GREAT LAKES FISHERY COMMISSION
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LAKE TROUT (*Salvelinus namaycush*) MORTALITY - A REVIEW

by

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ABSTRACT

Lake trout (Salvelinus namaycush) mortality estimates were summarized for a number of populations in an attempt to understand the dynamics of lake trout populations, and the influence of exploitation and sea lamprey predation. Estimates of mortality were extremely variable; however, it appears that natural mortality (from sources other than fishing or sea lamprey predation) is in the range of M = 0.10 - 0.25 for all populations examined. Fishing mortality is regulated by the management agencies and, therefore, was site specific. Lamprey induced mortality was more difficult to quantify with estimates ranging from L = 0.21 - 1.70 (mean = 0.721 ± 0.454; N = 12). It is apparent that lamprey contribute to the mortality of lake trout, however, the magnitude of that contribution is still uncertain.

INTRODUCTION

Until recently, little background information was available on the biology and population characteristics of the lake trout (Salvelinus namaycush) because this species can be extremely plastic throughout its range (Martin and Olver 1980). Further, the difficulty in accurately aging lake trout has contributed to the problems in understanding its population biology and, in particular, mortality within populations. Recent introductions of hatchery reared fish providing known-year stocks, and use of otoliths have enhanced ~~aided~~ our ability to age lake trout and thus better estimate mortality.

Mortality in lake trout stocks is attributed to natural or anthropogenic (exploitation) causes (Ricker 19??). Where sea lamprey exist, attempts have been made to further partition mortality. In the Great Lakes, indirect measures (wounding/scarring rates; carcass survey) are commonly used to infer mortality attributable to sea lamprey predation (see e.g. Bergstedt and Schneider 1988). While Martin and Olver (1980) tabulated selected etimates of lake trout mortality, they did not evaluate the contribution of exploitation or sea lamprey to mortality beyond natural causes. Therefore, in order to more clearly understand the impact of exploitation and sea lamprey predation, a review of the range of reported mortalities has been conducted. Differences between exploited and unexploited populations were summarized, and lake trout populations with/without sea lamprey were examined.

MORTALITY

One of the reasons for estimating population numbers is to determine mortality since knowledge of the mortality rates is important to understanding of population dynamics (Bagenal 1978). The mortality rate estimates the probability that any randomly chosen fish will die during a specified period of time (Regier and Robson 1967). In an exploited population, the mortality rate is a combination of mortality due to fishing and mortality due to natural causes. Separating these two components can be difficult. However, insight into the impact of the fishery on a population is obtained by a comparison of these two rates. This can be completed in one of two ways: (1) through comparison of total mortality in both exploited and unexploited populations; or (2) through calculation of fishing and natural mortality in exploited populations (Healey 1975). In addition, comparison of natural mortality rates among unexploited populations contributes to the understanding of the natural variation in population parameters and lends credence to the interpretation of data obtained from exploited populations. For lake trout, the impact of sea lamprey predation may be similarly defined by comparison of lake trout populations in the presence or absence of sea lamprey.

Mortality estimates and exploitation rates are presented as follows:

A = total annual mortality
n = conditional rate of natural mortality

m = conditional rate of fishing mortality
l = conditional rate of lamprey induced mortality
Z = instantaneous total mortality
M = instantaneous rate of natural mortality
F = instantaneous fishing mortality
L = instantaneous lamprey induced mortality
u = rate of exploitation of a fish stock or ratio of number recoveries to number of marked fish released (=R/M)

Unexploited Populations

Very little data are available for unexploited populations of lake trout. Mortality estimates included here were based on age structure and/or tag-recapture data (Johnson 1972; Johnson 1973; Bond 1975; McLeod et al. 1976; Falk et al. 1982). Calculations of two additional mortality estimates were completed using age structure data provided (Armstrong 1949; Martin 1952) following Ricker (1968). Mean total annual mortality (A) for the unexploited populations was 0.265 (Range=0.03-0.54; N=6). The mean instantaneous total mortality (Z) was 0.325 (Range=0.16-0.53; N=4).

Exploited Populations, No Sea Lamprey

Twenty six estimates of mortality from exploited populations without sea lamprey were obtained from tag-recapture, age structure, creel survey and/or commercial catch data. Additionally, total mortality estimates were calculated for 2 populations in which age structure data were provided (Martin 1952; Hanson and Cordone 1967).

The mean total annual mortality for those populations in the Northwest Territories was A=0.25 (Range=0.05-0.53; N=18), while mean instantaneous total mortality was Z=0.32 (Range=0.11-0.67; Miller and Kennedy 1948; Kennedy 1954; Falk et al. 1973; Johnson 1973; Wong and Whillans 1973; Moshenko and Gillman 1978; Yaremchuk 1986). Mean total mortality estimates from Ontario lakes were A=0.53 (Range=0.25-0.70; N=9) and Z=0.94 (Range=0.61-1.51; N=8; Martin 1952; Beverton and Holt 1957; Paloheimo 1958, 1961; Budd et al. 1968; Martin and Fry 1972, 1973; Hackney 1973; MacLean et al. 1981; Shuter et al. 1987; Olver unpubl.). For lakes in other regions, including Alberta (Paterson 1968), Saskatchewan (Rawson 1961), Manitoba (DeRoche unpubl.; DeRoche and Bond 1957) and California (Hanson and Cordone 1967), mean total mortality estimates were A=0.43 (Range=0.18-0.67; N=7) and Z=0.90 (Range=0.73-1.21; N=3). The overall mean total mortality estimates were A=0.369 (Range=0.05-0.70; N=48) and Z=0.691 (Range=0.11-1.51; N=22).

A number of authors (N=14) attempted to partition the mortality components into fishing and/or natural mortality. The mean conditional rate of fishing mortality (DeRoche unpubl.; DeRoche and Bond 1957; Budd et al. 1968; Paterson 1968) was m=0.243 (Range=0.02-0.40; N=6). Mean instantaneous fishing mortality (DeRoche unpubl.; Beverton and Holt 1957; Paloheimo 1958; Martin and Fry 1973; Hackney 1973) was F=0.327 (Range=0.22-0.58; N=12). The conditional rate of natural mortality (DeRoche unpubl.; Miller and Kennedy 1948; Kennedy 1954; DeRoche and Bond 1957; Budd et al. 1968; Paterson 1968; Wong and Shillans 1973; MacLean et al. 1981; Shutter et al. 1987) was n=0.351

(Range=0.11-0.56; N=20) and the mean instantaneous natural mortality (DeRoche unpubl.; Kennedy 1954; DeRoche and Bond 1957; Beverton and Holt 1957; Paloheimo 1958, 1961; Budd et al. 1968; Martin and Fry 1972; Hackney 1973; Yaremchuk 1986) was M=0.385 (Range=0.08-0.82; N=20).

Total annual mortality estimates in exploited populations were, on average, higher than total mortality in unexploited stocks. In addition, the estimates of natural mortality in exploited populations (n=0.351, M=0.385) were very similar to the estimates of total mortality in unexploited stocks (A=0.265, Z=0.325).

<u>Exploited Populations, With Sea Lamprey</u>

The majority of the estimates of mortality were obtained from the Great Lakes region (25 of 30 references). Mean total annual mortality for Lake Huron populations prior to sea lamprey (Budd et al. 1969; Berst and Spangler 1973) was A=0.225 (Range=0.20-0.25; N=2). In the presence of sea lamprey, mean total annual mortality (Fry 1953; Fry and Budd 1958; Budd 1960; Budd and Fry 1960; Budd et al. 1969; Berst and Spangler 1973) was A=0.723 (Range=0.25-0.98+; N=17). A similar pattern is observed in Lake Superior; i.e. total mortality estimates are much lower prior to sea lamprey invasion (A=0.17, Rahrer 1967; Z=0.70, Sakagawa and Pycha 1971) than after (A=0.57, Range=0.20-0.75, N=55, Loftus 1958; Rahrer 1965; Pycha 1972, 1980; Pycha and King 1975; Swanson and Swedberg 1980; Kruger et al 1986; MacCallum et al 1989; Z=1.74, Range=0.62-2.31, N=6, Loftus 1958; Pycha and King 1975; Pycha 1980). Few estimates are available for Lakes Michigan (Silliman 1969; Rybichie and Keller 1978; Moore and Lychwick 1981; Clark and Huang 1985) and Ontario (Christie unpubl., 1972). For these lakes, mean total mortality estimates were A=0.57 (Range=0.22-0.75; N=5) and Z=0.593 (Range=0.50-0.70; N=3). Mean total mortality for Cayuga Lake were A=0.46 (Range=0.26-0.60; N=3; Webster et al. 1959; Youngs and Olglesby 1972) and Z=0.598 (Range=0.31-0.867; N=10; Webster et al. 1959; Youngs 1980). Ninety-five (76%) of the 125 estimates of total annual mortality (A) were $\geq$ 0.50; while 23 (18.4%) were $\geq$ 0.75, indicating declining populations (Healey 1978).

Exploited populations with sea lamprey present are extremely complex, making it difficult to partition the mortality components. Total mortality estimates for these populations are on average higher than all other populations, however, again there is a great deal of overlap. Some investigators attempted to partition mortality into components. Estimates for fishing mortality are similar (m=0.19) to those for populations without sea lamprey (m=0.20). Estimates of natural mortality in these populations were generally higher than those for populations without sea lamprey. This is likely because a number of authors included sea lamprey induced mortality in estimates of natural mortality (e.g. Fry 1953; Budd and Fry 1958; Webster et al. 1959; Berst and Spangler 1970; Pycha and King 1975). Estimates of natural mortality excluding sea lamprey predation were n=0.20

(N=1; Swanson and Swedberg 1980) and M=0.25 (Range=0.24-0.26, N=2; Pycha 1980); values very similar to those found in other populations.

Estimates of lamprey induced mortality have been made by three (Pycha 1980; Swanson and Swedberg 1980; Hegstrom-Heg unpubl.). Mean estimates of mortality induced by sea lamprey were l=0.279 (Range=0.14-0.82; N=8) and L=0.721 (Range=0.21-1.71; N=12). The mean conditional rate of natural mortality (Webster et al. 1959; Budd et al. 1969; Pycha and King 1967, 1975; Swanson and Swedberg 1980) was n=0.461 (Range=0.20-0.90; N=16), while the mean instantaneous natural mortality (Fry 1953; Budd and Fry 1958; Webster et al. 1959; Pycha and King 1967, 1971; Budd et al. 1969; Silliman 1969; Berst and Spangler 1970; Rybickie and Keller 1978; Pycha 1980; Clark and Huang 1985) was M=0.602 (Range=0.10-2.30; N=27).

Factors Affecting Mortality Estimates

There is a very wide range in reported mortality rates among all classes of lake trout populations (unexploited, exploited, exploited with sea lamprey). The factors contributing to this variability must be examined. Biases in the data may then be identified and conclusions appropriately made.

Mortality estimates based on tag-recapture studies presume the assumptions of the Peterson type estimates are not seriously violated. Possible sources of error in tag-recapture estimates include tag loss, differential mortality of tagged fish, and failure by anglers/commercial fishermen to report recaptures. Violations of these assumptions would result in an overestimate of mortality rates. On the other hand, calculating mortality rates in a discrete area (e.g. Green Bay, L. Michigan; Moore and Lychwick 1980), assumes that there is no immigration and/or emmigration. If this assumption is violated, the mortality estimate will likely be low.

Mortality estimates based on creel surveys or commercial catch data are biased in at least two respects. Firstly, it is assumed that the reported catch statistics are accurate. Secondly, the data obtained is dependant on the type of fishery. For example, commercial fisheries may take fewer of the younger age groups than sports fisheries. Gear selectivity in both commercial and sports fisheries is an important factor in the age structure of the harvest. Age distribution in the catch and stock can can be dependent on exploitation rates as was seen after the opening of a comercial fishery on previously unexploited stocks (see Kennedy 1956; Keleher 1972; Johnson 1972, 1973).

Changing mortality with age and variable year class strength are two additional sources of variability in estimates of mortality. Mortality rates may be calculated over different spans of age as a result of the type of gear used (e.g. Black Bay, Lake Superior; MacCallum et al. 1989). Older fish may appear to have a somewhat higher mortality rate than intermediate-aged fish (e.g. A=0.37 for fish aged 13, A=0.65 for fish aged 24; Kennedy 1954); therefore, mortality estimates based on a wider age range should be lower than those based primarily on older fish. Changes in mortality with age are difficult to quantify because of problems with the aging technique using scales (see Yaremchuk 1986). Therefore, the amount of variation due to changing mortality with age is difficult to acertain. Mortality estimates based on a wide range of age classes should minimize this influencing factor.

Year class strength may be quite variable in some lake trout stocks (Fry 1953; Hale 1955; Martin 1966), markedly affecting the age structure of a population. However, Kennedy (1954), Rawson (1961) and Sakagawa and Pycha (1971) found year class strength was consistent in long lived stocks. For example, Johnson (1972, 1973) observed a continuous bimodal age distribution consisting of juveniles and adults in Keller Lake. Year class strength, however, may affect mortality estimates. For example, if only a few years (<3) of data are available, the presence of a strong year class which is vulnerable to the fishery may result in a mortality estimate that is higher than the true mortality rate. On the other hand, the presence of a weak year class which is vulnerable to the fishery my result in a mortality estimate that is lower than the true mortality rate if only a fey years of data are available.

The method for aging lake trout will also affect the mortality estimates. Use of scales tends to underestimate age, hence resulting in an overestimate of growth rate and mortality.

Otoliths provide a much more accurate age, thereby producing a more accurate estimate of mortality. The most accurate estimate of the age structure of a population is, of course, use of stocked lake trout.

Although biases and inconsistencies are evident in the mortality estimates, some conclusions can be drawn. In general, most biases inherent in the data will result in overestimates of mortality. Therefore, comparison of total mortality among populations can provide information as to the relative magnitude of the components of mortality (e.g. natural mortality, fishing mortality, sea lamprey induced mortality).

DISCUSSION

Lake trout are one of the most important freshwater commercial and sport fishes in Canada and the northeastern U.S., yet they are extremely sensitive to anthropogenic stresses and are highly susceptible to exploitation (Martin and Olver 1980). They are also inherently slow growing and late maturing. As a result, clear understanding of their biology is essestial for their management.

The suggested contribution of sea lamprey to the collapse of the lake trout population in the Great Lakes is still subject to debate. Sea lamprey contributed to their collapse, yet there is strong evidence that they may have co-existed in lakes such as Lake Ontario, Lake Champlain, and the Finger Lakes for hundreds of years (Brussard et al. 1981). Therefore, the influence of commercial and sport fishing pressure cannot be eliminated. Lake trout mortality estimates were summarized for a number of populations in an attempt to understand the dynamics of lake trout populations and the influence of fishing pressure and sea lamprey predation.

In virgin lake trout populations (unexploited, no sea lamprey), natural mortality estimates were considered to be equivalent to estimates of total mortality which were low. The low mortality rates are likely influenced by the relatively stable population structure in these unexploited lakes as a result of the long period required for maturation. Total mortality estimates for exploited lake trout populations were higher than those for unexploited populations. The higher total mortality can be attributed to exploitation. The estimates of natural mortality in these exploited populations without sea lamprey were roughly equivalent to those for unexploited populations.

Problems arise when examining data for populations in the presence of sea lamprey. The reported mortality values for lake trout populations in northern and arctic waters were generally lower than those from the Great Lakes (in which sea lamprey were present). For example, total mortality values for Great Slave lake ranged from 0.22 to 0.53 (Kennedy 1954; Falk et al. 1973). Similarly, the reported values in Great Bear Lake (A=0.19-0.25; Miller and Kennedy 1948; Falk et al. 1973; Johnson 1973), Keller Lake (A=0.25-0.31; Johnson 1972, 1973), and Kaminuriak Lake

(A=0.41; Bond 1975) were lower than those mortality rates for populations in which sea lamprey are present.

Budd et al. (1960) suggested that the coefficient of natural mortality for young hatchery (n=0.22) lake trout in South Bay where sea lamprey occur was not significantly different from the natural mortality rate in exploited lake trout stocks in the absence of sea lamprey (e.g. Lake Manitou n=0.22; Lake Opeongo n=0.17; Paloheimo 1958). In addition, a natural mortality value of 0.22 for young hatchery fish in South Bay (Budd et. al. 1969) and in Lake Superior (Pycha and King 1967), before these fish were vulnerable to sea lamprey attack, were similar natural mortality values for adult lake trout in Lake Superior prior to the sea lamprey invasion (0.10 to 0.25; Sakagawa and Pycha 1971) and for Lake Michigan (0.20; Silliman 1969).

Estimated natural mortality of lake trout was low in the Great Lakes prior to the invasion of sea lamprey. For example, Sakagawa and Pycha (1971) reported a natural mortality rate of M=0.10-0.25 for native lake trout age 9 y and older in Lake Superior. In South Bay, Lake Huron, Fry (1953) reported a pre-lamprey mortality value of M=0.25 for native lake trout while Budd et al. (1969) calculated mortality at M=0.23 for 3 y old hatchery lake trout of the 1954 year class. The calculated natural mortality of lake trout in Lake Michigan was M=0.20 (Silliman 1969), while natural mortality of planted lake trout in Lake Superior was M=0.23 (Pycha and King 1967). Based on these data, it is believed that natural mortality was likely 0.10 to

0.25 for lake trout less than 5 y of age in the Great Lakes prior to the sea lamprey invasion (Martin and Olver 1980).

The impact of sea lamprey has been considered by many. Fry (1953) reported that natural mortality in South Bay increased from M=0.25 to M=1.20 between 1948 to 1950. As well, estimated natural mortality increased with age to a maximum of M=2.30 for lake trout 7 y and older caught in the 1957 poundnet and gillnet fishery (Budd and Fry 1960). Budd et al. (1969) observed that, in South Bay, there appeared to be a direct correlation between annual sea lamprey wounding/scarring rates and annual natural mortality rates in lake trout less than 7 y of age. The increase in average total mortality rates between age 5 (A=0.62) and age 7 (A=0.92) has been attributed to sea lamprey predation (Budd et al. 1969). Loftus (1958) concluded that the decline of spawning stocks of lake trout in the Montreal and Dog Rivers of eastern Lake Superior was due to lamprey predation. Since these stocks were only lightly fished, the natural mortality rate would be close to the reported instantaneous total mortality value of Z=2.30. As well, Pycha and King (1975) suspected sea lamprey to be a major cause of natural mortality of large spawning lake trout on Gull Island shoal in Lake Superior.

There is evidence to suggest that the age at first maturity in teleosts is related to mortality and growth rate (Roff 1984). It is suggested that this maturity-mortality relationship has developed to optimize reproductive potential (Donald and Alger 1986). If mortality in lake trout populations is a function of age at first maturity, then this relationship may also be genetically determined. Survival and growth of stocked lake trout appear to be largely determined by competition (Gunn et al. 1987) Therefore, reported mortality estimates are likely influenced by the strain of lake trout used for stocking.

In conclusion, it is not possible at this time to draw firm conclusions regarding the validity of the estimates of mortality rates. The wide range of reported estimates contributes to the difficulty in interpretation of the data. The variability in all mortality estimates may be a result of a number of factors. Lake trout aged from scales may be underaged therefore growth rates and mortality estimates based on age structure data will tend to be high. The differences between populations may not be as great as they seem once more reliable estimates are made.

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LAKE TROUT MORTALITY ESTIMATES

EXPLOITED WITH SEA LAMPREY

Christie 1972	Lake Ontario		A=0.75* m=0.30
Christie, unpubl.	Lake Ontario		A=0.75
Fry 1953	Lake Huron -South Bay	 pre-S/L post-S/L	A=0.25-0.70* M=0.25 M=1.20 m=0.10
Budd & Fry 1960	Lake Huron -South Bay		A=0.70-0.90+* M=1.20-2.30
Fry & Budd 1958	Lake Huron -South Bay (stocked fish age IV)		A=0.60-0.98*
Budd 1960	Lake Huron -South Bay (stocked fish age II-V)		A=0.61-0.96*
Budd et al. 1969	Lake Huron -South Bay	pre-S/L post-S/L	A=0.20 n=0.20 M=0.23 A=0.62-0.92*
Budd et al. 1969	Lake Huron -South Bay (in presence of S/L)		A=0.58-0.82*
Berst & Spangler 1970	Lake Huron		A=0.70-0.95 F=0.03-0.77 M=0.57-0.78
Berst & Spangler 1973	Lake Huron	pre-S/L post-S/L	A=0.25 A=0.60-0.70
Loftus 1958	Lake Superior, ON -Montreal & Dog R.		A=0.90* Z=2.30* u=0.02-0.05
Rahrer 1965**	Lake Superior -Isle Royale (humper lake trout)		A=0.08-0.34
Rahrer 1967**	Lake Superior (pre-sea lamprey)		A=0.17
Pycha & King 1967	Lake Superior, WI		n<0.20 M=0.23

Sakagawa & Pycha 1971	Lake Superior pre-S/L	Z=0.70 F=0.45-0.60 M=0.10-0.25
Pycha 1972	Lake Superior	A=0.08-0.69
Pycha & King 1975	Lake Superior, WI	A=0.75 m=0.16 n=0.70 Z=1.39 F=0.18 M=1.21 u=0.10
Swanson & Swedberg 1980	Lake Superior -Gull Is. Reef	A=0.32-0.75 n=0.20 u=0.073 l=0.06-0.56
Pycha 1980	Lake Superior, MI	A=0.46-0.90 Z=0.62-2.31 F=0.17-0.42 M=0.24-0.26 L=0.21-1.70
Kruger et al. 1986	Lake Superior -Apostle Islands	A=0.55-0.65 Z=0.80-1.05
MacCallum et al. 1989	Lake Superior-Zone 1	A=0.55-0.80
	Zone 2	A=0.70-0.75
	Zone 3	A=0.65-0.73
	Zone 4	A=0.62-0.72
	Zone 5	A=0.58
	Zone 6	A=0.50-0.60
	Zone 7	A=0.40-0.70
	Zone 9	A=0.50-0.55
	Zone 12	A=0.54-0.58
	Zone 14	A=0.76
	Zone 16	A=0.46-0.64
	Zone 18	A=0.43
	Zone 19	A=0.67
	Zone 23	A=0.53
	Zone 24	A=0.54-0.55
	Zone 26	A=0.39-0.70
	Zone 27	A=0.70-0.75
	Zone 28	A=0.42-0.75
	Zone 29	A=0.60-0.77
	Zone 30	A=0.32-0.48
	Zone 31	A=0.55-0.67
	Zone 32	A=0.60-0.62
	Zone 33	A=0.50-0.80

	Zone 34	A=0.20-0.70
Silliman 1969	Lake Michigan	A=0.50 Z=0.70 F=0.50 M=0.20
Rybickie & Keller 1978	Lake Michigan -Charlevoix	Z=0.50 F=0.20 M=0.30-0.46
Moore & Lychwick 1980	Lake Michigan -Green Bay (age VI+)	A=0.22-0.65
Clark & Huang 1985	Lake Michigan -Frankfort Good Harbor Bay	Z=0.58 F=0.15-0.42 M=0.36
Webster et al. 1959	Cayuga Lake, NY	A=0.54 m=0.13 n=0.47 Z=0.78 F=0.14 M=0.64 u=0.10
Youngs & Olglesby 1972	Cayuga Lake, NY	A=0.25-0.60 u=0.04-0.10
Youngs 1972	Cayuga Lake, NY	u=0.12-0.16
Youngs 1980	Cayuga Lake, NY	Z=0.311-0.867 F=0.027-0.130
Engstrom-Heg unpubl. report	Seneca Lake, NY	l=0.014-0.236

EXPLOITED, NO SEA LAMPREY

Kennedy 1954	Great Slave Lake, NWT	A=0.33-0.53 n=0.33-0.53 Z=0.40-0.67 M=0.40-0.67
Falk et al. 1973	Great Slave Lake, NWT	A=0.22-0.32
Moshenko & Gillman 1978	Great Slave Lake, NWT	A=0.28-0.29
Miller & Kennedy 1948	Great Bear Lake, NWT	A=0.19 n=0.19
Falk et al. 1973	Great Bear Lake, NWT	A=0.19-0.30
Johnson 1973	Great Bear Lake, NWT -McVicar Arm	A=0.20-0.22 Z=0.22-0.25
Moshenko & Gillman 1978	Great Bear Lake, NWT	A=0.05-0.20
Yaremchuk 1986	Great Bear Lake, NWT (based on otoliths)	Z=0.11-0.25 M=0.08-0.12
Wong & Whillans 1973	Hottah Lake, NWT	A=0.32 m=0 n=0.32
Beverton & Holt 1957	Lake Opeongo, ON	F=0.06 M=0.25-0.45
Paloheimo 1958	Lake Opeongo, ON	A=0.50-0.70 Z=0.70-1.21 F=0.57-0.58 M=0.17-0.37 u=0.37-0.68
Paloheimo 1961	Lake Opeongo, ON	M=0.34
Martin & Fry 1972	Lake Opeongo, ON	A=0.50 Z=0.70 M=0.39
Martin & Fry 1973	Lake Opeongo, ON	A=0.50 Z=0.70 F=0.38-0.51
Hackney 1973	Lake Opeongo, ON	Z=0.61 F=0.36 M=0.25
Shuter et al. 1987	Lake Opeongo, ON	n=0.11$\pm$ 0.6

Budd et al. 1968	Lake Manitou, ON	A=0.25 M=0.25 m=0.02 n=0.20-0.23
Martin 1952**	Redrock Lake, ON	A=0.26
MacLean et al 1981	Lake Simcoe, ON	n=0.50
Olver unpubl.	Flack Lake ON	A=0.78 Z=1.51
Olver unpubl.	Semiwite Lake ON	A=0.62 Z=0.97
Olver unpubl.	Cheblow-Denman Lakes ON	A=0.67 Z=1.11
DeRoche unpubl.	Thompson Lake, Maine	A=0.67 m=0.20-0.26 n=0.56 Z=1.12 F=0.22-0.30 M=0.82 u=0.11-0.27
DeRoche & Bond 1957	Cold Stream Pond, Maine	A=0.57 m=0.40 n=0.22 Z=0.85 F=0.52 M=0.33 u=0.35
DeRoche unpubl.	Cold Stream Pond, Maine	A=0.52 m=0.21 n=0.39 Z=0.73 F=0.24 M=0.49 u=0.34-0.37
Paterson 1968	Swan Lake, AL	A=0.49 m=0.33 n=0.24 u=0.34
Rawson 1961	Lac La Ronge, Sask.	A=0.28-0.32
Hanson & Cordone 1967**	Lake Tahoe, CA	A=0.32

RELATIVELY UNEXPLOITED

Armstrong 1949*	Port Arthur Fish Hatchery, ON	A=0.03-0.05
Martin 1952	Louisa Lake, ON	A=0.52
Martin 1952**	Louisa Lake, ON	A=0.54
Johnson 1972	Keller Lake, NWT	A=0.25 m=0 n=0.25
Johnson 1973	Keller Lake, NWT	A=0.31 Z=0.37
Bond 1975	Kaminuriak Lake, NWT	A=0.41 Z=0.53
McLeod et al. 1976	Baker Lake, NWT	Z=0.24
Falk et al. 1982	Kasba Lake, NWT	Z=0.16

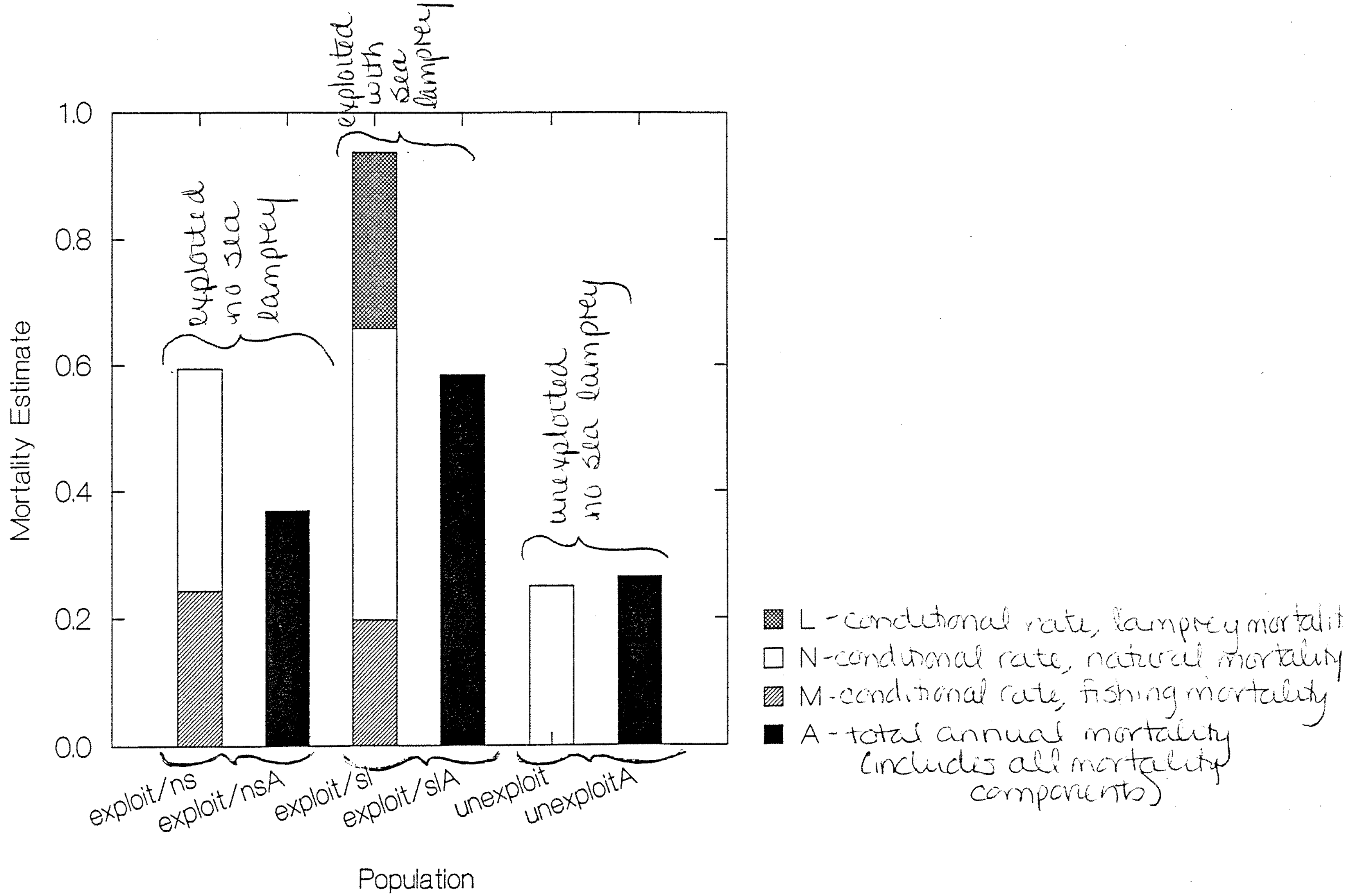
Note: ** mortality estimates calculated using length frequency data provided

* high mortality esitmates attributed to sea lamprey predatin by author

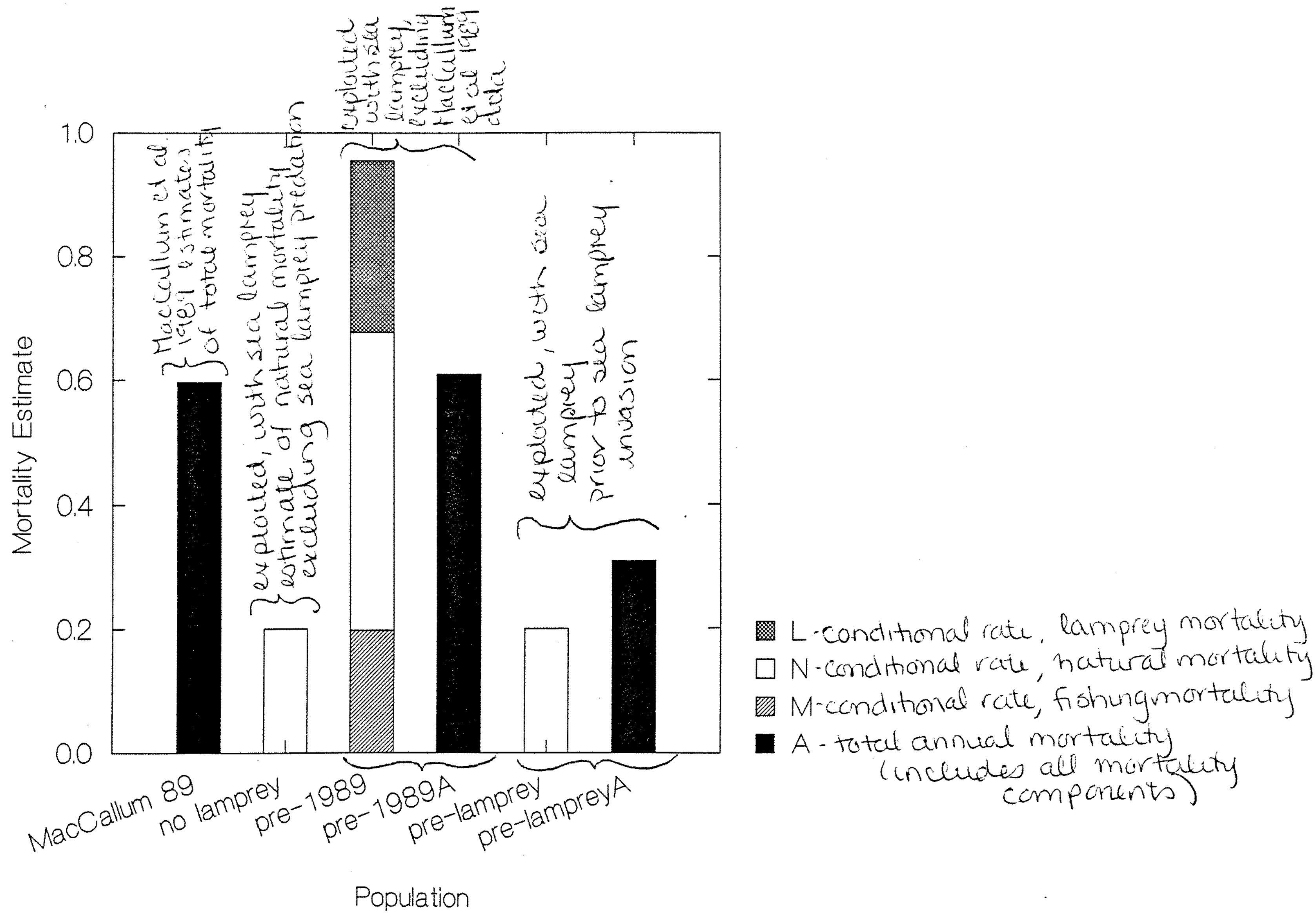
Unexploited Populations	Exploited No Sea Lamprey	Exploited With Sea Lamprey	
A = 0.03 - 0.54 mean=0.265 (N=6) sd=0.200	A = 0.05 - 0.70 mean=0.369 (N=48) sd=0.182	A = 0.08 - 0.98 mean=0.585 (N=125) sd=0.194	Total Mortality
Z = 0.16 - 0.53 mean=0.325 (N=4) sd=0.162	Z = 0.11 - 1.51 mean=0.691 (N=22) sd=0.359	Z = 0.50 - 2.31 mean=0.943 (N=32) sd=0.501	
	m = 0.02 - 0.40 mean=0.243 (N=6) sd=0.117	m = 0.10 - 0.30 mean=0.197 (N=3) sd=0.091	Fishing Mortality
	F = 0.22 - 0.58 mean=0.327 (N=12) sd=0.199	F = 0.03 - 0.77 mean=0.255 (N=36) sd=0.181	
n = 0.25 (N=1)	n = 0.11 - 0.56 mean=0.351 (N=20) sd=0.141	n = 0.20 - 0.90 mean=0.461 (n=16) sd=0.268	Natural Mortality
	M = 0.08 - 0.82 mean=0.385 (N=20) sd=0.214	M = 0.10 - 2.30 mean=0.602 (N=27) sd=0.563	
		l = 0.014 - 0.820 mean=0.279 (N=8) sd=0.273	Lamprey Mortality
		L = 0.21 - 1.70 mean=0.721 (N=12) sd=0.454	

	Exploited With Sea Lamprey Pre-Sea Lamprey	Exploited With Sea Lamprey Post-S/L, Pre-1989	Exploited With Sea Lamprey MacCallum 1989
Total Mortality	A = 0.17 - 0.62 mean=0.310 (N=4) sd=0.209	A = 0.08 - 0.98 mean=0.602 (N=52) sd=0.249	A = 0.20 - 0.80 mean=0.596 (N=69) sd=0.124
	Z = 0.70 (N=1)	Z = 0.62 - 2.31 mean=0.950 (N=31) sd=0.507	
Fishing Mortality		m = 0.10 -0.30 mean=0.197 (N=3) sd=0.091	
	F = 0.45 - 0.60 mean=0.525 (N=2) sd=0.106	F = 0.03 - 0.77 mean=0.239 (N=34) sd=0.173	
Natural Mortality	n = 0.20 (N=1)	n = 0.20 - 0.90 mean=0.479 (n=15) sd=0.268	
	M = 0.10 - 0.25 mean=0.190 (N=3) sd=0.079	M = 0.10 - 2.30 mean=0.654 (N=24) sd=0.577	
Lamprey Mortality		l = 0.014 - 0.820 mean=0.279 (N=8) sd=0.273	
		L=0.21 - 1.70 mean=0.721 (N=12) sd=0.454	

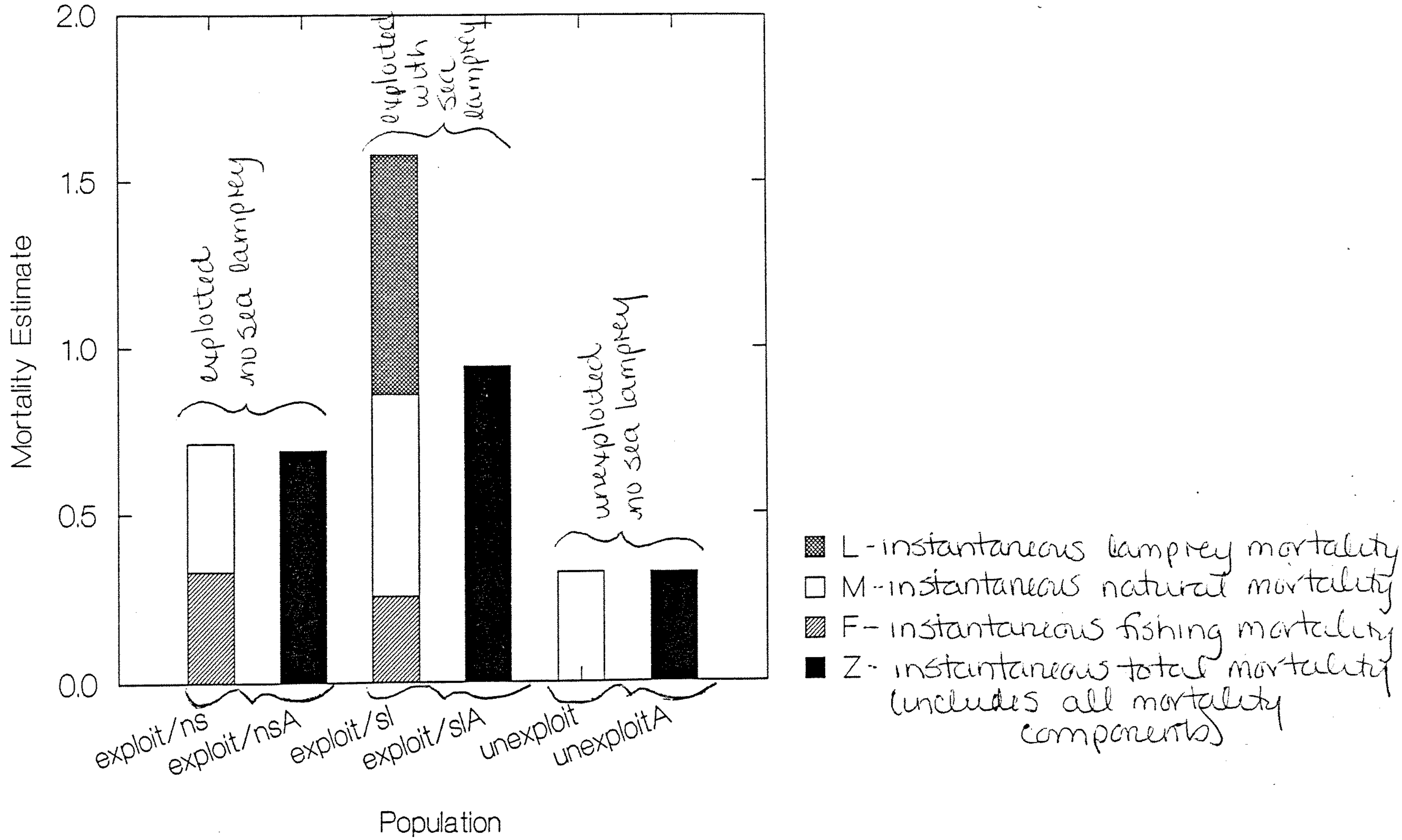
Mortality Estimates for Various Lake Trout Populations



Exploited Lake Trout Populations with Sea Lamprey



Mortality Estimates for Various Lake Trout Populations



Exploited Lake Trout Populations with Sea Lamprey