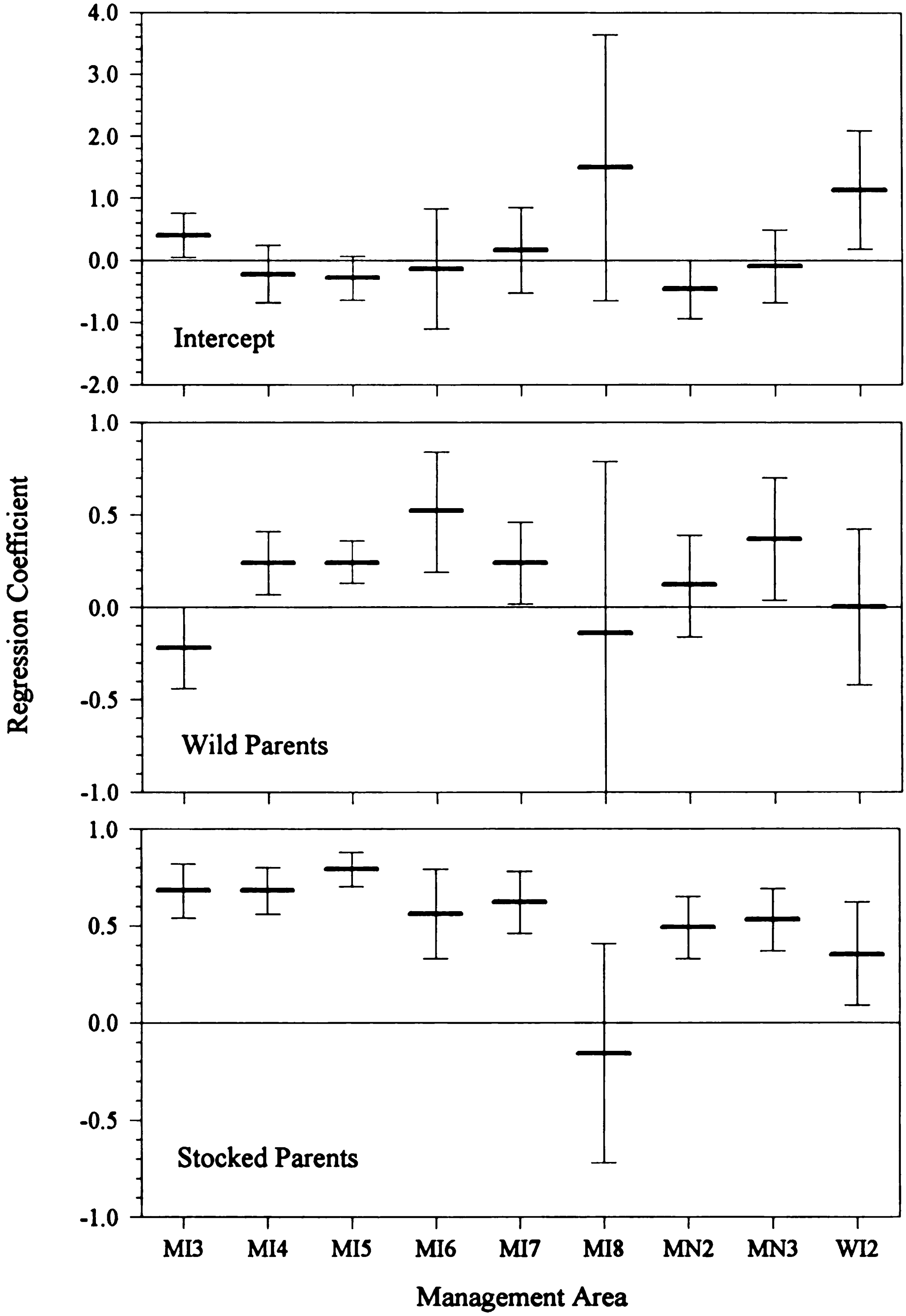

Figure 8. Multiple regression coefficients (±95% C.I.) of wild and stocked lake trout CPEs on recruit CPE in Michigan (MI3-MI8), Minnesota (MN2-MN3), and Wisconsin (WI2) waters of Lake Superior during 1959-93.

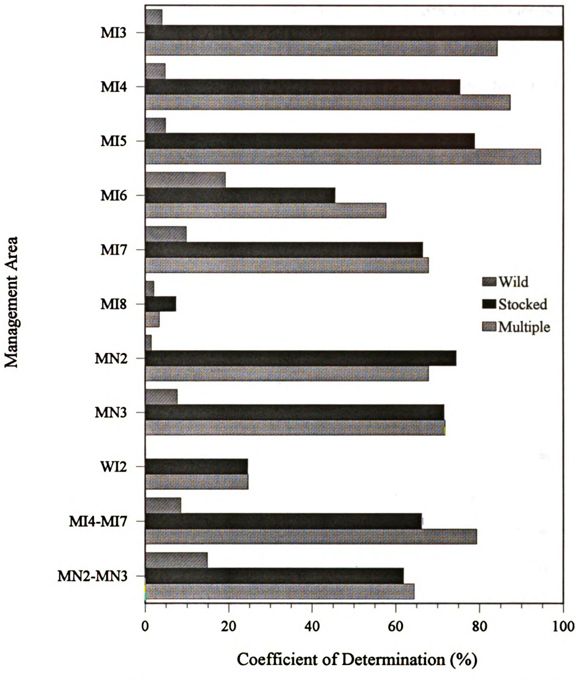

Figure 9. Coefficients of determination of wild and stocked lake trout CPEs on recruit CPE in Michigan (MI3-MI8), Minnesota (MN2-MN3), and Wisconsin (WI2) waters of Lake Superior during 1959-93.

explained by wild parents (r^2=0.09) (Appendix A, Table 17; Appendix B, Figure 24). In Minnesota areas MN2 and MN3, the CPEs of stocked and wild lake trout also explained the majority of the variation in CPE of progeny (R^2=0.63), of which most was explained by stocked parents (r^2=0.62) and little by wild parents (r^2=0.15) (Appendix A, Table 18; Appendix B, Figure 25). In Wisconsin area WI2, the CPEs of stocked and wild lake trout explained little of the variation in CPE of progeny (R^2=0.18) (Appendix A, Table 19; Appendix B, Figure 26).

Discussion

These results suggest that stocked lake trout produced more wild progeny in Lake Superior than wild lake trout, particularly in Minnesota and Michigan. The relatively weak contribution of stocked fish to recruitment in Wisconsin (WI2) may reflect the offshore, heterogeneous distribution of spawning grounds among the Apostle Islands (Coberly and Horrall 1980), compared to Michigan and Minnesota, where spawning grounds are more inshore and homogeneous (Krueger *et al.* 1986). Stocked lake trout were probably better able to locate inshore spawning grounds in Michigan and Minnesota than offshore shoals in Wisconsin. For example, stocked lake trout were rarely found on offshore spawning shoals in the Apostle Islands area of Wisconsin during the spawning season, but large concentrations of stocked lake trout could sometimes be found attempting to spawn on inshore, unsuitable habitat such as sand beaches as little as 5 km away (Krueger *et al.* 1986). In contrast, stocked lake trout spawned on virtually all spawning grounds in Michigan during the early 1970s

(Peck 1979), and spawner densities were as high or higher than those on Gull Island Shoal during the same spawning seasons (Swanson and Swedberg 1980). Different distributions of spawning habitat may thus explain why stock-recruitment relationships in Michigan and Minnesota were similar across broad areas. This further implies that lake trout stocks in Michigan and Minnesota interbreed more freely than in Wisconsin, and that knowledge of Wisconsin's population dynamics cannot be generalized to Michigan's or Minnesota's populations.

In contrast to the contribution of stocked fish, wild fish contributed relatively little to the production of wild progeny in Lake Superior. This was surprising, because stock-recruitment relationships have been documented for at least two spawning stocks in Wisconsin (Krueger *et al.* 1986; Schram *et al.*, in press). Wild lake trout accounted for 88% of the wild spawners recruited one generation later at Sand Cut Reef in Wisconsin during 1967-84, but stocked lake trout accounted for only 21% (Krueger *et al.* 1986). Data analyzed from Sand Cut Reef differed from ours in two respects. First, their analysis was of autumn CPEs from one spawning reef, whereas I analyzed spring CPEs from larger areas that likely represented multiple spawning stocks. The Sand Cut Reef analysis detected a relationship between a single spawning stock and recruitment, whereas my analysis failed to detect any stock-recruitment relationship, perhaps because several spawning stocks occur in the area, each with its own stock-recruitment relationship. Second, stocked fish were much more numerous than wild fish in both analyses, but wild lake trout were present in all years at Sand Cut Reef and absent in the early years of my analysis. The Sand Cut Reef data therefore has less overall contrast in lake trout abundance than mine, and may not reflect the colonizing success of stocked lake trout, in the absence of any wild lake trout.

In spite of widespread reproduction, however, stocked lake trout were unable to replace themselves (regression coefficients for stocked parents were all less than one, though both parents and recruits were indexed at the same sizes and ages; Ricker 1975). Recruitment must exceed parental stock sizes at some, usually low, parental stock sizes in order for a population to persist (Ricker 1975). However, parental stock sizes in Lake Superior were artificially bolstered through intensive stocking, which led to spawner densities in Michigan that approached 2.5 times the historic average (Chapter III). These artificially high spawner densities may have contributed to low reproductive efficiency through competition for spawning habitat or cannibalism on the progeny produced. Reproductive inefficiency of stocked lake trout in Lake Superior was previously noted by Krueger *et al.* (1986), who hypothesized that stocked spawners may have been unable to locate suitable spawning habitat on reefs.

Wild lake trout were even less able to replace themselves than stocked lake trout in inshore areas. Stock-recruitment regression coefficients for wild lake trout were even less than for stocked lake trout in all areas. During the 1970s, densities of wild lake trout were much lower than stocked lake trout, so wild lake trout spawners of the 1970s would likely have spawned with stocked lake trout spawners, so the contribution of rare, wild lake trout to recruitment may have been masked by the contribution of abundant, stocked lake trout. In contrast, the offshore Gull Island Shoal spawning stock reproduced successfully even when no female spawners were detected during spawning surveys (Swanson and Swedberg 1980). Inshore spawning stocks during the late 1980s and early 1990s were dominated by wild spawners and lower in density than during the 1970s. Consequently, I expect that stock-recruitment regression coefficients for wild lake trout spawning in Michigan during the 1980s will exceed one, as Krueger *et al.* (1986) found for the Sand Cut Reef spawning stock. The rate of stock recovery in Michigan and Minnesota should therefore improve during the late 1990s as wild lake trout spawners dominate recruitment.

My results suggest a robust biological relationship between numbers of parental lake trout and numbers of recruits, because stock-recruitment relationships for both stocked and wild parents were similar across much of Michigan and Minnesota in spite of the different time-frames of the relationships. The lack of a stock-recruitment relationship in Whitefish Bay (MI8) likely resulted from poor data (small samples, scattered in time), and from extremely low abundance of wild lake trout in all years analyzed. In western Michigan (MI3) and central Minnesota (MN2), relationships between wild parents and progeny were not significant, rather than between stocked parents and progeny, which was different than elsewhere in Michigan and Minnesota.

Management Implications

My results suggest that the availability of inshore spawning substrate is a critical determinant of successful reproduction by stocked lake trout in the Great Lakes. Other investigators have concluded that stocked lake trout were reproductively ineffective in Lake Superior (Krueger *et al.* 1986). This conclusion was subsequently held as the primary reason that lake trout restoration in the other Great Lakes had largely failed (Eshenroder *et al.* 1983). Unfortunately, previous stock-recruitment analyses in Lake Superior were restricted to the Apostle Islands area in Wisconsin, where spawning substrate is restricted to offshore shoals that demand homing ability by spawning lake trout. In Minnesota, Michigan, and Ontario, however, spawning substrate is widely distributed inshore, where little homing ability is required by inexperienced, stocked lake trout spawners.

Lake trout restoration has been deferred in both northern Lake Huron and northern Lake Michigan where inshore spawning grounds are found. Instead, these areas have been reserved for maximum sustained harvest of lake whitefish—mostly by gillnets that impose high incidental mortality on lake trout (Rybicki and Keller 1978). As a consequence, spawning stocks have not been permitted to develop in the areas where inshore spawning grounds occur and the likelihood of successful reproduction is greatest. Rather, lake trout restoration has been pursued mostly in the southern portions of both Lakes Huron and Michigan, where inshore spawning grounds are largely absent. Only since the mid-1980s has lake trout restoration been moved offshore to the large offshore reefs of Six-Fathom Bank in Lake Huron, the Beaver Islands in Lake Michigan, and the Mid-Lake Reefs in Lake Michigan. Stocking in these areas, in conjunction with protection from fishery exploitation, should provide for successful stock restoration, provided that the fish remain in these areas to spawn.

Stock restoration in northern Lake Huron and northern Lake Michigan can also succeed, provided that spawning grounds are still in suitable condition and that lake trout are afforded protection from fishery exploitation and sea lamprey predation. Surveys of historic lake trout spawning grounds in northern Lake Huron and Lake Michigan have shown that substrate quality has not been observably degraded (Edsall *et al.* 1992). Excessive fishery exploitation and sea lamprey predation may therefore explain the lack of successful reproduction by stocked lake trout in these areas. The success of future attempts to restore lake trout stocks in these areas may depend on the extent to which fishery managers are able to control total annual mortality resulting from fishery exploitation and sea lamprey predation. Stocking of hatchery-reared fish continues to be a viable tool for lake trout restoration in both lakes, provided that these controls on mortality are effective.

CHAPTER II:

DECLINING SURVIVAL OF LAKE TROUT STOCKED IN U.S. WATERS OF LAKE SUPERIOR

Abstract.—The survival of the 1963-82 year classes of stocked yearling lake trout (*Salvelinus namaycush*) declined significantly in Lake Superior. To investigate causes of these declines, a Ricker model of stock-recruitment was used to describe the catch per effort (CPE) of age-7 stocked lake trout in Minnesota, Michigan, and Wisconsin waters of Lake Superior as functions of the numbers of yearlings stocked six years earlier, the CPE of wild adult lake trout (an index of predation), and large-mesh gill-net fishing effort (an index of fishing mortality). Declining CPEs of stocked lake trout in Michigan and Wisconsin were significantly associated with increasing large-mesh gill-net fishing effort. Declining CPEs of stocked lake trout in Minnesota were significantly associated with increasing densities of wild lake trout. Sea lamprey abundance varied during the period, so predation by sea lampreys did not explain declining survival in any state. I conclude that stocked lake trout survival declined in Michigan and Wisconsin because of increased mortality in large-mesh gill fisheries, and can be enhanced by better controlling these fisheries. I conclude that survival of stocked lake trout declined in Minnesota because of increased predation by wild lake trout that recently recolonized the area. Predation by wild lake trout may also inhibit survival of stocked lake trout in Michigan and Wisconsin, but this effect appeared to be less important than large-mesh gill-net fishing mortality.

Introduction

Lake trout (*Salvelinus namaycush*) sustained 2 million kg of average annual yield to commercial fisheries during 1913-1950 in Lake Superior (Baldwin *et al.* 1979), but were nearly extirpated during the 1950s by fisheries and sea lampreys (*Petromyzon marinus*) (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990), which had colonized the lake during the 1940s and 1950s (Smith *et al.* 1974). Chemical control of the sea lamprey was begun in 1958 and reduced their abundance 85% by 1962 (Smith *et al.* 1974), at which time management authorities closed commercial lake trout fisheries (Pycha and King 1975). Hatchery-reared, yearling lake trout have been stocked in United States waters since 1952 (Lawrie and Rahrer 1972, 1973), and totalled 60 million by 1983 (Hansen *et al.* 1994b).

Stocked yearling lake trout survival was stable from 1959 through 1961, but declined after 1961, possibly because of predation by increasing numbers of older lake trout (Dryer and King 1968). The abundance of stocked lake trout increased rapidly during 1959-66, because of large plantings, and remained high from 1967 through 1970 even though few fish survived past age 9 because of high sea lamprey-induced mortality (Pycha and King 1975). The abundance of stocked lake trout in Michigan was high during the 1970s, but declined during the 1980s for unknown reasons (MacCallum and Selgeby 1987; Peck and Schorfhaar 1991). It has remained low since 1988 (Hansen *et al.* 1994b). Stocked lake trout abundance declined for unknown reasons in Wisconsin during the 1970s and 1980s and in Minnesota during the 1990s (Hansen *et al.* 1994b).

This declining survival may have been caused by increased competition for food with other salmonid species, wild lake trout, and previously stocked lake trout, and by predation by other species such as sea lamprey and large salmonids (Hansen *et al.* 1994a). In Michigan, the abundance of stocked fish declined coincident with reductions in stocking and growth rates, which slowed recruitment into sizes that were vulnerable to the assessment nets (MacCallum and Selgeby 1987). Declining abundance of stocked lake trout in most areas of Michigan also coincided with increased tribal commercial fishing effort (Peck and Schorfhaar 1991). In Wisconsin, the abundance of stocked lake trout coincided with reduced stocking and increased fishing mortality (MacCallum and Selgeby 1987).

Some of these causes of declining abundance of stocked lake trout are not easily controlled by fishery management actions. For instance, growth rates are limited by competition within and among species. In contrast, fishing mortality can be controlled by constraining the numbers and sizes of lake trout caught by sport and commercial fisheries. Sea lamprey-induced mortality can also be controlled by reducing the number of sea lampreys. Survival of stocked lake trout can be enhanced by increasing their average weight prior to stocking. It is important to determine what forces are currently influencing the survival of stocked lake trout in Lake Superior, to determine if that survival can be improved. Herein, abundance indices of stocked lake trout in United States waters of Lake Superior are modeled as functions of the number lake trout stocked, and of indices of competition, predation, and fishing.

Methods

Based on other investigations of lake trout survival, I developed *a priori* hypotheses to explain declining survival of lake trout stocked in U.S. waters of Lake Superior (Tyler and Crawford 1991). Declining survival of stocked lake trout in U.S. waters of Lake Superior was previously described as a function of reduced stocking and an unexplained year effect (Hansen *et al.* 1994a). Factors that were most likely to account for the year effect included those that affected survival of stocked yearlings during their first year in the lake, such as competition for prey between stocked and wild yearlings, size of yearlings at the time of their release, and predation by adult lake trout (either wild or stocked or both) on stocked yearlings during the first year after their release (Hansen *et al.* 1994a). Fishing mortality was not a likely cause of declining survival because survival was reduced before stocked lake trout were fully recruited into sport and commercial fisheries (Hansen *et al.* 1994a). Sea lamprey abundance varied without trend after 1961 (Klar and Weise 1994), so predation by sea lampreys did not explain declining survival.

Recruitment to Age 7

Recruitment was indexed as the relative abundance of age-7 lake trout stocked as yearlings (Hansen *et al.* 1994a). Catch per effort (CPE) during 1970-89 was defined as the number of fish caught per km of standard gill net in U.S. lake trout management areas (Figure 4). Ages were determined from a sample of scales removed from fish caught in the gill nets. Sample ages were validated by matching the fin clip observed on each fish to the year class on which that fin clip was used (all lake trout were marked by removal of a fin before stocking). Ages from the sample were expanded to the entire catch using an age-length key. Age-7 fish were used to index recruitment because catch curves revealed that age-7 fish were the first age class fully recruited to the gillnets (Pycha 1980), and fish were subject to higher rates of fishing- and sea lamprey-induced mortality after age 7 (Pycha and King 1975).

Previous analyses of recruitment to age 7 indicated that movement of fish among management areas precluded analysis of survival within management areas (Hansen *et al.* 1994a), but patterns of abundance were relatively homogenous within each state (Chapter I). Consequently, average recruitment was computed for Michigan, Minnesota, and Wisconsin waters for each of the 1963-86 year classes as the sum of the area-specific CPEs, weighted by the size of each area (Ricker 1975) (Tables 2-4). The 73-m contour was used for the size of each area because it approximates the maximum depth limit of lean lake trout in Lake Superior (Dryer 1966). Recruitment data was only available throughout 1970-93 for Minnesota areas MN2-MN3), Wisconsin area WI2, and Michigan areas MI3-MI7.

Factors Potentially Influencing Recruitment

Stock size was indexed as millions of yearlings of the 1963-86 year-classes stocked during 1964-87 (Tables 2-4). All lake trout included in the recruitment index were known to have come from plantings of fingerlings 7 years earlier and yearlings 6 years earlier, but yearlings were used as the index of stock size because they were previously shown to survive 4-10 times better than fingerlings in Lake Superior

Table 2. Stock and recruitment data used for modeling survival of yearling lake trout stocked in Michigan waters of Lake Superior.

Year Class	Age-7 Recruit CPE	Million Yearlings Stocked	Grams/ Yearling	Adult Lake Trout Wild CPE	Adult Lake Trout Stocked CPE	Juvenile Wild Lake Trout CPE	Gill Net Effort (1000 km)
1963	49.0	1.2	14.7	1.9	3.9	0.6	0.0
1964	32.3	0.7	16.6	1.2	7.3	1.4	0.0
1965	54.3	2.2	21.6	0.7	10.6	4.2	0.0
1966	34.7	2.1	19.2	0.3	23.2	4.6	0.0
1967	44.6	2.2	23.3	0.4	35.3	3.9	0.0
1968	46.5	1.9	24.2	0.3	38.7	6.4	0.0
1969	76.4	1.9	23.0	0.6	68.4	8.1	0.0
1970	25.9	1.1	21.4	1.4	59.8	11.0	0.0
1971	30.4	1.1	21.7	4.2	81.7	12.7	0.0
1972	39.0	0.9	21.0	4.6	83.1	21.0	0.0
1973	21.5	0.9	23.9	3.9	55.6	26.2	0.0
1974	35.3	0.8	22.4	6.4	75.4	36.4	0.1
1975	15.1	0.8	18.7	8.1	70.9	22.6	0.5
1976	16.4	0.7	21.7	11.0	88.2	19.1	0.8
1977	20.0	0.7	19.1	12.7	59.8	24.2	1.3
1978	11.6	0.8	16.5	21.0	65.1	31.1	1.9
1979	5.6	0.6	16.4	26.2	56.5	37.6	2.7
1980	2.0	0.6	18.4	36.4	57.4	29.3	3.7
1981	2.6	0.7	20.5	22.6	42.9	34.4	4.4
1982	1.5	0.8	19.6	19.1	27.7	30.3	5.4

Buettner 1961; Pycha and King 1967). Numbers of lake trout stocked previously appeared to be unrelated to recruitment at age 7 (Hansen *et al.* 1994a), but lack of contrast in numbers planted likely explained the lack of a significant relationship.

Size of stocked yearlings at release was indexed as the average weight, in grams, at release of each year class (total weight/total number stocked) (Tables 2-4). Size of yearlings at release was included because the percentage of lake trout returned from plantings in Lake Superior was more closely associated to the weight of the fish

Table 3. Stock and recruitment data used for modeling survival of yearling lake trout stocked in Minnesota waters of Lake Superior.

Year Class	Age-7 Recruit CPE	Million Yearlings Stocked	Grams/ Yearling	Adult Lake Trout Wild CPE	Adult Lake Trout Stocked CPE	Juvenile Wild Lake Trout CPE	Gill Net Effort (1000 km)
1963	2.4	0.2	6.4	11.9	1.8	0.4	0.0
1964	1.6	0.1	14.5	3.7	0.6	0.4	0.0
1965	2.0	0.1	20.4	1.7	1.4	0.9	0.0
1966	6.4	0.2	9.6	1.9	3.1	1.1	0.0
1967	10.1	0.2	19.3	0.5	3.2	1.4	0.0
1968	8.8	0.2	20.6	0.1	2.6	1.2	0.0
1969	10.5	0.2	20.5	0.4	10.4	1.1	0.0
1970	10.3	0.3	21.2	0.4	4.1	0.7	0.0
1971	14.8	0.3	22.4	0.9	5.8	0.8	0.0
1972	18.4	0.3	20.8	1.1	13.3	0.6	0.0
1973	9.4	0.3	22.9	1.4	16.1	0.9	0.0
1974	12.3	0.3	21.7	1.2	18.8	2.3	0.0
1975	23.1	0.3	22.0	1.1	16.5	2.3	0.0
1976	25.8	0.4	23.7	0.7	16.9	3.4	0.0
1977	27.0	0.4	15.5	0.8	19.8	1.9	0.0
1978	29.7	0.3	15.7	0.6	20.3	2.9	0.0
1979	22.1	0.4	17.8	0.9	26.6	7.4	0.0
1980	26.1	0.3	24.3	2.3	37.6	4.7	0.0
1981	9.3	0.3	23.5	2.3	43.0	7.7	0.0
1982	15.1	0.4	18.4	3.4	31.3	16.1	0.0

at release than to differences in stocking locations, seasons, or years, egg sources, rearing stations, or rearing diets (Pycha and King 1967).

Wild and stocked adult lake trout were indexed as predators as average CPEs of all sizes and ages caught in the adult lake trout assessment fishery (Chapter I) during years when stocked yearlings were released (1964-83) (Tables 2-4). Wild and stocked adult lake trout were included as independent potential predators because wild adults are distributed deeper than stocked adults (Krueger *et al.* 1986), and therefore

Table 4. Stock and recruitment data used for modeling survival of yearling lake trout stocked in Wisconsin waters of Lake Superior.

Year Class	Age-7 Recruit CPE	Million Yearlings Stocked	Grams/ Yearling	Adult Lake Trout Wild CPE	Adult Lake Trout Stocked CPE	Juvenile Wild Lake Trout CPE	Gill Net Effort (1000 km)
1963	49.9	0.7	20.3	7.1	9.5	4.5	0.9
1964	30.3	0.4	22.3	5.2	10.8	9.3	1.0
1965	16.2	0.3	18.4	5.1	21.5	8.5	1.6
1966	12.3	0.2	20.5	2.2	24.1	10.7	2.7
1967	17.4	0.3	20.7	0.4	15.0	9.0	4.5
1968	8.7	0.3	22.9	1.1	35.8	6.9	6.4
1969	11.0	0.2	26.0	4.5	59.4	9.1	8.5
1970	7.2	0.2	22.6	9.3	53.6	6.6	10.7
1971	10.3	0.3	22.0	8.5	32.7	8.0	12.4
1972	7.1	0.2	20.8	10.7	24.5	12.5	13.6
1973	3.8	0.4	20.7	9.0	28.4	11.3	14.0
1974	4.0	0.5	23.8	6.9	15.9	6.6	14.1
1975	8.7	0.6	28.7	9.1	16.7	3.5	14.4
1976	2.5	0.4	24.4	6.6	17.4	3.4	14.5
1977	14.7	0.4	22.8	8.0	19.6	3.9	14.5
1978	3.1	0.3	19.4	12.5	20.7	5.3	14.1
1979	5.8	0.3	22.3	11.3	15.2	12.2	13.6
1980	3.3	0.2	29.0	6.6	14.1	10.9	12.9
1981	2.6	0.2	23.9	3.5	7.6	9.7	12.9
1982	3.9	0.3	27.9	3.4	7.7	13.5	12.9

may have overlapped in space with stocked yearling lake trout differently than stocked adult lake trout. Wild lake trout were indexed as competitors in the same years when the stocked fish were indexed at age 7 (1970-89) because their interaction with stocked yearlings may not have been limited to the first year.

Fishing mortality was indexed as the average of the annual large-mesh gill-net effort (millions of meters) that was fished during the six years between stocking at age 1 and capture in the assessment nets at age 7 (Tables 2-4). Fishing effort was included because gill nets impose mortality on small (young) fish, even though the focus of their selectivity is on a relatively narrow range of sizes (ages) of fish (Hamley 1975). Gill nets impose increasingly selective mortality on lake trout as they grow in size (age) to fully recruited sizes (ages), so the gauntlet of gill-net fishing effort faced by each year class was treated as a moving average of the annual effort during years between stocking and recruitment. Fishing mortality was indexed using large-mesh gill-net effort because small-mesh gill nets were restricted to offshore chub fisheries and inshore floated lake herring (*Coregonus artedi*) fisheries that impose little mortality on lake trout. Trap nets are fished inshore but impose little mortality on lake trout (Schorfhaar and Peck 1993).

Statistical Analysis

A form of the Ricker (1975) stock-recruitment model was used to model the effects of size at release, predation, competition, and fishing on the survival of lake trout in Lake Superior (Walters *et al.* 1986; Hilborn and Walters 1992):

$$R = Se^{a-bS-cX} \tag{1}$$

The model describes recruitment (R) as a function of the parental stock (S), which is reduced by background, density-independent mortality (a), density-dependent mortality due to intraspecific competition or cannibalism (bS), and interspecific competition or predation (cX). Estimates of the model coefficients (a, b and c) can be found using multiple regression methods on the linear form of the model:

$$\log(R/S) = a - bS - cX + \varepsilon \qquad (2)$$

In the linear form of the model, the recruitment rate, log(R/S), is a decreasing function of the parental stock size and interactions with other species or fisheries. Random or unexplained influences on survival are described in the model as residual error (ε).

Potential explanatory variables were regressed sequentially on the logarithms of the recruitment rate, R/S (CPE at age 7 per million stocked), starting with the number of yearlings stocked (S), computing partial correlations with remaining X-variables, and adding the variable with the highest partial correlation and most biologically sensible coefficient to the model (Henderson and Velleman 1981). Model building was terminated when remaining variables accounted for little remaining residual error or had biologically meaningless partial correlations. Model fit was measured using the adjusted R^2 because the number of years sampled was small (N=20). Models were diagnosed for collinearity among predictor variables, and residual errors were diagnosed for normality, homogeneity of variance, independence, and linearity (Draper and Smith 1981; Systat, Inc. 1992; Kirby 1993).

Model performance was judged by predicting recruitment of the 1983-86 year-classes of stocked fish in each jurisdiction, and comparing the predicted values with observed values (Draper and Smith 1981). Models were therefore fitted to observed values of the 1963-82 year classes, and validated by comparing predicted to observed values of the 1983-86 year-classes. Recruitment rates of the 1986 year class were the lowest observed in all three states, so they provided good tests of model performance (Tyler 1992). Standardized residuals were computed ([observed value -

predicted value]/model SE) (Draper and Smith 1981) to aid in judging if predicted values of the 1983-86 year-classes were unusually large, compared to those of the 1963-82 year-classes. Predictions were considered satisfactory if their standardized residuals fell within the 95% *t*-interval for a sample of 20 observations.

Results

Michigan

Recruitment rates of stocked fish in Michigan were weakly associated with numbers released (r=0.26; N=20; P=0.26), but were strongly associated with large-mesh gill-net fishing effort (r=-0.93; N=20; $P \leq 0.01$) (Figure 10). Stocking and

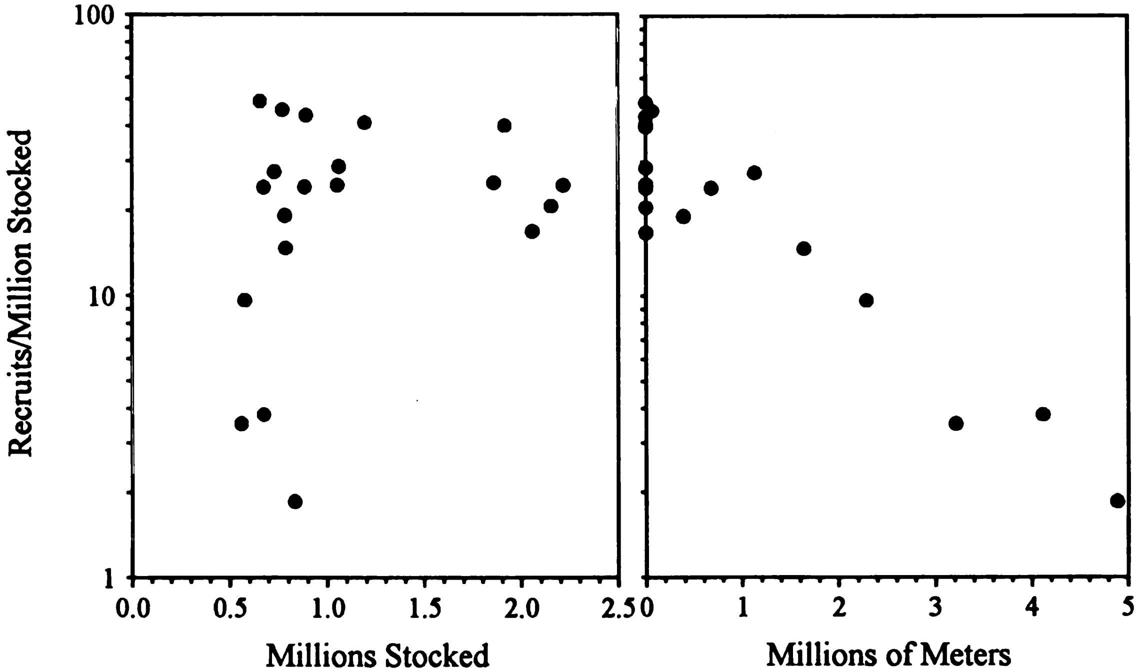

Figure 10. Recruitment rate of the 1963-82 year-classes of stocked yearling lake trout to age 7 compared to the number stocked (left panel) and large-mesh gill-net fishing effort (right panel) in Michigan waters of Lake Superior.

large-mesh gill-net fishing effort each accounted for significant variation in the recruitment of the 1963-82 year classes of stocked lake trout in Michigan (Figure 11; Table 5; Appendix A, Table 20). The coefficient for number stocked was negative, which suggests density dependent competition or cannibalism between the number released and their recruitment to age 7. However, large-mesh gill-net fishing exerted greater influence on recruitment than numbers stocked (the standardized coefficient was larger than for number stocked).

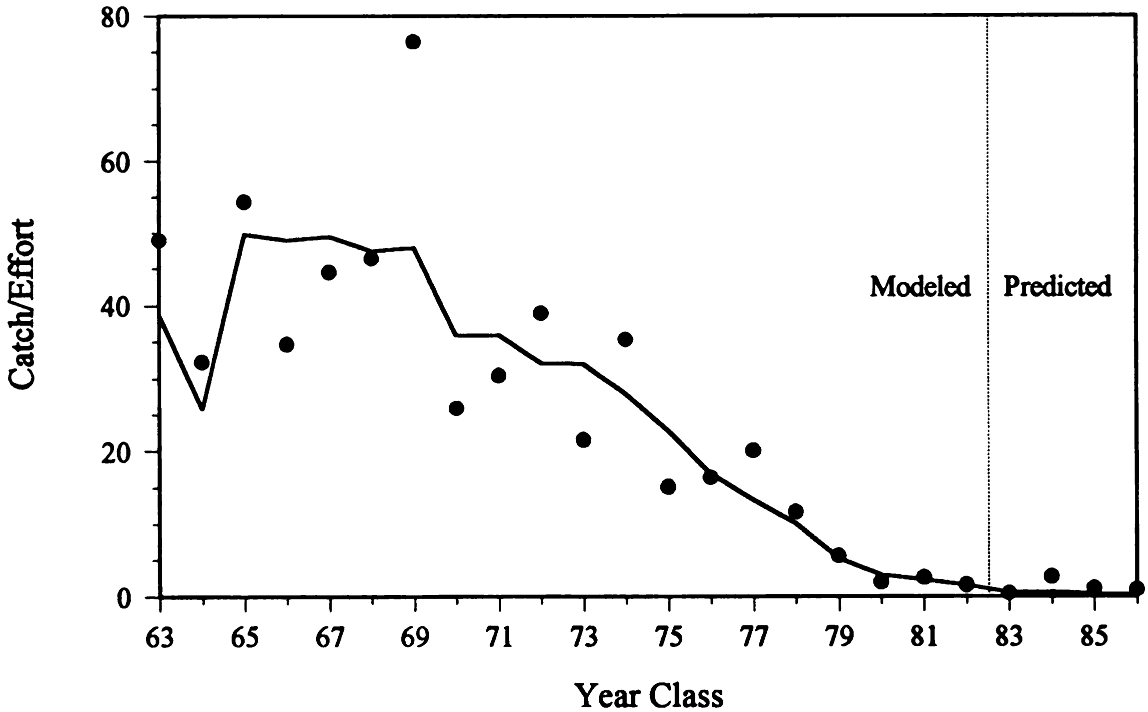

Figure 11. Catch per effort of age-7 stocked lake trout caught in assessment fisheries (dots) and predicted from yearling stocking and large-mesh gill-net fishing effort (line) in Michigan waters of Lake Superior.

Predicted and observed recruitment for the 1983-86 year classes were quite low (Figure 11), but predicted values for the latter three year classes were substantially

Table 5. Results of the multiple regression of stocked lake trout CPE at age 7 per million yearlings stocked (logarithms) on yearlings stocked six years earlier, gill net effort (millions of meters in Michigan and Wisconsin), and wild lake trout CPE (Minnesota) in Lake Superior.

Regression Parameter	Parameter Coefficient	SE	Standardized Coefficient	*t*	*P*
		Michigan (N=20; R^2=0.90; P<0.01)			
Intercept	3.90	0.18	0.00	21.37	0.00
Yearlings Stocked	-0.36	0.13	-0.23	-2.75	0.01
Gill Net Effort	-0.56	0.04	-1.04	-12.66	0.00
		Minnesota (N=20; R^2=0.67; P<0.01)			
Intercept	2.79	0.29	0.00	9.54	0.00
Yearlings Stocked	4.09	0.95	0.60	4.29	0.00
Wild Lake Trout CPE	-0.09	0.03	-0.43	-3.12	0.01
		Wisconsin (N=20; R^2=0.64; P<0.01)			
Intercept	4.82	0.357	0.00	13.08	0.00
Yearlings Stocked	-0.94	0.74	-0.17	-1.26	0.23
Gill Net Effort	-0.13	0.02	-0.82	-5.92	0.00

lower than observed values (Figure 12). This indicates that the model fitted to data for the 1963-82 year classes did not accurately describe data for the 1983-86 year classes. Recruitment rates for the 1983-86 year classes were among the lowest observed during 1963-86, and may have been lower than background rates of immigration into Michigan from neighboring jurisdictions. Immigration was not modeled explicitly, but could be as high as 10% of the numbers stocked into adjacent jurisdictions, based on tagging and marking studies (Eschmeyer *et al.* 1953; Buettner 1961; Pycha *et al.* 1965; Rahrer 1968; Swanson 1973; Ebener 1990; Peck and

Schorfhaar 1991). Such immigration could easily account for differences in predicted and observed recruitment in Michigan.

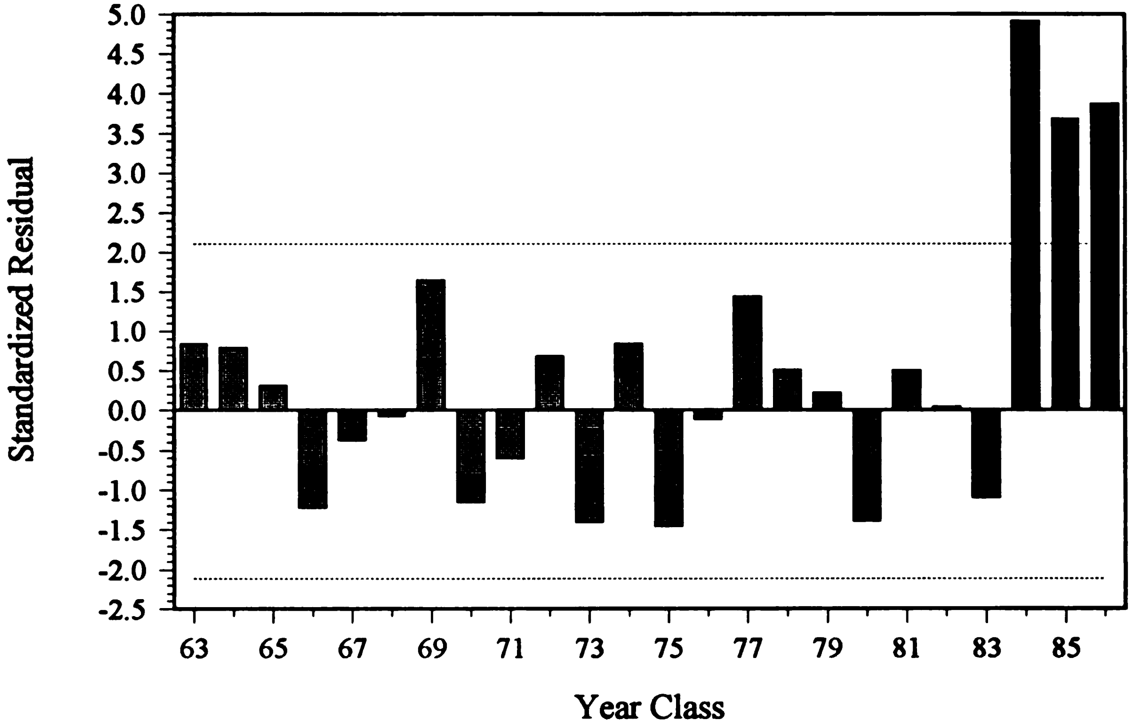

Figure 12. Standardized residuals for stocked lake trout recruitment, predicted from yearling stocking and large-mesh gill-net fishing effort in Michigan waters of Lake Superior (± the 95% *t*-interval).

Predation by wild lake trout may have been an important force of mortality on stocked lake trout in Michigan, but its effect was less significant than that of fishing mortality. Large-mesh gill-net fishing effort (r=-0.93; N=20; $P \leq 0.01$) and CPE of wild lake trout (r=-0.77; N=20; $P \leq 0.01$) were each correlated with recruitment, but wild lake trout CPE did not explain significant variation in the recruitment rate after accounting for gill-net effort. Other potential predictor variables for average size of stocked yearlings, competition with wild lake trout, and cannibalism by previously stocked lake trout were not well correlated with recruitment of stocked lake trout (Appendix B, Figure 27).

Minnesota

Recruitment rates of stocked lake trout in Minnesota were strongly related to the number of yearlings previously released (r=0.73; N=20; P≤0.01) and the density (CPE) of adult wild lake trout in the year of stocking (r=-0.62; N=20; P≤0.01) (Figure 13). The relative abundance of age-7 stocked lake trout in Minnesota was thus predicted from the number of yearlings released and the density of wild adult lake trout in the year when yearlings were released (Figure 14; Table 5; Appendix A, Table

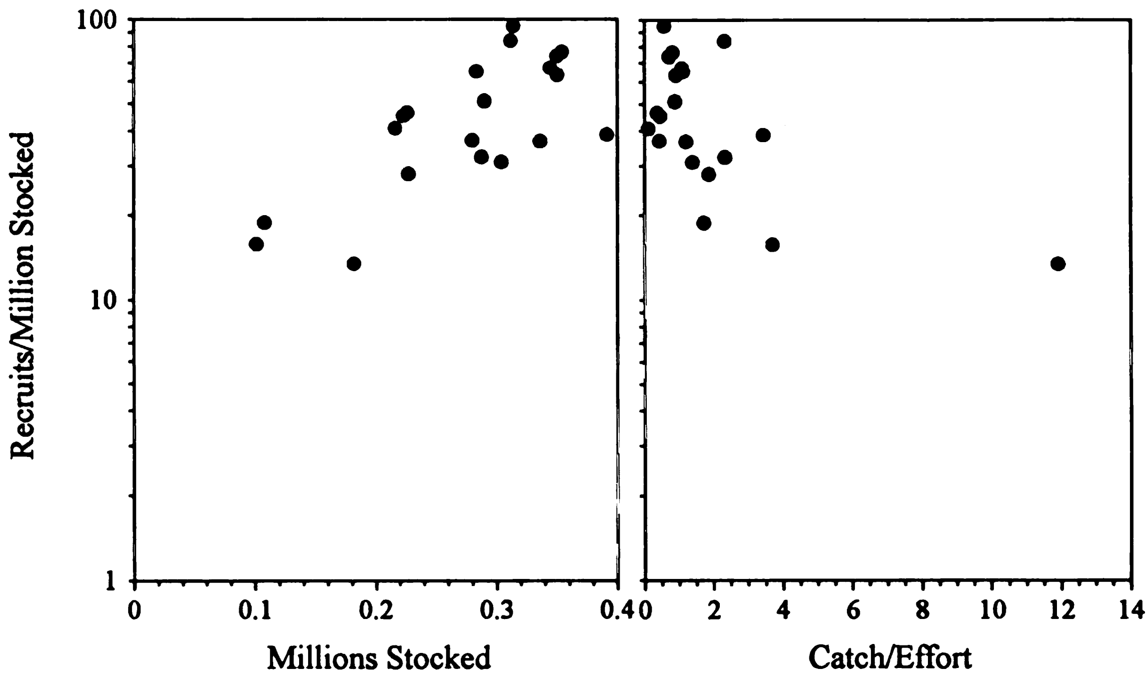

Figure 13. Recruitment rate of the 1963-82 year-classes of stocked yearling lake trout to age 7 compared to the number stocked (left panel) and wild lake trout density (right panel) in Minnesota waters of Lake Superior.

21). The coefficient for number stocked was positive, which suggests depensatory predation between the number released and their recruitment to age 7. Predation on stocked lake trout by wild adult lake trout was relatively similar to the effect of numbers of yearling lake trout released (standardized coefficients were of similar magnitude).

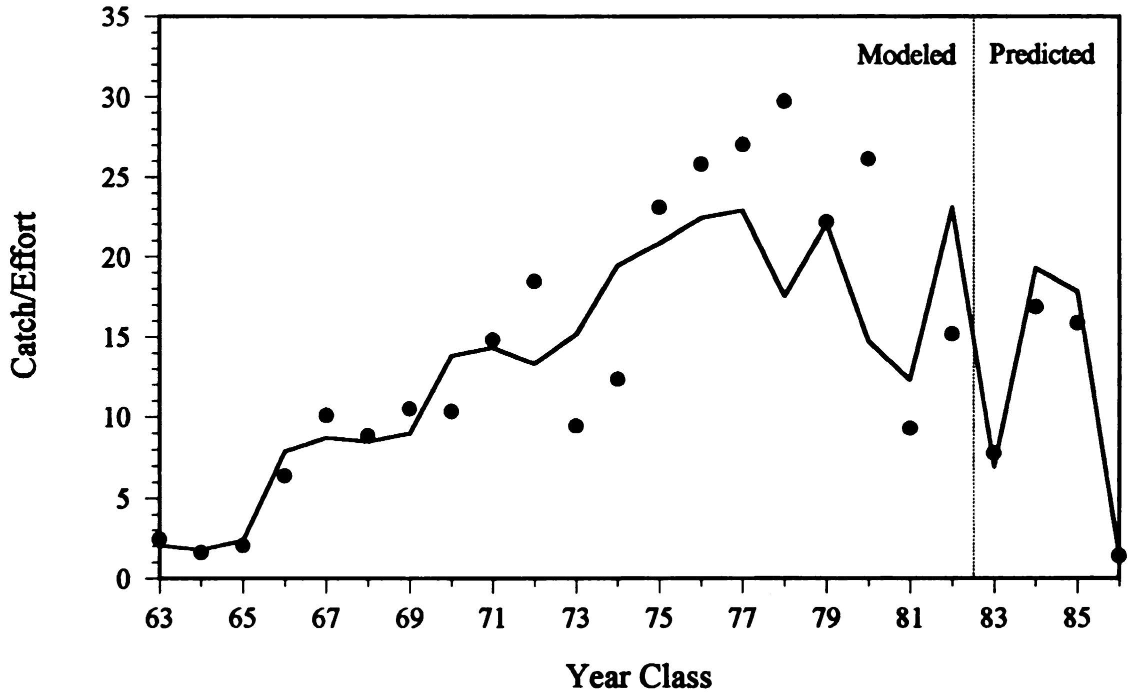

Figure 14. Catch per effort of age-7 stocked lake trout caught in assessment fisheries (dots) and predicted from yearling stocking and wild lake trout density (line) in Minnesota waters of Lake Superior.

Predicted and observed recruitment for the 1983-86 year classes were highly variable (Figure 14), but predicted values were remarkably similar to observed values (Figure 15). The recruitment rate for the 1986 year class was the lowest observed in Minnesota during 1963-86, yet was accurately predicted by stocking and predation,

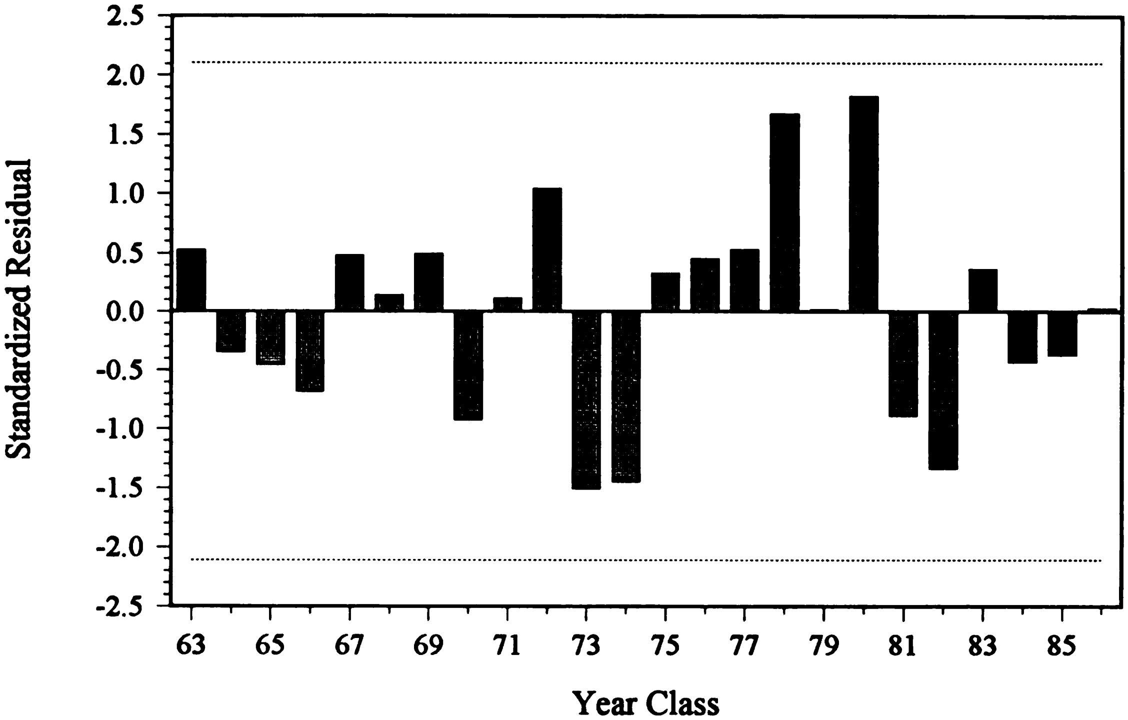

Figure 15. Standardized residuals for stocked lake trout recruitment, predicted from yearling stocking and large-mesh gill-net fishing effort in Minnesota waters of Lake Superior (± the 95% *t*-interval).

which indicates that the model fitted to data for the 1963-82 year classes accurately described data for the 1983-86 year classes.

Other potential predictor variables were not well correlated with recruitment of stocked lake trout (Appendix B, Figure 28). Therefore, the average size of stocked yearlings and wild juvenile lake trout competition were not implicated as causes of declining lake trout survival in Minnesota. Large-mesh gill-nets were not allowed in Minnesota, so fishing mortality was not related to survival of stocked lake trout.

Wisconsin

The recruitment of stocked lake trout to age 7 in Wisconsin was more strongly related to large-mesh gill-net fishing effort (r=-0.80; N=20; $P \leq 0.01$) than to the number of yearlings previously released (r=-0.087; N=20; P=0.71) (Figure 16). Recruitment rates of the 1963-82 year-classes of stocked lake trout in Wisconsin were thus predicted from the number of yearlings released and the average amount of large-mesh gill-net fishing effort in intervening years (Figure 17; Table 5; Appendix A, Table 22). The coefficient for number stocked was not significant, which suggests density independence between the number stocked and their recruitment to age 7. However, mortality on stocked lake trout caused by large-mesh gill nets largely explained trends

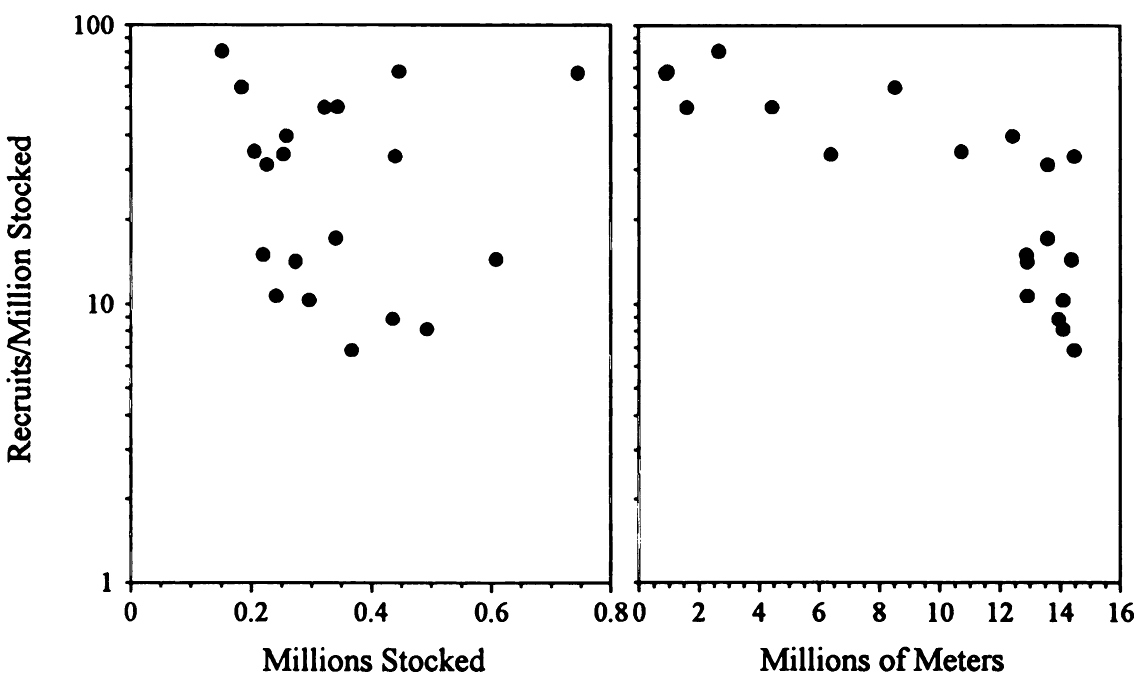

Figure 16. Recruitment rate of the 1963-82 year-classes of stocked yearling lake trout to age 7 compared to the number stocked (left panel) and large-mesh gill-net fishing effort (right panel) in Wisconsin waters of Lake Superior.

in stocked lake trout CPE in Wisconsin (large standardized coefficient), and may have masked the effect of numbers of lake trout stocked (small standardized coefficient).

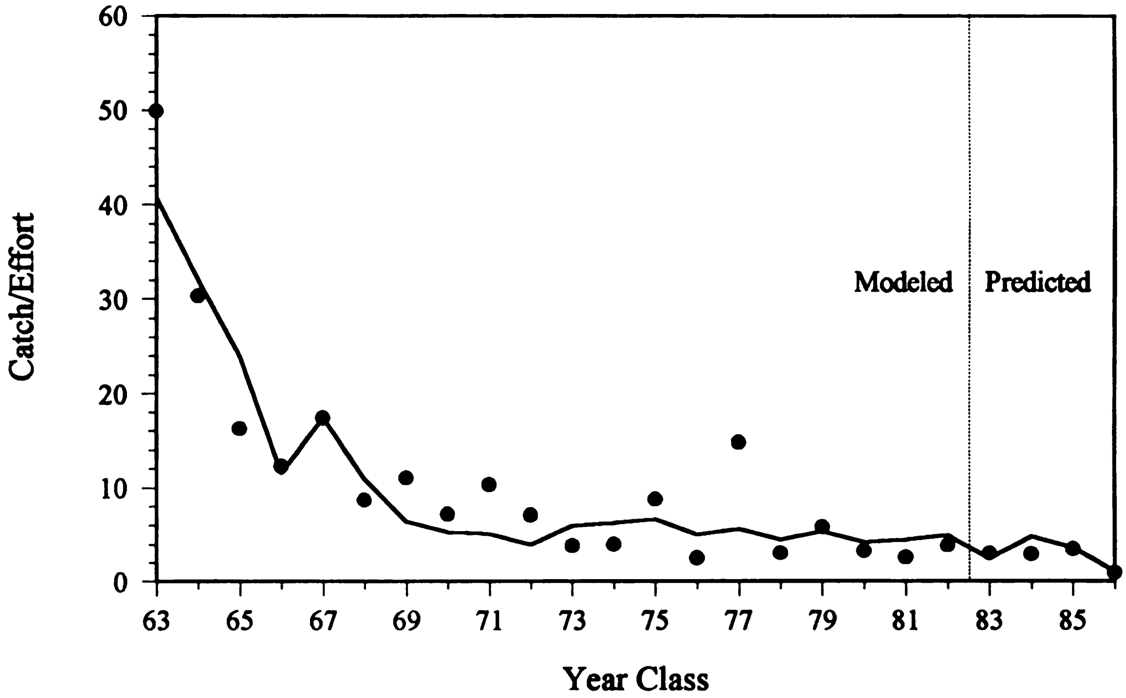

Figure 17. Catch per effort of age-7 stocked lake trout caught in assessment fisheries (dots) and predicted from yearling stocking and large-mesh gill-net fishing effort (line) in Wisconsin waters of Lake Superior.

Predicted and observed recruitment for the 1983-86 year classes were low, as in Michigan (Figure 17), but predicted values were remarkably similar to observed values, as in Minnesota (Figure 18). The recruitment rate for the 1986 year class was the lowest observed in Wisconsin during 1963-86, as it was in Minnesota, and yet was accurately predicted by stocking and predation. This indicates that the model fitted to data for the 1963-82 year classes accurately described data for the 1983-86 year classes in Wisconsin.

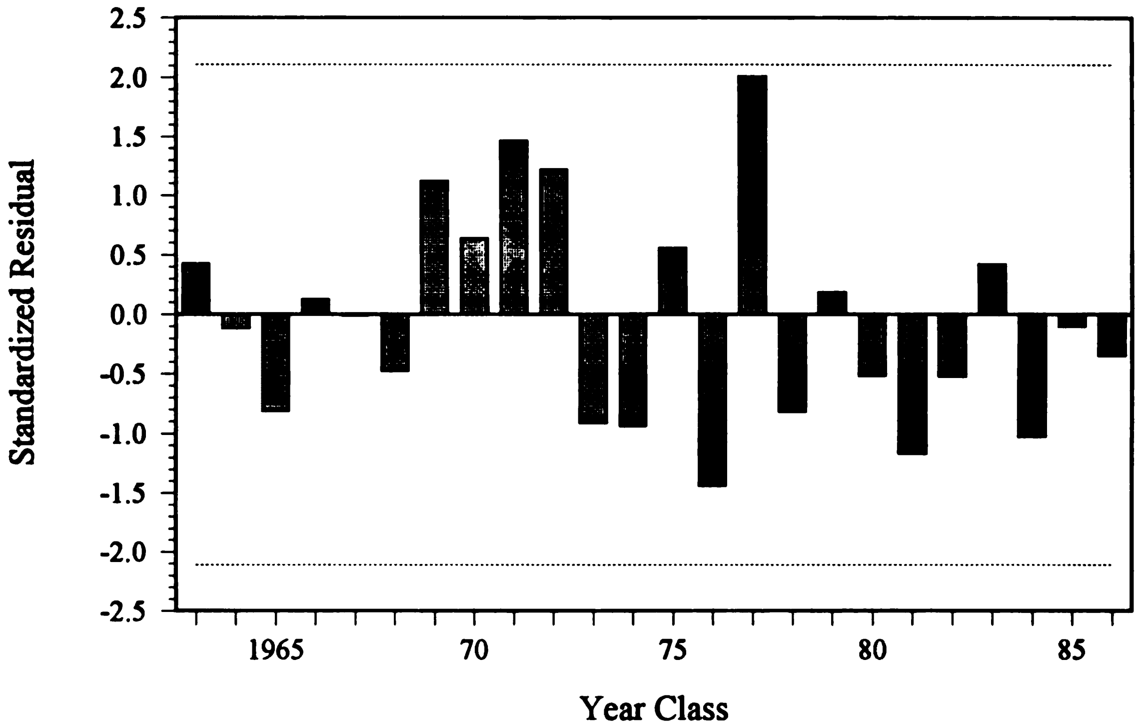

Figure 18. Standardized residuals for stocked lake trout recruitment, predicted from yearling stocking and large-mesh gill-net fishing effort in Wisconsin waters of Lake Superior (± the 95% *t*-interval).

Other potential predictor variables were not well correlated with recruitment of stocked lake trout (Appendix B, Figure 29). Consequently, the average size of stocked yearlings and wild juvenile lake trout competition were not implicated as causes of declining lake trout survival in Wisconsin.

Discussion

The present analysis suggests that survival of lake trout stocked in Michigan and Wisconsin declined primarily because of large-mesh gill-net fishing mortality, and in Minnesota because wild lake trout preyed on newly stocked lake trout. Survival of lake trout stocked in Michigan may also have been reduced by wild lake trout predation, but the effect was masked by fishing mortality, and therefore survival may have been no better even if gill-net fishing effort had been less. The present analysis did not implicate other factors that were previously suggested as significant sources of mortality on stocked lake trout, such as competition with wild yearling lake trout (Purych 1977; MacLean *et al.* 1981; Powell *et al.* 1986), predation by previously stocked lake trout (Elrod *et al.* 1993), or size of lake trout at the time of their release (Pycha and King 1967; Plosila 1977; Elrod *et al.* 1988; Gunn *et al.* 1987).

Fishing Mortality

The importance of fishing mortality on lake trout survival was surprising because declining survival had previously been shown to occur prior to ages 2-4, before the fish were recruited into the sport or commercial fisheries (Hansen *et al.* 1994a). However, survival declined most after the 1982 year class (Hansen *et al.* 1994a), and may have been undetectable by the present analysis. Fishing mortality was the primary cause of declining lake trout abundance in Lake Superior prior to the colonization of the lake by sea lampreys (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990), and large-mesh (≥114 mm stretch-measure) gill nets were the primary gear used to catch lake trout until 1962 when fisheries were closed (Pycha and King 1975). Large-mesh gill nets were not allowed in Minnesota after the fishery was closed in 1962, or in Michigan until tribal fisheries for lake whitefish (*Coregonus clupeaformis*) reopened during the late 1970s and 1980s (Peck and

Schorfhaar 1991). In contrast, large-mesh gill nets were allowed for harvesting lake whitefish in Wisconsin after 1970 (Hansen *et al.* in press).

Gill-net fishing effort significantly limited survival of lake trout stocked in Michigan and Wisconsin after 1963 even though these fisheries were targeted on lake whitefish. Gill nets are extremely selective for fish of certain sizes (Hamley 1975); for example, 114-mm stretch-mesh gill nets are highly selective for fish 457-610 mm TL (age 7-9; Pycha 1980). However, larger and smaller fish are also entangled, and many of these die, along with those that are gilled. The use of gill nets can therefore lead to high incidental mortality on a species, such as lake trout, even when the fishery intends to harvest another species, such as lake whitefish. Large-mesh gill-net effort increased earlier and was greater in Wisconsin; effort rose from an average of less than 1-million m during 1963-69 to more than 14-million m during 1973-86. Large-mesh gill-net effort increased later and was lower in Michigan; effort rose from nil during 1963-73 to an average of nearly 5-million m during 1982-89. Stocked lake trout apparently suffered high incidental mortality in large-mesh gill nets in both states, but were spared in Minnesota, where large-mesh gill nets were not used.

In Wisconsin, the effect of high incidental mortality on lake trout in large-mesh gill nets was evident in a truncated age distribution (Figure 19). In offshore waters, lake trout of the 1963-82 year-classes were protected by refuges (Swanson and Swedberg 1980), but inshore, were subjected to high incidental mortality in large-mesh gill-net fisheries targeted on lake whitefish. As a consequence, age distributions of inshore lake trout in spring 1990, the first year after those included in this analysis, were truncated compared to offshore lake trout. The age distribution of inshore lake

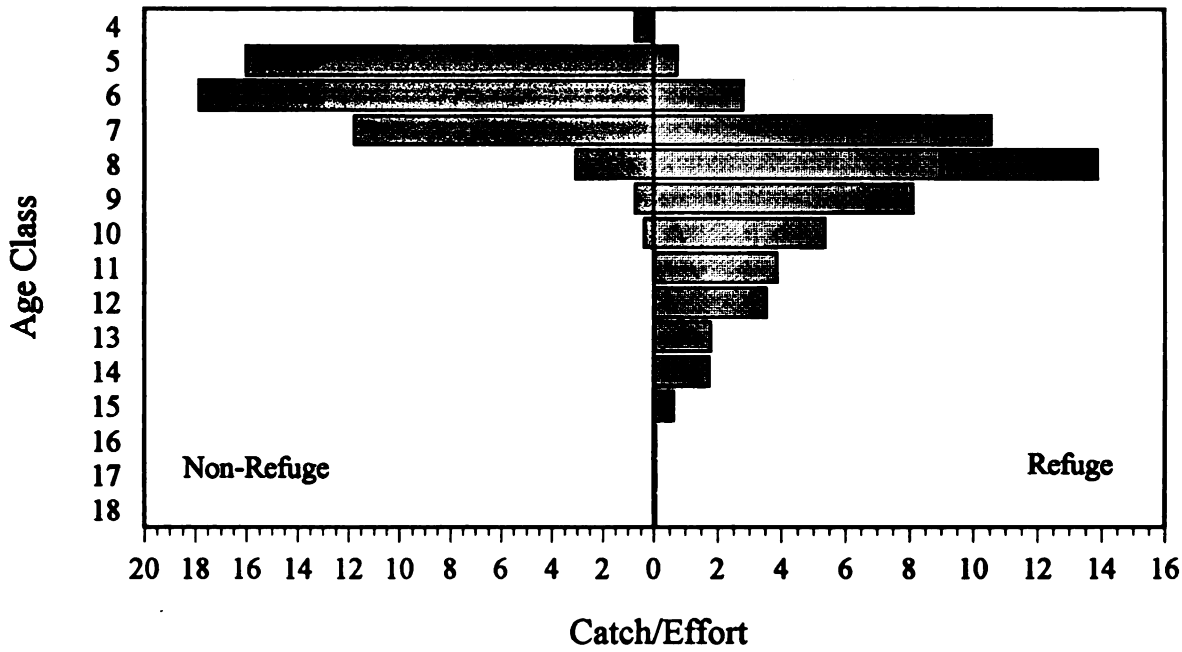

Figure 19. Catch/effort of lake trout in spring gill net assessment fisheries (number per km of net) inshore (non-refuge) and offshore (refuge) in eastern Wisconsin waters of Lake Superior in 1990.

trout shows that their growth rates had increased, such that the first fully recruited age had dropped by two years compared to offshore lake trout. In addition, ages beyond the first fully recruited age were truncated below age 10, whereas ages of offshore lake trout declined gradually from age 8 through age 18.

In Michigan, incidental mortality on lake trout in large-mesh gill nets was inversely related to recruitment, even though no refuges were present in which to contrast the resulting age structure (Figure 20). Large-mesh gill-net effort varied inversely to lake trout recruitment among management areas within Michigan waters. Recruitment rates in Michigan were lower for all year-classes after 1974 than for any previous year-classes, coincident with the onset of large-mesh gill-net fishing. As a

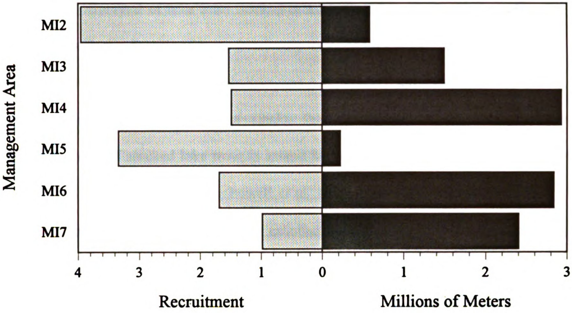

Figure 20. Recruitment of the 1982 lake trout year-class at age 7 (CPE/million yearlings stocked), compared to the average annual large-mesh gill-net fishing effort during 1983-88, in inshore Michigan areas of Lake Superior.

result, the recruitment of lake trout in Michigan was higher for year classes that were not subjected to large-mesh gill-net fishing and in areas where that fishing effort was lowest (MI2, MI5) than for year classes that were subjected to fishing effort and in areas where that fishing effort was higher (MI3, MI4, MI6, MI7).

Predation by Wild Lake Trout

Predation on newly stocked lake trout by mature wild lake trout may have been an important source of mortality in Minnesota, and possibly also in Michigan, waters of Lake Superior. Lake trout stocking success was inversely associated to abundances of older stocked lake trout during 1959-66, which suggested that cannibalism on newly stocked lake trout by previously stocked fish was important at that time (Dryer and

King 1968). Survival of lake trout stocked in Lake Ontario was also negatively associated with the density of large previously-stocked lake trout (≥550 mm total length), which suggested that cannibalism was a significant source of mortality on newly stocked lake trout (Elrod *et al.* 1993). Predation by native lake trout may have limited survival of stocked lake trout in inland lakes as well (Purych 1977; Martin and Olver 1980; MacLean *et al.* 1981; Powell *et al.* 1986; Evans and Willox 1991).

In spite of these suggestions that cannibalism was an important source of mortality, stocked juvenile lake trout have rarely been found in stomachs of wild adult lake trout (Powell *et al.* 1986; Elrod *et al.* 1993). In Lake Superior, stocked juvenile lake trout have rarely been encountered in surveys of lake trout feeding (Dryer *et al.* 1965; Conner *et al.* 1993; Gallinat 1993), which suggests that predation may not be an important source of mortality on newly stocked lake trout. A similar model of predation by Pacific cod (*Gadus macrocephalus*) on herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia, also suggested predation rates that were much higher than stomach contents had indicated (Walters *et al.* 1986). Walters *et al.* (1986) noted that their estimated rate of predation on herring by Pacific cod may have been too high if predation was spread across several years, if herring abundance had been overestimated, or if Pacific cod abundance had been underestimated.

Low occurrence of stocked yearling lake trout in wild adult lake trout stomachs may not adequately indicate the importance of wild lake trout predation to the overall survival of stocked lake trout. Stocked adult lake trout are distributed nearer to shore than wild adult lake trout (Krueger *et al.* 1986), and yearling lake trout move offshore, away from stocking sites, soon after their release (Pycha *et al.* 1965). Consequently, stocked yearling lake trout may only be vulnerable to cannibalism by stocked adult lake trout for a short time after stocking. Provided that stocked yearlings escape cannibalism near the stocking site, they would become more vulnerable to predation by wild adult lake trout during the remainder of their first year in the wild. However, stomach samples of Lake Superior lake trout have generally been obtained from sport fisheries that primarily operate inshore, or from spring gill-net assessments that coincide with yearling stocking (Conner *et al.* 1993; Gallinat 1993). Such sampling is unlikely to reflect of feeding on newly stocked lake trout by wild adult lake trout.

Management Implications

It appears that survival of lake trout stocked in Lake Superior declined significantly because of high incidental mortality in large-mesh gill nets and predation by wild adult lake trout. It is not clear, however, whether survival would have been better if gill-net fishing effort had been less, because predation by wild adult lake trout may have reduced survival in the absence of fishing mortality. Survival of stocked lake trout needs to be tested under conditions of lower gill-net fishing effort in Michigan, where densities of wild adult lake trout are highest, to determine whether predation by wild adult lake trout will compensate for reduced fishing mortality.

Such an adaptive management experiment may be focused on the wrong problem. Reduced survival of stocked lake trout because of excessive incidental mortality in large-mesh gill nets also indicates a problem for wild lake trout stocks in Lake Superior. Abundance of wild lake trout has also declined in Michigan and

Wisconsin (Hansen *et al.* 1994b), and likely indicates the same effects of excessive fishing mortality. Large-mesh gill-net fishing effort needs to be reduced in Michigan and Wisconsin to enhance survival of both wild and stocked lake trout. Reductions in large-mesh gill-net effort were imposed in Wisconsin on the state-licensed fishery in 1991 and the tribal-licensed fishery in 1992, but have yet been imposed in Michigan.

Reductions in incidental fishing mortality may lead to increased abundance of wild lake trout in both Michigan and Wisconsin. Predation by wild adult lake trout may subsequently increase, and reduce the survival of stocked lake trout that would otherwise have increased in the absence of fishing mortality. As a consequence of the interplay between fishing mortality and predation by wild adult lake trout, stocked lake trout survival may remain low in the future. Stocking may no longer be a useful stock enhancement technique in Lake Superior, particularly in areas with high densities of wild lake trout, regardless of the level of fishing mortality. Increasing density of wild lake trout in Minnesota may therefore lead to failures of stocked year classes, similar to those in Michigan and Wisconsin, absent excessive incidental fishing mortality.

The importance of predation by wild lake trout on stocked yearling lake trout needs to be better defined. Stomach samples should be obtained from wild lake trout throughout their bathymetric distribution and during the entire growing season. The bathymetric distribution of stocked yearling lake trout should also be determined to define their spatial overlap with wild adult lake trout. These studies should be done under conditions of both high and low large-mesh gill-net fishing effort to determine whether declining survival of stocked yearling lake trout can be improved in the face of increasing densities of wild lake trout in Lake Superior.

CHAPTER III:

STATUS OF LAKE TROUT

RESTORATION IN U.S. WATERS OF LAKE SUPERIOR

Abstract.—Lake trout (*Salvelinus namaycush*) populations in Lake Superior sustained 2 million kg of yield annually for four decades before collapsing during the 1950s due to excessive fishery exploitation and sea lamprey predation. Lake trout restoration was attempted during the ensuing decades through an interagency program of intensive stocking, sea lamprey control, and fishery regulation. Self-sustaining populations of lake trout have returned to most areas in Lake Superior, but progress toward historic yields has been difficult to measure because of losses to sea lamprey (*Petromyzon marinus*) predation and unreported harvest. Because of such inherent weaknesses in yield as a target for restoration, restoration targets were developed that are based on abundance during the period when historic yields were sustained. Long time-series of abundance data (1929-93) were developed from linear relationships between CPE in commercial and assessment fisheries in Michigan. Progress toward restoration of lake trout populations is described by comparing lake trout abundance during modern times (1970-93) with their abundance during a historic reference period (1929-43). Abundances of inshore stocks of wild lake trout exceeded historic abundances in some years and areas during the 1980s, but fell below historic abundances in all areas during the 1990s. Further progress in restoration can only be achieved if fishery managers adequately protect existing stocks of wild fish from predation by sea lampreys and exploitation by sport and commercial fisheries.

Introduction

Lake trout (*Salvelinus namaycush*) sustained 2 million kg of average annual yield during 1913-50 in Lake Superior (Baldwin *et al.* 1979), but collapsed nearly to extinction during 1951-62 because of excessive fishery exploitation and sea lamprey (*Petromyzon marinus*) predation (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990). Hatchery-reared, juvenile lake trout were stocked, in conjunction with controls on sea lampreys and fisheries, to restore populations into the lake (Lawrie and Rahrer 1972, 1973; Pycha and King 1975). Stocking has been relatively continuous since 1951 in Wisconsin, 1952 in Michigan, 1957 in Ontario, and 1962 in Minnesota (Lawrie and Rahrer 1972, 1973; Pycha and King 1975; Lawrie 1978). Sea lampreys reached peak abundance during 1958-61, and have been maintained at 15% of that level since 1962 using chemicals, barrier dams, and traps (Smith 1971; Smith *et al.* 1974; Smith and Tibbles 1980; Klar and Weise 1994). Commercial and sport lake trout fisheries were closed lakewide during 1962, and have been strictly regulated ever since (Pycha and King 1975; Hansen *et al.* 1994b).

The goal of lake trout restoration in Lake Superior is to restore self-sustaining stocks that can provide an average annual yield equal to that during 1929-43 (2 million kg) (LSLTTC 1986; Busiahn 1990). The reference period for lake trout restoration was set during 1929-43 because the yield during that period was consistent with the average annual yield dating back to 1913, and because lake trout stocks were thought to decline after 1943 (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978). However, this goal cannot be attained if sea lampreys kill a portion of the annual production, or if much of the yield from fisheries goes unreported, even if self-sustaining lake trout stocks are restored throughout the lake. For example, sea lampreys may have consumed as much lake trout production as humans in some areas during the 1990s (Hansen *et al.* 1994b)—lake trout stocks in these areas may have been much closer to historic abundances than was indicated by fishery yields. Alternatively, if the restoration goal were stated in terms of lake trout abundances that are capable of yielding 2 million kg annually (rather than actual yield), then progress could be measured regardless of losses to sea lamprey predation or unreported fishery harvest.

Progress in lake trout restoration could be better measured in terms of abundance, or an index of abundance such as CPE, than in terms of yield. Lawrie (1978) acknowledged that records of historical lake trout abundance were not available, but suggested that targets for stock restoration could be inferred from observations of stocks that had been lightly exploited and little affected by sea lamprey predation. He noted that the CPE of lake trout averaged 56.4 fish per km of multifilament nylon gill net during 1938-44 near Michipicoten Island, and ranged from 51.8 to 71.2 near Caribou Island (Lawrie 1978). In contrast, the CPE of lake trout averaged 241.1 on Superior Shoal during 1967-70 (Lawrie 1978). However, the lake trout at Superior Shoal averaged 17% smaller than those at either Michipicoten Island or Caribou Island, so the estimated CPEs of similar-sized lake trout would have been 201.1 at Michipicoten Island and 133.9 at Caribou Island (Lawrie 1978).

Such direct measures of lake trout abundance would facilitate measurement of progress in lake trout restoration in Lake Superior. My objective is to develop a quantitative means of evaluating the current status of lake trout stocks in inshore

Michigan waters by standardizing CPE data presented by Hile *et al.* (1951), Pycha and King (1975), and Hansen *et al.* (1994b) into a 65-year data set for each inshore Michigan management area in Lake Superior. These data series will allow direct comparison of contemporary lake trout abundance (CPE), monitored by ongoing gill-net assessment fisheries, with historic lake trout abundance, when populations yielded target levels of production. Progress toward these target levels of production can therefore be readily judged by the difference between the CPE in the assessment fishery and the average CPE during the historic (reference) period.

Methods

Study Area

Stock assessment of lake trout in Lake Superior is carried out in accordance with an inter-agency rehabilitation plan that specifies management areas for reporting progress in lake trout stock restoration (LSLTTC 1986) (Figure 4). These management areas are modifications of statistical districts previously used for reporting commercial fishery statistics in Michigan, Minnesota, and Wisconsin (Hile 1962). The difference between the two systems is that some statistical districts were divided into two smaller management areas that were closer in size to the range of lake trout movement in Lake Superior—90% of marked lake trout were recaptured within 80 km, regardless of the size at release or length of time at large (Eschmeyer *et al.* 1953; Buettner 1961; Pycha *et al.* 1965; Rahrer 1968; Swanson 1973; Ebener 1990; Peck and Schorfhaar 1991). Consequently, the statistical district for all of Wisconsin (WI) was divided into two management areas (WI1 and WI2), the statistical district surrounding the Keweenaw

Peninsula in Michigan (MS-3) was divided into two management areas (MI3 and MI4), and the statistical district in central Michigan waters (MS-4) was divided into two management areas (MI5 and MI6). Lake trout management areas in Ontario are the same areas used for management of lake whitefish commercial fishery quotas, and bear no resemblance to former statistical districts.

Data Description

I constructed 65-year data sets of lake trout abundance in Michigan from previous analyses of lake trout CPE by Hile *et al.* (1951), Pycha and King (1975), and Hansen *et al.* (1994b). Hile *et al.* (1951) estimated lake trout abundance during 1929-49 from commercial fisheries in Michigan statistical districts MS-1 through MS-6 from the catch per lift (CPE) in large-mesh gill nets (114-mm stretch-measure and greater), set-hooks, and pound nets, expressed as a percentage of the 1929-43 average, and averaged over statistical districts according to the yield in each area during 1929-43 (see Hile [1962] for a description of methods, and Jensen and Buettner [1976] for a tabulation of the data).

Pycha and King (1975) updated Hile et al.'s (1951) analysis through 1970 and expanded the analyses into Wisconsin, but used only large-mesh gill net CPE because that gear accounted for 96% of the production in 1956-70. The CPEs in gill nets were adjusted for increased efficiency of nylon twine (Pycha 1962), which replaced cotton twine during 1950-52. The commercial fishery was closed in 1962, but a few selected fishers were granted licenses to conduct assessment fishing thereafter. The CPEs of these fishers was generally higher than the average CPE of all commercial fishers, so

Pycha and King (1975) adjusted their CPEs during 1962-70 by the ratio of their CPEs to those of the entire fishery during 1959-61. The historic average CPE in adjacent area MI2 was used as the historic average in Wisconsin (Pycha and King 1975).

Hansen *et al.* (1994b) reported the CPE in gill net (114-mm stretch measure) assessment fisheries in Michigan, Minnesota, and Wisconsin during 1970-92, but did not link their data with those of Hile *et al.* (1951) and Pycha and King (1975). The analyses by Hansen *et al.* (1994b) were for lake trout management areas (LSLTTC 1986) (Figure 4), rather than the statistical districts used by Hile *et al.* (1951) and Pycha and King (1975). Consequently, I used data from statistical district MS-3 to construct the historic data series in management areas MI3 and MI4, district MS-4 for areas MI5 and MI6, district MS-5 for area MI7, and district MS-6 for area MI8. Hansen *et al.* (1994b) also computed the CPE as the geometric mean across all lifts in each management area, rather than the pooled catch over the pooled effort (Hile *et al.* 1951; Pycha and King 1975), to quantify the variance of catches.

Statistical Analysis

I analyzed commercial gill net fishery catch and effort data compiled by Jensen and Buettner (1976) for each of the Michigan statistical districts that were analyzed by Hile *et al.* (1951) and Pycha and King (1975). First, I reconstructed the data tabulated in Hile *et al.* (1951) to ensure that the historic data used in my analysis was the same. Next, I extended the data summaries through the end of the commercial gill net data series (1962), which provided statistics that should have been the same as those used by Pycha and King (1975) (Appendix A, Tables 23-24).

I used simple linear regression to relate the data series of Pycha and King (1975) (Appendix A, Tables 23-24) and Hansen *et al.* (1994b) (Appendix A, Tables 6-11, back-transformed values) during a period of overlap (1959-61), to extend the CPE of lake trout from 1929 through 1993. The period of overlap was the same one used by Pycha and King (1975) because it was a period before major restrictions were imposed on the fishery (1962), and assessment fishers worked as regular licensees within the overall commercial fishery. Catch and effort statistics were available for the 1959-61 overlap period in all management areas except MI8. For MI8, I used the next 3-year period (1962-64) for which data were available in both data sets. The linear relationship between the data series was then used to standardize the old data into the same units as the new data. The regression equation therefore provides an omnibus correction of catch from pounds to numbers, net length from feet to meters, CPE from the commercial fishery to the assessment fishery, and CPE from weighted averages to geometric means. Target CPEs in each area were computed as the average reconstructed CPE in the area during 1929-43. Because of the shortness of the overlap period (N=3), correlations were only judged to be acceptable if they were near unity.

Results

Average annual CPEs in the commercial and assessment fisheries during 1959-61 corresponded well for management areas MI3 (r=0.99), MI4 (r=0.94), MI5 (r=0.99), MI6 (r=0.99), and MI8 (r=1.00), but not in MI7 (r=0.72). The linear relations between commercial and assessment fisheries in 1959-61 were:

MI3: $CPE_a = -1.57 + (1.27 \times CPE_c)$

MI4: $CPE_a = -1.26 + (2.08 \times CPE_c)$

MI5: $CPE_a = -4.63 + (3.69 \times CPE_c)$

MI6: $CPE_a = -2.36 + (2.92 \times CPE_c)$

MI7: $CPE_a = -14.35 + (3.48 \times CPE_c)$

MI8: $CPE_a = -2.97 + (0.76 \times CPE_c)$

For each relation, CPE_a and CPE_c are average CPEs in the assessment and commercial fisheries during 1959-61. The slope of each linear relationship shows the efficiency of the assessment fishers in that management area, relative to the overall commercial fishery, provided that average weights of lake trout in the catch and the relationships between geometric means and weighted averages are relatively consistent among areas.

The target CPE for lake trout restoration (1929-43 average) was 18.40 in MI3, 31.56 in MI4, 70.98 in MI5, 57.36 in MI6, 103.31 in MI7, and 21.14 in MI8. In MI3 and MI4, the CPEs of wild lake trout exceeded the target in several years during the 1980s (1984-85 and 1989 in MI3; 1980-81 and 1986 in MI4), but by 1993, fell to only 35% of the target in MI3 and 57% of the target in MI4 (Figure 21). In MI5, the CPE of wild lake trout exceeded the target in 1985-86, and fell to 54% of the target in 1993 (Figure 22). In MI6, the CPE of wild lake trout never exceeded the target, but rose to 77% of the target in 1993 (Figure 22). In MI7 and MI8, the CPE of wild lake trout was lower than elsewhere, never exceeded the target in MI7, and exceeded the target in MI8 only in 1984 (Figure 23). The wild lake trout CPE in 1993 was only 16% of the target in MI7 and unknown in MI8 (Figure 23).

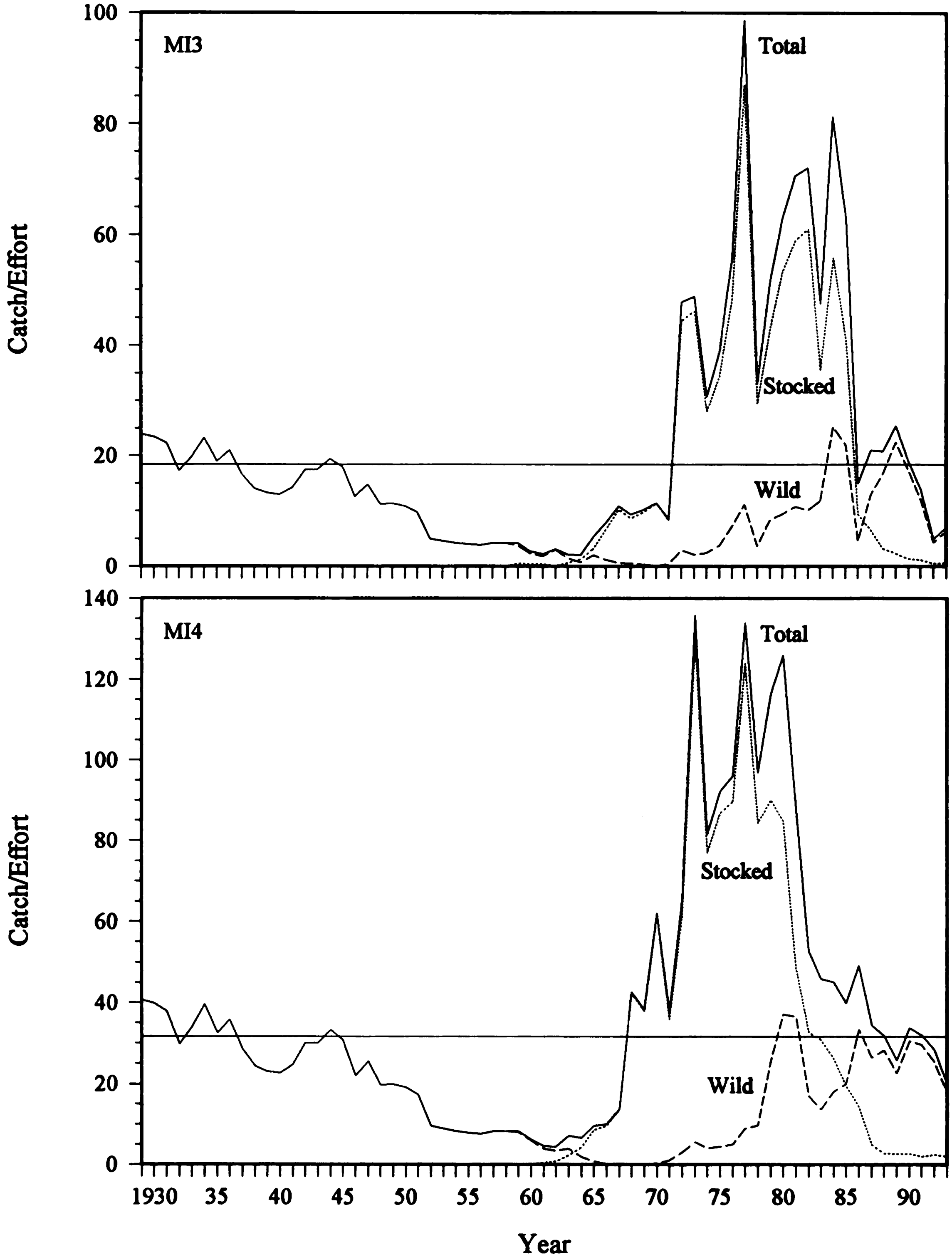

Figure 21. Abundance of stocked and wild lake trout in Michigan west (MI3) and east (MI4) of the Keweenaw Peninsula in Lake Superior during 1929-93, compared to the average abundance during 1929-43.

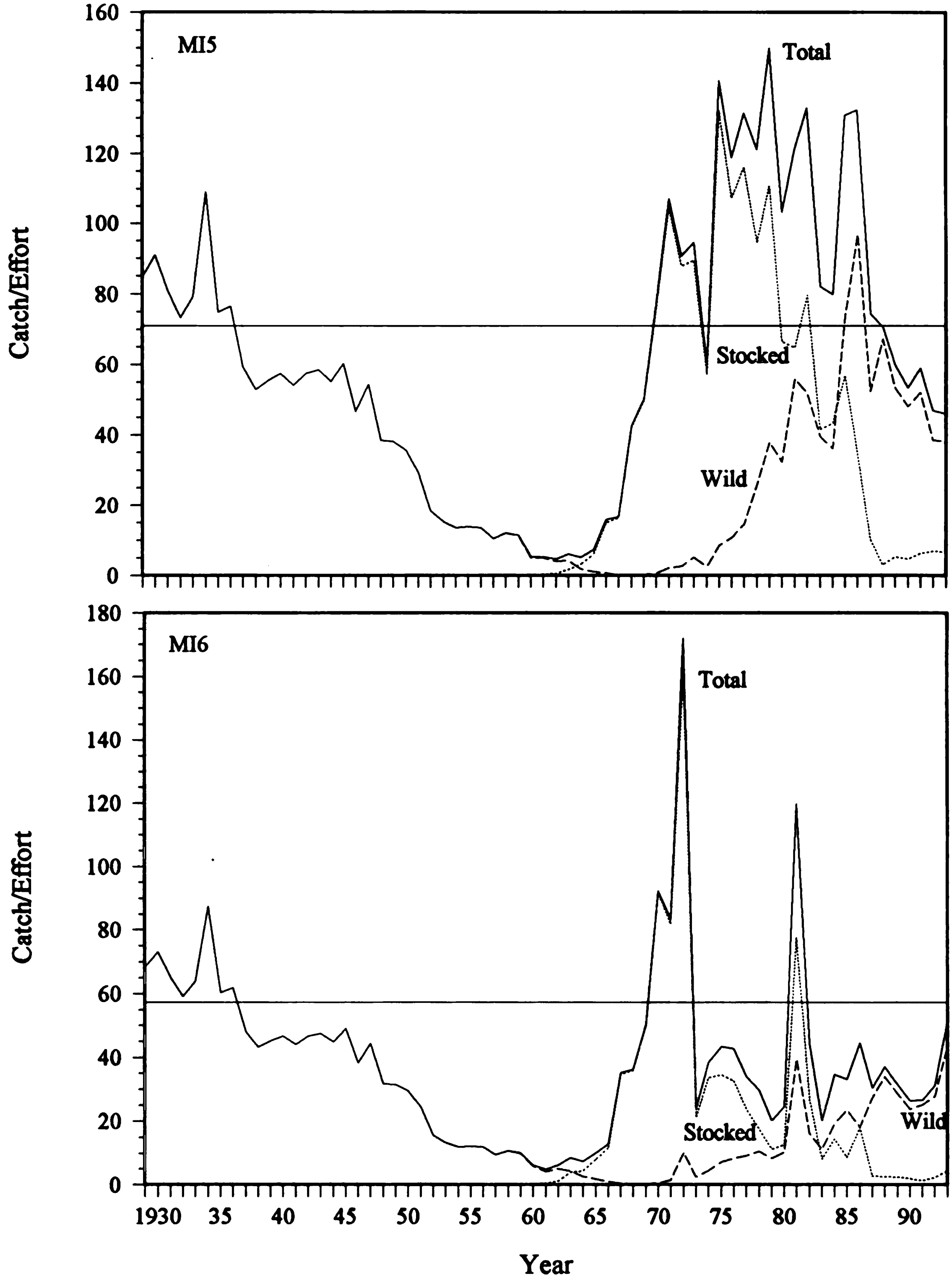

Figure 22. Abundance of stocked and wild lake trout in Michigan near Marquette (MI5) and Munising (MI6) in Lake Superior during 1929-93, compared to the average abundance during 1929-43.

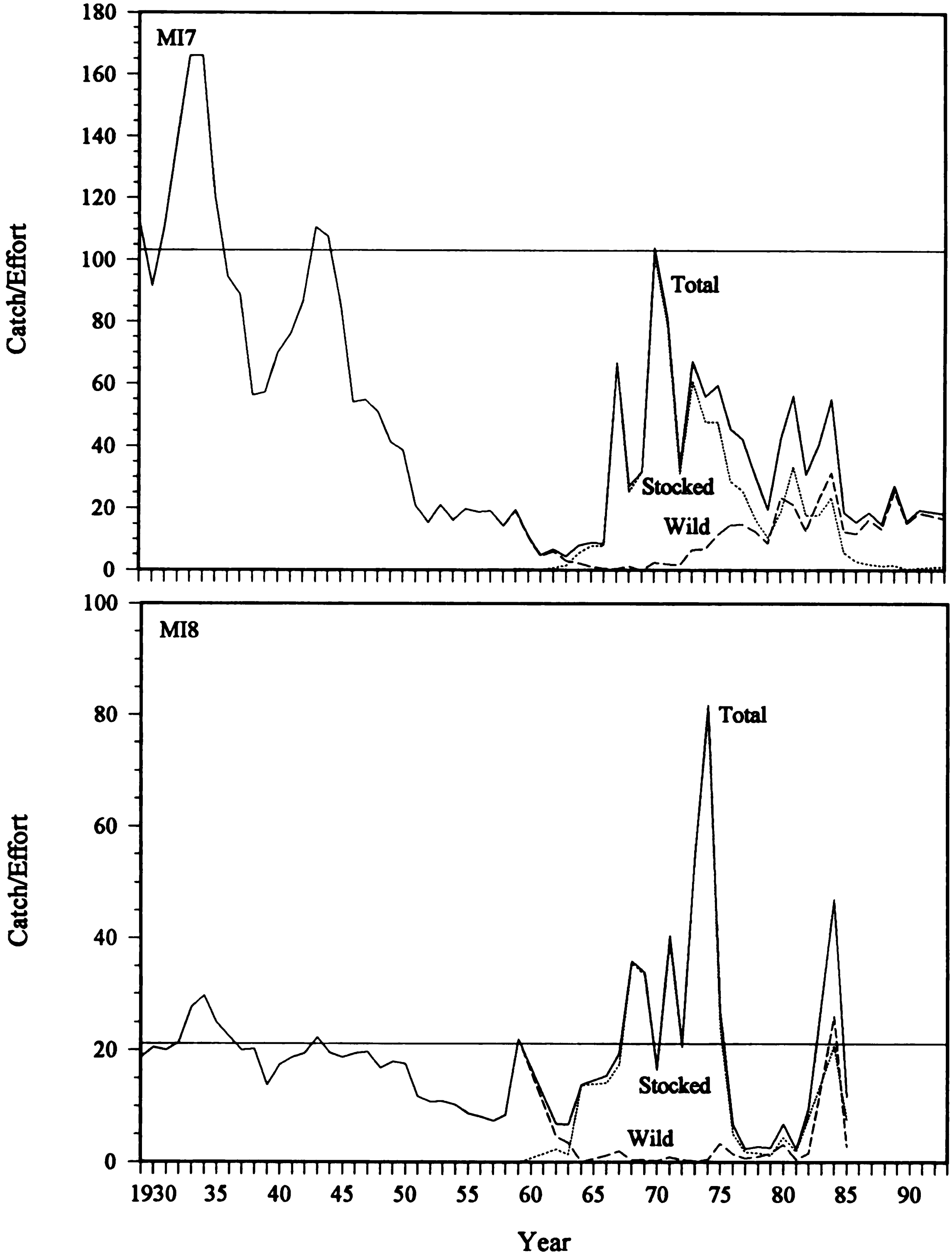

Figure 23. Abundance of stocked and wild lake trout in Michigan near Grand Marais (MI7) and in Whitefish Bay (MI8) in Lake Superior during 1929-93, compared to the average abundance during 1929-43.

Discussion

The perspective of the 1929-93 period shows that abundance of wild lake trout in Michigan declined steadily from the 1940s through the late 1960s and then improved from the 1970s through the 1980s. High abundances of stocked fish in the late 1960s produced increased numbers of wild fish in the 1970s (see Chapter I). Throughout the 1970s, abundances of stocked fish in many areas were much higher than during 1929-43, but declined sharply in the late 1970s and 1980s, and remained extremely low after 1988 (Chapter II). In most areas, numbers of wild lake trout increased steadily in the 1970s and early 1980s, but declined slowly in the late 1980s and early 1990s. The recent decline in the abundance of wild lake trout was partly caused by an earlier decline in the abundance of stocked lake trout, but was mitigated by reproduction by wild fish, the progeny of the first stocked spawners. Abundances of lake trout in Michigan in 1993 remain below the 1929-43 average in all areas, even though wild fish dominate the stocks.

Lake trout restoration was previously evaluated in Lake Superior in qualitative terms, primarily because stocks were far-removed from a restored condition. Early on, Dryer and King (1968) stated that "[t]he remarkable recovery of lake trout stocks in the Apostle Islands region makes the outlook for complete success of lake trout rehabilitation appear excellent. Natural reproduction, which has already been demonstrated, should soon replace hatchery plantings." A decade later, Lawrie (1978) stated that "there are now encouraging signs that natural reproduction of lake trout is increasing so that it may not be necessary to continue planting that species, at least, in perpetuity." Almost a decade later, MacCallum and Selgeby (1987) stated that "[i]ntensive planting of lake trout and increasing natural reproduction have led to a resurgence in lake trout abundance; annual harvests in the commercial and recreational fishery are now about one third of the harvest formerly sustained."

Of these accounts of progress in lake trout restoration, only MacCallum and Selgeby (1987) attempted to state progress in quantitative terms (relative to historic sustained yield). However, yield is greatly confounded by restrictions on fisheries, losses to sea lampreys, and non-reporting, which alter the maximum sustainable level of yield from one period to the next. Hansen *et al.* (1994b) attempted to overcome some of these problems by quantifying progress in terms of the total kill of lake trout in fisheries (both reported and unreported) and by sea lampreys. They found that the average yield in 1990-92 was only 25% of the historic average in Canada and 32% in the United States (Hansen *et al.* 1994b). Sea lampreys accounted for another 15% of the historic average yield in the United States (sea lamprey populations were not estimated in Canada) (Hansen *et al.* 1994b). Further, sea lampreys accounted for 42% of all the lake trout yield from United States waters west of the Keweenaw Peninsula and 18% from waters east of the peninsula (Hansen *et al.* 1994b).

My targets for wild lake trout abundance are similar, for some areas, to those suggested by Lawrie (1978). For areas MI5 and MI6, our targets were within the range of CPEs found on Michipicoten and Caribou Islands, whereas those for areas MI3, MI4 and MI8 were lower and that for area MI7 was higher. The target for area MI7 was weak due to poor correspondence between commercial and assessment fishery CPEs during the overlap period, but the average CPE during 1929-43 in the commercial fishery in area MI7 (statistical district MS-5) was higher than in any other district (Hile *et al.* 1951). This suggests that my target may be reasonable.

For many areas, target CPEs were quite similar to those that result from simple conversion of pounds per 1,000 feet of large-mesh gill nets into geometric mean number of fish per km of gill net. The yield per km is nearly the same as the number of fish per km because the average size of lake trout caught in 114-mm, stretch-mesh gill nets is approximately 1.1 kg. Also, the conversion from weighted average CPE to geometric mean CPE, a factor of approximately one-half, directly compensates for the conversion from commercial fishery CPE to assessment fishery CPE, a factor of approximately two. However, this similarity was not always true, as our target CPEs for areas MI5 (70.98) and MI6 (57.36) were much higher than the target CPE for district MS-4 computed by simple conversion of units (27.73). Targets for areas MI5 and MI6 were the closest to those suggested by Lawrie (1978).

Management Implications

Lake trout restoration has progressed substantially in several Michigan management areas. Wild lake trout stocks have been restored to within 23% of historic abundances in MI6, and abundances are still increasing. The prognosis for the future is good in this area so long as fishery managers continue to control commercial and sport fisheries and sea lampreys. In MI4 and MI5, lake trout stocks have been restored to within 43% and 46% of historic abundances, but stocks are declining in both areas. Mortality should be reduced in these areas if lake trout restoration is to move forward. Declining abundances in both areas began after 1985, coincident with the reopening of large-scale tribal commercial gill net fishing and increased catches in the sport fishery (Peck and Schorfhaar 1991). Regulation of each of these fisheries should be made more stringent in order to reduce fishing mortality on lake trout.

In remaining areas, lake trout stocks remain well below historic abundances, and will therefore require mortality to be reduced below current levels. In MI3, wild lake trout stocks recently declined, as in MI4 and MI5, and should also be targeted for more stringent fishery regulation. In MI7, the estimated historic CPEs are poor, so stock status is difficult to judge. Further analyses of modern and historic data should attempt to discover a more reliable target for abundance than the one derived herein. In the interim, fishery managers should ensure that fishery regulations are sufficient to sustain current abundances of wild lake trout. In MI8, lake trout restoration was deferred in 1985 as part of a negotiated settlement between the State of Michigan and local indian tribes. Lake trout stocks are unlikely to improve until fishery management changes substantially.

The reference period for lake trout restoration was set during 1929-43 because the yield during that period was consistent with the average annual yield dating back to 1913 (Hile *et al.* 1951), and because lake trout stocks were thought to decline after 1943 (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978). However, it is possible that yield during 1913-43 was sustained at an apparently stable level by sequentially fishing (and depleting) individual stocks, so that total abundance of lake trout in Lake Superior was declining over that period. For example, abundance of lake trout in Lake Superior may have begun to decline after 1939 (Coble *et al.* 1990), rather than 1945, as was previously thought (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978). Also, the 1929-93 data series show that abundance in central Michigan (MI5 and MI6) began to decline after 1934 (Figure 20).

Lake trout abundance in central Michigan may have declined earlier than in other areas because of the proximity of the major ports of Marquette (MI5) and Munising (MI6), but the decline in these areas was not evident when abundance was analyzed over a much broader area (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990). For this reason, the target CPEs for these two areas should be considered minimal estimates of stock sizes that are needed to sustain historical levels of lake trout production. However, records of commercial fishing catch and effort in Michigan only go back to 1929, so the data needed to investigate the sustainability of lake trout stocks prior to that year are not available.

SUMMARY AND CONCLUSIONS

Efforts to restore lake trout in Lake Superior have reestablished reproducing populations in most areas of the lake. Results of my stock-recruitment analyses suggest that stocked lake trout played a significant role in reestablishing these populations. Results of my survival analyses suggest that large-mesh gill-net fisheries reduced the abundance of stocked lake trout in both Michigan and Wisconsin. In Minnesota, such fisheries were not allowed to develop, so abundance of stocked lake trout declined later than in Michigan or Wisconsin, mostly in response to predation by increasing numbers of wild lake trout. Long-term data suggest that wild lake trout in Michigan during 1990-93, after more than 30 years of attempted stock restoration, were less abundant than during 1929-43, before stocks collapsed.

Sources of Recruitment

My results suggest that the availability of inshore spawning substrate in the Great Lakes is a critical determinant of successful reproduction by stocked lake trout. This is in contrast to the widespread belief that stocked lake trout are reproductively ineffective. Reproductive ineffectiveness of stocked lake trout was thought to explain the widespread failure of lake trout restoration in other Great Lakes (Eshenroder *et al.*

1983), but was based on stock-recruitment analyses in the Apostle Islands area of Lake Superior where spawning substrate is restricted to offshore shoals that require homing ability by spawning lake trout (Krueger *et al.* 1986). Spawning shoals in Minnesota, Michigan, and Ontario are widely distributed inshore, where little homing ability is required by inexperienced, stocked lake trout spawners that tend to wander inshore during the spawning season. Stocked lake trout reproduced effectively in all such areas of Lake Superior that had abundant inshore spawning habitat.

Lake trout restoration has been deferred in the northern parts of Lakes Huron and Michigan where inshore spawning grounds are most abundant; these areas have been reserved for intensive fisheries for lake whitefish, mostly by gillnets that impose high incidental mortality on lake trout (Rybicki and Keller 1978). Consequently, lake trout spawning stocks have not developed in these areas where inshore spawning shoals occur and the likelihood of successful reproduction is greatest. Rather, lake trout restoration has been pursued mostly in the southern parts of Lakes Huron and Michigan, where inshore spawning grounds are rare and the likelihood of successful reproduction is poorest. Only since the mid-1980s has lake trout restoration been pursued on large offshore reefs where stocked fish are likely to remain and spawn, such as Six-Fathom Bank, Lake Huron, the Beaver Islands, Lake Michigan, and the Mid-Lake Reefs, Lake Michigan. Stocking in these areas should provide for successful stock restoration if fish are protected from fisheries.

Stock restoration in northern Lake Huron and northern Lake Michigan can succeed if spawning grounds are still in suitable condition and lake trout are protected from fishery exploitation and sea lamprey predation. Surveys of historic lake trout spawning grounds in northern Lake Huron and Lake Michigan have shown that substrate quality has not been observably degraded (Edsall *et al.* 1992). Excessive fishery exploitation and sea lamprey predation more likely explain the lack of successful reproduction by stocked lake trout in these areas. The future success of lake trout restoration in these areas depends on the extent to which fishery managers can control total annual mortality resulting from fishery exploitation and sea lamprey predation. Stocking of hatchery-reared fish continues to be a viable tool for lake trout restoration in both lakes, provided that these controls on mortality are effective.

Causes of Declining Survival

My analyses suggest that survival of lake trout stocked in Lake Superior declined because of incidental mortality in large-mesh gill nets and predation by wild adult lake trout. It is not clear whether survival would have been better if gill-net fishing effort had been lower, because predation by wild adult lake trout may have reduced survival in the absence of fishing mortality. Survival of stocked lake trout should be tested under conditions of lower gill-net fishing effort to determine whether predation by wild adult lake trout will compensate for reduced fishing mortality.

Such an adaptive management experiment would be interesting, but may be focused on the wrong problem. Reduced survival of stocked lake trout due to high incidental mortality in large-mesh gill nets also poses a serious problem for wild lake trout in Lake Superior. Abundance of wild lake trout also declined in Michigan after 1988 (Hansen *et al.* 1994b), in conjunction with the abundance of stocked lake trout, most likely due to excessive fishing mortality on both wild and stocked fish. Large-mesh gill-net fishing effort should be reduced in Michigan and Wisconsin to enhance survival of both wild and stocked lake trout. Such reductions were imposed in Wisconsin on the state-licensed fishery in 1991 and the tribal-licensed fishery in 1992. No such reductions have yet been imposed in Michigan.

Reductions in incidental fishing mortality may lead to better survival and increased abundance of wild lake trout in Michigan and Wisconsin. However, wild adult lake trout will also increase, and increase their predation on stocked lake trout. As a consequence of the interplay between fishing mortality and predation by wild adult lake trout, stocked lake trout survival may remain low in the future. In the future, stocking may not be a useful enhancement technique in Lake Superior, particularly in areas with high densities of wild lake trout, regardless of the intensity of fishing mortality. Increasing density of wild lake trout in Minnesota may therefore lead to failures of stocked year classes, similar to those in Michigan and Wisconsin, in the absence of excessive incidental fishing mortality.

The importance of predation by wild lake trout on stocked yearling lake trout needs to be defined. Stomach samples should be obtained from wild lake trout throughout their bathymetric distribution and during the entire growing season. The bathymetric distribution of stocked yearling lake trout should also be determined to define their spatial overlap with wild adult lake trout. These studies should be done under conditions of both high and low wild lake trout density to determine whether declining survival of stocked yearling lake trout can be improved in the face of high densities of wild lake trout in Lake Superior.

Status of Restoration

Lake trout restoration has progressed substantially in several Michigan management areas. Wild lake trout stocks have been restored to within 23% of historic abundances in MI6, and abundances are still increasing. The prognosis for the future is good in this area so long as fishery managers continue to control fisheries and sea lampreys. In MI4 and MI5, lake trout stocks have been restored to within 43% and 46% of historic abundances, but stocks are declining in both areas. Declining abundances in both areas began after 1985 as large-mesh tribal commercial gill net fisheries were reopened (Peck and Schorfhaar 1991; Chapter II), so these fisheries should be regulated more stringently.

In all remaining areas of Michigan, lake trout stocks remain well below historic abundances. In MI3, wild lake trout stocks recently declined, as in MI4 and MI5, and should also be targeted for more stringent fishery regulation. In MI7, the estimated historic CPEs are not as reliable and current stock status therefore remains uncertain. More reliable targets should be developed through further investigation of historic data. In the interim, fishery managers should ensure that fishery regulations are sufficient to sustain current abundances of wild lake trout. Lake trout stocks in MI8 are unlikely to improve until fishery management changes substantially, because lake trout restoration was deferred in 1985 as part of a negotiated settlement between the State of Michigan and local Indian tribes. Large-mesh gill-net fisheries in MI8 should be converted to trap-net fisheries to advance lake trout restoration in this area.

The reference period for lake trout restoration was set during 1929-43 because yields during that period were consistent with average annual yields dating back to 1913 (Hile *et al.* 1951), and because lake trout stocks were thought to have declined after 1943 (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978). Yet, yield during 1913-43 may have been maintained at an unsustainable level by sequentially fishing and depleting individual stocks. Lake trout abundance may actually have declined over that period. For example, abundance of lake trout in Lake Superior may have begun to decline after 1934 in central Michigan, based on my 1929-93 data series.

Lake trout abundance in central Michigan may have declined earlier than in other areas because of the proximity of the major ports of Marquette (MI5) and Munising (MI6). The decline in these areas, however, was not evident when abundance was analyzed over a much broader area (Hile *et al.* 1951; Pycha and King 1975; Jensen 1978; Coble *et al.* 1990). For this reason, the target CPEs for these two areas should be considered conservative estimates of stock sizes that are needed to sustain historical levels of lake trout production. However, records of commercial fishing catch and effort in Michigan only go back to 1929, so the data needed to investigate the sustainability of lake trout stocks prior to that year are not available.

Conclusions

Self-sustaining lake trout stocks have been reestablished in much of Lake Superior, but prudent management is required to allow these stocks to recover to historic levels of abundance and to permit stocks to develop in the rest of the lake. Sea lamprey control and fishery regulation were effective enough to allow stocking to rapidly build inshore stocks of lake trout that reproduced in all areas with widely distributed inshore spawning habitat. However, survival of stocked lake trout declined sharply after 1970 in Wisconsin and after 1980 in Michigan, possibly due to mortality in large-mesh gill-net fisheries. Lake trout of hatchery origin are now extremely rare throughout Michigan, and declining rapidly elsewhere. Wild fish have replaced stocked fish in most areas, and, as the reproductive stocks of the future, should be protected from by sea lamprey predation and fishery exploitation. Stocking should be discontinued wherever wild fish dominate stocks, such as in Michigan and eastern Wisconsin, to protect wild stocks from hatchery diseases and outbreeding depression (Evans and Willox 1991; Krueger and May 1991).

State and tribal fishery management agencies, particularly in Michigan and Wisconsin, failed to control exploitation by commercial and angling fisheries after sea lamprey control and stocking caused inshore lake trout stocks to increase in abundance. Excessive fishery exploitation stalled lake trout restoration in the Apostle Islands area of Wisconsin, in waters surrounding the Keweenaw Peninsula in western Michigan, and in Grand Marais and Whitefish Bay in eastern Michigan. Virtually all excessive fishery exploitation in Lake Superior, both historically and presently, is coincident with the use of unregulated amounts of large-mesh gill nets, which impose incidental mortality on lake trout even when they are set for other species (usually lake whitefish). Large-mesh gill-net effort was recently reduced in eastern Wisconsin, by imposing limits on the total amount of net that can be set in a year by each fisher. Similar measures should be imposed on tribal fisheries that operate in waters around the Keweenaw Peninsula, to reverse the downward trend in abundance of wild lake trout in these waters. State and tribal fishery management agencies should renegotiate the consent order for eastern Michigan waters around Grand Marais and Whitefish Bay, where lake trout restoration was foregone in favor of intensive large-mesh gill-net fisheries for lake whitefish. Lake trout exploitation in Minnesota and Ontario should be contained at current levels to sustain progress in these jurisdictions.

APPENDIX A - ADDITIONAL TABLES

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Table 6. Catch/effort of lake trout in spring gill-net assessment fisheries in western Keweenaw Peninsula waters (MI3) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	1.65815	0.09522	1.55456	0.09524	0.41082	0.05743	23
1960	1.31851	0.22253	1.21731	0.21453	0.32797	0.11852	7
1961	1.18169	0.13975	1.05655	0.13114	0.38783	0.06800	25
1962	1.40563	0.15078	1.38454	0.14935	0.09095	0.04137	8
1963	1.13636	0.12167	0.90477	0.11224	0.48904	0.10806	8
1964	1.13037	0.22124	0.56342	0.04007	0.84421	0.26453	3
1965	1.85769	0.11548	1.11303	0.11562	1.43843	0.11734	19
1966	2.17703	0.13515	0.79354	0.09245	2.02967	0.13835	19
1967	2.47818	0.15730	0.51092	0.10327	2.42120	0.15457	7
1968	2.33833	0.13688	0.43418	0.19288	2.27240	0.12856	9
1969	2.42128	0.16948	0.28307	0.07290	2.37318	0.18888	11
1970	2.52076	0.14914	0.07389	0.02944	2.51388	0.14948	15
1971	2.26862	0.24898	0.32466	0.10363	2.23577	0.24696	15
1972	3.88793	0.27468	1.35064	0.24161	3.81507	0.28432	9
1973	3.90670	0.08070	1.14032	0.12014	3.85412	0.08315	16
1974	3.45539	0.10120	1.22993	0.11199	3.36496	0.10417	21
1975	3.68601	0.08362	1.56575	0.10750	3.56921	0.08854	25
1976	4.04048	0.11987	2.11523	0.13660	3.89896	0.11723	15
1977	4.60240	0.21362	2.49987	0.27748	4.47820	0.20548	8
1978	3.52819	0.16756	1.54969	0.16505	3.41366	0.16243	22
1979	3.96728	0.35273	2.25771	0.35426	3.78706	0.35239	6
1980	4.15853	0.27944	2.34882	0.29323	3.99543	0.27154	8
1981	4.26983	0.12340	2.47167	0.19361	4.09267	0.12093	8
1982	4.29120	0.10517	2.41122	0.14789	4.12725	0.11775	8
1983	3.88229	0.06649	2.55119	0.06367	3.59888	0.07683	7
1984	4.41067	0.13726	3.26706	0.16325	4.03952	0.13772	4
1985	4.16164	0.17631	3.13411	0.11819	3.73569	0.21060	5
1986	2.77006	0.14128	1.73353	0.24386	2.34523	0.11709	12
1987	3.08942	0.12718	2.64085	0.15889	2.02757	0.17606	14
1988	3.08170	0.11415	2.87756	0.12753	1.44186	0.11396	24
1989	3.27533	0.10425	3.15884	0.10078	1.21429	0.17653	21
1990	2.99475	0.14164	2.90336	0.14512	0.86970	0.13751	22
1991	2.70692	0.11155	2.56737	0.13136	0.79364	0.10891	31
1992	1.79607	0.14300	1.67280	0.14846	0.42576	0.09163	32
1993	2.09718	0.11753	2.00907	0.11603	0.46735	0.09724	32

APPENDIX A

Table 7. Catch/effort of lake trout in spring gill-net assessment fisheries in Keweenaw Bay in Michigan waters (MI4) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	2.22326	0.03069	2.20045	0.03122	0.17397	0.01243	165
1960	1.98110	0.04972	1.93689	0.05057	0.25756	0.01897	97
1961	1.73064	0.05741	1.60769	0.06019	0.44482	0.04035	74
1962	1.70851	0.05026	1.49638	0.05491	0.60826	0.04204	111
1963	2.09071	0.04983	1.61586	0.06667	1.18545	0.05493	111
1964	2.02670	0.05788	1.05103	0.06877	1.68176	0.05544	106
1965	2.36461	0.06154	0.61022	0.04773	2.25977	0.06390	95
1966	2.39127	0.07537	0.22503	0.03417	2.36247	0.07631	104
1967	2.68408	0.06891	0.11161	0.02658	2.67370	0.06909	90
1968	3.77557	0.07614	0.23455	0.05009	3.76754	0.07625	51
1969	3.66895	0.08015	0.20448	0.04092	3.66311	0.08011	44
1970	4.14492	0.12757	0.32234	0.07567	4.13845	0.12732	32
1971	3.65229	0.15241	0.71035	0.07273	3.60918	0.15744	36
1972	4.19486	0.17343	1.40345	0.15131	4.13547	0.17894	20
1973	4.91854	0.15190	1.89237	0.12372	4.87196	0.15657	11
1974	4.41376	0.10466	1.62242	0.10080	4.35637	0.10664	32
1975	4.53550	0.14604	1.69359	0.12123	4.47525	0.15357	15
1976	4.57485	0.11832	1.79799	0.11512	4.50846	0.12162	38
1977	4.90583	0.14447	2.29728	0.10085	4.82770	0.15112	25
1978	4.58469	0.17765	2.37451	0.17998	4.44700	0.18283	29
1979	4.76572	0.17426	3.28558	0.17486	4.51309	0.17514	9
1980	4.84470	0.14393	3.64199	0.16717	4.45386	0.15337	21
1981	4.48602	0.11391	3.62538	0.09876	3.90788	0.13866	25
1982	3.98564	0.11477	2.89007	0.12534	3.51686	0.13057	33
1983	3.84741	0.09799	2.68187	0.12717	3.45842	0.09843	41
1984	3.83152	0.10528	2.94875	0.08676	3.30258	0.12538	24
1985	3.71091	0.14733	3.05067	0.15459	3.02067	0.13952	21
1986	3.91797	0.13934	3.53914	0.13807	2.73090	0.16397	22
1987	3.56890	0.09936	3.31502	0.13054	1.79623	0.14171	27
1988	3.49149	0.11326	3.37657	0.11775	1.34643	0.10066	60
1989	3.29207	0.08213	3.16646	0.08231	1.30139	0.08783	79
1990	3.55046	0.11482	3.45307	0.11983	1.28833	0.09225	48
1991	3.49642	0.09792	3.42301	0.09883	1.09865	0.09553	46
1992	3.38372	0.07818	3.27647	0.07964	1.21306	0.11920	36
1993	3.04780	0.10776	2.93713	0.10746	1.10677	0.10737	40

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Table 8. Catch/effort of lake trout in spring gill-net assessment fisheries around Marquette in Michigan waters (MI5) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

Year	Total		Wild		Stocked		*N*
	Mean	SE	Mean	SE	Mean	SE	
1959	2.50959	0.06206	2.49714	0.06264	0.12792	0.01078	80
1960	1.83574	0.05176	1.79430	0.05255	0.22066	0.01703	105
1961	1.85016	0.07152	1.78804	0.07044	0.34963	0.03279	57
1962	1.73265	0.06899	1.61678	0.06930	0.49117	0.03553	42
1963	1.95621	0.07726	1.67700	0.07271	0.99697	0.07193	26
1964	1.81756	0.08120	1.05781	0.06281	1.42534	0.08992	44
1965	2.12056	0.06255	0.72011	0.08678	1.95471	0.06816	26
1966	2.82464	0.08095	0.54737	0.06620	2.77375	0.08512	20
1967	2.87104	0.16779	0.19199	0.04391	2.85674	0.16900	20
1968	3.77511	0.21477	0.26603	0.09411	3.76656	0.21569	18
1969	3.93535	0.15682	0.31281	0.07009	3.92782	0.15723	16
1970	4.35491	0.15180	0.48191	0.13238	4.34384	0.15388	13
1971	4.68368	0.10440	1.14275	0.27833	4.65857	0.10205	7
1972	4.51882	0.17657	1.28019	0.23934	4.48873	0.17399	8
1973	4.55978	0.21008	1.81549	0.19979	4.50469	0.20959	7
1974	4.10870	0.13820	1.22137	0.16913	4.06429	0.13645	24
1975	4.95481	0.24507	2.24572	0.30759	4.89227	0.23984	7
1976	4.78553	0.12116	2.46104	0.13169	4.68430	0.12313	24
1977	4.88655	0.12650	2.74029	0.11022	4.76364	0.13216	17
1978	4.80567	0.12265	3.28831	0.10755	4.55923	0.13100	18
1979	5.01752	0.11647	3.66424	0.11959	4.71841	0.11950	18
1980	4.64550	0.16379	3.50660	0.29514	4.21120	0.12848	12
1981	4.80818	0.16129	4.04239	0.15844	4.18470	0.16813	10
1982	4.89686	0.09953	3.96699	0.14458	4.39061	0.07770	10
1983	4.41998	0.08089	3.70556	0.08571	3.75010	0.09284	16
1984	4.39164	0.14784	3.61548	0.13985	3.79247	0.15802	8
1985	4.88179	0.12620	4.31424	0.13547	4.05865	0.12110	5
1986	4.89299	0.26440	4.58382	0.24165	3.57663	0.32298	5
1987	4.32244	0.11719	3.97585	0.24101	2.42378	0.34804	8
1988	4.27323	0.18539	4.22284	0.17940	1.41495	0.26371	14
1989	4.10792	0.11329	3.99451	0.11585	1.83660	0.17052	22
1990	3.99449	0.12067	3.89193	0.12418	1.75126	0.11750	22
1991	4.09348	0.12120	3.97082	0.11786	1.97591	0.17938	18
1992	3.86685	0.11318	3.67614	0.11614	2.04972	0.16552	24
1993	3.85013	0.08291	3.66876	0.08231	2.04311	0.14284	24

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Table 9. Catch/effort of lake trout in spring gill-net assessment fisheries around Munising in Michigan waters (MI6) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	2.40920	0.08179	2.39499	0.08158	0.15281	0.02383	35
1960	1.98054	0.12128	1.93577	0.12323	0.26782	0.04140	25
1961	1.76284	0.05675	1.65217	0.06440	0.40420	0.03880	42
1962	1.98196	0.07845	1.80699	0.08047	0.75354	0.05915	26
1963	2.26695	0.11169	1.66861	0.12755	1.62358	0.12848	13
1964	2.12138	0.08635	1.30878	0.08460	1.69841	0.10029	16
1965	2.40671	0.12086	1.03195	0.12557	2.20302	0.12549	14
1966	2.62936	0.13193	0.70342	0.15359	2.53724	0.12839	13
1967	3.59159	0.14771	0.44839	0.09855	3.57568	0.14658	12
1968	3.61735	0.15744	0.28243	0.09418	3.60648	0.15752	13
1969	3.94331	0.11118	0.29011	0.08675	3.93316	0.11278	19
1970	4.53598	0.13407	0.45132	0.11962	4.52814	0.13429	16
1971	4.43790	0.16956	0.91879	0.20357	4.41790	0.16911	7
1972	5.15415	0.13642	2.42154	0.10768	5.09090	0.15266	2
1973	3.22126	0.23429	1.27070	0.22765	3.09869	0.23149	11
1974	3.67528	0.15370	1.71492	0.13695	3.54800	0.15713	14
1975	3.79169	0.19829	2.11652	0.18961	3.56845	0.21974	16
1976	3.77443	0.09250	2.25177	0.11328	3.51798	0.10312	24
1977	3.55868	0.15712	2.32995	0.16212	3.20705	0.16848	26
1978	3.42437	0.13321	2.45831	0.13743	2.92368	0.14672	30
1979	3.05305	0.11590	2.23523	0.11652	2.51169	0.12540	25
1980	3.24519	0.15158	2.43972	0.18607	2.61589	0.16733	20
1981	4.79360	0.40552	3.69966	0.59724	4.36540	0.28645	3
1982	3.81498	0.26811	2.84831	0.30333	3.32361	0.27976	10
1983	3.05491	0.11223	2.51278	0.08566	2.22440	0.18690	12
1984	3.57591	0.13391	3.01025	0.18501	2.74160	0.11819	8
1985	3.53315	0.22845	3.20521	0.22336	2.27413	0.27641	8
1986	3.81769	0.64868	2.95744	0.89925	2.94694	0.70860	3
1987	3.44753	0.21208	3.34787	0.19952	1.35948	0.28344	8
1988	3.63784	0.25458	3.55666	0.24573	1.33128	0.30382	12
1989	3.48294	0.17826	3.38756	0.17570	1.27317	0.21862	14
1990	3.31388	0.12057	3.20597	0.12324	1.12574	0.15206	32
1991	3.31830	0.14170	3.26303	0.13402	0.84191	0.18704	28
1992	3.47285	0.13680	3.35931	0.13826	1.23088	0.18729	26
1993	3.99368	0.24742	3.49311	0.28332	2.50282	0.29555	16

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Table 10. Catch/effort of lake trout in spring gill-net assessment fisheries around Grand Marais in Michigan waters (MI7) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	3.02396	0.08323	3.00193	0.08027	0.35036	0.09787	15
1960	2.49080	0.20953	2.45609	0.19675	0.40729	0.18560	7
1961	1.77336	0.06848	1.71144	0.06748	0.30116	0.03961	17
1962	2.06121	0.09878	1.95634	0.10099	0.57689	0.05305	7
1963	1.68686	0.22576	1.38601	0.21609	0.92617	0.14905	9
1964	2.21341	0.10595	1.20670	0.10551	1.85873	0.17761	7
1965	2.30910	0.24365	0.74003	0.08447	2.19350	0.25534	4
1966	2.27985	0.17124	0.48683	0.10918	2.18891	0.19730	10
1967	4.21703		0.40966		4.20954		1
1968	3.34110	0.21314	0.79242	0.22453	3.27251	0.22648	8
1969	3.48781	0.66473	0.00000	0.00000	3.48781	0.66473	2
1970	4.65451	0.10009	1.25723	0.09808	4.63032	0.09919	2
1971	4.41104	0.38244	1.11705	0.26274	4.38277	0.38582	6
1972	3.53635	0.21583	0.94822	0.15229	3.47254	0.23736	5
1973	4.22605	0.19046	2.03058	0.22885	4.12368	0.18439	6
1974	4.04188	0.14076	2.07900	0.24574	3.89005	0.14550	7
1975	4.10662	0.19030	2.51368	0.29279	3.88898	0.17078	4
1976	3.84157	0.12214	2.75550	0.13020	3.39827	0.13275	28
1977	3.76532	0.23018	2.77035	0.24389	3.28624	0.22936	21
1978	3.44020	0.10767	2.61066	0.11914	2.86051	0.12240	33
1979	3.02287	0.23872	2.28836	0.27168	2.45421	0.18496	17
1980	3.77898	0.19053	3.20248	0.16932	2.98670	0.21180	10
1981	4.04852	0.14325	3.10829	0.16198	3.54300	0.15932	10
1982	3.46228	0.13044	2.62005	0.13708	2.92498	0.13662	18
1983	3.73363	0.17833	3.17746	0.18660	2.92763	0.16885	7
1984	4.02964	0.10866	3.48514	0.09527	3.20171	0.12612	4
1985	2.97874	0.20064	2.61455	0.19071	1.90616	0.22439	6
1986	2.81679	0.16125	2.55924	0.20475	1.34199	0.14062	12
1987	2.97889	0.17775	2.86579	0.17551	1.09015	0.18360	11
1988	2.77748	0.18510	2.67280	0.18936	0.89043	0.12138	26
1989	3.35019	0.13016	3.28331	0.13051	0.94719	0.14679	19
1990	2.82840	0.16567	2.79805	0.16290	0.38024	0.13138	16
1991	3.02187	0.12789	2.96418	0.13604	0.54945	0.10423	24
1992							0
1993	2.96119	0.10529	2.87519	0.11670	0.81137	0.10388	16

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Table 11. Catch/effort of lake trout in spring gill-net assessment fisheries in Whitefish Bay in Michigan waters (MI8) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	3.13542		3.13542		0.00000		1
1960							0
1961							0
1962	2.06108	0.13671	1.72890	0.09632	1.17462	0.16224	8
1963	2.04469	0.23042	1.49016	0.39512	0.85570	0.28516	7
1964	2.69995	0.16713	0.10663	0.03164	2.69331	0.16691	11
1965							0
1966	2.80662	0.12714	0.79105	0.25867	2.71765	0.11268	5
1967	3.01989	0.36914	1.07910	0.17403	2.91758	0.38297	4
1968	3.60980	0.40050	0.33660	0.05952	3.59809	0.40321	3
1969	3.55050	0.32337	0.39473	0.14385	3.53968	0.32143	5
1970	2.88287	0.28134	0.26766	0.11008	2.86484	0.28123	4
1971	3.72519	0.04700	0.62873	0.03535	3.70364	0.04928	3
1972	3.08924	0.23343	0.40225	0.17040	3.07116	0.23002	9
1973	4.02848	0.24489	0.21971	0.13817	4.02467	0.24358	3
1974	4.41691	0.18981	0.36368	0.19803	4.40534	0.19633	6
1975	3.33476	0.74234	1.45768	0.85609	3.22101	0.68342	4
1976	2.05392	0.23869	0.89890	0.19483	1.81252	0.24328	28
1977	1.21782	0.23835	0.56276	0.15617	1.01461	0.21689	26
1978	1.31471	0.20913	0.68749	0.15799	0.99412	0.20187	21
1979	1.27147	0.36880	0.93912	0.34320	0.78728	0.30047	8
1980	2.06516	0.52983	1.41968	0.50379	1.69442	0.45669	8
1981	1.21848	0.20439	0.44529	0.15361	1.05159	0.17509	7
1982	2.35852	0.29992	0.93690	0.17091	2.20057	0.30408	13
1983							0
1984	3.87324	0.15725	3.29820	0.06730	3.08273	0.26155	2
1985	2.54371	0.20600	1.29711	0.24820	2.14766	0.25839	12
1986							0
1987							0
1988							0
1989							0
1990							0
1991							0
1992							0
1993							0

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Table 12. Catch/effort of lake trout in spring gill-net assessment fisheries in western Minnesota waters (MN1) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959							0
1960							0
1961							0
1962							0
1963	2.13421		1.99149		1.22153		1
1964	1.28594		1.14950		0.84696		1
1965	1.85637	0.12922	1.38629	0.09185	1.55121	0.11183	3
1966	1.22079	0.23829	0.70235	0.17891	1.10840	0.21485	9
1967	1.73369	0.38639	0.69175	0.17648	1.69037	0.37513	8
1968	1.53096	0.16685	0.10965	0.10965	1.51752	0.16205	12
1969							0
1970							0
1971							0
1972							0
1973							0
1974							0
1975							0
1976							0
1977							0
1978							0
1979							0
1980							0
1981							0
1982	3.24487	0.11753	0.60100	0.26306	3.22396	0.13714	7
1983	3.39494	0.11918	0.57962	0.26724	3.35330	0.11890	8
1984	3.24952	0.16855	0.78099	0.29723	3.18529	0.14957	9
1985	3.22732	0.15487	0.63093	0.24228	3.18838	0.14859	9
1986	3.34878	0.30876	1.08136	0.25184	3.28135	0.29635	10
1987	4.52471	0.17492	1.67257	0.06156	4.44341	0.18175	5
1988	3.37286	0.19643	1.19889	0.34657	3.27561	0.20960	4
1989	4.01863	0.25227	1.76029	0.31187	3.78070	0.23809	16
1990	3.36930	0.15078	0.99519	0.25043	3.22331	0.14677	20
1991	3.75891	0.14852	1.76814	0.26554	3.40212	0.15993	24
1992	4.26398	0.24542	1.87918	0.33530	3.99179	0.23391	16
1993	4.00479	0.18298	1.91229	0.23035	3.76588	0.18348	17

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Table 13. Catch/effort of lake trout in spring gill-net assessment fisheries in central Minnesota waters (MN2) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959							0
1960							0
1961							0
1962							0
1963	1.48827	0.23398	1.44966	0.21019	0.17486	0.17486	4
1964	2.80293		2.45379		1.76824		1
1965	1.50206	0.03382	1.31749	0.00000	0.56126	0.08654	2
1966	1.71933	1.02712	1.12974	0.99008	1.44236	0.82448	3
1967	2.16000	0.44499	0.87846	0.11804	1.97778	0.49220	2
1968	1.79962	0.27827	0.47764	0.13822	1.69702	0.27519	15
1969	1.39464	0.10525	0.18959	0.04785	1.33314	0.10421	55
1970	2.37400	0.16207	0.18728	0.12806	2.35249	0.15793	9
1971	1.24194	0.13706	0.22363	0.10400	1.12647	0.15385	14
1972	1.49825	0.12547	0.19383	0.09355	1.36632	0.15729	20
1973	2.64273	0.08686	0.36363	0.08919	2.58096	0.09278	42
1974	2.47972	0.10740	0.64646	0.13808	2.36813	0.10524	30
1975	2.39594	0.10228	0.28559	0.06330	2.35153	0.10292	54
1976	2.37053	0.12507	0.19645	0.05996	2.35032	0.12385	45
1977	2.16994	0.12670	0.07140	0.04006	2.15960	0.12690	31
1978	2.68245	0.09809	0.18174	0.05288	2.66296	0.09839	44
1979	2.88629	0.13482	0.13102	0.05559	2.87265	0.13547	39
1980	3.29792	0.13294	0.25084	0.07494	3.28164	0.13433	45
1981	3.58677	0.14389	0.37030	0.09900	3.57448	0.14255	45
1982	3.82338	0.10000	0.62340	0.10142	3.79131	0.10218	45
1983	3.39298	0.10204	0.46311	0.09109	3.35341	0.10434	52
1984	3.02769	0.11742	0.38761	0.08430	2.98589	0.11858	53
1985	3.40769	0.11622	0.70357	0.11974	3.35866	0.11637	46
1986	3.46693	0.15103	0.83734	0.15083	3.39450	0.15197	51
1987	3.75557	0.11752	1.42009	0.15246	3.63111	0.11951	57
1988	3.88449	0.11930	1.19780	0.18054	3.79270	0.11961	41
1989	3.77279	0.11126	1.64107	0.15915	3.59473	0.11520	54
1990	3.93366	0.10126	1.72628	0.18536	3.74475	0.10914	49
1991	3.62288	0.15389	1.62375	0.18735	3.45724	0.15449	42
1992	2.99145	0.09427	1.00801	0.11264	2.83871	0.09592	98
1993	3.49893	0.06444	1.26402	0.13954	3.35600	0.06370	66

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Table 14. Catch/effort of lake trout in spring gill-net assessment fisheries in eastern Minnesota waters (MN3) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959							0
1960							0
1961							0
1962							0
1963	2.26912	0.21733	2.22047	0.21387	0.25358	0.14025	16
1964	2.62719	0.15511	2.61223	0.15525	0.16147	0.06441	15
1965	1.74612	0.16791	1.65369	0.16658	0.45463	0.07676	29
1966	1.04989	0.09504	0.92571	0.08531	0.31542	0.06578	62
1967	1.52372	0.10939	1.13604	0.09935	0.85478	0.11657	30
1968	1.41537	0.12856	0.32367	0.07881	1.25337	0.13959	35
1969	1.26519	0.08384	0.07459	0.02140	1.23878	0.08334	152
1970	2.52752	0.14925	0.38416	0.11242	2.48028	0.14822	22
1971	1.93037	0.11696	0.43014	0.08221	1.81474	0.12438	39
1972	2.35543	0.22772	0.81397	0.10305	2.12993	0.29422	14
1973	2.84794	0.10538	0.91471	0.10348	2.70553	0.11153	65
1974	3.14425	0.12065	0.97829	0.10529	3.02619	0.12883	56
1975	3.30157	0.09300	0.98915	0.09005	3.21436	0.09371	109
1976	3.14335	0.10542	0.94090	0.09185	3.05873	0.10587	74
1977	3.20042	0.10167	0.72600	0.09681	3.13514	0.10361	68
1978	3.24837	0.08731	0.77049	0.08849	3.19270	0.08608	59
1979	3.22692	0.12387	0.60118	0.09705	3.14539	0.13730	51
1980	3.40749	0.10350	0.81728	0.11549	3.33709	0.10416	63
1981	3.80714	0.08511	1.46819	0.14268	3.69229	0.08705	45
1982	3.87316	0.14906	1.41995	0.19544	3.77981	0.15060	34
1983	3.72832	0.12475	1.78974	0.15135	3.53500	0.13967	41
1984	3.40059	0.10659	1.28998	0.11566	3.25596	0.11886	56
1985	4.44092	0.13794	1.60737	0.50313	4.30845	0.12380	10
1986	4.10813	0.13655	2.45976	0.24713	3.80233	0.12848	29
1987	4.26080	0.12646	1.88910	0.33185	4.03527	0.14013	19
1988	3.99709	0.08124	2.45250	0.18722	3.47547	0.12939	53
1989	4.20329	0.09354	3.16337	0.13024	3.64855	0.10648	45
1990	3.74262	0.09749	2.50042	0.15914	3.12733	0.12833	56
1991	3.74691	0.10550	2.55249	0.15177	3.21853	0.14095	50
1992	3.92961	0.12460	2.79414	0.17784	3.33047	0.16008	47
1993	3.02392	0.17808	2.25513	0.18257	2.20830	0.18113	66

APPENDIX A

Table 15. Catch/effort of lake trout in spring gill-net assessment fisheries in western Wisconsin waters (WI1) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959							0
1960							0
1961							0
1962							0
1963							0
1964							0
1965							0
1966							0
1967							0
1968							0
1969	2.54968	0.93087	0.20281	0.00000	2.52342	0.95018	2
1970	3.71692	0.26702	0.94969	0.19955	3.67816	0.26605	4
1971	2.59677	0.15427	0.34784	0.12847	2.56087	0.16002	4
1972	2.89253	0.34385	0.69492	0.29479	2.84773	0.32658	5
1973							0
1974							0
1975							0
1976							0
1977							0
1978							0
1979							0
1980							0
1981							0
1982							0
1983							0
1984							0
1985							0
1986							0
1987	1.62860	0.11003	0.80364	0.06825	1.50353	0.13749	19
1988	1.34175	0.14223	0.48900	0.08756	1.26320	0.14698	19
1989	1.22386	0.17788	0.37683	0.08583	1.16796	0.18070	19
1990	1.28287	0.13002	0.62118	0.08988	1.16590	0.14706	19
1991	1.35549	0.12284	0.69563	0.10711	1.25422	0.12137	19
1992	1.25868	0.08207	0.65917	0.12017	1.12180	0.07592	19
1993	1.56063	0.10081	0.87594	0.10529	1.44948	0.10552	19

APPENDIX A

Table 16. Catch/effort of lake trout in spring gill-net assessment fisheries in eastern Wisconsin waters (WI2) of Lake Superior (mean and SE across N lifts of $\log_e$-transformed values).

	Total		Wild		Stocked		
Year	Mean	SE	Mean	SE	Mean	SE	*N*
1959	1.56379	0.11514	1.18054	0.11124	0.86882	0.10159	25
1960	2.22424	0.21331	1.73151	0.21328	1.56687	0.18961	40
1961	1.66293	0.14312	1.43376	0.14424	0.75453	0.09285	22
1962	2.48650	0.11003	2.26394	0.10555	1.21761	0.10374	24
1963	2.37126	0.15680	1.71750	0.14020	1.81157	0.14729	24
1964	2.95438	0.08891	2.08849	0.12321	2.34984	0.10930	32
1965	2.88788	0.15906	1.81951	0.10340	2.47144	0.18757	27
1966	3.35376	0.10317	1.80454	0.13770	3.11488	0.11955	14
1967	3.31669	0.14354	1.16256	0.10973	3.22265	0.14975	15
1968	2.80103	0.07271	0.36041	0.03872	2.76996	0.07349	82
1969	3.63678	0.08310	0.73358	0.07882	3.60421	0.08356	31
1970	4.17979	0.10140	1.69638	0.08977	4.10020	0.10432	39
1971	4.17873	0.11905	2.32817	0.12021	3.99952	0.12363	38
1972	3.76564	0.08295	2.25532	0.10366	3.51710	0.08292	38
1973	3.62363	0.10444	2.45782	0.11711	3.23917	0.10981	38
1974	3.70943	0.06833	2.30612	0.11772	3.38082	0.08599	36
1975	3.23261	0.08073	2.06895	0.13309	2.82559	0.07588	36
1976	3.33201	0.11083	2.31336	0.10930	2.87530	0.12932	36
1977	3.39590	0.08860	2.03258	0.15422	2.91034	0.12227	36
1978	3.46160	0.12417	2.19468	0.14573	3.02389	0.14647	36
1979	3.67895	0.07212	2.59976	0.12611	3.07706	0.12493	36
1980	3.42029	0.08798	2.50642	0.10018	2.78316	0.14791	28
1981	3.22153	0.13797	2.02474	0.18693	2.71305	0.19835	18
1982	2.52910	0.13323	1.49430	0.13442	2.15015	0.13726	30
1983	2.62689	0.13398	1.47825	0.18133	2.16257	0.17187	28
1984	2.97113	0.14812	1.59465	0.20089	2.60183	0.15362	30
1985	2.87342	0.14581	1.83430	0.16239	2.44888	0.14668	36
1986	3.36504	0.13622	2.58348	0.15390	2.74063	0.13017	40
1987	3.21625	0.15891	2.47915	0.20658	2.49202	0.13116	31
1988	3.01955	0.13036	2.36810	0.15199	2.24600	0.13026	31
1989	3.29216	0.16499	2.67114	0.18220	2.42473	0.16646	31
1990	3.06239	0.15467	2.49005	0.19969	2.10282	0.13182	31
1991	3.15796	0.15966	2.60588	0.21012	2.16677	0.11351	31
1992	3.08006	0.14477	2.61669	0.18521	1.93280	0.11039	31
1993	3.10047	0.10533	2.72104	0.14013	1.84273	0.08831	31

APPENDIX A

Table 17. Results of the multiple regression of recruit CPE ($\log_e$) during 1967-93 on native and stocked spawner CPEs ($\log_e$) during 1959-85 in Michigan areas MI4-MI7 of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

	1	2	3
	2.71745	0.19829	0.08426

CONDITION INDICES

	1	2	3
	1.00000	3.70191	5.67897

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.01643	0.00946	0.97412
NATIVE	0.02850	0.70965	0.26185
STOCKED	0.02277	0.37743	0.59980

DEP VAR:RECRUITS N:107 MULTIPLE R: 0.890 SQUARED MULTIPLE R: 0.793
ADJUSTED SQUARED MULTIPLE R: 0.789 STANDARD ERROR OF ESTIMATE: 0.54461

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	-0.13959	0.14682	0.00000	.	-0.95076	0.34393
NATIVE	0.32294	0.04949	0.29251	0.99083	6.52552	0.00000
STOCKED	0.66752	0.03678	0.81352	0.99083	.18E+02	0.00000

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	NATIVE	STOCKED
CONSTANT	1.00000		
NATIVE	-0.56533	1.00000	
STOCKED	-0.68529	-0.09575	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	118.13219	2	59.06609	199.14349	0.00000
RESIDUAL	30.84647	104	0.29660		

WARNING: CASE 95 IS AN OUTLIER (STUDENTIZED RESIDUAL = -3.108)
WARNING: CASE 108 IS AN OUTLIER (STUDENTIZED RESIDUAL = 2.662)

DURBIN-WATSON D STATISTIC 1.654
FIRST ORDER AUTOCORRELATION .155

APPENDIX A

Table 18. Results of the multiple regression of recruit CPE ($\log_e$) during 1967-93 on native and stocked spawner CPEs ($\log_e$) during 1959-85 in Minnesota areas MN2-MN3 of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

	1	2	3
	2.57711	0.34908	0.07380

CONDITION INDICES

	1	2	3
	1.00000	2.71708	5.90923

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.01688	0.00878	0.97435
NATIVE	0.04084	0.63215	0.32701
STOCKED	0.02342	0.17889	0.79769

DEP VAR:RECRUITS N: 46 MULTIPLE R: 0.802 SQUARED MULTIPLE R: 0.644
ADJUSTED SQUARED MULTIPLE R: 0.627 STANDARD ERROR OF ESTIMATE: 0.49353

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	-0.58930	0.21141	0.00000	.	-2.78739	0.00788
NATIVE	0.49141	0.11839	0.38600	0.95782	4.15062	0.00015
STOCKED	0.56539	0.06680	0.78715	0.95782	8.46426	0.00000

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	NATIVE	STOCKED
CONSTANT	1.00000		
NATIVE	-0.61269	1.00000	
STOCKED	-0.82210	0.20538	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	18.93019	2	9.46510	38.85943	0.00000
RESIDUAL	10.47363	43	0.24357		

WARNING: CASE 155 IS AN OUTLIER (STUDENTIZED RESIDUAL = -3.563)
WARNING: CASE 178 HAS LARGE LEVERAGE (LEVERAGE = 0.238)

DURBIN-WATSON D STATISTIC 1.150
FIRST ORDER AUTOCORRELATION .418

APPENDIX A

Table 19. Results of the multiple regression of recruit CPE ($\log_e$) during 1967-93 on native and stocked spawner CPEs ($\log_e$) during 1959-85 in Wisconsin area WI2 of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

	1	2	3
	2.89864	0.06698	0.03438

CONDITION INDICES

	1	2	3
	1.00000	6.57850	9.18194

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.00604	0.00784	0.98612
NATIVE	0.00846	0.46551	0.52603
STOCKED	0.00988	0.73325	0.25687

DEP VAR:RECRUITS N: 27 MULTIPLE R: 0.497 SQUARED MULTIPLE R: 0.247
ADJUSTED SQUARED MULTIPLE R: 0.184 STANDARD ERROR OF ESTIMATE: 0.54779

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	1.13280	0.46262	0.00000	.	2.44868	0.02202
NATIVE	0.00246	0.20344	0.00219	0.95694	0.01211	0.99044
STOCKED	0.35313	0.12893	0.49609	0.95694	2.73897	0.01144

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	NATIVE	STOCKED
CONSTANT	1.00000		
NATIVE	-0.65266	1.00000	
STOCKED	-0.57140	-0.20751	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	2.35683	2	1.17842	3.92704	0.03346
RESIDUAL	7.20186	24	0.30008		

WARNING: CASE 201 IS AN OUTLIER (STUDENTIZED RESIDUAL = -2.937)

DURBIN-WATSON D STATISTIC .642
FIRST ORDER AUTOCORRELATION .637

APPENDIX A

Table 20. Results of the multiple regression of recruitment rate ($\log_e$) of the 1963-82 year classes on numbers of yearlings stocked and large-mesh gill-net fishing effort in Michigan waters of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

1	2	3
2.18925	0.74232	0.06842

CONDITION INDICES

1	2	3
1.00000	1.71732	5.65647

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.02408	0.00389	0.97203
YEARLING	0.02614	0.04690	0.92696
GILLNETS	0.05086	0.56388	0.38526

DEP VAR:SURVIVAL N: 20 MULTIPLE R: 0.954 SQUARED MULTIPLE R: 0.911
ADJUSTED SQUARED MULTIPLE R: 0.900 STANDARD ERROR OF ESTIMATE: 0.28529

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	3.90143	0.18255	0.00000	.	.21E+02	0.00000
YEARLING	-0.35604	0.12942	-0.22594	0.77774	-2.75098	0.01364
GILLNETS	-0.55799	0.04407	-1.03985	0.77774	-.13E+02	0.00000

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	YEARLING	GILLNETS
CONSTANT	1.00000		
YEARLING	-0.91064	1.00000	
GILLNETS	-0.62376	0.47145	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	14.13014	2	7.06507	86.80651	0.00000
RESIDUAL	1.38361	17	0.08139		

DURBIN-WATSON D STATISTIC 2.447
FIRST ORDER AUTOCORRELATION -.244

APPENDIX A

Table 21. Results of the multiple regression of recruitment rate ($\log_e$) of the 1963-82 year classes on numbers of yearlings stocked and density (CPE) of wild adult lake trout in Minnesota waters of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

	1	2	3
	2.40207	0.56615	0.03178

CONDITION INDICES

	1	2	3
	1.00000	2.05980	8.69427

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.00953	0.00754	0.98293
YEARLING	0.01038	0.02096	0.96866
WILDPRED	0.05756	0.76723	0.17521

DEP VAR:SURVIVAL N: 20 MULTIPLE R: 0.839 SQUARED MULTIPLE R: 0.703
ADJUSTED SQUARED MULTIPLE R: 0.668 STANDARD ERROR OF ESTIMATE: 0.31606

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	2.79147	0.29246	0.00000	.	9.54490	0.00000
YEARLING	4.09200	0.95323	0.59640	0.90415	4.29277	0.00049
WILDPRED	-0.09290	0.02979	-0.43320	0.90415	-3.11812	0.00626

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	YEARLING	WILDPRED
CONSTANT	1.00000		
YEARLING	-0.95325	1.00000	
WILDPRED	-0.46765	0.30959	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	4.02587	2	2.01294	20.15074	0.00003
RESIDUAL	1.69820	17	0.09989		

WARNING: CASE 1 HAS LARGE LEVERAGE (LEVERAGE = 0.862)

DURBIN-WATSON D STATISTIC 1.800
FIRST ORDER AUTOCORRELATION .040

APPENDIX A

Table 22. Results of the multiple regression of recruitment rate ($\log_e$) of the 1963-82 year classes on numbers of yearlings stocked and large-mesh gill-net fishing effort in Wisconsin waters of Lake Superior.

EIGENVALUES OF UNIT SCALED X'X

	1	2	3
	2.74717	0.19692	0.05591

CONDITION INDICES

	1	2	3
	1.00000	3.73509	7.00940

VARIANCE PROPORTIONS

	1	2	3
CONSTANT	0.01094	0.00291	0.98615
YEARLING	0.01808	0.33191	0.65000
GILLNETS	0.02311	0.56335	0.41354

DEP VAR:SURVIVAL N: 20 MULTIPLE R: 0.822 SQUARED MULTIPLE R: 0.676
ADJUSTED SQUARED MULTIPLE R:0.638 STANDARD ERROR OF ESTIMATE: 0.48235

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	4.81613	0.36827	0.00000	.	.13E+02	0.00000
YEARLING	-0.93529	0.74312	-0.17471	0.98866	-1.25860	0.22519
GILLNETS	-0.12848	0.02169	-0.82233	0.98866	-5.92419	0.00002

CORRELATION MATRIX OF REGRESSION COEFFICIENTS

	CONSTANT	YEARLING	GILLNETS
CONSTANT	1.00000		
YEARLING	-0.75546	1.00000	
GILLNETS	-0.66321	0.10649	1.00000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	8.25806	2	4.12903	17.74731	0.00007
RESIDUAL	3.95516	17	0.23266		

WARNING: CASE 1 HAS LARGE LEVERAGE (LEVERAGE = 0.547)

DURBIN-WATSON D STATISTIC 2.244
FIRST ORDER AUTOCORRELATION -.135

APPENDIX A

Table 23. Commercial fishery lake trout catch (pounds) and large-mesh gill-net effort (1,000 feet) in Michigan statistical districts MS-1 through MS-3 of Lake Superior during 1929-61 (compiled from Jensen and Buettner 1976).

	MS-1			MS-2			MS-3		
Year	Catch	Effort	C/f	Catch	Effort	C/f	Catch	Effort	C/f
1929	306,596	13,993	219	61,700	4,139	149	319,275	15,853	201
1930	263,783	12,988	203	93,793	5,938	158	323,978	16,429	197
1931	188,821	10,586	178	65,818	4,808	137	438,577	23,304	188
1932	203,689	8,892	229	38,896	2,723	143	361,739	24,245	149
1933	220,566	10,259	215	47,993	2,324	207	328,570	19,454	169
1934	256,388	10,473	245	47,411	2,563	185	360,858	18,402	196
1935	302,833	11,183	271	44,013	2,870	153	325,075	20,040	162
1936	262,293	9,970	263	112,652	6,366	177	325,946	18,271	178
1937	222,586	10,094	221	108,642	7,560	144	252,051	17,601	143
1938	234,901	10,553	223	67,001	5,091	132	225,592	18,311	123
1939	218,379	11,117	196	91,232	5,351	170	221,538	18,919	117
1940	213,902	10,368	206	122,597	7,798	157	240,754	20,973	115
1941	205,653	9,386	219	102,214	7,284	140	322,943	25,877	125
1942	238,812	9,639	248	81,099	5,253	154	444,437	29,728	150
1943	257,240	9,381	274	96,842	5,646	172	496,905	33,149	150
1944	339,394	12,570	270	143,397	6,450	222	590,641	35,474	166
1945	271,017	10,372	261	159,697	7,973	200	611,669	39,642	154
1946	263,141	12,717	207	147,082	10,200	144	659,628	50,146	132
1947	242,180	10,729	226	127,391	9,516	134	583,512	45,339	129
1948	286,004	12,156	235	142,452	11,295	126	496,398	49,197	101
1949	236,469	12,755	185	125,680	9,108	138	558,009	54,818	102
1950	293,943	11,399	196	112,120	7,237	118	704,146	54,489	98
1951	298,186	13,151	140	103,475	7,055	90	659,034	45,568	89
1952	343,724	15,154	101	75,085	5,637	59	649,508	55,071	52
1953	288,873	15,644	82	62,304	4,430	63	572,158	52,413	49
1954	249,482	15,241	73	37,758	3,196	53	543,795	52,088	46
1955	211,828	11,847	79	57,113	3,229	79	491,937	49,140	44
1956	214,202	16,858	56	89,038	4,494	88	384,114	39,701	43
1957	80,525	6,976	51	35,668	2,601	61	323,711	31,331	46
1958	57,940	4,445	58	30,071	1,842	73	311,422	30,036	46
1959	21,165	2,390	39	12,640	952	59	253,463	24,306	46
1960	11,063	1,542	32	5,112	683	33	108,743	14,448	33
1961	7,980	1,190	30	4,108	520	35	88,591	12,650	31

APPENDIX A

Table 24. Commercial fishery lake trout catch (pounds) and large-mesh gill-net effort (1,000 feet) in Michigan statistical districts MS-4 through MS-6 of Lake Superior during 1929-61 (compiled from Jensen and Buettner 1976).

	MS-4			MS-5			MS-6		
Year	Catch	Effort	C/f	Catch	Effort	C/f	Catch	Effort	C/f
1929	159,686	6,610	242	377,323	10,321	366	12,231	587	208
1930	249,042	9,612	259	292,085	9,590	305	18,065	783	231
1931	271,700	11,701	232	367,330	10,150	362	38,646	1,721	225
1932	231,366	10,955	211	520,108	11,718	444	62,322	2,568	243
1933	182,149	8,035	227	293,138	5,650	519	98,856	3,031	326
1934	210,721	6,839	308	516,675	9,955	519	86,819	2,461	353
1935	210,811	9,792	215	493,884	12,739	388	57,652	1,996	289
1936	196,174	8,937	220	335,200	10,716	313	100,533	3,916	257
1937	169,728	9,792	173	389,099	13,099	297	109,258	4,862	225
1938	177,118	11,343	156	360,967	17,747	203	73,276	3,220	228
1939	216,422	13,244	163	372,646	18,092	206	21,984	1,542	143
1940	213,459	12,710	168	340,563	14,020	243	63,764	3,347	191
1941	252,311	15,911	159	369,341	14,222	260	119,411	5,705	209
1942	282,828	16,803	168	422,361	14,567	290	98,190	4,522	217
1943	256,610	15,015	171	390,692	10,865	360	107,001	4,190	255
1944	291,167	17,988	162	491,733	14,015	351	127,770	5,850	218
1945	345,763	19,612	176	323,181	11,280	287	135,941	6,519	209
1946	349,819	25,198	139	335,623	17,048	197	192,135	8,843	217
1947	259,940	16,241	160	272,073	13,669	199	114,707	5,192	221
1948	245,241	20,913	117	299,473	15,896	188	140,196	7,661	183
1949	283,864	24,501	116	341,650	21,315	160	125,009	6,306	198
1950	382,602	26,861	109	311,622	15,480	153	164,400	6,482	193
1951	464,708	31,022	92	279,019	17,009	101	138,104	7,299	116
1952	455,988	32,617	62	214,249	11,119	86	144,227	6,168	104
1953	388,830	32,032	54	177,932	7,769	102	151,604	6,560	103
1954	331,568	29,909	49	222,217	11,214	88	151,681	7,027	96
1955	293,287	26,171	50	189,428	8,562	98	85,641	5,015	76
1956	260,844	23,811	49	163,153	7,671	95	73,180	4,748	69
1957	208,638	22,577	41	136,220	6,307	96	54,847	4,144	59
1958	188,162	18,515	45	135,155	7,215	83	35,557	2,154	73
1959	208,260	21,413	43	136,644	6,601	92	30,748	2,068	66
1960	68,065	10,702	28	67,094	4,821	62	5,798	444	58
1961	53,126	9,234	26	48,498	3,006	72	14,365	1,131	56

APPENDIX B - ADDITIONAL FIGURES

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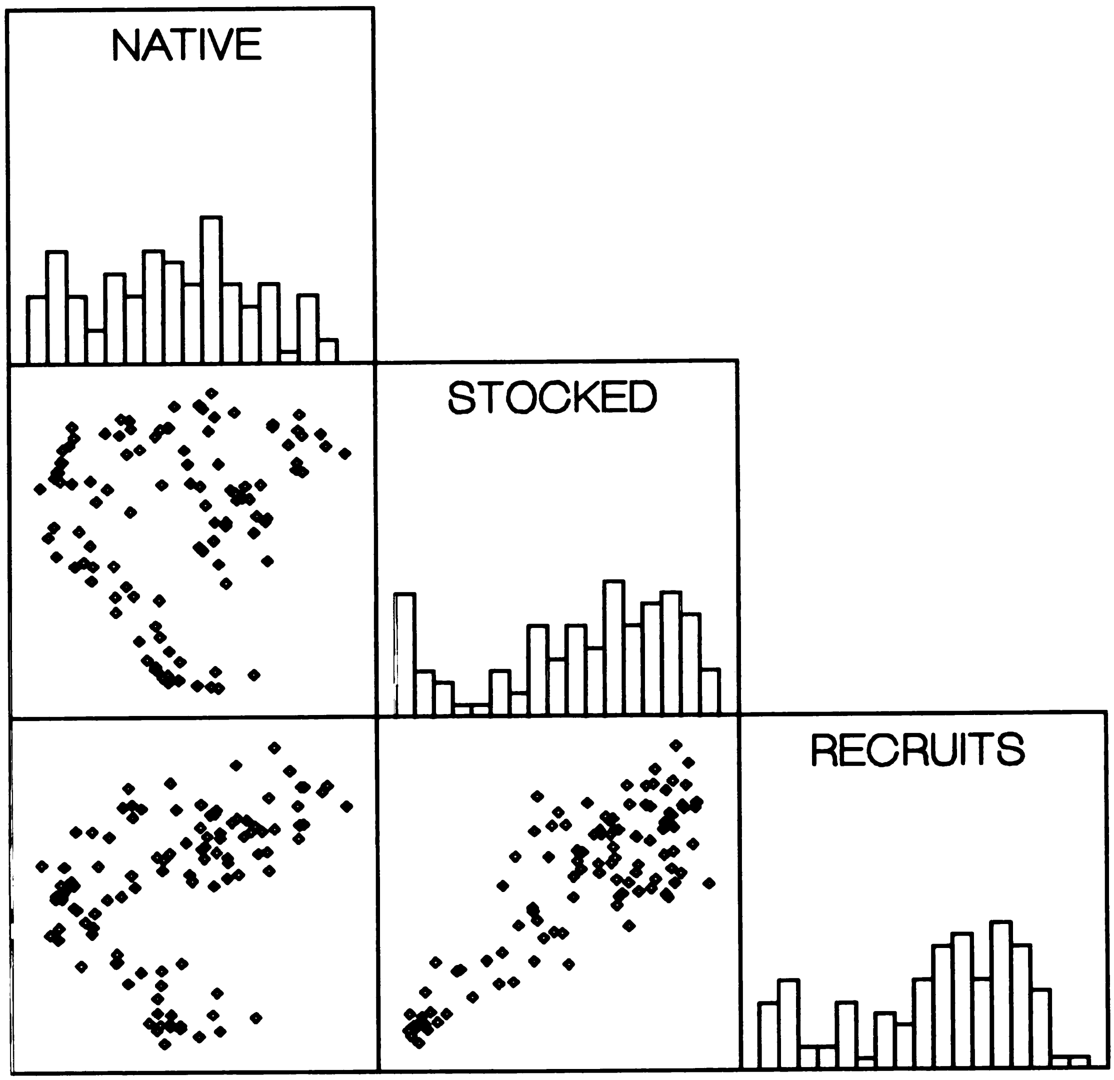

Figure 24. Scatter-plot matrix of native and stocked spawner CPEs ($\log_e$) during 1959-85 and recruit CPE ($\log_e$) during 1967-93 in Michigan areas MI4-MI7 of Lake Superior.

APPENDIX B

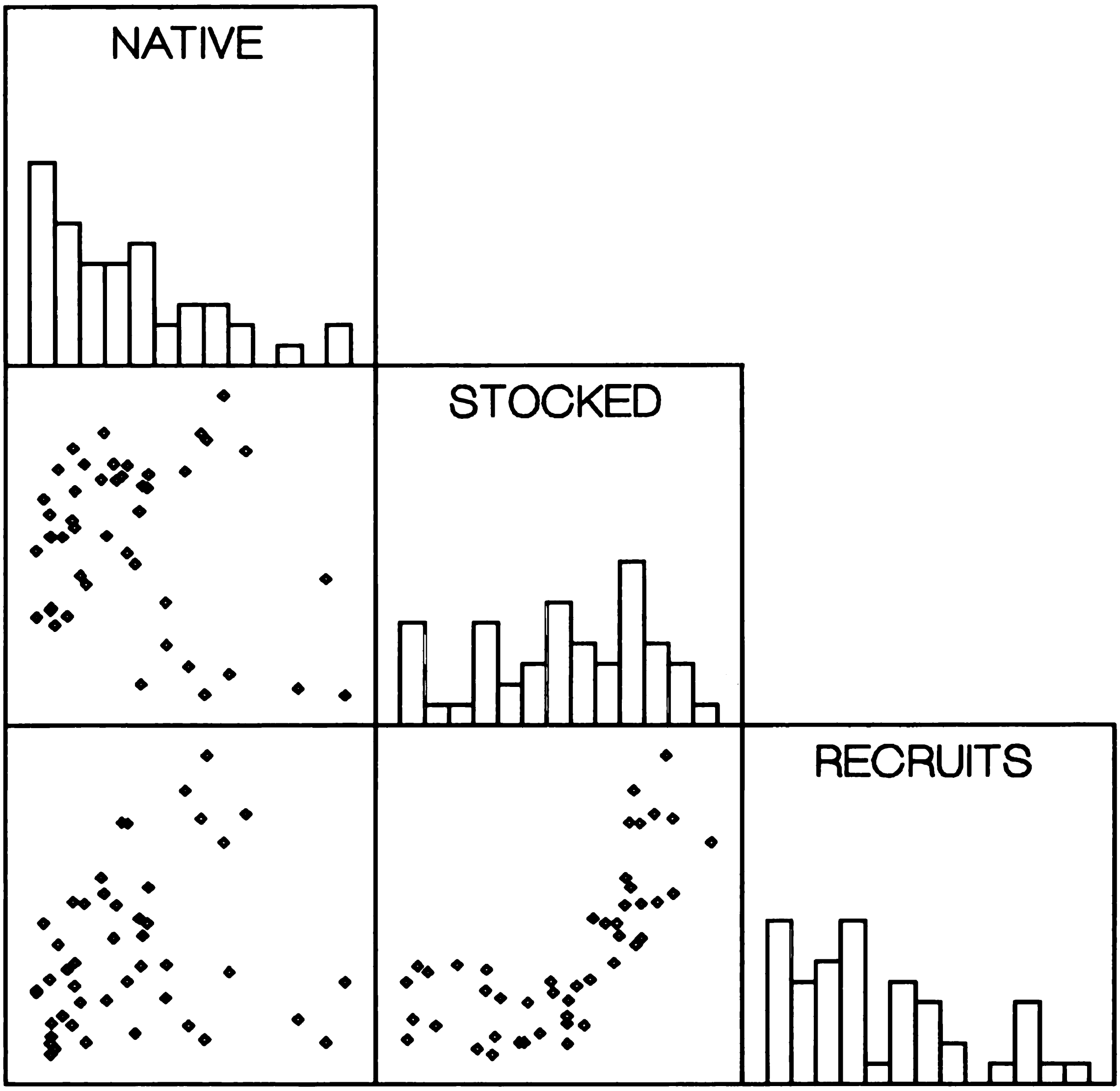

Figure 25. Scatter-plot matrix of native and stocked spawner CPEs ($\log_e$) during 1959-85 and recruit CPE ($\log_e$) during 1967-93 in Minnesota areas MN2-MN3 of Lake Superior.

APPENDIX B

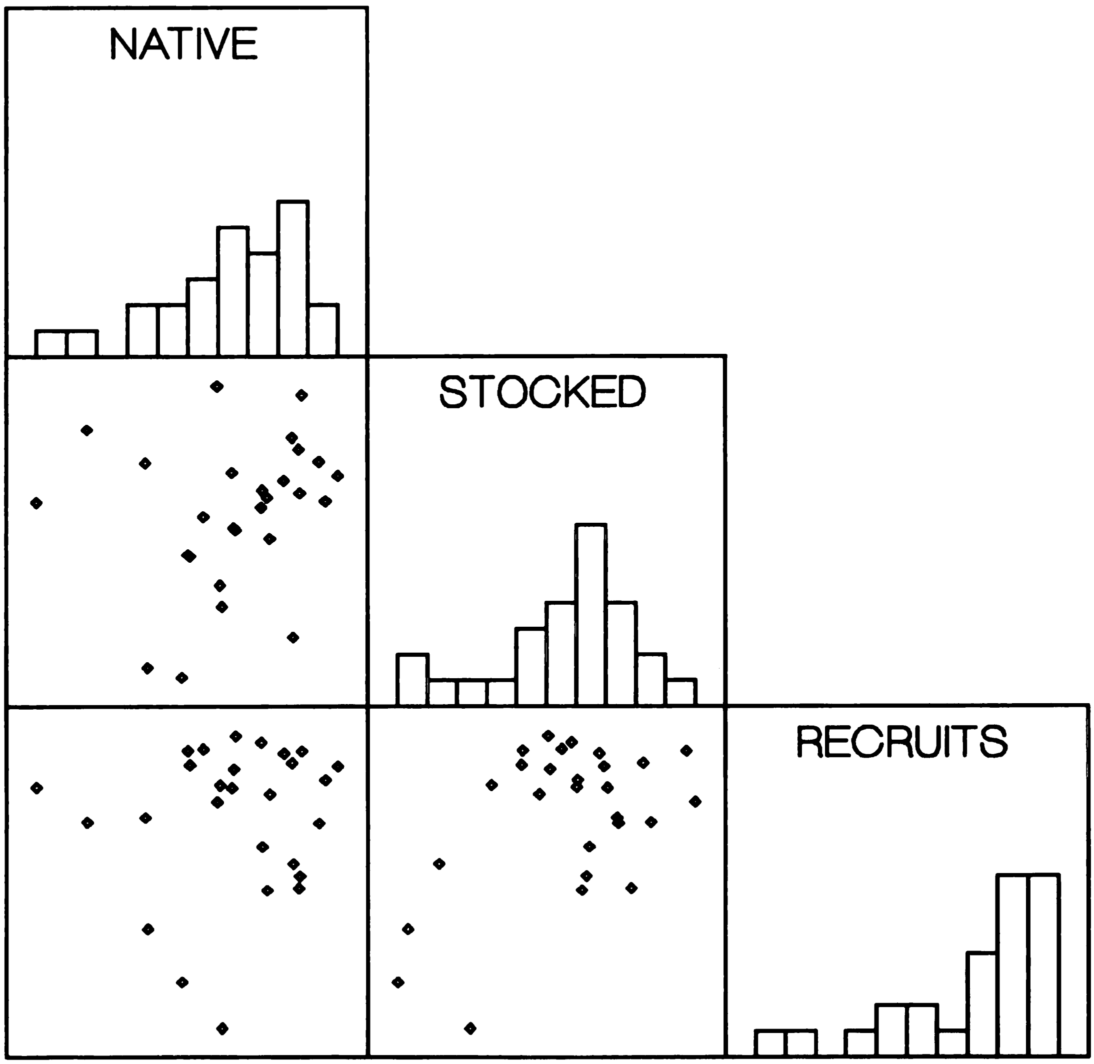

Figure 26. Scatter-plot matrix of native and stocked spawner CPEs (log_e) during 1959-85 and recruit CPE (log_e) during 1967-93 in Wisconsin area WI2 of Lake Superior.

APPENDIX B

Figure 27. Scatter-plot matrix of stocked lake trout survival, millions of yearlings stocked, average grams/yearling, wild adult lake trout CPE, stocked adult lake trout CPE, wild juvenile lake trout CPE, and large-mesh gill-net fishing effort in Michigan waters of Lake Superior during 1963-89.

APPENDIX B

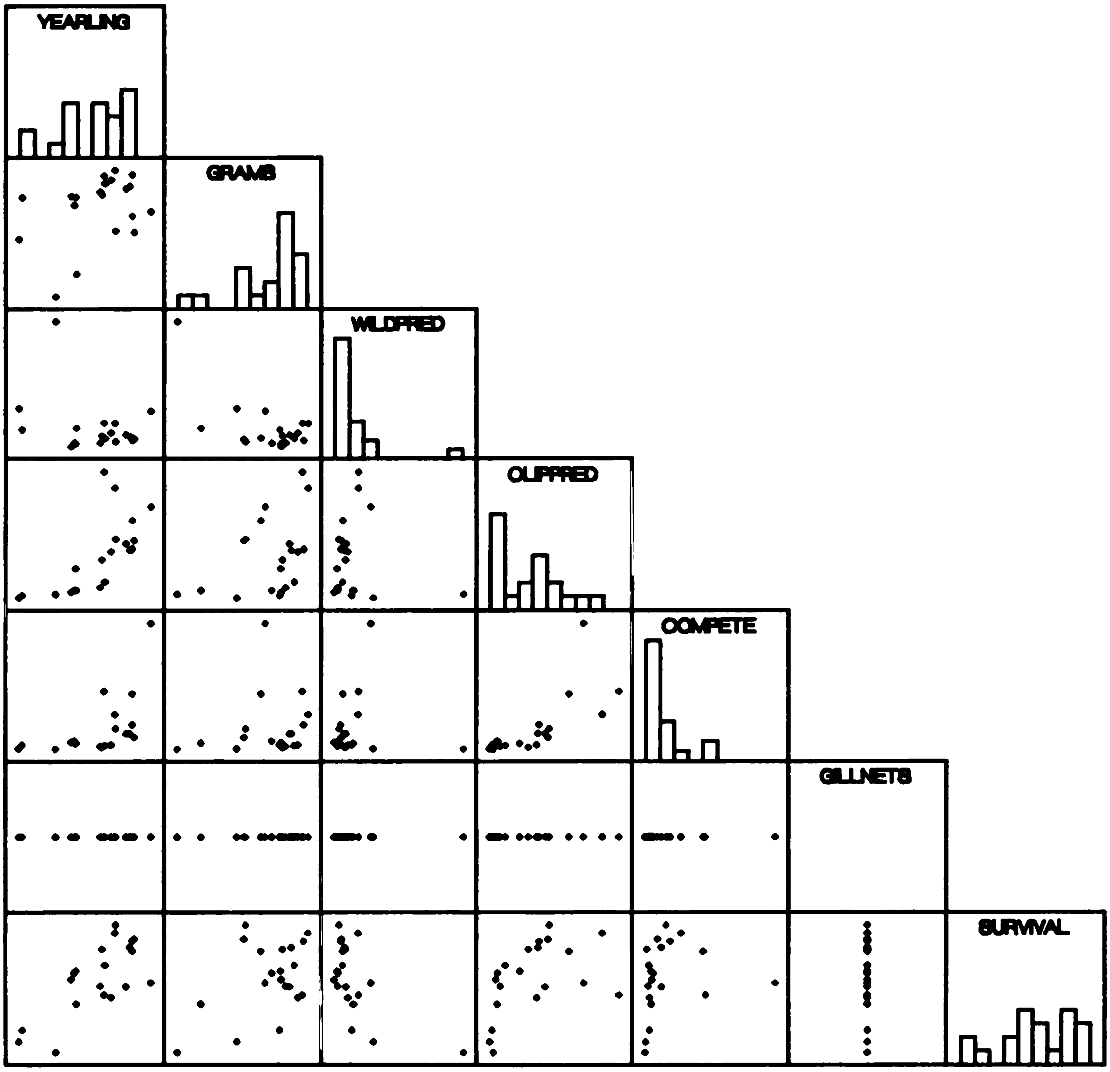

Figure 28. Scatter-plot matrix of stocked lake trout survival, millions of yearlings stocked, average grams/yearling, wild adult lake trout CPE, stocked adult lake trout CPE, wild juvenile lake trout CPE, and large-mesh gill-net fishing effort in Minnesota waters of Lake Superior during 1963-89.

APPENDIX B

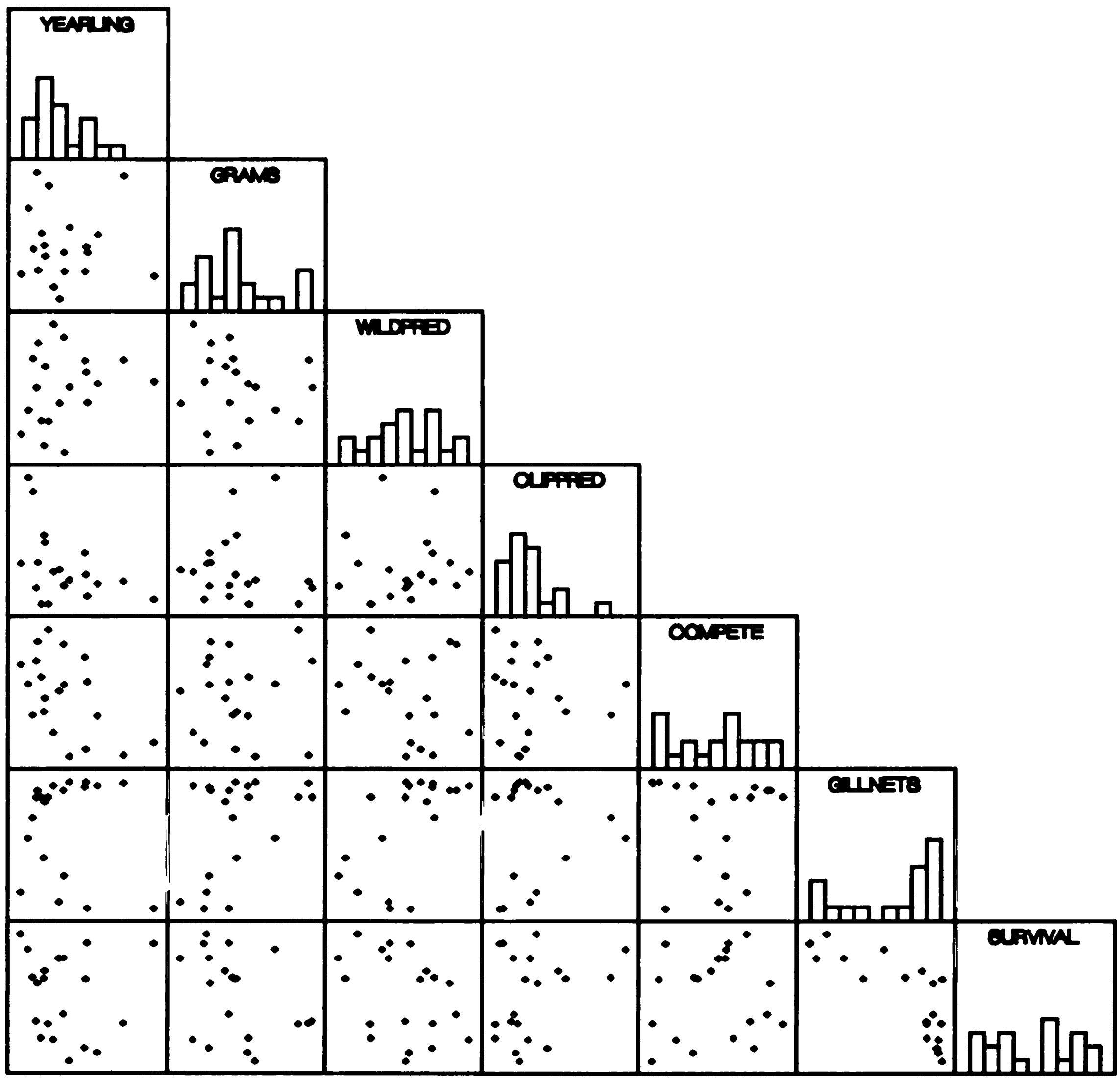

Figure 29. Scatter-plot matrix of stocked lake trout survival, millions of yearlings stocked, average grams/yearling, wild adult lake trout CPE, stocked adult lake trout CPE, wild juvenile lake trout CPE, and large-mesh gill-net fishing effort in Wisconsin waters of Lake Superior during 1963-89.

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